

Age of acquisition effects on the functional organization of language in the adult brain

Rachel I. Mayberry^{a,*}, Jen-Kai Chen^{b,c}, Pamela Witcher^b, Denise Klein^{b,c}

^a University of California, San Diego, United States

^b Department of Neurology and Neurosurgery, McGill University, Montreal, Canada

^c Cognitive Neuroscience Unit, Montreal Neurological Institute, Montreal, Canada

ARTICLE INFO

Article history:

Accepted 23 May 2011

Available online 25 June 2011

Keywords:

Age of acquisition

Critical period

fMRI

Sign language

ASL

Grammatical judgment

Language processing

Broca's area

Visual processing

Brain development

ABSTRACT

Using functional magnetic resonance imaging (fMRI), we neuroimaged deaf adults as they performed two linguistic tasks with sentences in American Sign Language, grammatical judgment and phonemic-hand judgment. Participants' age-onset of sign language acquisition ranged from birth to 14 years; length of sign language experience was substantial and did not vary in relation to age of acquisition. For both tasks, a more left lateralized pattern of activation was observed, with activity for grammatical judgment being more anterior than that observed for phonemic-hand judgment, which was more posterior by comparison. Age of acquisition was linearly and negatively related to activation levels in anterior language regions and positively related to activation levels in posterior visual regions for both tasks.

© 2011 Elsevier Inc. All rights reserved.

1. Introduction

Whether a dearth of language acquisition during post-natal brain growth affects language processing in the adult brain is unknown. The question is germane to the critical period hypothesis for language acquisition (Lenneberg, 1967). Although the hypothesis is decades old, it has been difficult to investigate because spoken language is ubiquitous in the environment of infants. In the absence of brain damage, one situation isolates infants from spoken language and often has the effect of delaying the onset of language acquisition, namely congenital deafness. Infants who are born deaf cannot hear the languages spoken around them and the visual signal of speech conveys insufficient phonetic detail to support spontaneous language acquisition. For many such children, language acquisition begins after exposure to, and immersion in, a sign language at ages well beyond infancy (Mayberry, 2007, 2010). Here we ask whether variation in the age-onset of language acquisition affects language processing in the adult brain.

Research has discovered that the grammar of sign languages, like that of spoken ones, is hierarchically organized. Sign language utterances are structured at the sentence (syntax), word

(morphology), sub-word (phonology), and semantic (word and sentence meaning) levels (Brentari, 1998; Davidson, Capronigro, & Mayberry, 2008; Klima & Bellugi, 1979; Sandler & Lillo-Martin, 2006; Stokoe, Casterline, & Croneberg, 1965; Zeshan, 2006). Although the grammatical properties of sign languages are similar to those of spoken ones, their age-onset of acquisition is typically different. A small percentage (less than 10%) of deaf children acquire sign language from birth because they had deaf parents who signed to them (Schein, 1989). For the remaining 90% of deaf children, sign language acquisition begins at a range of ages beyond infancy depending upon their first exposure to it. No underlying biological anomaly causes this variation in the age of acquisition, AoA, of sign languages. Instead the reasons are socio-cultural. For example, the child's hearing loss may have been detected late, or the child may not have been enrolled in school until an older age. A school that used sign language may not have been accessible to the family. Alternatively, the family and/or professionals may have elected to isolate the child from sign language despite a notable lack of functional speech in the erroneous belief that doing so would impede spoken language development (Mayberry, 2007, 2010).

Variation in the age-onset of sign language acquisition has multiple effects on psycholinguistic processing in adulthood. As acquisition begins at older ages, morphological and syntactic abilities decline (Boudreault & Mayberry, 2006; Emmorey, Bellugi, Friederici, & Horn, 1995; Newport, 1990). Later AoA is associated with the

* Corresponding author. Address: Department of Linguistics, University of California, San Diego, 9500 Gilman Drive, La Jolla, CA 92093-0108, United States. Fax: +1 858 534 4789.

E-mail address: rmayberry@ucsd.edu (R.I. Mayberry).

commission of lexical errors made during off-line processing tasks that are dissociated from syntactic structure and sentence meaning and instead linked to the sub-lexical form of signs. Sentence and discourse-level sign language comprehension decrease in tandem with these phonologically-based lexical errors (Mayberry & Eichen, 1991; Mayberry & Fischer, 1989).

Key to investigating a possible critical period for language is the finding that AoA effects on sign language processing are especially large in cases where little or no language was acquired prior to the acquisition of sign language at older ages. These effects are unlike the well-documented AoA effects for the outcome of second-language, L2, learning (Mayberry, 1993). For example, learning an L2 at older ages can lead to near-native proficiency depending upon factors such as the grammatical relationship of the L2 to the first language and the degree of education undertaken in the L2 (Birdsong & Molis, 2001; Flege, Yeni-Komshian, & Liu, 1999). Consistent with how a critical period might be hypothesized to affect language development, research with deaf signers has found that an early onset of language is associated with near-native language proficiency, as in L2 learning. However, a dearth of language acquisition during early life is associated with low levels of language proficiency across all languages subsequently learned independent of sensory-motor modality (Mayberry & Lock, 2003; Mayberry, Lock, & Kazmi, 2002). The crucial question is whether the unique and life-long psycholinguistic effects associated with a lack of language in early life reflect differential neural language processing by the adult brain.

In order to predict how AoA effects might appear in the results of an fMRI experiment, we turn to research investigating the neural processing of sign language. Converging evidence shows that the neural processing loci of sign languages largely overlap those of spoken languages. These findings come from a variety of neurolinguistic paradigms, including brain lesion and cortical language mapping studies, and the neuroimaging of healthy adults with PET and fMRI. The bulk of this research has been conducted with participants with an early age-onset of sign language acquisition.

Case studies of brain lesions in deaf adults, who are described as being “lifelong signers,” show a leftward asymmetry for sign language processing. Left hemisphere, LH, but not right hemisphere, RH, lesions have been found to disrupt sign language comprehension (Poizner, Klima, & Bellugi, 1987). Lesions in the LH temporal lobe affect the comprehension of single signs and complex sentences (Hickok, Bellugi, & Klima, 1998; Hickok, Love-Geffen, & Klima, 2002). Similar results were obtained in a cortical mapping study. Direct stimulation of Broca and Wernicke’s areas in the LH disrupted sign production in a deaf patient undergoing surgery for epilepsy (Corina et al., 1999). Two case studies, one in American and one in Japanese Sign Language, found that deaf adults with lesions in the left occipital cortex exhibited difficulty recognizing signs (Hickok, Klima, Kritchevsky, & Bellugi, 1995; Saito, Otsuki, & Uneo, 2007).

One controlled means of comparing the neural processing of signed and spoken languages is to neuroimage them in the same brain. Hearing native signers, (i.e., hearing adults with deaf parents who signed to them from birth) were scanned as they produced spontaneous autobiographical narratives, once in ASL and once in spoken English. The PET results revealed largely overlapping LH activation for ASL and spoken English, with ASL showing somewhat more dispersed activation patterns (Braun, Guillemin, Hosey, & Varga, 2001). PET activation patterns during sign (i.e., word) retrieval in deaf native signers (i.e., deaf individuals with deaf parents who signed to them from birth) performing tool and action naming tasks in ASL were largely indistinguishable from the PET activation patterns of hearing English speakers performing the same task (Damasio et al., 1996). Importantly, the activation patterns associated with sign retrieval were unaffected by any iconic

relationship between the sign’s phonological form and its meaning (Emmorey et al., 2003, 2004). This indicates that higher levels of linguistic processing are modality independent, although some lower levels of sign processing are both modality independent and dependent, such as the maintenance of sign items in immediate memory (Pa et al., 2008).

fMRI studies of deaf native signers have also found activation in the classic language areas of the LH with a trend toward bilateral activation in frontal and temporal lobes. These results have been found for distinct sign languages, namely American, British, and Japanese, using various tasks and stimuli (Kassubek, Hickok, & Erhard, 2004; MacSweeney et al., 2002; McCullough, Emmorey, & Sereno, 2005; Sakai, Tatsuno, Suzuki, Kimura, & Ichida, 2005). Although sign language is visual, activation in the occipital cortex is not routinely found across studies for linguistic processing in highly proficient signers. Occipital cortex activation has been reported in hearing signers for whom sign language is a non-dominant language, and in hearing non-signers (Klann, Kastrau, & Huber, 2005; MacSweeney et al., 2002). Activation in occipital cortex when the task involves higher level linguistic processing may be associated with lower proficiency. This is not entirely due to the subtraction of visual activation by way of a moving baseline task. Use of a moving baseline does not predict a lack of activation reported for occipital cortex in deaf native signers (Corina et al., 2007; MacSweeney et al., 2006; Sakai et al., 2005).

Some studies have compared the neurolinguistic processing of native and non-native signers with inconsistent results. While passively viewing ASL stimuli, hearing native signers of ASL showed activation in the right angular gyrus, whereas hearing L2 signers did not (Newman, Bavelier, Corina, Jezzard, & Neville, 2002). It is possible that the RH activation shown by the hearing native signers was elicited by ASL stimuli that were more discourse- than sentence-like. The RH is involved in the processing of prosody and inter-sentential relations (Baum & Pell, 1999; Caplan & Dapretto, 2001). Consistent with this interpretation are the results of an fMRI study that directly compared activation patterns for ASL at the discourse and sentence levels. Discourse-level stimuli with prosodic contours in sign language elicited RH activation patterns whereas sentence-level stimuli elicited LH activation in deaf native signers (Newman, Supalla, Hauser, Newport, & Bavelier, 2010). In a PET study of working memory in Swedish Sign Language, hearing native signers showed a left parietal bias which was not found when hearing L2 signers were included in the group analyses (Rönnberg, Rudner, & Ingvar, 2004).

On a phonological similarity task, where the participants decided whether the signs for pairs of line drawings shared articulatory parameters (akin to rhyme judgments for spoken words), deaf native signers showed less activation in the left, posterior inferior frontal gyrus compared to deaf non-native signers of British Sign Language (who acquired spoken English in childhood and BSL in late adolescence or adulthood; MacSweeney, Waters, Brammer, Woll, & Goswami, 2008).¹ Greater activation in these brain regions is sometimes reported for L2 learners of a spoken language relative to native speakers of the language (Indefrey, 2006). On a task requiring detection of reversed signs in German Sign Language dialogs, deaf non-native signers showed a variety of individual activation patterns. This could be due to the fact that AoA was uncontrolled. Notably, some participants with late AoA showed primarily left occipital activation (Meyer et al., 2007). Given

¹ It is important to note that being born deaf and learning a sign language at an older age does not necessarily mean that it is a *first* language acquired at a late age in the absence of earlier language. Some deaf individuals acquire spoken language in early childhood; their subsequent sign language learning is more akin to L2 learning, even though their L1 proficiency in spoken language is less than native-like (Mayberry et al., 2002).

the inconsistent results of neuroimaging studies of non-native signers, the effect of AoA on adult neural sign language processing remains unknown.

The goal of the present fMRI study was to determine whether the unique psycholinguistic effects associated with a delayed age-onset of language acquisition is associated with differential neural activation patterns for language processing in the adult brain. In order to replicate our previous behavioral results in the scanner, we used a grammatical judgment task (Boudreault & Mayberry, 2006). Additional advantages of using this task are that it yields multiple measurements of language processing, including decision accuracy for grammatical and ungrammatical stimuli and response time, RT. Second, the task has been widely used to measure proficiency in L2 behavioral research and in fMRI research investigating L2 neural processing (Luke, Liu, Wai, Wan, & Tan, 2002; Rüschemeyer, Fiebach, Kempe, & Friederici, 2005; Wartenburger et al., 2004).

Attenuated language proficiency is a hallmark of deaf individuals with a delayed age-onset of sign language acquisition subsequent to minimal previous spoken language acquisition (Mayberry, 2007). This is a potential confound in neuroimaging research where proficiency can affect activation patterns. In order to obtain the clearest portrait of neural language processing in this population, we created a novel task with reduced linguistic demands, *phonemic-hand* judgment. Here the decision is whether the phonological form of the final sign of a sentence is made with one hand. The number of hands used to form signs is rule-governed (Battison, 1978). Linguists consider these rules to be part of the phonological system of sign languages because they do not represent physiological limitations on the hands (Ann, 1996; Brentari, 1998; Channon, 2004; Rozelle, 2003). In addition, morphological rules differentially apply to signs depending upon the number of hands in the base sign (Pfau & Steinbach, 2006).

Consistent with previous neurolinguistic research, we hypothesized that deaf native signers, whose age-onset of language acquisition was from birth, would primarily show activation in the brain's classic LH language regions. Given our previous psycholinguistic research, we further hypothesized that deaf non-native signers whose age-onset of language acquisition was beyond infancy, and who acquired little functional spoken language in the interim, would show neural activation patterns that deviate from the classic one in some, as yet unknown, systematic fashion. Finally, if language acquisition in early life is necessary for the classic pattern of neural processing to fully develop, then we should observe AoA effects independent of task performance levels.

2. Methods

2.1. Participants

Twenty-two adults (11 females) who were right-handed volunteered for the study. All participants were born profoundly deaf (>90 dB) according to audiological reports they supplied. The participants had used ASL for 19 or more years after first being immersed in it between the ages of birth and 14 years at home or school. As in previous research (Mayberry & Lock, 2003), participants were recruited to represent three developmental epochs, infancy, birth to 3 years; early childhood, 4 to 7 years; and late childhood, 8 to 14 years. Participants gave informed consent and were compensated for their time. The Research Ethics Board of the Montreal Neurological Institute approved the protocol.

AoA ranged from birth to 14 years with a mean of 5.86 years. Six participants had deaf parents who signed to them from birth, native signers; 14 participants had hearing parents. One participant's hearing parents signed with him/her from the age of three. The

Table 1

Participant variables. Linear regression results for participant variables in relation to AoA.

Variable	Mean (SD)	R	t	p
Age	38.59 (11.75)	.35	1.67	.11
Years of ASL	32.73 (11.03)	-.07	-.30	.77
IQ screening	11.26 (1.97)	-.36	-1.51	.15

Table 2

Participant language skills. Linear regression results for participants' self-rated language skills in relation to AoA.

Language comprehension scale	Mean (SD)	R	t	p
Spoken English of strangers	1.92 (1.44)	.14	.50	.63
Spoken English of acquaintances	3.15 (2.88)	.35	1.23	.25
ASL	9.00 (1.00)	-.60	-2.07	.07

Note. Rating: 1 = not at all; 10 = easily.

remaining 13 participants acquired ASL outside the home, non-native signers. Mean age was 38 years, and mean length of ASL experience was 33 years (see Table 1). All participants were screened for nonverbal IQ with two subtests of the nonverbal scale of the WAIS (Picture Completion and Arrangement). Mean scaled score was 11.26. The normed average for the hearing population on these subtests is 10.0, SD = 3. Participant recruitment thus produced a sample balanced for age, years of ASL experience, and screening nonverbal IQ. Linear regression results showed that the participant variables were not significantly related to AoA (see Table 1).

Self- and parental report of language onset, history, and proficiency is widely used in L1 and L2 research and has been found to correlate with objective measures of language proficiency (Fenson et al., 1993; Marian, Blumenfeld, & Kaushanskaya, 2007). In lieu of testing the participant's language skills across languages and modalities prior to scanning, we asked them to rate their language abilities with a Language Background Questionnaire used in previous research using a 10-point scale: 1 = not at all; 10 = perfectly (Chamberlain & Mayberry, 2008). The participants' mean rating of their ability to comprehend the spoken English of strangers was 1.92 and that of acquaintances was 3.15 (Table 2). The fact that participants rated their ability to comprehend the speech of strangers significantly lower than that of acquaintances (paired $t = -1.92$, $p < .04$) indicates that the Language Background Questionnaire is sensitive to variation in language proficiency. Unsurprisingly, the participants rated their ability to comprehend ASL with a mean of 9.0 on a 10 point scale, and significantly higher than their ability to comprehend spoken English of acquaintances (paired $t = -7.80$, $p < .0001$). The results of linear regressions using AoA as the predictor variable showed that it was unrelated to self-rated proficiency for spoken English. AoA showed a non-significant trend to negatively predict ASL comprehension (Table 2) such that earlier AoA was associated with higher self-reported levels of ASL comprehension. In sum, the participants had normal intelligence, could not understand spoken language sufficiently for functional communication through it, and were ASL dominant.

2.2. Stimuli

The stimuli were a subset of sentence structures used in previous research investigating AoA effects on ASL sentence processing (Boudreault & Mayberry, 2006). The ASL sentences consisted of familiar signs and no fingerspelling, were mono-clausal, and 6–9 morphemes in length with a mean duration of 4683 ms. The

sentences were of four ASL sentence types: simple, negative, inflecting verb, and WH-questions. The same syntactic violation was applied to all the exemplars of a given sentence type to create ungrammatical stimuli in the following fashion. (1) The simple sentences used SVO word order with plain (non-inflecting) verbs, such as “The two boys from the deaf school are conversing.” The simple sentences were all made ungrammatical with a word-order violation by moving the verb to the middle of the subject noun phrase, as in *“The two are chatting boys from the deaf school.” (2) The negative sentences all contained a single ASL plain verb; half the verbs were negated with a simultaneous headshake and half were negated with the negative sign NOT preceding the verb. The two forms of negation are processed similarly in ASL (Boudreault & Mayberry, 2006). The negative sentences were all made ungrammatical by moving the headshake or the sign NOT to the subject-noun phrase, as in “The old car’s windshield-wiper washers don’t work,” versus *“The old not car’s windshield-wiper washers work.” (3) The inflecting-verb sentences used ASL verbs that require case and number inflections which are affixed to the verb stem, as in “The man gave the heavy box to the boy,” where the verb “give” is inflected with morphemes for singular, 1st person-subject and singular 3rd person objective cases. These sentences were made ungrammatical by altering the objective case inflection so that it no longer agreed with the object-noun phrase, as in *“The man gave-to-it the heavy box the boy.” (4) In ASL, WH-questions are formed by placing a WH-sign at the beginning or end of a sentence, as in “Many business are going bankrupt, why?” The WH-questions were made ungrammatical by moving the WH-sign to the middle of the subject noun phrase, as in *“Many why businesses are going bankrupt?” In sum, the stimulus ASL sentences were short, single clauses while the ungrammatical counterparts consisted of word order violations for three sentence structures and verb inflection violations for the fourth sentence structure. There were 11 grammatical and 11 ungrammatical counterparts

for each sentence type, except for simple sentences, for which there were 12 grammatical and 12 ungrammatical counterparts, for a total of 90 ASL stimuli.

2.3. Tasks

Participants performed three tasks in the scanner, grammatical judgment, phonemic-hand judgment, and watching a still image. For grammatical judgment, participants decided with a button press whether the stimulus was grammatical in ASL. For phonemic-hand judgment, participants decided with a button press whether the final sign of the stimulus sentence was made with one hand. For the baseline task, participants quietly watched a still image of the signer (see Fig. 1). The 45 grammatical and 45 ungrammatical stimuli were randomized for the grammatical judgment task. The same stimuli were re-randomized for the phonemic-hand judgment task. The baseline condition was a still image of the signer whose facial expression was neutral and whose body posture had arms at rest (Fig. 1).

2.4. Procedure

There were three runs each of which consisted of three blocks of grammatical judgment, three blocks of phonemic-hand judgment, and the baseline task. Task order was randomized within each run. The stimuli for each judgment task were blocked into groups of 10 items for a total of 90 trials per judgment task. At the beginning of each block, participants saw a brief video of ASL instructions for the task; these were excluded from the analysis. The instructions were shown in black and white video to contrast with the ASL stimuli, which were shown in color, as was the baseline task (Fig. 1). Stimuli were presented visually on the center of a screen back-projected onto a tilted mirror with $40^\circ \times 30^\circ$ of visual angle.

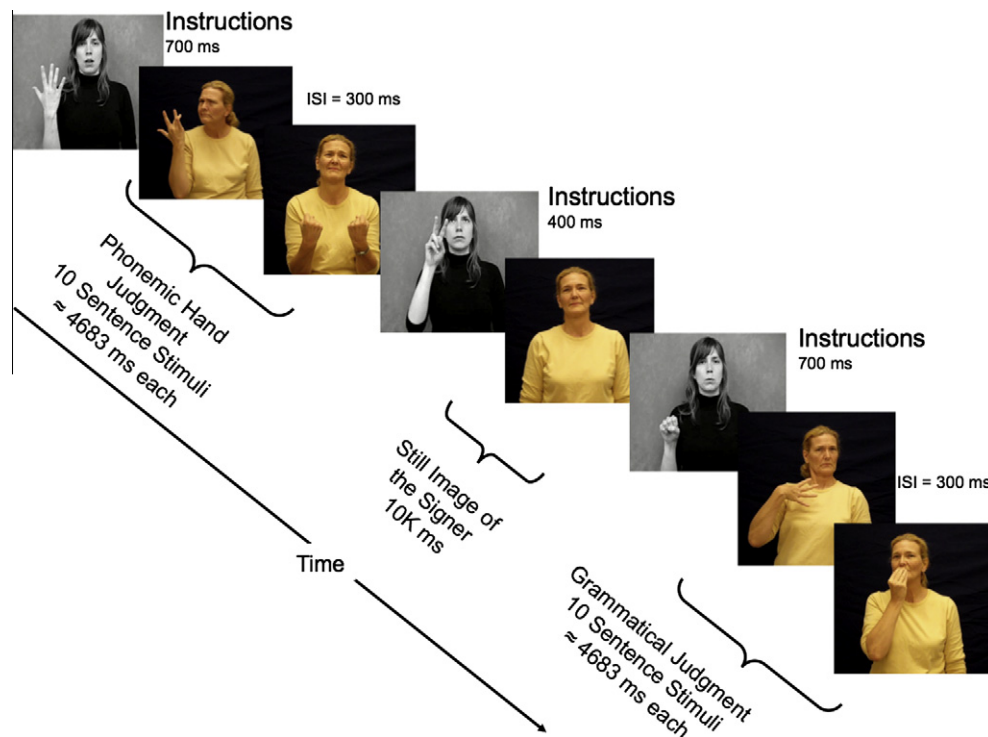


Fig. 1. Study experimental design. Schematic timeline showing the sequence of instructions and blocks for the phonemic-hand judgment task, the baseline condition, and the grammatical judgment task. Each photo is one video frame taken from the three ASL conditions. As shown here, instructions were given in black and white to contrast with the stimuli which were shown in color. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

2.5. Behavioral dependent measures

2.5.1. Grammatical judgment

Prior to each block of grammatical judgment, participants were instructed to respond to each ASL sentence with a finger button press indicating *yes* if the stimulus was grammatical and *no* if it was not. Accuracy was the dependent variable.

2.5.2. Phonemic-hand judgment

Participants were instructed prior to each block of phonemic-hand judgment to press the *yes* button if the final sign of the stimulus was made with one hand and to press the *no* button if it was not. Accuracy was the dependent variable.

2.5.3. Response time

The length of time the participants took to make each judgment was also recorded. Timing began from the onset of the ungrammatical element in the ungrammatical stimulus and from the same locus in the grammatical counterpart (see stimulus description above).

2.6. Testing procedure

A native ASL signer, who was deaf, assisted by a fluent L2 ASL signer, who was hearing, tested the participants. Prior to entering the scanner, participants were given instructions in ASL and trained on a computer with the behavioral tasks using practice stimuli not included in the scanning experiments. Scanning began only after the participant demonstrated he or she understood the three tasks, grammatical and phonemic-hand judgment, and watching a still image of a signer. ASL instructions were presented again in the scanner via a video before each block. An iBook recorded the participants' key press and response time using PowerLaboratory 1.0.3 experimental software (Chute & Daniel, 1996).

2.7. fMRI procedure

2.7.1. Scanning

Participants were scanned at the Montreal Neurological Institute using a 1.5T Siemens Sonata imager. A high-resolution T1-weighted 3D volume was acquired for anatomical localization of functional data (TR: 22 ms, TE: 9.2 ms, FA: 30, matrix size $256 \times 256 \times 170$, voxel size $1 \times 1 \times 1 \text{ mm}^3$). Changes in neural activity were measured using blood oxygenation level dependent (BOLD) fMRI by means of a T2* weighted gradient echo (GE) echo-planar imaging (EPI, TR: 5000 ms, TE: 51 ms, FA: 90). Functional images were acquired in a plane parallel to the anterior–posterior commissural plane, with 32, 4-mm slices positioned for maximum coverage of the brain.

2.7.2. fMRI data analysis

The functional data for each participant were processed using an in-house software package. The steps included motion correction by realigning all functional volumes to the third volume of that run followed by spatial smoothing of the images with a 6-mm full-width at half-maximum Gaussian filter. Voxel-wise statistical analysis of the motion corrected fMRI time series was performed with fMRIstat (Worsley, Evans, Marrett, & Neelin, 1992; available at www.math.mcgill.ca/keith/fmristat). The BOLD data were first converted to percentage of the whole volume. Significant percent BOLD changes between experimental (i.e., grammatical judgment and phonemic-hand judgment) and baseline (i.e., watching a still image of a signer) conditions were determined at each voxel based on a linear model with correlated errors. A design matrix of the linear model containing the onset time and duration of

each task condition was convolved with a hemodynamic response function modeled as a difference of two gamma functions and corrected for slice-timing to coincide with the acquisition of each slice (Friston et al., 1998). Temporal and spatial drifts were removed by modeling them as an autoregressive process of degree 1. At each voxel, the autocorrelation parameter was estimated from the least squares residuals using the Yule-Walker equations, after a bias correction for correlations induced by the linear model. The autocorrelation parameter was first regularized by spatial smoothing, and then used to whiten the data and the design matrix. Next, the linear model was re-estimated using least squares on the whitened data to produce estimates of effects and their standard errors for the following comparisons: (1) grammatical judgment minus baseline and, (2) phonemic-hand judgment minus baseline. In the next step, functional runs within each participant were combined using a fixed effects analysis.

Finally, average across participants was achieved by first normalizing individual data through linear registration to the Montreal Neurological Institute template (MNI305) using an in-house algorithm (Collins, Neelin, Peters, & Evans, 1994). The normalized data of the participants were then combined using a mixed effects linear model with fixed effects standard deviations taken from the previous analysis. A random effects analysis was performed by first estimating the ratio of the random effects variance to the fixed effects variance, then regularizing this ratio by spatial smoothing with a Gaussian filter. The variance of the effect was then estimated by the smoothed ratio multiplied by the fixed effects variance. The amount of smoothing was chosen to achieve 100 effective degrees of freedom. The resulting *T* statistic images were thresholded using the minimum given by a Bonferroni correction and random field theory to correct for multiple comparisons, taking into account the non-isotropic spatial correlation of the errors (Worsley et al., 2002). Threshold for significance was established at $t = 4.14$ for the activation peaks, or $t = 3.10$ for activation clusters greater than 222 mm^3 , based on the number of resolution elements in the acquisition volume (2880 resels).

3. Results

The results are presented in three sections. The behavioral results for the grammatical and phonemic-hand judgments are presented first. fMRI neuroimaging analyses comparing the activation patterns for the two linguistic tasks are presented second. AoA effects on the neural activation patterns for both tasks are presented last.

3.1. Behavioral results

3.1.1. Grammatical judgment

Mean proportion of grammatical judgment errors was 25%. Performance on grammatical and ungrammatical stimuli was analyzed with *d'* which ranged from 3.25 to 0.09 across the participants with a mean of 1.56. Grammatical judgment performance was negatively related to AoA ($R = -.65$, $p < .001$; Fig. 2), indicating that as AoA began at later ages, sensitivity to the ASL syntactic structure declined. Mean RT for accurate grammatical judgments was 1544 ms and positively related to AoA ($R = .30$, $p < .04$). That is, as AoA began at later ages, the time needed to make accurate grammatical judgments increased (Table 3; Fig. 2a). Length of experience was not a significant covariate in the regression analyses. These results are consistent with our previous research showing a negative relation between AoA and ASL grammatical judgment when the participants' length of experience was 15 years or more and uncorrelated with AoA (Boudreau & Mayberry, 2006).

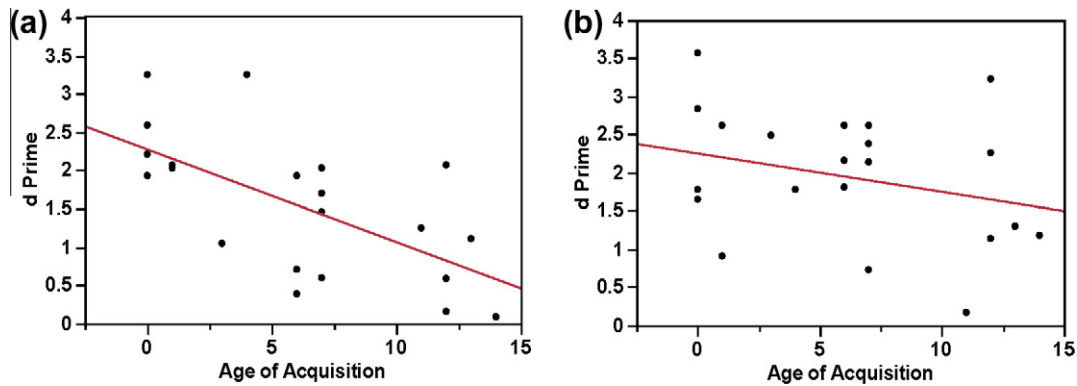


Fig. 2. Linguistic task performance. (a) Scatterplot and regression line for grammatical judgment performance measured in d' as a function of AoA. (b) Scatterplot and regression line for phonemic-hand judgment performance measured in d' as a function of AoA (see Table 3).

Table 3

Grammatical and phonemic-hand judgment performance. Linear regression results for grammatical and phonemic-hand judgment sensitivity (d') and response time, RT (ms), in relation to AoA.

Task/measure	Mean (SD)	R	t	p
<i>Grammatical judgment</i>				
d'	1.56 (.91)	-.65	-3.81	.001
RT	1544 (338)	.30	2.07	.04
<i>Phonemic-hand judgment</i>				
d'	1.96 (.84)	-.29	-1.36	.19
RT	1490 (333)	.10	.63	.53

3.1.2. Phonemic-hand judgment

As predicted, the mean proportion of phonemic-hand judgment errors was less than that for grammatical judgment at 12%. Phonemic-hand judgments of the final signs of grammatical and ungrammatical stimuli were analyzed with d' and showed a range from 3.57 to 0.17 across the participants with a mean of 1.96. Performance on this lower-level linguistic task was not significantly related to AoA ($R = -.29$, $p = .19$; Table 3; Fig. 2b). Mean RT to make accurate phonemic-hand judgments was 1490 ms. and not significantly related to AoA ($R = .10$, $p = .53$; Table 3).

To determine whether the slopes of the linear regressions for the judgment tasks in relation to AoA were different, we performed an analysis of covariance. The results showed a significant effect for AoA, $t = -3.50$, $p < .001$, a marginal effect of task, $t = -1.70$, $p = .09$, and no significant interaction between AoA and task, $t = -.14$, $p = .16$.

To summarize the behavioral results, AoA affected sensitivity to basic ASL syntactic structures but not to the number of hands used in sign formation. Next we compared the hemodynamic activation patterns for these two ASL linguistic tasks which allowed us to determine similarities and differences in the neural process that underlie grammatical judgment in sign language in contrast to those that underlie phonemic processing in sign language both in the context of the same ASL stimuli.

3.2. Significant activation peaks for the judgment tasks

The first step in the fMRI data analysis was to discover the general patterns of activation across the participants for each task compared to the baseline condition. To this end, statistical maps of the BOLD signal for the grammatical judgment condition against the baseline condition, and for the phonemic-hand judgment condition against the baseline, were constructed by averaging the data across the three runs for each participant. The group-average

statistical images were obtained by computing an omnibus test on individual t maps. The significant activation peaks for all the participants when performing the grammatical and phonemic-hand judgments in comparison to the baseline condition are shown in Table 4.

3.2.1. Grammatical judgment activation compared to baseline

When grammatical judgment was compared to the baseline, there was significant bilateral activity in the inferior frontal gyrus and in the anterior insular/opercular region bilaterally. Significant activations were also observed in the left motor cortex, the right supplementary motor area (SMA) and the right cerebellum (Table 4; see Fig. 3).

3.2.2. Phonemic-hand judgment activation compared to baseline

When phonemic-hand judgment was contrasted with the baseline condition, significant activity was again observed bilaterally in the anterior insular/opercular region. Peaks were also observed in the left motor cortex, right SMA and right cerebellum. In contrast to the predominantly frontal lobe activity observed when participants performed the grammatical judgment task, phonemic-hand judgment activated more posterior brain regions. When judging the number of hands used to articulate the final sign of ASL sentences, there is an absence of activity in the inferior frontal region in contrast to what was activated for grammatical judgment. There are, however, activations for phonemic-hand judgment in the left post-central gyrus, left parietal lobule, right caudate, bilateral inferior temporal gyrus and right occipital cortex (lingual gyrus; Table 4, Fig. 3).

The general pattern that emerges from these analyses is that some brain regions are commonly activated by both tasks, and that some regions are more specific to one task relative to the other (Table 4). Regions common to both tasks include activity bilaterally in the anterior insula, right SMA (anterior peak), left motor strip (likely related to hand movement for making response) and right cerebellum. Unique to grammatical judgment is activity bilaterally in the inferior frontal gyrus. For phonemic-hand judgment, activated regions are concentrated in more posterior regions. Unique to phonemic-hand judgment is activity in right SMA (posterior), right caudate, left post-central gyrus (possibly face area), left inferior parietal cortex, bilateral inferior temporal gyri, and the right occipital (lingual) cortex.

3.2.3. Direct comparison of grammatical and phonemic-hand judgment tasks

In order to confirm that specific activations were unique to each kind of linguistic task in ASL, we directly compared the tasks by subtracting the activation for phonemic-hand judgment from that

Table 4Activations for grammatical and phonemic-hand judgment. *t*-Statistic results for grammatical and phonemic-hand judgments against baseline (*N* = 22).

Brain region	Grammatical judgment > baseline				Phonemic-hand judgment > baseline			
	<i>x</i>	<i>y</i>	<i>z</i>	<i>t</i>	<i>x</i>	<i>y</i>	<i>z</i>	<i>t</i>
Left inferior frontal gyrus, BA 44	–48	14	0	5.34				
Right inferior frontal gyrus, BA 44	48	14	0	6.07				
Left anterior insula	–38	16	2	6.95	–30	18	6	4.16
Right anterior insula	38	16	2	5.34	38	14	6	4.65
Right SMA (anterior)	2	20	46	7.90	2	16	48	5.35
Left motor cortex	–36	–24	66	6.22	–36	–24	66	5.91
Left motor cortex	–34	–10	62	5.41	–34	–12	66	5.35
Right cerebellum	20	–54	–24	5.78	20	–54	–24	5.84
Right SMA (posterior)					2	–4	58	5.14
Right caudate					18	16	12	5.00
Left post-central gyrus, BA 1, BA 2					–56	–22	18	6.05
Left inferior parietal lobule, BA 7, BA 40					–46	–36	56	5.21
Left inferior temporal gyrus, BA 37					–52	–72	4	4.09
Right inferior temporal gyrus, BA 37					52	–68	0	4.36
Right lingual gyrus, BA 18 (occipital)					16	–72	10	4.65

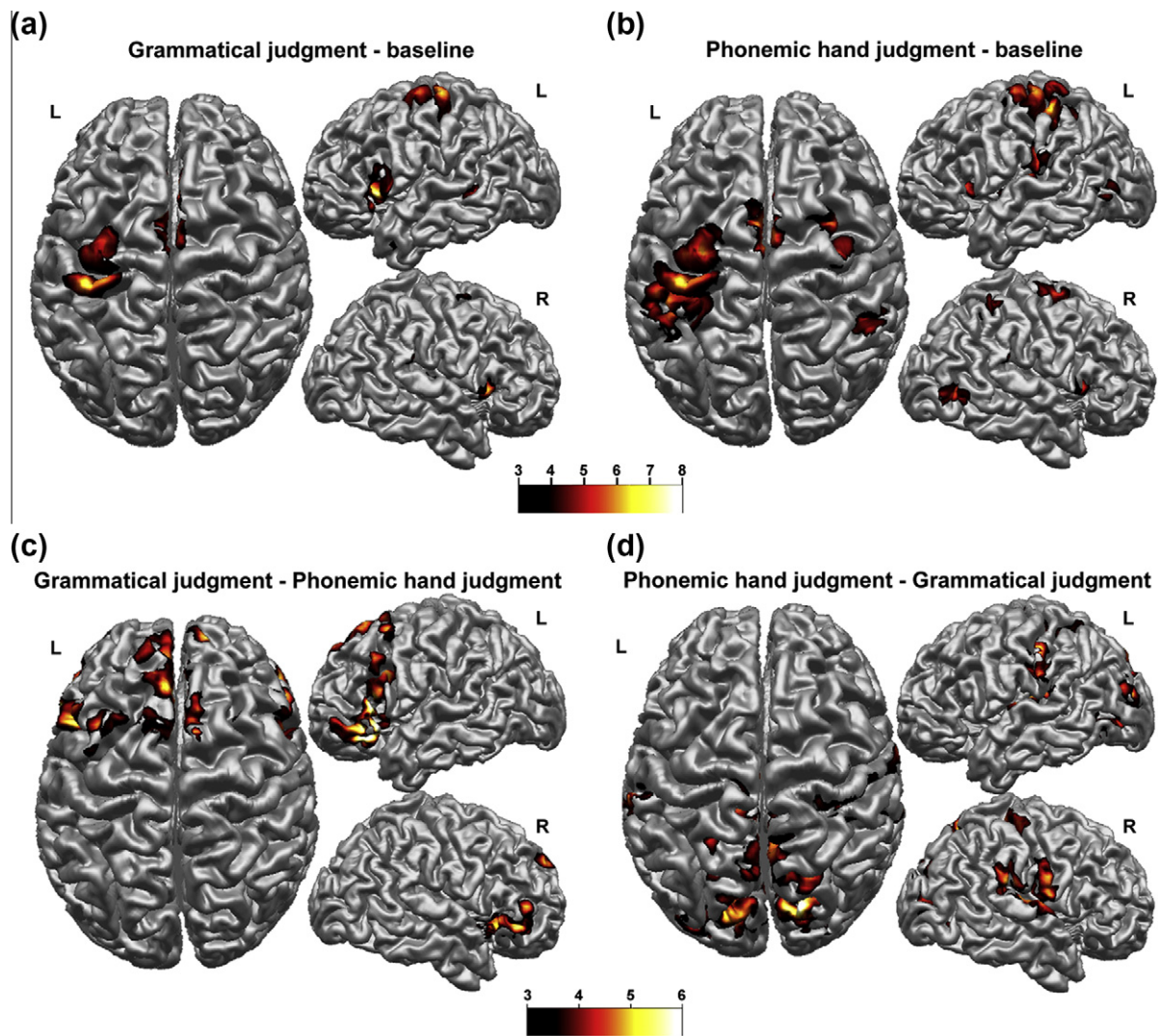


Fig. 3. Activations unique to the linguistic conditions. (a) 3-D rendered image showing BOLD activation patterns for grammatical judgment with baseline subtracted. (b) 3-D rendered image showing BOLD activation patterns for phonemic-hand judgment with baseline subtracted. (c) 3-D rendered image showing BOLD activation patterns for grammatical judgment with phonemic hand judgment subtracted. (d) 3-D rendered image showing BOLD activation patterns for phonemic-hand judgment with grammatical judgment subtracted. The color bar encodes *t*-statistic scores indicating the significance level with a threshold at $t > 4.14$ for the peak and $t > 3.10$ for activation clusters greater than 222 mm³. L = left hemisphere; R = right hemisphere.

of the grammatical judgment and vice versa using data from all the participants ($N = 22$). These results showed more clearly the anterior–posterior differences in activation patterns between the two judgment tasks, with predominantly frontal-lobe activity for grammatical judgment and posterior cortex activity for phonemic judgment (see Table 5, Fig. 3). Also striking in this direct comparison is how grammatical judgment is lateralized to the left hemisphere. In the grammatical judgment minus phonemic-hand judgment subtraction, there are several activations in the left inferior frontal region, one activation in the right inferior frontal region and a midline SMA activation. In the phonemic-hand judgment minus the grammatical judgment subtraction there are of note several activations in the left occipital cortex (Table 5, Fig. 3).

3.3. AoA effects on linguistic task activations

To identify brain regions where AoA modulated BOLD signal changes, the data were analyzed with whole-brain, voxel-wise linear regressions using AoA as the predictor variable and task performance (d') and length of experience as the covariates in separate analyses for each judgment condition against the still baseline. In addition, to obtain a preliminary picture of the relationship between BOLD signal-change and AoA, we descriptively examined the percent signal-change within a 8 mm^3 sphere centered at the voxel of each of these regions of interest (VOI obtained from the whole-brain regression map).

3.3.1. AoA effects on grammatical judgment activation

Using whole-brain regression analyses, eight brain regions were identified as having a linear relationship with AoA for grammaticality judgment, six of which showed a negative relation to AoA and two of which showed a positive relation to AoA. Five regions in the anterior left hemisphere showed hemodynamic activity levels that decreased as a linear function of AoA (see Table 6, Fig. 4): VOI 1, dorsolateral prefrontal cortex; VOI 2, anterior insula/frontal operculum; VOI 3, inferior frontal gyrus (BA 44); VOI 4, ventral premotor region (BA 6); and VOI 5, superior temporal gyrus (BA 22). One VOI was also found in the right anterior cortex, namely VOI 6 in the superior temporal gyrus (BA 22). For these VOIs, later AoA was associated with decreased BOLD signal change. For each regression, performance and length of experience were non-significant covariates except for VOI 1, left dorsolateral prefrontal cortex, and VOI 4, left ventral premotor region, where performance correlated with the activation.

Two regions in the posterior left hemisphere showed hemodynamic activity levels that increased as a linear function of AoA for grammatical judgment (Table 6, Fig. 4): VOI 8, left lingual gyrus (BA 18); and VOI 9, left middle occipital gyrus (BA 19). Task performance and length of experience were non-significant covariates in these analyses. For these posterior VOIs, later AoA was associated with increased BOLD signal change.

3.3.2. AoA effects on phonemic-hand judgment activation

For phonemic-hand judgment, eight regions of interest were identified, six of which showed a negative relation with AoA and two of which showed a positive relation with AoA.

Four regions in the left hemisphere showed hemodynamic activity levels that decreased as a linear function of AoA (see Table 6, Fig. 5): VOI 2, anterior insula/frontal operculum; VOI 3, inferior frontal gyrus (BA 44); and VOI 4, ventral premotor region (BA 6); VOI 5 in superior temporal gyrus (BA 22). Two VOIs were also found in the right anterior cortex; namely in the superior temporal gyrus (BA 22), VOI 6; and in the dorsolateral prefrontal cortex (BA9/46), VOI 7. As was the case for grammatical judgment, later AoA was associated with decreased BOLD signal change in these anterior VOIs for phonemic-hand judgment.

Two regions showed hemodynamic activity levels that increased as a linear function of AoA for phonemic-hand judgment, namely VOI 8, left lingual gyrus (BA 18); and VOI 9, left middle occipital gyrus (BA 19), (Table 6, Fig. 5). As was the case for grammatical judgment, later AoA was associated with increased activation in BOLD signal change in these posterior VOIs.

In sum, many regions of interest overlap between the two linguistic tasks with respect to AoA effects. Where they do overlap, the same VOI is used (Table 6). The BOLD signal in the VOIs in anterior regions show an increase in the BOLD signal with early AoA and a decrease in the BOLD signal with later AoA. The BOLD signal in the VOIs in posterior regions show AoA effects in the reverse direction, that is, a decrease in the BOLD signal with early AoA and an increase in the BOLD signal relation to later AoA. VOI 1 (left dorsolateral prefrontal, BA 9) is only observed for AoA effects on grammaticality judgment activation. VOI 7 (right dorsolateral prefrontal, BA 9) is only observed for AoA effects on phonemic-hand judgment activation. VOIs in the left occipital cortex show a trend for AoA effects in phonemic-hand judgment, but are only significant for AoA effects in the grammaticality judgment condition.

Thus, AoA affects hemodynamic activation for the higher-level task of grammatical judgment task and the lower-level task of phonemic-hand judgment task in a similar fashion. Early AoA is

Table 5

Activations unique to grammatical and to phonemic-hand judgment. t -Statistic results for grammatical judgment minus baseline vs. phonemic-hand judgment minus baseline and vice versa ($N = 22$).

Brain region	Grammatical judgment > hand judgment				Phonemic-hand judgment > grammatical judgment			
	x	y	z	t	x	y	z	t
Left inferior frontal gyrus, BA 44	−56	20	8	5.21				
Left inferior frontal gyrus, BA 44	−46	24	−12	5.53				
Left inferior frontal gyrus, BA 44	−48	14	28	4.82				
Left anterior insula	−46	16	−6	5.69				
Right inferior frontal gyrus, BA 44	50	18	0	5.06				
SMA	0	24	56	5.69				
SMA	0	24	48	5.77				
Left post-central gyrus, BA 1, BA 2					−50	−18	18	6.51
Left caudate					−6	16	4	4.23
Left fusiform gyrus, BA 37					−30	−52	−18	5.43
Left primary visual cortex, BA 17					−10	−68	16	4.95
Left superior occipital gyrus, BA 19					−16	−82	56	5.55
Left inferior occipital gyrus, BA 18					−30	−90	2	4.76
Right post-central gyrus, BA 1, BA 2					48	−18	14	5.01
Right superior parietal lobule, BA 7					16	−78	48	6.33

Table 6
Linear regression results for AoA on whole brain analyses for grammatical and phonemic-hand judgment ($N = 22$).

VOI	Region	Grammatical judgment – baseline					Phonemic-hand judgment – baseline				
		<i>x</i>	<i>y</i>	<i>z</i>	<i>R</i>	<i>p</i>	<i>x</i>	<i>y</i>	<i>z</i>	<i>R</i>	<i>p</i>
<i>Negative BOLD/age of acquisition relationship</i>											
1	Left dorsolateral prefrontal, BA 9	–26	48	18	–0.92	0.00					
2	Left anterior insula/frontal operculum	–36	20	12	–0.83	0.00	–34	20	12	–0.71	0.00
3	Left inferior frontal gyrus, BA 44	–46	4	32	–0.89	0.00	–48	4	32	–0.65	0.00
4	Left ventral premotor region, BA 6	–34	–8	20	–0.85	0.00	–34	–10	12	–0.64	0.00
5	Left superior temporal gyrus, BA 22	–42	–36	2	–0.86	0.00	–40	–36	0	–0.64	0.00
6	Right dorsolateral prefrontal, BA 9/46						28	24	40	–0.65	0.00
7	Right superior temporal gyrus, BA 22	54	–36	16	–0.81	0.00	52	–34	18	–0.60	0.01
<i>Positive BOLD/age acquisition relationship</i>											
8	Left lingual gyrus, BA 18	–14	–76	2	0.62	0.01	–16	–74	–6	0.45	0.05
9	Left middle occipital gyrus, BA 18/19	–22	–84	12	0.75	0.01	–22	–84	16	0.58	0.01

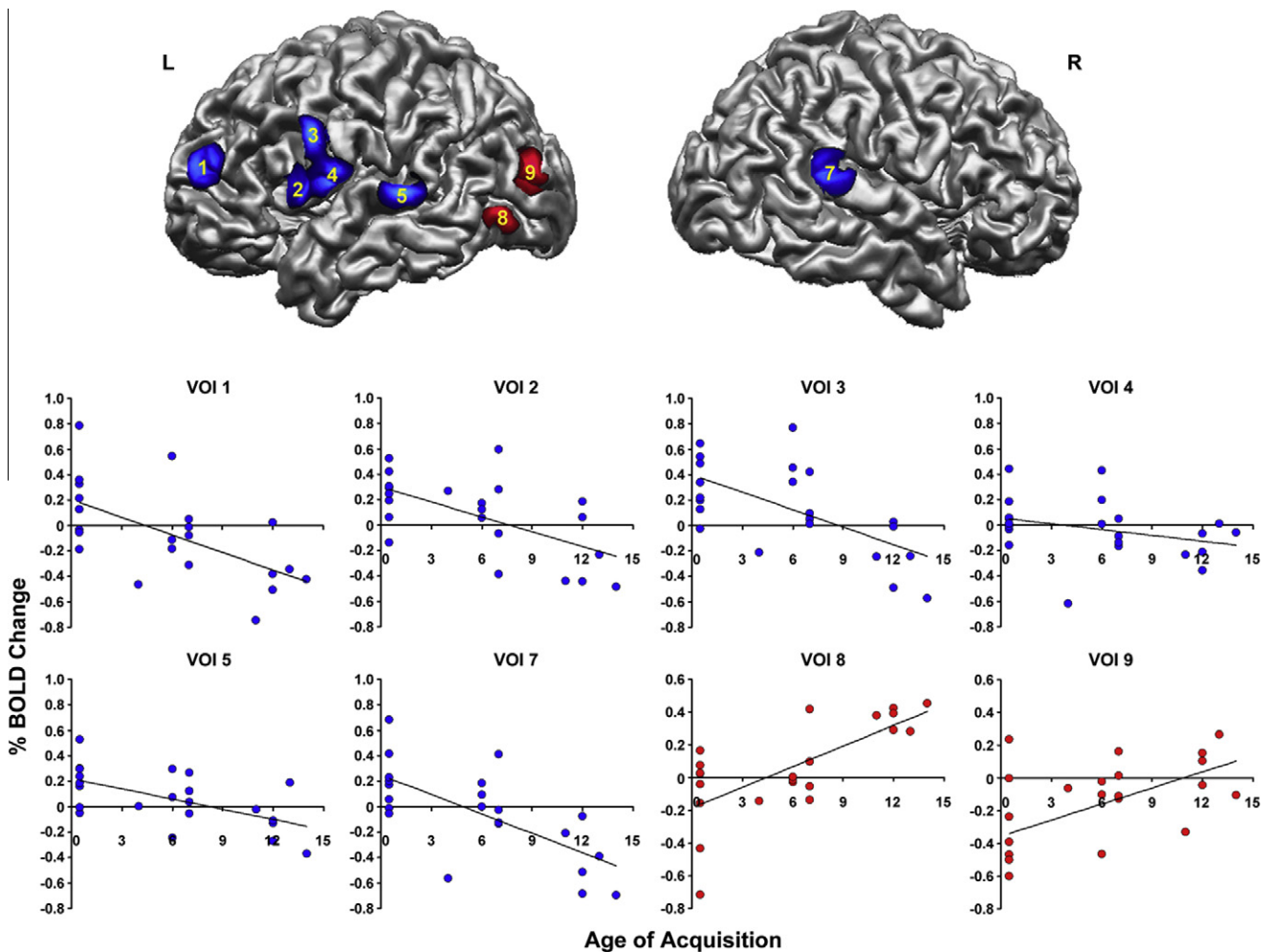


Fig. 4. AoA effects on grammatical judgment activation. 3-D rendered image showing brain areas sensitive to AoA for grammatical judgment; *L* = left hemisphere; *R* = right hemisphere; Blue = negative linear relation to AoA; Red = positive linear relation to AoA; Regression scatterplots show brain activity in all the VOI's for the grammatical judgment task as a function of AoA; % BOLD change (*y*-axis) in relation to AoA (*x*-axis). Of particular note is VOI 2 (left frontal operculum) and VOI 9 (left occipital cortex, BA 18).

associated with increased activation in anterior VOIs in the classic language areas and decreased activation in posterior VOIs. Late AoA shows effects in the reverse direction with decreased activation in anterior VOIs in the classic language areas and increased activation in posterior VOIs. In the final set of fMRI analyses, we sought to determine whether AoA effects would be observed for the baseline task of watching a still image of a signer. Because the task did not involve linguistic processing, we expected an absence of AoA effects.

3.3.3. Baseline comparisons in relation to the judgment conditions

To determine whether the baseline condition was similar for the two conditions, and whether AoA affected them, we generated *t*-maps for the whole group by subtracting the grammatical judgment activation from that of the baseline, and subtracting the phonemic-hand judgment activation from that of the baseline. The resulting activation patterns are similar for each condition and include the rostral anterior cingulate cortex (rACC), midline posterior cingulate and precuneus, and bilateral extrastriate visual areas (see

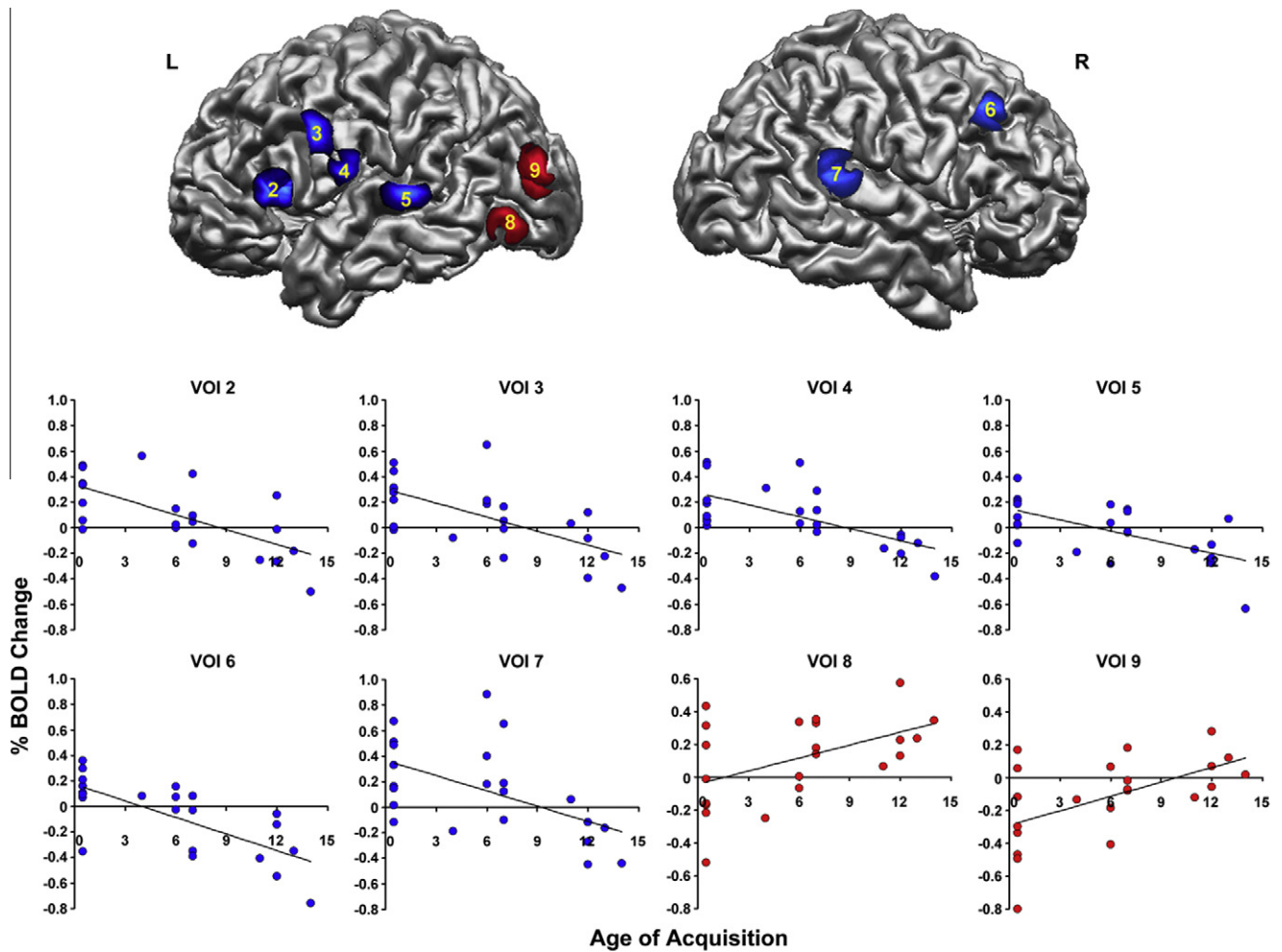


Fig. 5. AoA effects on phonemic-hand judgment activation. 3-D rendered image showing brain areas sensitive to AoA for phonemic-hand judgment; VOI's 2–9; L = left hemisphere; R = right hemisphere; Blue = negative linear relation to AoA; Red = positive linear relation to AoA; Regression scatterplots showing brain activity in all the VOI's for the phonemic-hand judgment task as a function of AoA; % BOLD change (y-axis) in relation to AoA (x-axis). Of particular note is VOI 2 (left frontal operculum) and VOI 9 (left occipital cortex, BA 18).

Fig. 6. This activation pattern is reminiscent of what has been described as the brain's default activation network (Raichle, MacLeod, Snyder, Powers, & Gusnard, 2001).

To rule out possible effects related to AoA in baseline activations, we performed linear regressions on them using AoA as the predictor variable. AoA showed no effects on the activation patterns for the baseline condition when grammatical judgment was subtracted. Similarly, AoA showed no effects on the activation patterns for the baseline condition when phonemic-hand judgment was subtracted. These results indicate that AoA has no discernable effects on the activation patterns for the baseline condition. This was an expected finding because the baseline task did not involve linguistic processing, which is specifically what AoA affects. Thus we do not observe differences in hemodynamic activations across the participants when they are engaged in the non-linguistic and low-level visual analysis involved when watching a still image of a person.

4. Discussion

The results fit our predictions and elucidate how a dearth of language exposure in early life affects language processing in the adult brain. Consistent with previous neurolinguistic research, the sign language processing of individuals born deaf whose age-

onset of language acquisition began in early life showed neural activation in the brain's classic language regions. By contrast, the sign language processing of those individuals born deaf whose age-onset of language acquisition began well beyond infancy, and who acquired little functional spoken language in the interim, showed neural activation patterns that deviated from the classic one in a systematic fashion. Specifically, the degree of departure from the classic pattern of neural language processing was a linear function of the length of language deprivation during early childhood. These striking results were of two types: negative effects in anterior brain regions responsible for higher level linguistic processing and positive ones in posterior brain regions responsible for lower level linguistic processing. Finally, the effects of AoA on neural language processing were independent of the linguistic level of the task, that is, whether it required attention to syntactic structure or sub-lexical form, performance accuracy, or length of experience. These results provide new insights into the nature of the critical period for language, which are best understood by comparing AoA effects on the activation patterns for the two linguistic tasks.

First, as has been well attested in previous research, a number of brain regions, most notably in the LH but also in the RH, were recruited for sign language processing. However, the present study is the first to neuroimage grammatical judgment in a sign language.

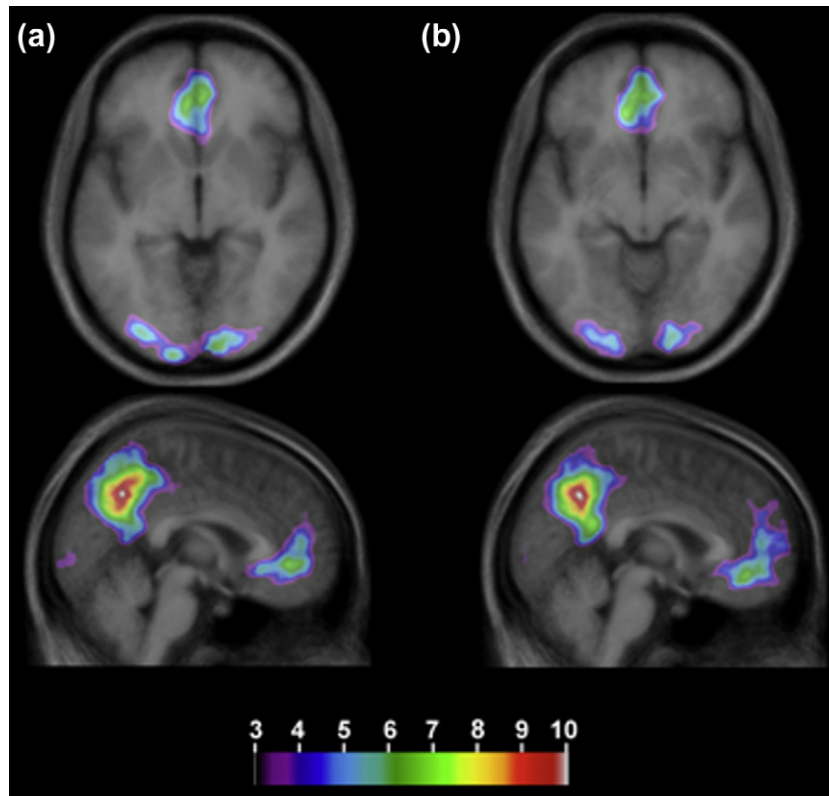


Fig. 6. Baseline activations. (a) Functional t -map overlaid on the anatomical MRI for the entire group of subjects showing baseline activation with grammatical judgment subtracted. (b) Functional t -map overlaid on the anatomical MRI for the entire group of subjects showing baseline activation with phonemic-hand judgment subtracted. The color bar encodes t -statistic scores indicating the significance level.

Grammatical judgment in ASL showed a bilateral pattern of activation with a leftward asymmetry in left-inferior frontal gyrus, LIFG. This activation pattern is similar to that observed for grammatical judgment performed in spoken language by hearing speakers (Wartenburger et al., 2004). In addition, the present study is the first to contrast syntactic processing in a sign language with phonemic processing. The phonemic-hand judgment task involved lower level linguistic skills because it was sub-lexical by nature, rather than syntactic, although the task was performed in the context of the same ASL sentence stimuli as the grammatical judgment task. The neural activation results for this novel phonemic processing task were consistent with the explanation that it required shallower linguistic analysis than grammatical judgment. Phonemic-hand judgment did not activate the left inferior frontal gyrus, as is typical for syntactic processing, but instead activated the inferior temporal gyrus and regions in the parietal and occipital lobes.

The contrastive patterns of neural activation for syntactic processing, being more anterior, as compared to phonemic processing in ASL, being more posterior, suggest that models of neural language processing developed to explain the functional anatomy of spoken language can also explain much of the functional anatomy of sign language (Hagoort, 2005; Hickok & Poeppel, 2004; Hickok et al., 2002). The crucial contribution of the present results is the finding that the overlap in functional anatomy for spoken and signed language processing is only observed when language acquisition begins in early life.

Importantly, the results also reveal that AoA affects the posterior to anterior dimension of neural language processing. Adults with an early age-onset of language acquisition showed activation patterns concentrated in somewhat more left lateralized anterior brain regions, a pattern characteristic of native speakers. This

reflects what is known about their psycholinguistic processing, namely that it is deep and thorough. As the age-onset of language acquisition began at older ages, activations across these anterior brain areas decreased. These striking results, apparent for both tasks, suggest that when the timing of post-natal brain growth and the onset of language acquisition are asynchronous during early childhood, different regions of the brain's classic language network are recruited for linguistic processing in the adult brain. A late age-onset of language acquisition attenuates activation in adult brain areas that typically sub-serve syntactic, semantic, and phonological processing even when the language has been used as a primary one for more than two decades.

AoA affects neural language processing in the adult brain in two ways that are predicted by previous research. When activation in anterior language areas is attenuated with later AoA, activation in posterior areas responsible for visual perceptual processing increases. Late AoA produces a shallower level of language processing. Behavioral work has found that adult signers who were born deaf and have a late onset of language acquisition commit lexical errors suggestive of heightened awareness of the phonological structure of signs, which correlates negatively with comprehension (Mayberry, 1993; Mayberry & Eichen, 1991; Mayberry & Fischer, 1989). Categorical perception studies have also discovered that late learners of sign language, who were born deaf and first began to acquire language at a late age, are hypersensitive to the psychophysical properties of signs. Adult signers, deaf or hearing, who acquired language in early childhood, signed or spoken, do not exhibit this hypersensitivity to the visual properties of signs (Best, Mathur, Miranda, & Lillo-Martin, 2010; Morford, Grieve-Smith, MacFarlane, Stanley, & Waters, 2008). Late learners of language showed increased activation in occipital areas, and lesions to the

left occipital cortex are known to cause deficits in identifying the phonological structure of signs (Hickok et al., 1995; Saito et al., 2007).

The present results integrate all these findings with the discovery that the behavioral processing bias associated with late language acquisition processing, a bias toward the visual and sub-lexical phonemic features of words (i.e., signs), reflects an underlying, differential allocation of resources to the initial stages of the neural language processing stream. This was found in another fMRI study, although not attributed to late AoA. In a neuroimaging study of German Sign Language, Meyer et al. (2007) found more posterior activation in occipital cortex compared to anterior regions in one deaf signer with a reported AoA of 13 years, and in several other participants whose AoA was unspecified. These unexpected findings for language processing were suggested as being due to deafness. However, the present results suggest another explanation, namely that the observed posterior activation for sign language was due to the late onset of language acquisition in the participants. When language acquisition begins atypically late, the present results show that more neuronal resources are allocated to the initial stages of language processing, such as phonemic processing, such that fewer resources are available for the downstream processes of semantic and syntactic analyses. Increased neural activation for the initial stages of language processing may arise from inefficient neuronal organization, as suggested by Indefrey (2006).

An alternative explanation for the neurolinguistic processing patterns associated with a late AoA could be that they arise from reduced language proficiency, a common outcome of L2 learning. Indeed, recent neuroimaging research indicates that L2 word recognition entails more visual activation relative to L1 word recognition at the beginning of L2 learning (Leonard et al., 2010). However, unlike typical L2 learners, the present participants did not possess native-like fluency in any other language acquired early in life, and they had on average two or more decades of ASL experience. In other words, the present participants were not L2 learners. Another counter-argument comes from the results of the present phonemic-hand judgment task where performance was unrelated to AoA. Nonetheless, the neural activation patterns associated with it were similar to those for the grammatical judgment. Although clearly in need of further research, the present results suggest that the neural activation patterns associated with a late age-onset of language acquisition are not transient, like L2 learning, but instead reflect a stable end-state of brain language processing that results from early brain growth in the absence of language acquisition during early childhood.

Finally, the more posterior activation patterns we find here for language processing are not unique to sign language and have been observed in several neuroimaging studies of normally hearing children. Consideration of these findings helps situate the critical period effects we find here in a broader developmental context. For example, when listening to spoken language, hearing toddlers (21 months old) showed greater hemodynamic activation in occipital regions compared to three year olds (Redcay, Haist, & Courchesne, 2008). Hearing children (7–10 years) also showed greater hemodynamic activation in occipital regions compared to adults on a visually presented, spoken verb generation task (Brown et al., 2005; Schlaggar et al., 2002). Likewise, when listening to sentences, healthy hearing children and those with perinatal brain damage (9–12 years) showed greater hemodynamic activation in inferior occipital cortex compared to adults (Booth, MacWhinney, Thulborn, Sacco, & Feldman, 2000). Similar neuroimaging results have been reported for hearing adolescents and adults with underdeveloped language. When deciding the semantic category of visually presented words, males with autism spectrum disorder (14–44 years), several of whom were reported to have underdeveloped

language associated with low verbal IQ scores (6/10 participants), showed greater activation in inferior occipital cortex and reduced activation in perisylvian language areas compared to age-matched male controls (Gaffrey et al., 2007).

Evidence is thus emerging that as language processing develops and becomes more sophisticated and automatic for larger linguistic units, such as for entire sentences, and becomes less tied to the sensory, perceptual, and phonemic units of language, that the primary weight of neural activation patterns shift from more posterior to more anterior brain regions. This interpretation emphasizes development of the automaticity of processing linguistic structures, including lexical ones, but is compatible with interpretations that beginning word learning requires visual, sensory and conceptual associations and support (Brown et al., 2005; Gaffrey et al., 2007). Note that this hypothesized posterior to anterior growth in the development of brain language processing transcends the sensory-motor modalities of the language stimuli, i.e., auditory vs. visual presentation, as demonstrated by the studies of children's neural language processing, and the sensory-motor modality of linguistic structure itself, i.e., signed vs. spoken language, as demonstrated by the present results. These developmental findings suggest that the activation patterns we find here for adults with a late age-onset of language acquisition, rather than being anomalous, are the product of underdeveloped neural language processing that has failed to grow forward in the adult brain due to an absence of language experience during critical moments throughout early brain development.

The present findings suggest that the timing of two key phenomena characteristic of early human development, brain growth and language acquisition, need to be in temporal synchrony in order for the classic neural network of language processing to reach its maximum potential in the adult brain. Our findings do not address the possible mechanisms by which these neuronal and linguistic developmental phenomena occur or the ways in which they interact. These crucial questions await more research.

Acknowledgments

We are indebted to the individuals from several Canadian Deaf communities who volunteered for this research, and D. Ilkbasaran and the staff at the Brain Imaging Center of the Montreal Neurological Institute for testing assistance. We also thank several individuals for helpful discussions about the data and analyses: T. Brown, N. Ferjan, F. Haist, R. Kluender, R. Zatorre, and P. Hagoort, K-M. Petersson and the Neurobiology of Language Group of the Max Planck Institute for Psycholinguistics. The research reported here was supported by grants from NSERC (171239 to RIM; 264061 to DK), SSHRC (410-2004-1775 to RIM), the GW Stairs Memorial Fund (216624 to DK and RIM), the Center for Research on Language Mind and Brain (to RIM and DK), and funds from the Division of Social Sciences, UCSD (RIM).

References

- Ann, J. (1996). On the relation between ease of articulation and frequency of occurrence of handshapes in two sign languages. *Lingua*, *98*, 19–42.
- Battison, R. (1978). *Lexical borrowing in American Sign Language*. Silver Spring, MD: Linstok Press.
- Baum, S. R., & Pell, M. D. (1999). The neural bases of prosody: Insights from lesion studies and neuroimaging. *Aphasiology*, *13*, 581–608.
- Best, C. T., Mathur, G., Miranda, K. A., & Lillo-Martin, D. (2010). Effects of sign language experience on categorical perception of dynamic ASL pseudosigns. *Attention, Perception, & Psychophysics*, *72*, 747–762.
- Birdsong, D., & Molis, M. (2001). On the evidence for maturational constraints in second language acquisition. *Journal of Memory & Language*, *44*, 235–249.
- Booth, J. R., MacWhinney, B., Thulborn, K. R., Sacco, K., & Feldman, H. M. (2000). Developmental and lesion effects in brain activation during sentence comprehension and mental rotation. *Developmental Neuropsychology*, *18*, 139–169.

- Boudreault, P., & Mayberry, R. I. (2006). Grammatical processing in American Sign Language: Age of first-language acquisition effects in relation to syntactic structure. *Language and Cognitive Processes*, 21, 608–635.
- Braun, A., Guillemin, A., Hoesly, L., & Varga, M. (2001). The neural organization of discourse: An H2 15 O-PET study of narrative production in English and American Sign Language. *Brain*, 124, 2028–2044.
- Brentari, D. (1998). *A prosodic model of sign language phonology*. Cambridge, MA: MIT Press.
- Brown, T. T., Lugar, H. M., Coalson, R. S., Miezin, F. M., Peterson, S. E., & Schlaggar, B. (2005). Developmental changes in human cerebral functional organization for word generation. *Cerebral Cortex*, 15, 275–290.
- Caplan, D. N., & Dapretto, M. (2001). Making sense during conversation: An fMRI study. *Neuroreport*, 12, 3625–3632.
- Chamberlain, C., & Mayberry, R. I. (2008). ASL syntactic and narrative comprehension in skilled and less skilled adult readers: Bilingual-bimodal evidence for the linguistic basis of reading. *Applied Psycholinguistics*, 28, 537–549.
- Channon, R. (2004). The symmetry and dominance conditions revisited. In N. Adams (Ed.), *Chicago Linguistic Society (Vol. 40)* (pp. 45–57). Chicago: Chicago Linguistic Society.
- Chute, D. L., & Daniel, R. S. (1996). *B/C PowerLaboratory*. Pacific Grove, CA: Brooks/Cole Publishing Co.
- Collins, D. L., Neelin, P., Peters, T. M., & Evans, A. C. (1994). Automatic 3D inter-subject registration of MR volumetric data in standardized talairach space. *Journal of Computer Assisted Tomography*, 18, 192–205.
- Corina, D., Chiu, Y.-S., Knapp, H., Greenwald, R., San Jose-Robertson, L., & Braun, A. (2007). Neural correlates of human action observation in hearing and deaf subjects. *Brain Research*, 1152, 111–129.
- Corina, D., McBurney, S. L., Dodrill, C., Hinshaw, K., Brinkley, J., & Ojemann, G. (1999). Functional roles of Broca's area and SMG: Evidence from cortical stimulation mapping in a deaf signer. *NeuroImage*, 10, 570–581.
- Damasio, H., Grabowski, T., Tranel, D., Hichwa, R. D., & Damasio, A. R. (1996). A neural basis for lexical retrieval. *Nature*, 380, 499–505.
- Davidson, K., Capronigro, I., & Mayberry, R. I. (2008). On the syntax and semantics of question–answer pairs in American Sign Language. In T. Friedman & S. Ito (Eds.), *Proceedings from semantics and linguistic theory (SALT)* (Vol. XVIII, pp. 212–229). Ithaca, NY: Cornell University.
- Emmorey, K., Bellugi, U., Friederici, A. D., & Horn, P. (1995). Effects of age of acquisition on grammatical sensitivity: Evidence from on-line and off-line tasks. *Applied Psycholinguistics*, 16, 1–23.
- Emmorey, K., Grabowski, T., McCullough, S., Damasio, H., Ponto, L. L. B., Hichwa, R. D., et al. (2003). Neural systems underlying lexical retrieval for sign language. *Neuropsychologia*, 41, 85–95.
- Emmorey, K., Grabowski, T., McCullough, S., Damasio, H., Ponto, L. L. B., Hichwa, R. D., et al. (2004). Motor-iconicity of sign language does not alter the neural systems underlying tool and action naming. *Brain and Language*, 89, 27–37.
- Fenson, L., Dale, P., Reznick, J. S., Thal, D., Bates, E., Hartung, J., et al. (1993). *MacArthur communicative inventories*. San Diego: Singular.
- Flege, J. E., Yeni-Komshian, G. H., & Liu, S. (1999). Age constraints on second-language acquisition. *Journal of Memory and Language*, 41, 78–104.
- Friston, K. J., Fletcher, P., Josephs, O., Holmes, A., Rugg, M. D., & Turner, R. (1998). Event-related fMRI: Characterizing differential responses. *NeuroImage*, 7, 30–40.
- Gaffrey, M. S., Kleinhans, N. M., Haist, F., Akshoomoff, N., Campbell, A., Courchesne, E., et al. (2007). Atypical participation of visual cortex during word processing in autism: An fMRI study of semantic decision. *Neuropsychologia*, 45, 1672–1684.
- Hagoort, P. (2005). On broca, brain, and binding: A new framework. *Trends in Cognitive Science*, 9, 416–423.
- Hickok, G., Bellugi, U., & Klima, E. S. (1998). What's right about the neural organization of sign language? A perspective on recent neuroimaging results. *Trends in Cognitive Science*, 2, 465–486.
- Hickok, G., Klima, E. S., Kritchevsky, M., & Bellugi, U. (1995). A case of 'sign blindness' following left occipital damage in a deaf signer. *Neuropsychologia*, 13, 1597–1606.
- Hickok, G., Love-Geffen, T., & Klima, E. S. (2002). Role of the left hemisphere in sign language comprehension. *Brain and Language*, 82, 167–178.
- Hickok, G., & Poeppel, D. (2004). Dorsal and ventral streams: A framework for understanding aspects of the functional anatomy of language. *Cognition*, 92, 67–99.
- Indefrey, P. (2006). A meta-analysis of hemodynamic studies on first and second language processing: Which suggested differences can we trust and what do they mean? *Language Learning*, 56, 279–304.
- Kassubek, J., Hickok, G., & Erhard, P. (2004). Involvement of classical anterior and posterior language areas in sign language production, as investigated by 4 T functional magnetic resonance imaging. *Neuroscience Letters*, 364, 168–172.
- Klann, J., Kastrau, F., & Huber, W. (2005). Lexical decision with no iconicity effect in German Sign Language: An fMRI-study. *Brain and Language*, 95, 167–169.
- Klima, E. S., & Bellugi, U. (1979). *The signs of language*. Cambridge: Harvard University Press.
- Lenneberg, E. H. (1967). *Biological foundations of language*. New York: John Wiley & Sons, Inc.
- Leonard, M. K., Brown, T. T., Travis, K. E., Gharapetian, L., Hagler, D. J., Dale, A., et al. (2010). Spatiotemporal dynamics of bilingual word processing. *NeuroImage*, 49, 3286–3294.
- Luke, K.-K., Liu, H.-L., Wai, Y.-Y., Wan, Y.-L., & Tan, L. H. (2002). Functional anatomy of syntactic and semantic processing in language comprehension. *Human Brain Mapping*, 16, 133–145.
- MacSweeney, M., Campbell, R., Woll, B., Brammer, M. J., Giampietro, V., David, A. S., et al. (2006). Lexical and sentential processing in British Sign Language. *Human Brain Mapping*, 27, 63–76.
- MacSweeney, M., Waters, D., Brammer, M. J., Woll, B., & Goswami, U. (2008). Phonological processing in deaf signers and the impact of age of first language acquisition. *NeuroImage*, 40, 1369–1379.
- MacSweeney, M., Woll, B., Campbell, R., McGuire, P. K., David, A. S., Williams, S. C. R., et al. (2002). Neural systems underlying British Sign Language and audio-visual English processing in native users. *Brain*, 125, 1583–1593.
- Marian, V., Blumenfeld, H. K., & Kaushanskaya, M. (2007). The language experience and proficiency questionnaire (LEAP-Q): Assessing language profiles in bilinguals and multilinguals. *Journal of Speech, Language, and Hearing Research*, 50, 940–967.
- Mayberry, R. I. (1993). First-language acquisition after childhood differs from second-language acquisition: The case of American Sign Language. *Journal of Speech and Hearing Research*, 36, 1258–1270.
- Mayberry, R. I. (2007). When timing is everything: Age of first-language acquisition effects on second-language learning. *Applied Psycholinguistics*, 28, 537–549.
- Mayberry, R. I. (2010). Early language acquisition and adult language ability: What sign language reveals about the critical period for language. In M. Marschark & P. Spencer (Eds.), *Oxford handbook of deaf studies, language and education* (Vol. 2, pp. 281–290). New York: Oxford University Press.
- Mayberry, R. I., & Eichen, E. B. (1991). The long-lasting advantage of learning sign language in childhood: Another look at the critical period for language acquisition. *Journal of Memory and Language*, 30, 486–512.
- Mayberry, R. I., & Fischer, S. D. (1989). Looking through phonological shape to lexical meaning: The bottleneck of nonnative sign language processing. *Memory and Cognition*, 17, 740–754.
- Mayberry, R. I., & Lock, E. (2003). Age constraints on first versus second language acquisition: Evidence for linguistic plasticity and epigenesis. *Brain and Language*, 87, 369–383.
- Mayberry, R. I., Lock, E., & Kazmi, H. (2002). Linguistic ability and early language exposure. *Nature*, 417, 38.
- McCullough, S., Emmorey, K., & Sereno, M. (2005). Neural organization for recognition of grammatical and emotional facial expressions in deaf ASL signers and hearing nonsigners. *Cognitive Brain Research*, 22, 193–203.
- Meyer, M., Toepel, U., Keler, J., Nussbaumer, D., Zysset, S., & Friederici, A. D. (2007). Neuroplasticity of sign language: Implications from structural and functional brain imaging. *Restorative Neurology and Neuroscience*, 25, 335–351.
- Morford, J., Grieve-Smith, A. B., MacFarlane, J., Stanley, J., & Waters, G. (2008). Effects of language experience on the perception of American Sign Language. *Cognition*, 109, 41–53.
- Newman, A. J., Bavelier, D., Corina, D., Jezzard, P., & Neville, H. J. (2002). A critical period for right hemisphere recruitment in American Sign Language processing. *Nature Neuroscience*, 5, 76–80.
- Newman, A. J., Supalla, T., Hauser, P., Newport, E. L., & Bavelier, D. (2010). Prosodic and narrative processing in American Sign Language: An fMRI study. *NeuroImage*, 52, 669–676.
- Newport, E. L. (1990). Maturation constraints on language learning. *Cognitive Science*, 14, 11–28.
- Pa, J., Wilson, S. M., Pickell, H., Bellugi, U., & Hickok, G. (2008). Neural organization of linguistic short-term memory is sensory modality-dependent: Evidence from signed and spoken language. *Journal of Cognitive Neuroscience*, 20, 2198–2210.
- Pfau, R., & Steinbach, M. (2006). Pluralization in sign and speech: A cross-modal typological study. *Linguistic Typology*, 10, 135–182.
- Poizner, H., Klima, E. S., & Bellugi, U. (1987). *What the hands reveal about the brain*. Cambridge, MA: MIT Press.
- Raichle, M. E., MacLeod, A. M., Snyder, A. Z., Powers, W. J., & Gusnard, D. A. (2001). A default mode of brain function. *Proceedings of the National Academy of Sciences*, 98, 676–682.
- Redcay, E., Haist, F., & Courchesne, E. (2008). Functional neuroimaging of speech perception during a pivotal period in language acquisition. *Developmental Science*, 11, 237–252.
- Rönnberg, J., Rudner, M., & Ingvar, M. (2004). Neural correlates of working memory for sign language. *Cognitive Brain Research*, 20, 165–182.
- Rozelle, L. (2003). *The structure of sign language lexicons: Inventory and distribution of handshape and location*. Unpublished Dissertation, University of Washington, Seattle.
- Rüschmeyer, S. A., Fiebach, C. J., Kempe, V., & Friederici, A. D. (2005). Processing lexical semantic and syntactic information in first and second language: fMRI evidence from German and Russian. *Human Brain Mapping*, 25, 266–286.
- Saito, K., Otsuki, M., & Ueno, S. (2007). Sign language aphasia due to left occipital lesion in a deaf signer. *Neurology*, 69, 1466–1468.
- Sakai, K. L., Tatsuno, Y., Suzuki, K., Kimura, H., & Ichida, Y. (2005). Sign and speech: Amodal commonality in left hemisphere dominance for comprehension of sentences. *Brain*, 128, 1407–1417.
- Sandler, W., & Lillo-Martin, D. (2006). *Sign language and linguistic universals*. Cambridge: Cambridge University Press.
- Schein, J. D. (1989). *At home among strangers: Exploring the Deaf community in the United States*. Washington, DC: Gallaudet University Press.
- Schlaggar, B. L., Brown, T. T., Lugar, H. M., Visscher, K. M., Miezin, F. M., & Peterson, S. E. (2002). Functional neuroanatomical differences between adults and school-age children in the processing of single words. *Science*, 296, 1476–1479.
- Stokoe, W. C., Casterline, D. C., & Croneberg, C. G. (1965). *A dictionary of American Sign Language on linguistic principles*. Washington, DC: Gallaudet University Press.

- Wartenburger, I., Heekeren, H. R., Burchert, F., Heinemann, S., Bleser, R., & Villringer, A. (2004). Neural correlates of syntactic transformations. *Human Brain Mapping, 22*, 72–81.
- Worsley, K. J., Evans, A. C., Marrett, S., & Neelin, P. (1992). A three-dimensional statistical analysis for CBF activation studies in human brain. *Journal of Cerebral Blood Flow and Metabolism, 12*, 900–918.
- Worsley, K. J., Liao, C. H., Aston, J., Petre, V., Duncan, G. H., Morales, F., et al. (2002). A general statistical analysis for fMRI data. *Neuroimage, 15*, 1–15.
- Zeshan, U. (2006). Sign languages of the world. In R. E. Asher (Ed.), *Encyclopedia of language and linguistics* (2nd ed., pp. 335–365). Oxford: Elsevier.