Neural Systems Mediating American Sign Language: Effects of Sensory Experience and Age of Acquisition

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ERPs were recorded from deaf and hearing native signers and from hearing subjects who acquired ASL late or not at all as they viewed ASL signs that formed sentences. The results were compared across these groups and with those from hearing subjects reading English sentences. The results suggest that there are constraints on the organization of the neural systems that mediate formal languages and that these are independent of the modality through which language is acquired. These include different specializations of anterior and posterior cortical regions in aspects of grammatical and semantic processing and a bias for the left hemisphere to mediate aspects of mnemonic functions in language. Additionally, the results suggest that the nature and timing of sensory and language experience significantly impact the development of the language systems of the brain. Effects of the early acquisition of ASL include an increased role for the right hemisphere and for parietal cortex and this occurs in both hearing and deaf native signers. An increased role of posterior temporal and occipital areas occurs in deaf native signers only and thus may be attributable to auditory deprivation. © 1997 Academic Press

INTRODUCTION

A central goal of cognitive neurosciences is to ascertain the degree to which intrinsic constraints govern the functional specializations of different neural systems and the complementary role of environmental inputs in specifying these specializations. Within the domain of sensory processing, current evidence suggests there are distinct biases that operate in neural development

but that the nature and timing of sensory experience are critical in specifying the identity and the functional architecture of brain systems (Kaas, 1995; Sur, Pallas, & Roe, 1990; Schlaggar & O'Leary, 1991; Rauschecker, 1995). At this point in time, it is reasonable to suppose that factors important in the development and maintenance of specialized systems for sensory processing also operate in the development of brain systems important for cognition, including language. That is, it is likely that there exist biological biases in the development of neurocognitive systems, but these biases are dependent on and modifiable by the nature and timing of specific experiences.

A major issue in psycholinguistic research has been the extent to which there exist biological constraints on the forms of natural languages. Theoretical considerations, formal structures, developmental data and behavioral data from normal and brain-lesioned adults have been brought to bear on this question. Cross-linguistic comparisons have provided important opportunities to address this issue. Additionally, several recent studies have explored this question by comparing the acquisition and processing of language acquired through different modalities, i.e., aural-oral language and the visual-manual or sign languages of the deaf. This literature has documented an impressive number of parallels between the formal characteristics, acquisition, and breakdown of ASL and spoken languages (Bellugi, Poizner, & Klima, 1989; 1990; Poizner, Klima, & Bellugi, 1987).

Thus, for example, ASL exhibits grammatical structure at all linguistic levels: syntax, morphology, and phonology (see Klima & Bellugi, 1988). Grammatical properties and principles that hold for spoken languages are also found in signed languages (see Lillo-Martin, 1991). Furthermore, children acquiring ASL as a native language from their deaf parents go through similar developmental stages as hearing children acquiring a spoken language (Bellugi, van Hoek, Lillo-Martin, & O'Grady, 1988). These results suggest there are constraints on the organization of all natural languages and that these operate independently of the modality through which language is acquired.

At the same time, the modality of transmission clearly impacts other aspects of language acquisition and processing. For example, the modality of the language affects the nature of the grammatical devices that the language exploits. Morphological and phonological distinctions are most often conveyed simultaneously within signed languages, reflecting the capacity of the visual system to present information simultaneously (Emmorey & Corina, 1990). Grammatical distinctions are conveyed by planes of signing space and spatial loci within these planes.

The pattern of similarities and differences implies that there should be parallels in the identity and operation of the neural systems that mediate spoken and signed languages, but that there are likely to be some differences as well.

One approach to this issue has been to compare the effects of damage to specific brain regions on particular aspects of oral- and sign-language production and comprehension. The initial studies along these lines reported similar patterns of hemispheric asymmetries and also similar patterns of anterior-posterior dependencies in language breakdown following cortical damage in speaking and signing patients. More recently, additional studies have reported discrepancies between the findings for aural-oral and sign-language breakdown. For example, deficits have been noted in spatial classifiers following right-hemisphere damage (Corina, in press).

Studies of neurologically intact signers have also addressed some of these issues. Hemifield studies of sign stimuli present a confusing array of results. Much of the variability is likely due to heterogeneity in the etiology and age of onset of deafness and task demands (see Neville et al., 1982a, b; Poizner & Battison, 1980). However, even carefully controlled studies have reported discrepant results, e.g., some reporting a left-, some a right-field advantage for sign perception.

The event-related potential (ERP) technique has been employed in a few studies of deaf signers. These have documented distinct effects of auditory deprivation and the acquisition of sign language on nonlanguage visual sensory and attentional processing (Neville et al., 1983, Neville & Lawson, 1987; Neville, 1995). A preliminary study of ERPs to signs presented to the hemifields reported behavioral and ERP asymmetries in deaf signers that were parallel to results from hearing subjects reading English words, i.e., a strong left-hemisphere bias (Neville, 1991b). Hearing subjects who learned ASL as a first language from their deaf parents displayed similar results. By contrast, when deaf subjects read English words presented to the two hemifields or when hearing subjects who learned ASL late or not at all were presented with ASL signs to the hemifields, the typical behavioral and ERP asymmetries were not evident. These results raised the hypothesis that the early acquisition of the grammar of a language may be a key factor in the development of language-relevant brain systems within the left hemisphere.

Recently this hypothesis was explored further in a study of the processing of English sentences using the ERP technique (Neville, Mills, & Lawson, 1992). ERPs to ''open class'' words, including nouns, verbs, and adjectives that make reference to specific objects and events, were compared with ERPs to ''closed class'' words including articles, conjunctions, and auxiliaries that specify relations between objects and events. It has been suggested that in English the closed class words support the initial syntactic parsing of sentences and thus play a major role in grammar. Neville et al. (1992) reported that open and closed class words in sentences elicited distinct patterns of ERPs normal hearing adults. These included an N400 response over posterior regions of both hemispheres in response to open class words and an

earlier response, N280, over anterior regions of the left hemisphere in response to closed class words. Congenitally deaf subjects who learned English late and imperfectly displayed ERPs to the open class words that were similar to those of the hearing subjects. In addition, the N400 responses elicited by sentence final anomalous words were identical in the deaf and hearing subjects. By contrast, however, the ERP responses of the deaf subjects to the closed class words lacked the asymmetrical N280 response over anterior regions of the left hemisphere. These results were interpreted as evidence that nonidentical neural systems mediate the processing of grammatical and semantic information in English and that these distinct neural systems have different developmental vulnerabilities to the altered early language experience of the deaf.

In the present study we employed ASL glosses of the English sentences used in the Neville et al. (1992) study to determine the nature and extent of similarities and differences in the pattern of ERPs to open and closed class signs and sentence final anomalies. In light of the studies summarized above, we hypothesized that there should be similarities in the neural systems utilized in processing ASL and English by subjects who learned those languages at the normal age for language acquisition. At the same time, in view of the markedly different mode through which language is acquired, alterations in the organization of language-relevant systems were expected, and the timing of acquisition of ASL was expected to interact with these. On the other hand, we also predicted that there may be differences in the neural systems utilized by deaf subjects that may be attributable to auditory deprivation, as we have previously reported. In order to assess the effects of auditory deprivation, we compared responses from deaf and hearing native signers born to deaf parents. In order to assess the effects of age of acquisition of ASL on the organization of these systems, we compared results from hearing native signers to hearing individuals who learned ASL in young adulthood (''hearing late learners'') to become certified interpreters of the deaf. Additionally, a comparison of results from the hearing late-learners and hearing subjects who did not know ASL (''hearing nonsigners'') helped to separately assess the effects of linguistic meaning from the neural events elicited by the complex stimuli that included moving human faces and hands.

Since many prior studies have demonstrated the importance of motion information in the perception of ASL, we presented a sequence of digitized images that captured the identifying motion of each sign. Additionally, signs were coded as open or closed for comparison with the English study. However, in ASL, as in many other languages, the distinction is less clear than it is in English, as ASL is a highly inflected language. Therefore, as described more fully under Methods, we classified as open class those signs belonging to the lexical category noun, verb, or adjective, and closed class items were pronouns, conjunctions, and auxiliaries.

METHODS

Subjects

(a) Deaf Subjects

All ten deaf subjects (five males, age range 23 to 37 years) were born profoundly deaf (>90dB loss bilaterally) due to a genetic etiology in which the CNS is not directly affected. These subjects learned American Sign Language (ASL) from their deaf parents at the same age that normal hearing children acquire spoken language. Nine of the subjects were right-handed and one was ambidextrous (as assessed by the Edinburgh Inventory of Handedness, 1971).

(b) Hearing Native Signers

The second group of subjects comprised ten hearing subjects (5 males, age range 21 to 38 years), who were all born to deaf parents and learned ASL as their first language. Eight of the subjects were right-handed and two of them left-handed. All subjects learned English as their second language at a later age. All had normal hearing.

(c) Hearing Late Learners (Hg LL)

The nine hearing late learners (4 males, 23 to 36 years) were born to normal-hearing parents. They were right-handed, native English speakers who learned ASL after the age of 17 years. At the time of testing they were all fluent in ASL and most worked as interpreters for the deaf.

(d) Hearing Nonsigners

The eight hearing subjects (4 males, age range 22 to 29 years) were born to normal-hearing parents and all were right-handed. This group had no knowledge of or experience with ASL.

All 37 subjects in each of the four groups had normal visual acuity and no neurological problems. They were paid $12.00 an hour for their participation in this experiment.

Stimuli

The stimuli were sentences presented one sign at a time on a monitor under the control of a computer. Each sign consisted of eight frames of digitized film (240 msec). Signs appeared in the center of a rectangle that indicated subjects were not to blink or move their eyes. The monitor was 57 in. from the subject, so signs subtended about 7 degrees visual angle vertically and 6–7 degrees of visual angle horizontally.

Sign Digitization

The signed sentences were recorded on 16 mm black and white film. A Grinnell image digitizer connected to a PDP 1134A was employed to select eight frames that represented the identifying movements of each sign. A native deaf signer chose the frames. Each frame was 256 by 256 bits with four bits of grey scale.

Procedure

Subjects sat comfortably in a copper-shielded, sound-attenuating room and were given instructions describing the task along with one practice session. All three groups that were familiar with ASL were shown a videotape with instructions in ASL before beginning the experiment. The hearing group with no experience with ASL was given instructions in English. Subjects were presented with 100 sentences in four blocks, each separated by a short break. A trial began with the onset of the rectangle in the center of the screen followed 1400–2000 msec later by the first sign of the sentence. Sentences ranged in length from 6 to 13 signs.

In between signs the subjects saw a still image of the signer. The interval from the onset of one sign to the onset of the next was 1000 msec. Two seconds after the onset of the final sign of the sentence the rectangle was turned off and the subject was prompted to press one of two buttons to indicate whether or not the sentence made sense. The hearing nonsigners were told that, although they did not know the language, they should make a guess as to whether or not the sentence made sense. Many subjects indicated they tried to guess the meaning intended from the facial expressions of the signer. Half of the final signs of the sentences were highly expected given the preceding context (e.g., MILK GLASS–BROUGHT–OVER–PUT–DOWN$_a$ (classifier construction) LEAVE$_a$ LATER SOUR. (The milk was left out and turned sour.)) and half were semantically anomalous (e.g., $\overline{\text{MAN HE}_a}^{\text{topic}}$ POLITICAL COMPETE WIN NOW HE$_a$ WRITE HIS ACCEPT WOOD. (The winning candidate was preparing his acceptance *wood*.)) Prior to the final signs all sentences were well formed and meaningful. The hand used to respond was counterbalanced across subjects. Each of the signs in the sentences except the first and last were coded for membership in the open class (N = 308 including nouns, verbs, and adjectives) or closed class (N = 116 including pronouns, conjunctions, etc.). Classifier signs, compound signs, and inflected verbs were excluded from the analysis. Classifiers and inflected verbs contain grammatical information coded in the morphology, and compound signs were digitized as if they were two signs such that ERPs were recorded separately for each part of the compound. Thus the closed class ASL signs consisted of pronouns, conjunctions, prepositions, and auxiliaries. Open class signs consisted of nouns, verbs without agreement or aspect morphology, adverbs, and adjectives.

ERP Recordings

Scalp electrical activity was recorded with Ag/AgCl electrodes from over several sites within and between the two hemispheres and from around the eyes. The scalp sites included six locations based on the International 10–20 System: Left and right frontal (F7/F8), posterior temporal (T5/T6), and occipital (01/02). Recordings were also taken from six other locations over left and right anterior temporal regions (50% of the distance from F7(8) to T3(4), left and right temporal (33% of the interaural distance lateral to CZ), and left and right temporoparietal areas (33% of the interaural distance lateral to a point 13% of the nasion-inion distance posterior to CZ). These nonstandard lateral sites were selected because they overlie brain regions thought to be important in language and have shown sensitivity to experimental variables in several ERP studies of language (Neville et al., 1982a, b; Neville, Kutas, Chesney, & Schmidt, 1986; Neville et al., 1992). Recordings from these electrodes and the vertical EOG from beneath the left eye were referenced to the linked mastoids. The horizontal EOG was recorded between electrodes placed at the outer canthus of each eye. Electrical activity was amplified with a band pass of 0.01–100 Hz and was digitized at 225 Hz.

Data Analysis

The EEG was sampled 100 msec prior to and 700 msec following each stimulus. Trials on which excessive eye movement or muscle artifact occurred were excluded from the averages (approximately 2–5% of all trials). ERPs were averaged separately for open class and closed class signs at each electrode site (6) over each hemisphere (2). Final signs that were and were not semantically anomalous were averaged separately.

Amplitudes of negative and positive values of ERP components were quantified by computer as either peak (maximal) amplitudes within a latency range or as area measures (the mean voltage within the same latency range), relative to 100 msec prestimulus baseline voltage. ERP component latencies were measured as the time of occurrence of the maximal negative or positive voltage within a given latency range. For the open and closed class signs the measurement windows were 50–150 msec for P100 at posterior (i.e., parietal, temporoparietal,

and occipital) electrodes, 50–200 for anterior N100 and posterior N130, 150–250 for P200, 200–350 msec for N250; 350–550 msec for N400; 400–800 for the late positive component (P550). For the final signs the peak amplitude, latency, and mean area within 300–600 and 600–900 msec (N400) were measured on both the ERPs and the difference waves (i.e., formed by subtracting the ERP to semantically appropriate signs from ERPs to semantically anomalous signs). This removes ERP activity that is the same to both signs and retains only the activity associated with semantic anomalies.

ERP measures were subjected to a three-way analysis of variance (ANOVA) with repeated measures on two levels of sign class, two levels of hemisphere, and six levels of electrode. Subanalyses of variance were performed to further clarify significant interactions. The Geisser–Greenhouse correction (Geisser & Greenhouse, 1959) was applied to all repeated measures with greater than one degree of freedom.

RESULTS

Here we present under I the results for signs in the middle of the sentence, and under II results for the final signs. We present under (A) the results from the deaf subjects, followed by a discussion of how these compare with the results from hearing subjects reading English (from Neville et al., 1992). Under (B) we compare the results of deaf native signers and hearing native signers. Under (C) we compare the results from hearing native signers with hearing interpreters who learned ASL late (''hearing late learners'') and under (D) we compare the results from hearing late learners with those of hearing nonsigners who did not know ASL.

I. Middle Words

A. Deaf Adults

Behavior. The deaf subjects correctly accepted 92% of the semantically appropriate sentences and correctly rejected 96% of semantically anomalous sentences (see Table 1).

ERP components. As seen in Fig. 1, the signs elicited a series of negative and positive deflections that varied as a function of electrode position and sign class membership. Over posterior regions, around 100 msec a positivity were elicited (P100) followed by a negativity at 130 msec (N130), and positivity at 200 (P200). These were followed by a negative peak at 250 msec (N250), a positivity at 350 (P350), a negativity around 400 msec (N400), and a broad positivity that was maximal around 550 msec (P550). Over ante-

TABLE 1
ASL Sentences
Percent Correct Responses

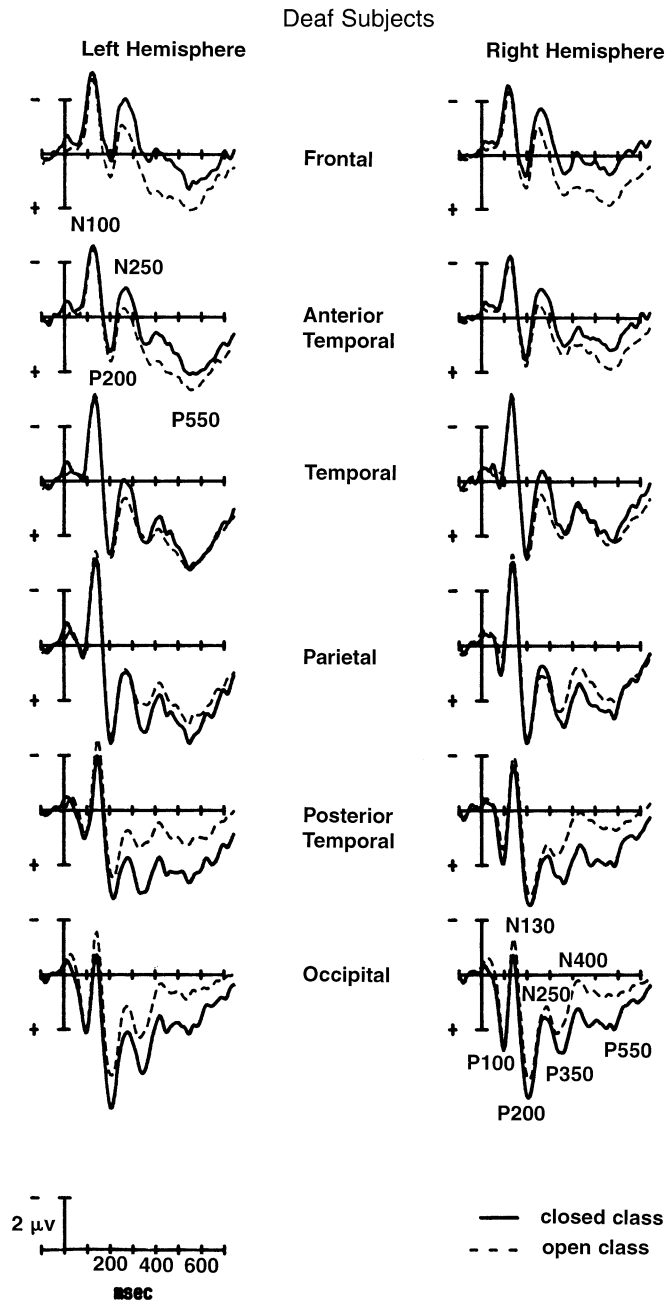|	Deaf	Hearing native signers	Hearing late learners	Hearing nonsigners
Semantically appropriate	92	85	89	54
Semantically anomalous	96	92	95	55

Deaf Subjects

Fig. 1. ERPs to closed/open class signs in the middle of ASL sentences. ERPs averaged across ten deaf subjects. Recordings from frontal, anterior temporal, temporal, parietal, posterior temporal and occipital areas of the left and right hemispheres.

rior regions an initial negativity (N100) was followed by P200, N250, and P550. The N400 response was reduced anteriorly.

Effects of sign class (deaf subjects). By 100 msec there were significant differences in the ERPs to open and closed class signs. The amplitude of posterior P100 was larger for closed than for open class signs (sign class $\times$ electrode $F(2, 18) = 5.05, p < .02$). Posterior N130 was more negative for open than closed class signs (sign class $\times$ electrode $F(5, 45) = 5.15, p < .02$). Posterior P200 was larger for closed class signs but over frontal areas it displayed the opposite pattern (sign class $\times$ electrode $F(5, 45) = 10.41, p < .001$). Thus over posterior regions the early ERP components to open class signs tended to be more negative than those to closed class signs, while over anterior regions the closed class signs were more negative.

The N250 was largest over anterior regions (electrode $F(5, 45) = 6.18, p < .01$). The N250 response was larger to closed than open class signs over anterior sites (sign class $\times$ electrode $F(5, 45) = 9.7, p < .001$; anterior sites, sign class $F(1, 9) = 10.90, p < .009$). Over the three posterior sites, only posterior temporal and occipital sites displayed the opposite pattern, i.e., N250 was larger for open than closed class signs.

The posterior N400 response was larger for open than closed signs (sign class $\times$ electrode $F(5, 45) = 12.35, p < .0003$). The late positivity (P550) displayed a similar pattern, i.e., greater negativity for open class signs over posterior areas, but displayed the opposite pattern anteriorly (sign class $\times$ electrode $F(5, 45) = 11.36, p < .001$). In addition P550 was larger from over the left than from over the right hemisphere (hemisphere, peak amplitude $F(1, 9) = 24.74, p < .008$; area $p < .01$).

Discussion of deaf results. These results demonstrate that the open and closed class signs elicited different ERPs by 100 msec after sign onset. As seen in Fig. 2 the prominent pattern whereby open class signs elicited more negative responses over posterior regions, while closed class signs were more negative over anterior regions, is similar to that observed in normal hearing subjects when they read open and closed class words in English sentences. This similarity of pattern as a function of word/sign class membership was superimposed upon several marked differences in the morphology of the ERPs to words and signs. A prominent difference in the responses from hearing and deaf subjects is that the N280 response was absent from posterior areas in the hearing subjects but the N250 response was present at all posterior sites in the deaf subjects. In addition, the N280 response of hearing subjects was absent or small in ERPs to open class words, but the N250 response was present to both open and closed class signs in the deaf. An additional difference is that the N280 response was strongly lateralized to the left hemisphere in hearing subjects, but the N250 response of the deaf to ASL was symmetrical (see Fig. 1). These several differences suggest that the N280 and N250 responses per se are not indexing the same underlying neural events. However, they are similarly modulated by class membership.
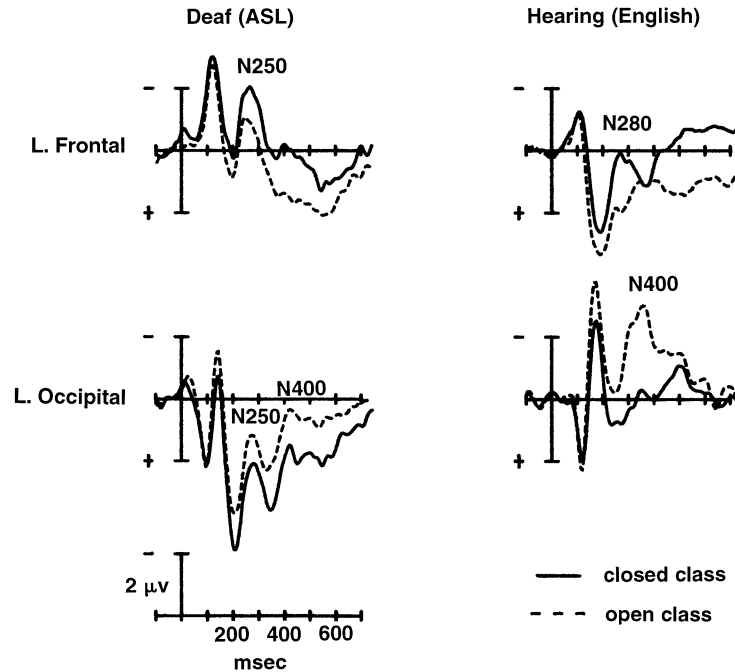
FIG. 2. ERPs to open and closed class signs in ASL sentences averaged across 10 deaf subjects from left frontal and occipital areas. ERPs to open and closed class words in English sentences from 17 normally hearing subjects reported in Neville, Mills, and Lawson, 1992.

In a recent study of ERPs during a face perception task (Sarfaty, Mills, Knaudt, & Neville, 1992) we have observed a response similar in latency and distribution to the N250 elicited by the signs (which included faces). In view of these results and the fact that the N250 was elicited by signs in subjects who did not know ASL (see below), it is likely that this response is indexing the operation of neural systems active in face processing. We hypothesize, however, that the increased N250 amplitude anteriorly in response to closed class signs may arise from the addition of activity specifically linked to the processing of information provided by the closed class signs. Evidence on this hypothesis is provided by an analysis of sign class effects in subjects who are not proficient or less proficient in ASL (see below).

The negativity around 400 msec (N400) to open class signs is similar in its latency and posterior distribution to the response elicited in both deaf and hearing subjects by open class words in English sentences (see Neville, 1992, and Fig. 2). It differs in the fact that it was prominent in response to closed class signs as well. Closed class words in English elicit a very small N400 response. This difference may be attributable to the comparatively weaker

distinction between open and closed class signs in ASL. Nonetheless, N400 was larger for open than for closed class signs, as is the case for English words.

Following N250 and N400 a positivity was apparent around 550 msec in response to ASL. This positivity was larger from the left than from the right hemisphere. A similar late positive component (LPC) is elicited by English words and displays the same asymmetry (Neville et al., 1992). In view of the strong link that has been demonstrated between the LPC response and mnemonic processing (Neville et al., 1986; Karis, Fabiani, & Donchin, 1984; Paller, McCarthy, & Wood, 1988), this component may index the operation of similar, lateralized processes associated with updating memories for both signs and words.

In summary, the results from the deaf subjects displayed a pattern of differential responsiveness to open and closed class signs that resembled, in overall pattern, the results for hearing subjects reading English words. These results are consistent with the proposal that there is significant overlap in the identity and organization of the neural systems that mediate the processing of all formal languages, independently of the modality through which they are acquired. The several differences between these results and those for English words may be in part attributable to the fact that there is a less clear distinction between open and closed class signs than exists for English words, and to the prominent ERP response elicited in conjunction with the processing of moving stimuli that included faces.

Additionally, the fact that the deaf subjects had sustained auditory deprivation since birth may have contributed to aspects of the differences observed. We have previously reported several such effects that include increased activity of posterior visual areas, perhaps due to compensatory hypertrophy like that observed after unimodal deprivation in other animals (Neville, 1990, 1995). Effects that may be attributable to auditory deprivation will be indexed in main effects of group in a comparison of the results from the hearing native signers who were born to deaf parents and who also acquired ASL as a first language, but who have had normal auditory sensory experience. On the other hand, any differences between deaf and hearing signers that interact with sign class may be attributable to differences in the extent of experience with and use of ASL and/or to differences in the degree of bilingualism in the two groups.

B. Hearing Native Signers

Behavior. The hearing native signers correctly accepted 85% of the semantically appropriate sentences and correctly rejected 92% of semantically anomalous sentences (see Table 1).

ERP components. Over anterior and central brain regions the signs elicited ERPs in deaf and hearing native signers that were similar. However, over posterior regions there was a marked difference (see Fig. 3). The occipital
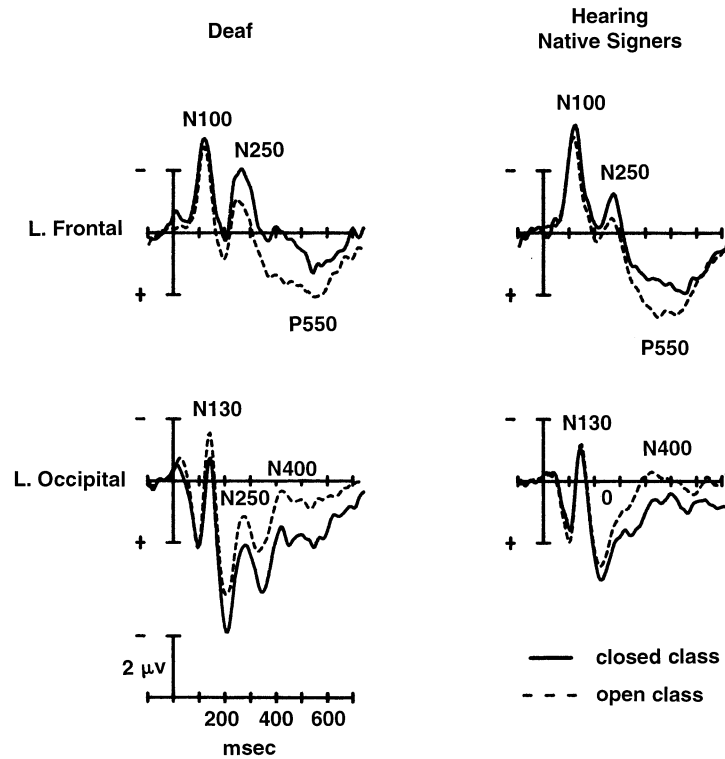
FIG. 3. ERPs to open and closed class signs in ASL sentences averaged across 10 deaf and 10 hearing native signers born to deaf parents. Recordings from left frontal and occipital electrodes.

N250 response and the following P380 were absent or attenuated in the hearing native signers (mean N250-P350 amplitude deaf = 2.2 μV, hearing native signers = .7 μV, $F(1, 18) = 5.06, p < .03$).

Over anterior areas the effects of sign class were similar in the two groups, i.e., the ERPs to closed class signs were more negative than ERPs to open class signs. However, these effects occurred later in the hearing than in the deaf group. In contrast to the results for the deaf, in the hearing native signers there were no significant sign class effects on P100, N100, or P200 amplitude (all n.s.). However the anterior N250 was, in the hearing as in the deaf native signers, larger to closed than open class words (word class, $F(1, 9) = 7.37$, $p < .02$). The posterior N400 response was, in the hearing as in the deaf native signers, larger for open than closed class signs (sign class × electrode amplitude $F(5, 45) = 7.65, p < .03$, area $p < .01$). As in the deaf, the following positivity displayed a reciprocal pattern, i.e., more negative to the closed class signs over anterior regions, more negative to open class signs over posterior regions (sign class × electrode, amplitude $F(5, 45) = 7.07$,

$p < .01$); area $F(5, 45) = 7.65, p < .01$). As in the deaf, the P550 also tended to be larger from the left hemisphere, primarily for open class words, over anterior sites (electrode $\times$ hemisphere, $F(5, 45) = 1.44, p < .06$; area, sign class $\times$ electrode $\times$ hemisphere, $F(5, 45) = 3.74, p < .03$).

Discussion (hearing and deaf native signers). A major group difference between the deaf and hearing native signers occurred independently of sign class membership and is therefore likely to be a consequence of auditory deprivation. The extension to the occipital regions of the N250 response in the deaf but not the hearing subjects is a result in line with previous studies of nonlanguage processing that suggest there is increased activity of posterior visual areas in the deaf. These results extend these findings to language materials.

The effects of sign class displayed a similar pattern in the two groups, but they occurred around 100 msec later in the hearing native signers. This effect is reminiscent of latency shifts reported in studies of bilinguals (Ardal, Donald, Meuter, Muldrew, & Luce, 1990; Weber-Fox & Neville, 1996) and may be attributable to less reliance on and use of ASL in the hearing than in the deaf subjects. Nonetheless the hearing subjects acquired ASL as a first language from their parents and many of these subjects use it extensively. This similarity of age of exposure and experience probably underlies the strong congruence of responsiveness in these groups. We assessed the effects of age of acquisition of ASL on these patterns by examining responses from hearing late learners of ASL whose experience with the use of ASL is extensive, but who learned ASL beyond the middle teen years.

C. Hearing Late Learners

Behavior. The hearing late learners correctly accepted 89% of the semantically appropriate sentences and correctly rejected 95% of semantically anomalous sentences (see Table 1).

ERP components. As seen in Fig. 4 the ERPs from the hearing late learners and hearing native signers displayed similar morphologies, including the prominent N250 response over anterior areas. A major difference between the groups was that, in contrast to the results for the deaf and hearing native signers, the N250 was not different for open and closed class signs in the hearing late learners (anterior sites, sign class $\times$ group $F(1, 17) = 5.08, p < .03$). Additionally, as seen in Fig. 5, over posterior regions, in response to closed class signs, the N250 response was smaller in hearing late learners than in hearing native signers (sign class $\times$ group $F(1, 17) = 4.93, p < .04$). This effect was significant only over parietal regions where it was larger from the right hemisphere (hemisphere $\times$ group $F(1, 17) = 7.5, p < .01$).

The N400 response displayed similar effects in the two groups (see Fig. 4) i.e., was larger for open class signs (N400 amplitude sign class $\times$ electrode $F(5, 40) = 9.20, p = .005$; area $F(5, 40) = 13.20, p < .002$). P550, as in
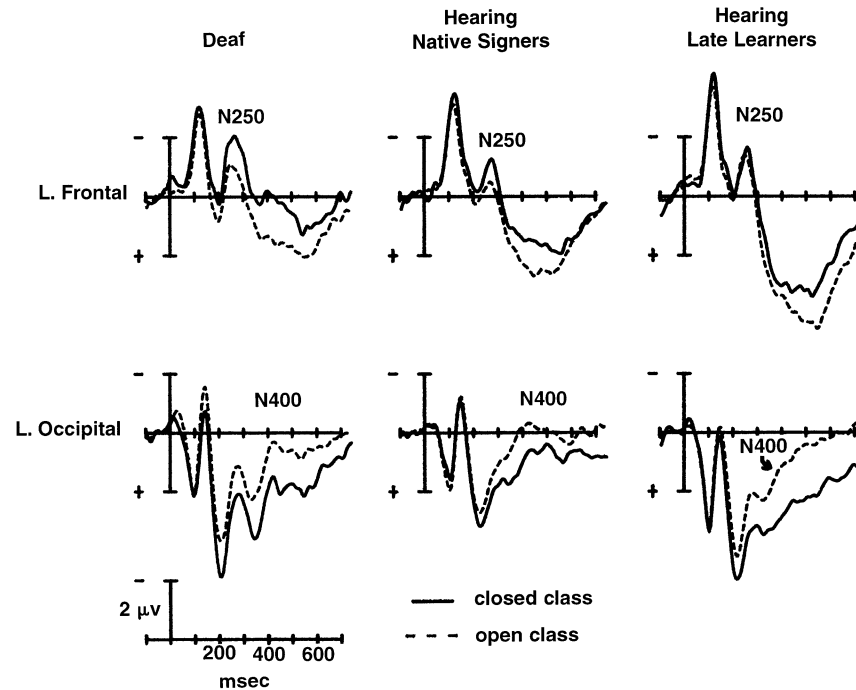
FIG. 4. ERPs to open and closed class signs in ASL sentences from 10 deaf and 10 hearing native signers and from 9 hearing ASL interpreters who learned ASL in the late teenage years ("Hearing Late Learners"). Recordings from left frontal and occipital areas.

the hearing native signers, displayed the reciprocal pattern (sign class $\times$ electrode $F(5, 40) = 12.12, p < .002$) and was also asymmetric in the same direction, i.e., left larger than right (hemisphere peak $F(1, 8) = 8.31, p < .02$; area $F(1, 8) = 7.5, p < .02$).

Discussion. There were two major differences between the early and late hearing learners of ASL. Late learners did not show the modulation of the anterior N250 response by sign class, (i.e., where in deaf and hearing native signers ERPs elicited by closed class signs were more negative). By contrast, this pattern was seen for both English and ASL by native learners, and would therefore appear to be a pattern strongly linked to early acquisition of a language, but to be independent of modality. The other major difference was the reduction in late learners of ASL of the N250 response to closed class words over parietal regions of the right hemisphere. The fact that this response was largest in those who acquired ASL early suggests that early exposure may result in recruitment of right parietal cortical areas for ASL. This effect may be a consequence of the important role that the perception of motion, space, and faces plays in the perception of ASL. This altered organization occurred independently of auditory deprivation and stands in
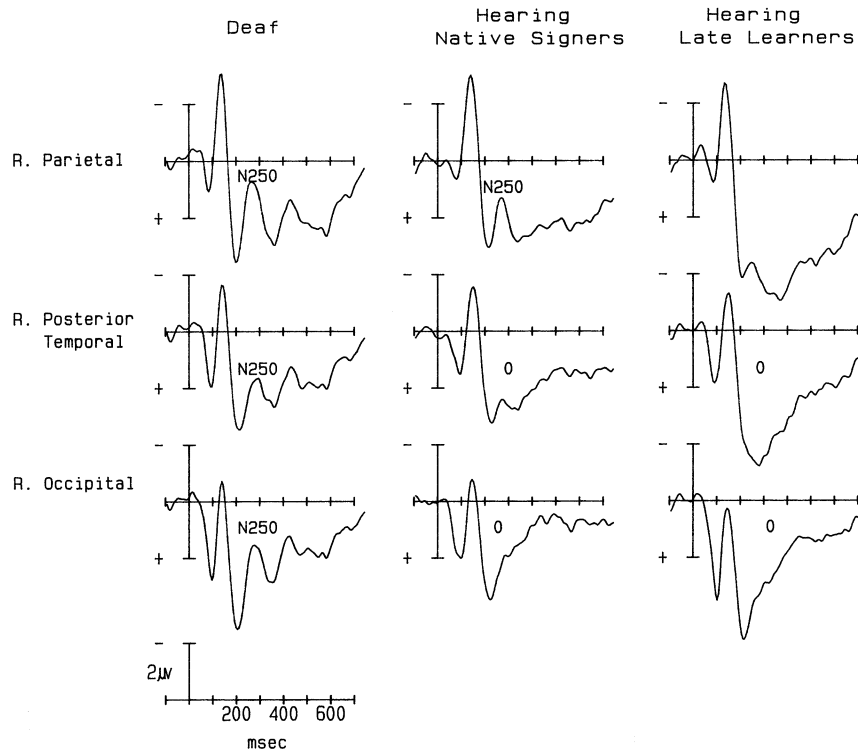
FIG. 5. ERPs to closed class signs in ASL sentences from 10 deaf and 10 hearing native signers and 10 late learners of ASL. Recordings from parietal, posterior temporal and occipital areas of the right hemisphere.

contrast to the increase in N250 over occipital areas which was only observed in the deaf (see Fig. 5).

D. Hearing Nonsigners

Behavior. The hearing nonsigners correctly accepted 54% of the semantically appropriate sentences and correctly rejected 55% of semantically anomalous sentences (see Table 1).

ERP components. The hearing nonsigners displayed early ERP responses that were similar to the other groups. As for the hearing late learners, the N250 response displayed an anterior distribution. The N250 response was later in the hearing nonsigners than hearing late learners (electrode $\times$ group $F(5, 75) = 5.21, p < .005$). Neither N250 nor any earlier components displayed effects of sign class in the hearing subjects. As seen in Fig. 6, following N250 the ERPs from the hearing subjects returned to baseline over anterior areas and were slightly positive over posterior areas. By contrast,
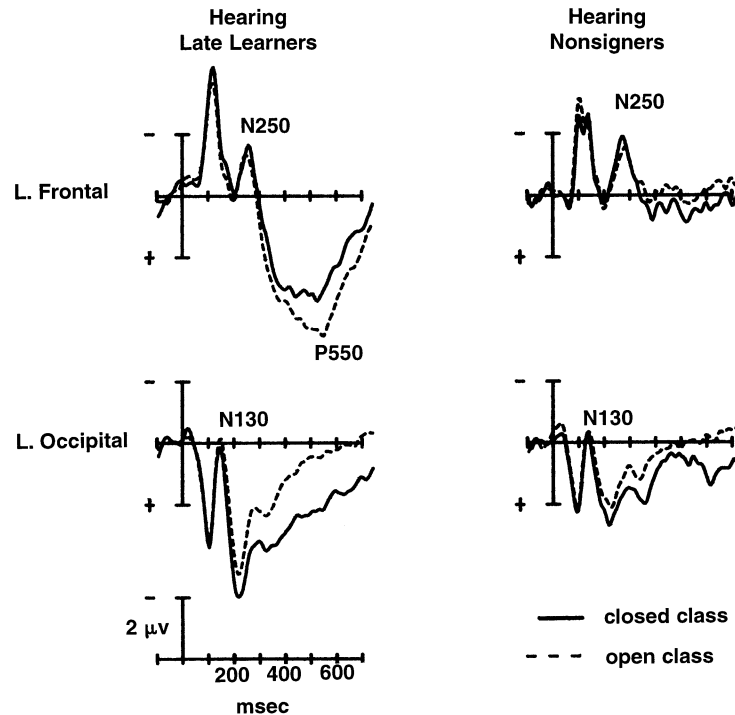
FIG. 6. ERPs to open and closed class signs in ASL sentences averaged across 10 hearing late learners of ASL and 8 hearing subjects who never learned ASL. Recordings from left frontal and occipital areas.

beginning around 300 msec the hearing late learners displayed a large positive response. Thus the measures of the N400 and P500 displayed significant group differences indicating a larger positivity for the hearing late learners (N400 area group effect $F(1, 15) = 11.92, p < .003$; P550 area group $F(1, 15) = 8.42, p < .01$). Additionally, whereas the late positive area was larger from the left hemisphere in hearing late learners, it was symmetrical in the hearing nonsigners (hemisphere $\times$ group, N400 area, $F(1, 15) = 6.43, p < .02$; P550 area, $F(1, 15) = 6.27, p < .02$).

Surprisingly, both N400 and P550 displayed significant effects of sign class over posterior areas in the hearing nonsigners (N400 area $F(1, 7) = 8.39, p < .02$; P550 area $F(1, 7) = 9.76, p < .01$). These effects were in the same direction as for the other groups, i.e., open class more negative than closed class over posterior areas. However, over posterior areas the sign class effects were larger in the hearing late learners than in the hearing nonsigners (sign class $\times$ electrode $\times$ group, N400 area $F(5, 75) = 9.54, p < .001$; P550 area $F(5, 75) = 6.04, p < .008$).

Discussion. As would be expected from a group who did not know ASL, neither N250 nor ERP components prior to it differed as a function of sign class. The unexpected result was that later in the ERPs, in the time region of N400 and P550, sign class membership did affect the amplitude of ERP activity. These results imply that the signs differed along some nonlinguistic dimension that influenced the N400-like response. Several studies have reported N400-like responses to nonlanguage stimuli, including faces, that were an integral part of the present stimuli. Moreover, the late negative responses to these stimuli diminish with repetition (Rugg, Furda, & Lorist, 1988; Bentin & Moscovitch, 1988; Sarfaty et al., 1992). Since the closed class signs are, in ASL as in English, more frequent in general and in these sentences, this sign class effect may be due to greater repetition effects on the N400 to closed class signs. The fact that the difference between the sign classes was larger for the hearing late learners suggests that additional, possibly linguistic, factors were operating in them and not in the hearing nonsigners. If this were the case the modulation of N400 by semantic expectancies should not be similar in the hearing groups who do and do not know ASL. The results for the final words that were semantically appropriate and anomalous are reported below.

II. Sentence Final Words

Figure 7 displays the ERPs to signs at the end of the sentences that were semantically appropriate and anomalous, and the difference ERPs formed by subtracting the appropriate from the anomalous signs. The hearing subjects who did not know ASL did not display any differences between the sentence endings (all sentence-type effects n.s.). The deaf subjects were the only group to display a significant increase in N250 amplitude to anomalous endings (N250 peak, sentence-type effect $F(1, 8) = 7.4, p < .02$). By about 300 msec each of the groups that knew ASL displayed significant differences in the same direction, i.e., the ERPs to the anomalous signs were more negative (N400 peak measure, sentence-type effect: deaf $F(1, 8) = 22.61, p < .001$; hearing native signers $F(1, 8) = 87.30, p < .001$; hearing late learners $F(1, 8) = 11.51, p < .009$; P550 area, deaf $F(1, 8) = 29.38, p < .0006$; hearing native signers $F(1, 8) = 66.55, p < .0001$; hearing late learners $F(1, 8) = 16.25, p < .003$). These effects were broadly distributed and did not interact with electrode site in any of the groups. Measures of the difference waves revealed that the peak amplitude of the N400 effect tended to occur earlier in the deaf than the hearing native signers (mean 534 vs. 600 msec, group $F(1, 16) = 3.5, p < .08$). Measures of the overall amplitude of the difference ERP did not reveal significant group differences. Analyses of the early (300–600 msec) and later (600–900 msec) phases of N400 suggested that the effect lasted longer in the hearing native signers than in the deaf subjects (area 600–900 group, $F(1, 16) = 7.1, p < .01$).
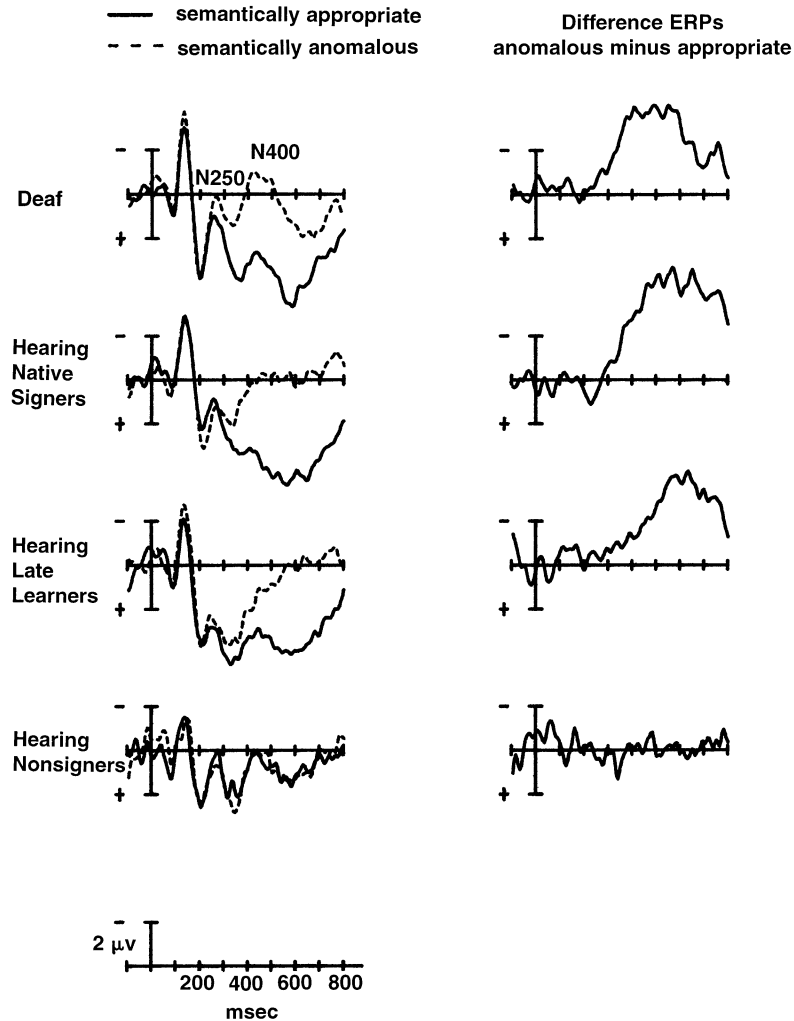
Fig. 7. ERPs from 10 deaf and 10 hearing native signers, 9 hearing late learners of ASL and 8 hearing subjects who did not know ASL. Left: Responses to final signs of ASL sentences that were either semantically appropriate or anomalous. Right: Difference ERPs formed by subtracting ERPs to semantically appropriate signs from semantically anomalous signs. Recordings are from right parietal electrode.

Discussion

With the exception of the hearing nonsigners, the results from the different groups displayed similar effects of semantic anomaly suggesting that later stages of semantic processing are relatively unaffected by the effects of auditory deprivation and the late acquisition of language. The one group differ-

ence was that the N400 effect began earlier and its late phase was reduced in the deaf subjects. This effect is reminiscent of the earlier onset of the sign class effects in the deaf than in the other groups. Since these group effects interacted with sign/sentence type, they suggest that the deaf subjects' greater use of and reliance on ASL was the important factor in producing the earlier effects in them.

The N400 effect in ASL peaked and terminated later than has been observed for semantic anomalies in written English, and instead displayed latencies more similar to those observed for auditory language (Holcomb & Neville, 1990, 1991). It is likely that, just as in auditory speech, the high degree of variability in the timing of the recognition point of the different signs contributed to this variability. By contrast, in written presentation all the information is available at one point in time.

GENERAL DISCUSSION

The ASL signs elicited ERPs that differed in overall morphology from those elicited by written or spoken English words, as would be expected given the large physical differences between the eliciting events. These physical-stimulus effects on the ERPs no doubt arise from the fact that different neural systems are activated from the earliest stages of sensory presentation.

Modality Independent Effects

Of interest with respect to the question of the extent of overlap in the neural systems that mediate language independent of the modality of transmission are the results showing highly similar effects of open vs. closed class membership on ERPs to words and signs. Native speakers of English and native ASL signers, both hearing and deaf, displayed a similar pattern of responsiveness whereby an early anterior negativity (N250 and N280) was larger to closed class elements, while a later, posterior negativity (N400) was larger to open class elements. Neither late learners of English (the deaf) nor late learners of ASL (the hearing interpreters) displayed an increased, early anterior negativity to closed class elements. By contrast, both groups of late learners display a greater later posterior negativity to open class elements. Additionally, both groups of late learners display the increase in the late posterior negativity (N400) to semantic anomalies. A further distinction between the early anterior and late posterior systems is that the latter displayed effects of sign class even in subjects who did not know ASL. These effects are most likely due to repetition priming of the closed class signs. However, no such effects were observed on the anterior N250.

These results are consistent with evidence from lesion studies (Poizner et al., 1987) and previous ERP results (Neville, 1991a, b; 1995) and recent fMRI research (Neville et al., 1995; Neville & Bavelier, in press) that suggest that there are substantial similarities in the organization and activation of

the neural systems that mediate the processing of language by native users, independent of the modality through which language is acquired. Moreover both the lesion data and recent ERP studies comparing the effects of syntactic and semantic anomalies (Neville et al., 1991; Garrett, 1995) suggest a greater role for anterior brain areas in the processing of grammatical information and a greater role for more posterior areas during processing of semantic/referential information.

Modality Dependent Effects

A number of differences in the results for English and ASL inform hypotheses about the nature and extent of the role of language and sensory experience in the organization of language relevant brain systems. A major difference between the results for native users of English and ASL occurred in the nature of lateral asymmetries. When reading, native English speakers display asymmetrical ERPs, whereby the left hemisphere is more negative than the right. These asymmetries are often evident by 150 msec post word onset (Neville et al., 1982; Neville et al., 1986; Neville et al., 1992). Moreover, the N280 response to closed class words is strongly lateralized to the left hemisphere (Neville et al., 1992). Additionally, the late positive component is larger from the left hemisphere (Kutas & Hillyard, 1980; Neville et al., 1986, 1992). The present results from deaf native signers did not display any asymmetries prior to the late positivity (P550) which, as for English, was also larger from the left hemisphere. These results imply that the earliest stages of ASL sentence-processing may be more bilaterally organized than is the case for English. This early symmetry may arise from the recruitment of specialized areas within the right hemisphere in the analyses of shape, motion, and location information that is central to ASL. Recent clinical evidence (Corina et al., 1990) and fMRI evidence (Neville et al., 1995; Neville & Bavelier, in press) is consistent with this interpretation.

The ERPs to ASL displayed asymmetries of the late positive potential, P550. Several studies have linked responses similar to the P550 to mnemonic processes (Karis et al., 1984; Neville et al., 1986; Paller et al., 1988). For example, the amplitude of similar, late positive components to the initial presentation of a stimulus is positively correlated with the likelihood that that item will be subsequently recognized or recalled. For verbal materials this component and this effect of memory is larger over the left hemisphere, and may therefore index the updating of language relevant memory systems. The asymmetries in cortical function for ASL reported in the clinical literature and the behavioral literature may therefore arise from asymmetries of language-relevant memory systems. An additional difference between the clinical studies and the ERP and fMRI studies is the etiology and age of onset of deafness of the subjects. Most of the clinical subjects were not congenitally deaf native signers. By contrast the nonclinical subjects in our stud-

ies were all born deaf to deaf parents from whom they acquired ASL at an early age. It may be that the maintenance or recruitment of additional cortical areas into the language systems can only occur when ASL is acquired early (see below).

Effects of Age of Acquisition

The results from late learners, both deaf subjects reading English and hearing late learners of ASL, suggest that there are marked effects of age of acquisition of language on the development of the early anterior responsiveness to closed class elements. By contrast the later posterior effects on open class words and the effects of semantic anomaly are relatively unaffected by this factor. More specifically, those aspects of semantic processing that are indexed by the N400 response appear less vulnerable to the effects of age of language acquisition than is the system indexed by the closed class modulation of the anterior negativity. We have recently reported a similar result in Chinese/English bilinguals. Delays in the acquisition of English of only 4 years were associated with reduction of the left lateralized anterior response to grammatical anomalies. However, the amplitude and distribution of the response to semantic anomalies was unaffected by delays of exposure up to 16 years. Thus the present results are consistent with several different lines of evidence that indicate that different neural systems with different developmental timecourses mediate aspects of semantic and grammatical processing (Neville et al., 1991, 1992; Curtiss, 1977; Brown, 1973; Friederici, 1985; Weber-Fox & Neville, 1996).

Additional differences between the hearing subjects who acquired ASL early and those who acquired it later suggest that there may be developmental time limits on the recruitment of different brain areas in the processing of ASL. Thus the hearing native signers had a larger N250 response over parietal cortex than did hearing late learners. Moreover, this effect was most evident in ERPs to closed class signs. These results suggest that there are time limits on the recruitment of parietal areas in processing the grammar of ASL.

Effects of Auditory Deprivation

Finally, we also observed differences in the distribution of ERP activity that are likely to be consequences of auditory deprivation since they were evident only in the deaf subjects and occurred independently of sign class. The extension of the N250 response to posterior temporal and occipital areas in the deaf only suggest increased activity of visual cortical areas following lack of auditory input. We have previously reported increased activity over these areas in congenitally deaf subjects during nonlanguage tasks. We have compared these to results in experimental animals and have suggested several mechanisms whereby such changes may occur (Neville, 1990, 1995).

These results imply that the language relevant systems of the brain may also benefit from the compensatory changes in visual processing that occur with auditory deprivation.

In summary, these results suggest that there are constraints on the organization of the neural systems that mediate formal languages. The biases operate independently of the modality through which language is acquired and may include different specializations of anterior and posterior cortical regions in the processing of aspects of grammatical and semantic information. They may also include a bias for the left hemisphere to mediate aspects of mnemonic functions in language. Additionally, the results suggest that the nature of sensory and language inputs significantly impacts the development of the language systems of the brain. The effects of the early acquisition of ASL include an increased role for the right hemisphere and for the parietal cortex that occurs in both hearing and deaf native signers. An increased role of posterior temporal and occipital areas occurred in deaf native signers only and thus may be attributable to auditory deprivation.

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