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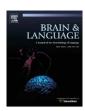
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The role of personal experience in the neural processing of action-related language

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ABSTRACT

We investigated how auditory language processing is modified by a listener's previous experience with the specific activities mentioned in the speech. In particular, we asked whether neural responses related to language processing depend on one's experience with the action-based content of this language. Icehockey players and novices passively listened to sentences about ice-hockey and everyday situations during functional magnetic resonance imaging (fMRI). When listening to action-related sentences, neural activation in left inferior frontal gyrus (IFG) and left dorsal premotor cortex (PMd) depended on one's actual (physical) experience with the action described in the sentence: hockey experts showed greater activity in these regions than novices for hockey sentences, but not for everyday-action sentences. Thus, personal experience with linguistic content modulated activity both in regions associated with language comprehension (IFG) and in those related to complex action planning (PMd). Moreover, hockey experts (who have extensive experience with both hockey and everyday situations) showed greater activity in left IFG regions for hockey relative to everyday sentences. This suggests that the degree to which one finds information personally relevant (i.e., over and above one's direct experience with it) also modulates processing in brain regions related to semantic-level processing.

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1. Introduction

The language we hear and use in daily life varies substantially in terms of its relationship to our own personal experiences. In fact, some of the language we encounter depicts situations with which we have little personal experience or interest. Nevertheless, we seem to understand this language as clearly and easily as sentences conveying information about which we do have direct experience. For instance, one need not have driven a race car, gone sky-diving, or played ice-hockey to understand simple sentences about these topics (e.g., 'The race-car driver braked sharply', 'The sky-diver put on the harness', 'The hockey player skated to the right'). Indeed, language is important because of its ability to convey information of infinite variety and therefore cannot be limited in scope to the conveyance of things we merely have experience with or care about. Because the content of language is so flexible and varied, it is perhaps not surprising that the basic properties of language are described in terms of linguistic structure rather than content (e.g., Chomsky, 1957; Hockett, 1960) or that theories of language processing often focus on the different levels of language, rather than the kinds of messages the language conveys (e.g., Hagoort, 2005; Hickok & Poeppel, 2007).

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Research examining the neural substrates of speech processing has revealed a network of brain regions thought to be central to understanding auditory language. Regions in this network include the left inferior frontal gyrus (IFG) and bilateral anterior superior temporal gyri (STG) (see Hickok & Poeppel, 2007; Vigneau et al., 2006). Although the specific constituent brain regions (or their attributed functions) differ somewhat across language theories, for over 130 years, it has been a relatively common assumption that there is a core network of brain regions underlying language comprehension - and that linguistic processing in this network does not vary as a function of language content or the non-linguistic experience of the language listener (Freud, 1891/1953; Geschwind, 1970).

Recent work suggests we may need to rethink this assumption. For example, Dominey and Hoen (2006) review evidence and put forth a comprehensive neurolinguistic model derived from construction grammar theory that posits a strong interaction between semantic structures and syntactic forms. This interaction, they propose, is mediated by an integrated neural network containing several subdivisions of the inferior frontal gyrus. In addition, language understanding may involve brain regions outside traditional language areas - regions more typically associated with motor behavior and action than language processing. This suggests that experience performing particular actions may provide some of the neural substrates for semantic understanding (e.g., Aziz-Zadeh, Wilson, Rizzolatti, & Iacoboni, 2006; Tettamanti et al., 2005).

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Indeed, a listener's personal experience with the activities being linguistically conveyed seems to modulate the neural processes called upon during comprehension. For example, recent work in our lab has shown that sports experience enhances action-related language understanding by recruitment of left dorsal premotor cortex (PMd), a region normally devoted to higher-level action selection and implementation – even when there is no intention to perform a real action (Beilock, Lyons, Mattarella-Micke, Nusbaum, & Small, 2008). In that study, both expert ice-hockey players and novices were presented with spoken sentences about icehockey situations ("The hockey player passed with his backhand") and everyday situations ("The individual opened the fridge") inside the scanner. Some of these sentences were action-related and some were not. Critically, premotor regions were not only active during action-language listening, they were also tied to understanding. Specifically, PMd activity mediated the relationship between sensorimotor expertise and facilitation on a later comprehension task for sentences describing hockey-related actions. Thus, one's experience performing non-linguistic activities changes the neural regions recruited when one understands language about such activities, and as a result, the quality of compre-

In the present work, we move beyond Beilock et al.'s (2008) goal of identifying the neural regions that mediate the relationship between motor expertise and action-language comprehension (i.e., comprehension of language that depicts situations involving overt actions). Specifically, we re-examine the raw data acquired in Beilock et al. to address three new questions about how one's non-linguistic personal experience with the actual physical activities conveyed in auditory language might impact the neural network called upon to process that information. We do this by focusing on the direct contrasts in neural activity between experts and novices listening to hockey-related sentences and everyday sentences – something that was not done in Beilock et al. (2008).

Our first goal in the present study was to assess whether neural activity during language listening depends on participants' degree of experience with the content of linguistic stimuli. Given that hockey players have more hockey experience (and particularly more sensorimotor experience with the content of hockey sentences) than novices, but presumably equal experience with the content of the everyday sentences, this sets the stage to ask two more questions about experience and language understanding.

Specifically, in a second question we ask whether direct experience with the subject matter of auditory sentences affects the biology of language comprehension as a function of whether the sentences are about physical actions or other information. Finally, we ask whether processing more *personally relevant* information shows greater activity in the regions identified in the above analyses – over and above what may be explained due to differences in personal experience alone. That is, although a hockey player may have significant experience hitting hockey pucks and opening the fridge, the former may be more relevant to him than the latter – a fact that may bias processing of language about these two situations.

1.1. Personal experience (Question 1)

How does one's experience with particular activities (e.g., a particular sport) impact the neural processing of linguistic descriptions of those activities? In other words, does experience with linguistic content (by 'content' we mean here the actual situations to which a sentence refers) affect the way in which language is processed? Previous work has shown that shared cultural experience with certain types of *linguistic* input (e.g., lexical frequency) can affect comprehension (e.g., Bates et al., 2003; Cuetos, Alvarez, González-Nosti, Méot, & Bonin, 2006; Lapata, Keller, & Walde, 2001;

Lee, Chiang, & Hung, 2008). In the current study, however, we are more directly concerned with the impact that actual experience (e.g., whether one has in fact driven a race-car, been sky-diving, or played ice-hockey) has on regions thought to be central for processing linguistic meaning. This is in spite of the subjective sense of understanding that often arises for language content that we in fact have no actual experience with.

One way in which personal experience might affect language processing is through the biasing of attention. If one has considerable experience with situations of a particular type (e.g., football or ice-hockey situations; Holt & Beilock, 2006), then hearing language related to situations of that type may activate a broader range of associations relative to a novice with no such experience.

It is a robust and well-documented finding that priming one piece of information orients attention to semantically-related information (for a review, see Maxfield, 1997). Thus, one might expect attention to be drawn to stimuli related to domains in which one has considerable experience. If a hockey player always has hockey on the mind, then linguistically-conveyed hockey information may always be primed. Such an effect has in fact been demonstrated behaviorally with sports aficionados: Baseball fans have a hard time coming up with a word that forms a compound word with "plate," "broken," and "shot" because they cannot help but think about "home plate." Unfortunately, the word "home" does not go with "shot" (whereas the word "glass" fits with all three: Wiley, 1998). In addition, the effect of change-blindness (the inability to report a sudden change in visual stimuli) is attenuated in football experts when viewing specifically football-related images (Werner & Thies, 2000). This is because football experts are able to attend to football scenarios in such a way that they do not miss subtle changes in the scenes presented to them. Taken together, these studies suggest that personal experiences may alter the way one attends to specific types of information; in other words, experience can bias one to attend differently to stimuli that are in one's domain of expertise versus stimuli that are outside it. Thus, in terms of language understanding, the extent of one's personal experience with the linguistic content one hears may be reflected in the activity of neural regions recruited during comprehension.

In the present study, we expected activity to increase in regions related to processing the meaning of language content in a domain with which subjects had considerable experience (relative to individuals with less experience in said domain). This is because attention is widely believed to increase neural activity in regions that process the type of information to which one is attending (Chelazzi, 1995; Poghoysyan & Ioannides, 2008; Posner & Driver, 1992; Rowe, Friston, Frackowiak, & Passingham, 2002). To answer Question 1, then, we investigated how experience modulates regional brain activity during language processing. We were specifically interested in regions where neural activity was dependent on hockey experience and sentence content i.e., where hockey experts showed greater activity than novices for hockey sentences but not for everyday sentences. To do this, we examined the entire brain for an experience (i.e., hockey players versus novices) × content (Hockey sentences versus Everyday sentences) interaction.

1.2. Action (Question 2)

Given that sport is an action-based domain, we can ask whether the action (versus non-action) content of sentences affects how direct experience with that content might impact the neural regions called upon to process it. Put another way, in a second question we ask whether the effect of personal experience on language processing differs when language is action based. I.M. Lyons et al./Brain & Language xxx (2009) xxx-xxx

Why might we classify sentences into those describing actions and those that do not? Recent work has provided intriguing evidence that the neural regions recruited in accessing the meaning of words can include the sensory systems that underlie related concepts. For example, González et al. (2006) reveal that olfactory areas are activated when participants accessed the meaning of words such as 'cinnamon'. With respect to language about action specifically, a number of researchers have shown that processing of sentences and words about specific actions activates motor regions involved in the execution of those actions (Meister & Iacoboni, 2007; Pulvermüller, 2005; Pulvermüller, Hauk, Nikulin, & Ilmoniemi, 2005). Recently, it has been shown that activity in a region of left dorsal premotor cortex (PMd - an area believed central to selection of higher-level action plans; e.g., Grafton, Fagg, & Arbib, 1998; O'Shea, Johansen-Berg, Trief, Gobel, & Rushworth, 2007; O'Shea, Sebastian, Boorman, Johansen-Berg, & Rushworth, 2007) mediates the increased comprehension of hockey-specific action language that is observed as hockey experience increases (Beilock et al., 2008). However, to our knowledge, it has not yet been empirically tested whether regions thought central to semantic-level language processing (i.e., the core language network mentioned above: Hickok & Poeppel, 2007; Vigneau et al., 2006) are also modulated by personal experience with a specific category of action-related language. Thus, in the present study, we asked whether action-related sentences show an interaction effect similar to that described in Section 1.2. For completeness, this was asked of non-action sentences as well.

1.3. The influence of personal relevance (Question 3)

In language, no sentence ever really stands alone. Sentences are linked to one another and we understand particular sentences within a broader discourse framework that involves several different types of information (see Pickering & Garrod, 2004). In any set of sentences that are strung together, there is varying content which a listener may find more or less personally relevant. All subjects in the current study, hockey players and novices alike, had substantial experience with everyday sentence content such as opening umbrellas and walking dogs. Spending hundreds of hours on the ice-rink should not minimize one's experience or identity associated with performing everyday activities such as opening a refrigerator (Beilock & McConnell, 2004). However, because hockey is a mainstay of a professional player's life, one can imagine that a hockey player would gear his attention toward information he finds most personally relevant. Thus, processing hockey-related information might actually impact the processing of language about everyday experiences. It is not known, presently, whether differences in sentence relevance alone (i.e., given similar levels of experience with the content) relate to differences in neural activity in core language processing circuits. To test this, we compared hockey sentences with everyday sentences in expert hockey players. This comparison extends the investigation from one's experience with the situations described in linguistic content to its relevance to the listener.

In summary, ice-hockey experts and novices listened to sentences depicting hockey and everyday situations. Half of these sentences described actions while the remainder did not. We asked (1) whether neural activity depends on participants' degree of personal experience with the content of linguistic stimuli, (2) whether action-related language changes the regions observed in this way, and (3) whether processing more personally relevant information shows greater activity in these regions than processing of less relevant information - over and above what may be explained due to differences in personal experience alone.

2. Methods

2.1. Participants

Subjects were 21 right-handed males (18-35 years). Ice-hockey experts (n = 12) played professional or Division I intercollegiate hockey (15.7 \pm 1.9 years playing experience). Novices (n = 9) had no playing or watching experience.

2.2. Stimuli and procedure

Stimuli were 176 spoken sentences. Eighty eight of these described ice-hockey situations; the remaining 88 sentences described everyday situations. Hockey and Everyday sentences were orthogonally divided further into action and non-action sentences (with 44 total sentences for each of the four possible sentence-types). Example sentences are given in Table 1. Sentences were equated across categories in terms of complexity, length, and number of syllables. In addition, presence of hockey-specific jargon (e.g., 'the blue line', 'line change', 'in the crease') was carefully minimized. This was done to increase the probability that differences in neural activation would be due to differences in experience with the actual situations depicted, and not simply be attributable to differences in lexical familiarity.

During scanning, sentences were equally divided over two functional runs and presented in fixed random order using a jittered inter-stimulus interval (Range: 0-16.11 s; Mean: 2.21 s). Sentences were presented only once. Subjects were told to lie still and instructed to pay attention to the sentences because their memory for the sentences might be tested at a later time. After scanning, participants completed 2 behavioral tasks: (1) a sentence-picture matching task, and (2) a recognition memory task.

Although the picture-matching task was not the focus of the current work and is thus not described in detail further (see Beilock et al., 2008 for more complete treatment of these data), it is important to note that experts and novices did not differ in comprehension accuracy on the hockey-related sentences. In the recognition memory task, participants were visually presented with 96 sentences, half of which were taken from the set presented during scanning, and the other half were highly similar but new sentences. Participants' task was to indicate whether a sentence occurred during the previous scanning session with a yes/no button press. Overall participants performed well above chance on this task (Mean = 68.1% correct, SE = 2.1%, t(20) = 8.15, p < .001), suggesting that they were attending to the stimuli presented during scanning as instructed. Moreover, a 2 (Experience: Experts,

Table 1 Example stimuli.

The hockey player needed the rest

The hockey player supported the plan

The hockey player took blame for the loss

The hockey player took pride in the win

Example sentences	
Hockey action (H-A)	Everyday action (E-A)
The hockey player knocked down the net	The individual opened the fridge
The hockey player followed through the shot	The individual stepped on the chair
The hockey player stopped slowly on the ice	The individual brushed his hair
The hockey player tightened his skate	The individual wiped off the counte
The hockey player held onto the puck	The individual closed the book
The hockey player changed hands	The individual jumped over the stream
Hockey non-action (H-nA)	Everyday non-action (E-nA)
The hockey player enjoyed victory	The individual earned the acclaim
The hockey player won the award	The individual earned the reward

The individual understood the plan

The individual abandoned hope

The individual valued support

The individual found peace

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Novices) \times 2 (Sentence Type: Hockey sentences, Everyday sentences) analysis of variance (ANOVA) on recognition accuracy revealed no significant effects (all ps > .05) of experience, sentence type, or their interaction. In other words, both groups had similar recognition memory accuracy for all sentence types.

In addition, participants were visually observed during scanning to ensure they were awake with eyes open. Between scans they were reminded of the task. Although passive listening has the disadvantage that attention is not overtly monitored, it has a number of advantages that we feel outweigh the disadvantages. We have argued that inclusion of an overt manual response can skew the BOLD signal in key motor areas that are also part of the speech-processing network (Small & Nusbaum, 2004). Since we are explicitly interested in the role of motor-related experience and its influence on language processing, we opted for the passive listening approach. Furthermore, we (and others) have shown that subjects are generally attentive and compliant in passive listening situations (e.g., Hasson, Nusbaum, & Small, 2006).

2.3. fMRI acquisition, preprocessing and analysis

MRI data were acquired from a GE-LX 3T scanner (Fairfield, Connecticut, USA) using a standard quadrature head coil. A forward T2*-weighted spiral sequence (Noll, Cohen, Meyer, & Schneider, 1995) was used to acquire functional images covering the whole brain (30 axial slices) with a repetition time (TR) of 2000 ms and an echo time of 30 ms. In-plane resolution with the spiral sequence is 3.75×3.75 mm and the slice thickness was 4mm (no skip) for an isometric voxel size of $3.75 \times 3.75 \times 4$ mm. Hi-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.

Preprocessing and statistical analyses were conducted using BrainVoyager QX, 1.9.10 (Brain Innovation, Maastricht, The Netherlands). Preprocessing of data involved spatial smoothing using a 5 mm full-width at half-maximum (FWHM) Gaussian kernel, slice scan-time correction, correction for three-dimensional head-motion, mean intensity adjustment at the volume level to correct for scanner-related fluctuations, linear trend removal, and temporal high-pass filtering to remove non-linear drifts of three cycles or fewer per time-course. Functional images were manually aligned to the high-resolution T1 structural images and transformed into Talairach space (Talairach & Tournoux, 1988).

Data were first analyzed strictly in terms of domain or content area (i.e., Hockey versus Everyday sentences) (Question 1 from the Introduction). To do this, after preprocessing, data from all subjects were submitted to a group-level, whole-brain, random-effects general linear model (GLM) (Friston et al., 1994), with separate predictors for Hockey and Everyday sentences. The resultant betaweights for these two predictors were then submitted to a 2 (Experience: Experts, Novices) × 2 (Sentence Type: Hockey sentences, Everyday sentences) ANOVA (with Experience as a between-subjects factor and Sentence Type as a within-subjects factor). Regions showing a significant interaction were identified using an initial uncorrected voxel-wise threshold of F(1, 20) = 10.07, p < .005. Regions thus identified were subsequently cluster-level corrected for multiple comparisons using a Monte-Carlo simulation procedure with a family-wise false-positive rate of .01 (thus requiring 7 or more contiguous functional voxels to be considered significant at the whole-brain level) (Forman et al., 1995).

Next, we subdivided the Hockey and Everyday sentences into those describing actions and those describing scenes without an overt action performed (Question 2) (Table 1). We conducted two additional ANOVAs (Experience by Sentence Type). The first ANOVA included only sentences describing hockey-action situations (H-A condition) and everyday-action situations (E-A condition). The second included only sentences describing hockey non-action

situations (H-nA condition) and everyday non-action situations (E-nA condition). For these ANOVAs, regions showing a significant interaction term were identified using the same p < .005 threshold (cluster-level corrected at $\alpha = .01$) as in the first analysis.

In order to test the effect of processing more versus less relevant sentence content (Question 3), two whole-brain contrasts (testing action and non-action sentences separately) were conducted for the hockey expert subjects only (n = 12): (1) H-A > E-A and (2) H-nA > E-nA. The resulting t-statistic maps used a voxelwise cut-off of p < .005, and were subsequently cluster-level corrected at ($\alpha = .01$).

3. Results

3.1. Personal experience (combined regions in Fig. 1; Question 1)

Regarding the role of personal experience, three regions showed a significant Expertise \times Sentence-Type interaction at the wholebrain level. These included a region in the pars orbitalis of the left inferior frontal gyrus (IFG) (BA47), which extended to include a portion of the pars triangularis (BA 45). Activity in this region was characterized by significantly greater activity for Experts than Novices when listening to hockey sentences [t(19) = 3.11, p = .006] but not when listening to everyday sentences (t = -0.89, p = .386).

Significant interaction effects were also seen in the caudate nuclei bilaterally. As there was no effect of hemisphere (all F < 1), right and left caudate activity was averaged together (referred to hereafter simply as caudate). Overall, this region showed a pattern similar to the left IFG, with significantly greater activity for Experts relative to Novices during hockey sentences [t(19) = 3.66, p = .003] but not everyday sentences [t(19) = -1.85, p = .082]. Regions are shown in yellow and green in Fig. 1a; condition means are shown in Fig. 1b; region details are summarized in Table 2 (top).

3.2. Action sentences (action regions in Fig. 1; Question 2)

Looking at sentences describing only *action*-related situations, two regions showed a significant Expertise (ice-hockey experts, novices) × Sentence Type (hockey, everyday) interaction. The first region was located in left IFG. This region was located within anterior pars triangularis (Brodmann's Area 45), being slightly superior and anterior to that reported in Section 3.1. (Note also that, as can be seen in Fig. 1a, this region is distinct from that seen specifically for non-action sentences in Section 3.3 below; therefore, to distinguish 'action' and 'non-action' IFG regions, the current region is referred to hereafter as *dorsal* left IFG, or left IFGd.) In IFGd, Experts showed greater activity than Novices while listening to H-A sentences [t(19) = 2.32, p = .040]. Novices showed greater activity than Experts while listening to E-A sentences [t(19) = -2.35, p = .036].

The second region was located in the anterior portion of the left dorsal premotor cortex (PMd). In this region, Experts showed significantly greater activity than Novices while listening to H-A sentences [t(19) = 3.35, p = .006]. For E-A sentences, the trend toward greater activity for Novices than Experts was marginally significant [t(19) = -2.04, p = .058]. Regions are shown in red in Fig. 1a; condition means are shown in Fig. 1c; region details are summarized in Table 2 (middle).

3.3. Non-action sentences (non-action regions in Fig. 1; Question 2)

Looking at those sentences describing only *non action*-related situations, four regions showed a significant Expertise × Sentence Type interaction. These included a large region in left IFG. This region showed considerable overlap with the left IFG region revealed in Section 3.1 located at the junction of BA45 and BA47, although

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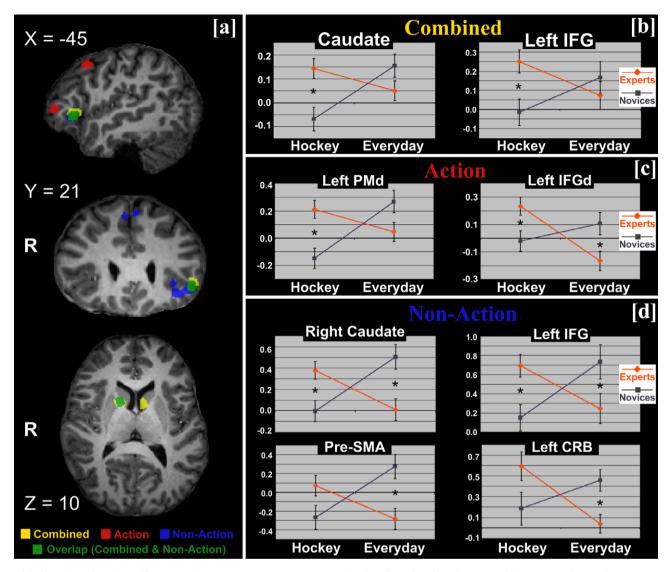


Fig. 1. (a) All regions showed a significant Expertise \times Sentence-Type interaction. Regions in yellow showed an interaction when action and non-action sentences were combined (the category hockey included H-A and H-nA sentences, and the category everyday included E-A and E-nA sentences). Regions in red showed an interaction when only action sentences were considered. Regions in blue showed an interaction when only non-action sentences were considered. Overlapping regions from the combined and Non-action analyzes are shown in green. (b-d) Condition means for combined (b), action (c), and non-Action regions (d). Y-axes depict beta-estimates. For each subject, beta-estimates were averaged across all voxels in the region for a given condition; thus, one value for each condition and each subject was generated. These values were used to test for differences between groups and were averaged across subjects in each group to generate the mean values depicted in (b-d). Asterisks indicate a significant difference between groups for that sentence-type at p < .05. Error bars represent standard errors of the mean.

Table 2Regions showing a significant expertise (expert, novice) by sentence-type (hockey, everyday) interaction for each analysis (combined, action, non-action).

		•		,
ROI (Brod. area)	Center gravity			ROI size (mm³)
	x	у	Z	
Combined sentences				
L. IFG (47)	-44	19	1	536
R. Caudate	15	7	10	758
L. Caudate	-8	5	9	357
Action sentences				
L. IFGd (45)	-45	34	5	209
L. PMd (6)	-44	9	44	533
Non-Action sentences				
L. IFG (47)	-37	22	-3	1598
R. Caudate	14	7	11	778
Pre-SMA (6)	1	25	52	301
L. Cerebellum	-12	-57	-10	562

the current region extended more rostro-medially to include a greater portion of BA47 than the region show in the first analysis (see Fig. 1). In this region, Experts showed greater activity than Novices while listening to H-nA sentences [t(19) = 3.16, p = .005] and Novices showed greater activity than Experts while listening to E-nA sentences [t(19) = -2.11, p = .049].

A significant interaction was also seen in the right caudate nucleus. This cluster overlapped almost completely with that seen in the first analysis (Fig. 1). Activity in this region showed a similar pattern, with greater activity for Experts during H-nA sentences [t(19) = 2.94, p = .009], and greater activity for Novices during E-nA sentences [t(19) = -3.24, p = .005].

The two remaining regions included the pre-supplementary motor area (preSMA) and a cluster located in the medial anterior portion of the left cerebellum (CRB). In both of these regions, Experts showed marginally greater activity than Novices for H-nA sentences [preSMA: t(19) = 2.07, p = .052; Left CRB: t(19) = 1.96, p = .065], and Novices showed significantly greater activity than

Experts for E-nA sentences [preSMA: t(19) = -3.31, p = .004; left CRB: t(19) = -2.88, p = .012]. Regions are shown in blue and green in Fig. 1a; condition means are shown in Fig. 1d; region details are summarized in Table 2 (bottom).

3.4. Personal relevance (Question 3)

For hockey experts, activity during hockey sentences was contrasted with activity during everyday sentences. Results for action sentences showed an effect in the same dorsal left IFG region previously identified in the interaction analyses above, with significantly greater activity for hockey relative to everyday action sentences. For non-action sentences, several regions showed a similar effect, including IFG, caudate and anterior superior temporal sulci (STSa), and rostral anterior cingulate cortex (ACC), all bilaterally. Significant regions are summarized in Table 3. Regions that overlapped with brain areas also showing a significant interaction effect from the preceding analyses are denoted in Table 3 using italics.

4. Discussion

Most theories of the neural processing of language do not take into account the listener's personal experience with the situation depicted in linguistic content (e.g., Dominey & Hoen, 2006; Hagoort, 2005; Hickok & Poeppel, 2007). That is, in assessing the meaning of a sentence, individual differences in listeners' experiences within a specific domain of expertise would be considered at most only as a factor that comes into play at a post-linguistic stage of processing; thus, experience with language content would be unlikely to influence the normal operation of the language comprehension network. In the current work we show that regions central to reconstructing the meaning of sentences are indeed modulated by the listener's personal experience with sentence content.

4.1. Personal experience (Question 1)

Activity in left inferior frontal gyrus (IFG) and bilateral caudate nuclei showed sensitivity to one's experience with the content of linguistic information (Fig. 1a and b). As predicted, hockey experts showed greater activity in these regions than novices for hockey but not everyday sentences. In other words, in the domain in which subjects were selected to differ most in terms of personal experience (hockey), participants with the greatest amount of experience (experts) showed significantly higher activation during language

processing about that domain. Of particular interest was the finding that this effect occurred in the pars orbitalis and pars triangularis of left IFG. It has been argued that activity in this anterior portion of left IFG during language comprehension is centrally related to semantic comprehension (Cai, Kochiyama, Osaka, & Wu, 2007; Dominey, Inui, & Hoen, 2009; Hagoort, 2005; Hickok & Poeppel, 2007; Kuperberg, Sitnikova, & Lakshmanan, 2008; McDermott, Petersen, Watson, & Ojemann, 2003; Poldrack et al., 1999; Vigneau et al., 2006; Wu, Cai, Kochiyama, & Osaka, 2007). This suggests that personal experience can play a key role in determining the meaning of what one hears.

It seems plausible that personal experience focuses attention toward content with which one has previously established numerous meaningful associations. This may have led to activity increases in semantic-related neural areas in experts during hockey sentence presentation. This interpretation is consistent with the view of left IFG function in language processing proposed by Thompson-Schill and colleagues. In their account, left anterior IFG serves to integrate contextual information as a top-down biasing mechanism that inhibits competing activations during selection of appropriate word meaning (Novick, Trueswell, & Thompson-Schill, 2005; Thompson-Schill, Bedney, & Goldberg, 2005). In this respect, Bedny, Hulbert, and Thompson-Schill (2007) showed that patients with left IFG lesions were impaired in integrating contextual information while performing a triplet lexical decision task. In addition, Cristescu, Devlin, and Nobre (2006) report evidence that anterior left IFG is active when participants are instructed to orient attention to semantic categories but not spatial locations. Taken together, this literature supports the interpretation of our findings that personal experience leads to attentional biases which results in greater semantic processing of linguistic information most relevant to oneself (see also Section 4.3).

Importantly, however, it is likely not the case that all participants were, for example, attending only to the hockey sentences (activity for which was then modulated by experience). In nearly all regions showing the critical Experience by sentence-type interaction, not only did hockey experts show relatively greater activation for hockey relative to everyday sentences, novices also showed the opposite trend: greater activation for everyday relative to hockey sentences. This crossover effect indicates that any attentional effects due to personal experience had to be specific to the type of sentence with which a subject was most distinctly an expert. So did novices just attend to everyday sentences and ignore hockey sentences (and did experts simply do the reverse)? Note

Table 3Regions showing a significant difference between sentence type (hockey, everyday) for experts (*n* = 12) (action and non-action sentences were treated separately). Italicized regions also showed a significant interaction effect (see Table 2). The rightmost two columns show condition means for the relevant sentence type (standard errors of the mean are shown in parentheses). Means were obtained for each condition by first averaging over all voxels in the region for each subject. These values were then averaged across expert subjects.

ROI (Brod. area) Center gravity			ROI size (mm³)		Activity	
	x	у	z		Mean (Std. err.)	
Experts: H-A > E-A					H-A	E-A
L. IFGd (45)	-47	35	5	527	.570(.130)	190(.128)
Experts: H-nA > E-nA					H-nA	E-nA
L. IFG (47)	-34	22	-3	1276	.627(.108)	.089 (.099)
R. IFG (47)	40	26	-5	234	.378(.093)	013 (.095)
Rostral ACC (32)	4	30	18	918	.234(.074)	233 (.074)
L. Caudate	-13	2	17	753	.398(.083)	008 (.101)
R. Caudate	15	8	13	325	.615(.105)	.044 (.098)
L. STSa (38)	-48	-8	-12	792	.865(.115)	.258 (.126)
R. STSa (38)	46	7	-9	312	.646(.080)	.088 (.111)
L. ITS (20/21)	-60	-21	-12	338	.364(.095)	221(.089)
L. Cerebellum	-15	-55	-10	868	.758(.166)	.100 (.078)

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that the post-scan memory test did not show differences in memory accuracy as a function of either expertise or sentence-type. This suggests that our effects cannot be solely accounted for by attentional processes. Rather, as mentioned in the paragraph above, it appears more plausible that experience-dependent biases in attentional processing were present, but these led to differences in semantic-level processing, which in turn would appear to account for the crossover effects seen in terms of neural activity.

Finally, in terms of differences in bilateral caudate activation as a function of hockey experience and sentence type, the caudate has been identified as a reward area and greater activity in this region typically accompanies positive outcomes (e.g., Lau & Glimcher, 2007, 2008; Tricomi, Delgado, McCandliss, McClelland, & Fiez, 2006). Hockey players who have extensive hockey experience (and hockey success given the high skill-level at which we sampled) may in fact draw upon reward areas when understanding sentences about their expert skill domain. Although admittedly speculative, such a conclusion is very much in line with our finding that, during language comprehension, personal experience with language content results in the involvement of brain areas outside core language networks.

4.2. Action-related language (Question 2)

As this study focuses on processing of action-related language, the following discussion is primarily limited to findings for action sentences. However, in the context of distinguishing between action and non-action related content with respect to the effect of personal experience in language processing, two distinct regions in anterior left IFG were seen for action and non-action sentences (Fig. 1a). These left IFG regions did not overlap even when the threshold was reduced to p < .05 (uncorrected). While language areas related to semantic processing may be modulated by personal experience regardless of whether content is action-related or not (i.e., both regions were found in left anterior IFG), the precise neural locus of this influence seems to vary depending on whether content is action-related.

A recent upsurge in work has related action understanding and language comprehension in terms of overlapping cognitive and neural processes (for representative examples, see Beilock, 2008; Buccino et al., 2005; Glenberg & Kaschak, 2002; Pulvermüller, 2005). Much of this work (e.g., Breier & Papanicolaou, 2008; Hamzei et al., 2003; Kuhn & Brass, 2008; Skipper, Goldin-Meadow, Nusbaum, & Small, 2007; for recent reviews, see also Friederici, 2006; Grodzinsky, 2006) has focused on activity in posterior IFG, such as pars opercularis and posterior pars triangularis (roughly BA44 and inferior BA6), that has traditionally been associated with more phonetic and motor-production aspects of language processing (Burton, Small, & Blumstein, 2000; Burton & Small, 2006; Hickok & Poeppel, 2007; Price, 2000; Vigneau et al., 2006). Interestingly, we found here that personal experience modulates activity during action-related language-listening in a more anterior portion of left IFG. This portion of left IFG has previously shown to activate during attentional modulation of action observation (Chong, Williams, Cunnington, & Mattingley, 2008; Molnar-Szakacs, Iacoboni, Koski, & Mazziotta, 2005) and when action observation (in the form of language-relevant gesture) is integrated with speech (Willems, Özyürek, & Hagoort, 2007). This suggests that attentional modulation of semantic-level processing of specifically action-related language may be facilitated by top-down control of action-based simulation of relevant content.

Consistent with this view, left dorsal premotor cortex (PMd) showed a pattern similar to that seen in left IFGd for action sentences. Activity in this region is considered important for retrieval of complex action plans (Grafton et al., 1998; O'Shea, Johansen-Berg et al., 2007; O'Shea, Sebastian et al., 2007; Rushworth, Johan-

sen-Berg, Gobel, & Devlin, 2003; Schluter, Krams, Rushworth, & Passingham, 2001; Toni et al., 2002; Wise & Murray, 2000). Furthermore, we have shown that this region mediates the relation between sports experience and the understanding of action-related language (Beilock et al., 2008), and Grabowski, Damasio, and Damasio (1998) report evidence that naming both tools and actions activates an area of the left PMd in the vicinity of the left PMd activation we report here.

Expert hockey players are expert performers of hockey-related and everyday motor actions. Novices, on the other hand, by definition are only experts in performing everyday actions. Thus, the effect of personal experience in left PMd presents the interesting possibility that the greater depth of semantic processing in left IFGd for relevant action sentences may have been further enriched by activation of personal experience forming and retrieving complex action plans. This interpretation is supported by a positive functional correlation between activity in these regions during hockey action [r(19) = .488, p = .025] but not hockey non-action sentences [r(19) = .250, p = .275]. Broadly speaking, this result is consistent with a view of linguistic processing that posits comprehension of action-related content is facilitated by recruitment of representations which, while not immediately relevant to language processing per se, are relevant to the particular actions being processed and thus may aid in comprehension of this content.

4.3. Personal relevance (Question 3)

Hockey experts should have considerable experience with both the hockey and everyday situations depicted by sentences presented in the current study. However, one may note that several regions in Fig. 1 (see especially left IFG regions in Fig. 1c and d) show greater activity in experts for hockey relative to everyday sentences. Why might this be the case? As noted in the Introduction, one explanation is that, over and above the role of experience, the degree of endogenous personal relevance of the linguistic content - content seen as relatively more important by the listener may also impact the processing of linguistic meaning. By definition, hockey-related situations take a central place in the lives of professional and semi-professional hockey players, who spend hundreds of hours on the ice-rink (Beilock & McConnell, 2004). It is thus plausible that hockey experts find language about a hockey player knocking down the net more personally relevant than language about an individual opening the fridge (see Table 1 for sen-

To test the effect of personal relevance in hockey experts more conservatively, hockey sentences were contrasted with everyday sentences in experts (we specifically focus on hockey players because, as mentioned above, this group should have experience with both hockey and everyday situations). Both left IFG regions (i.e., those seen for action and non-action sentences) showed significantly greater activation for hockey relative to everyday sentences in the expert group at the whole-brain level. However, within anterior IFG the neural locus of this difference was specific to whether sentences were action-related (as was the case for the interaction analysis discussed in Section 4.2), with action sentences showing an effect of personal relevance in a region slightly dorsal and anterior to that observed for non-action sentences. In sum, not only do one's experiences with sentence content affect semantic-level language processing, but even the degree to which one finds this content personally relevant can lead to increased processing relative to less relevant content.

Furthermore, in the left IFGd region, for everyday-action sentences, experts showed activity in this region below baseline [one-sample (two-tailed) test: t(11) = -3.04, p = .011; see Fig. 1c, Table 3]. That is, processing of sentences within one's domain of expertise – at least for sentences of action-related content – may

in fact lead to inhibition of sentences outside that domain. In general, then, these data lend support to an attention-based account of the effect of experience and perceived personal relevance on semantic-level language processing. Top-down attentional mechanisms may act either to up- or down-regulate processing of stimuli after it had been categorized as personally relevant or not.

However, it is important to point out that because the above interpretation assumes a specific time-course of processing that cannot be tested in the current data set, there is an alternative explanation. Specifically, it may be that personally relevant information has an inherently higher threshold, which would place the influence of one's experience with content on language processing at a relatively *pre*-attentive stage (note that both postand pre-attentive processes might simultaneously be at work as well.) Given the strict constraints on temporal resolution in fMRI, however, differentiating between these possibilities is not possible using the paradigm we have employed in the current study. Precisely how and when personal relevance of linguistic content impacts semantic processes is an important topic for further inquiry.

5. Conclusions

These data show that personal experience with linguistic content modulates language processing both in left anterior IFG regions believed central to semantic processing, and in regions whose presumed function is strongly related to the content being described. With respect to action-related language in particular, left dorsal premotor cortex was sensitive to personal experience during processing of sentences depicting action-related situations - a finding in keeping with recent work showing activity in this region mediates the impact of sports-expertise on action-language comprehension (Beilock et al., 2008). Broadly speaking, these data are consistent with the hypothesis that both personal experience with, and the personal relevance of, language content serves as a key factor in orienting attention toward greater semantic processing of individually meaningful categories of linguistic stimuli. In general, this selection process may be reflected in activity in anterior regions of the left IFG, though the precise locus of this activation may itself depend on the type of content being processed e.g., whether or not one is attempting to comprehend action-related language.

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