Response from Corina, Neville and Bavelier

The commentary by Hickok, Bellugi and Klima raises several issues regarding our recently published functional neuroimaging study of ASL and English comprehension in native signers using the highest field-strength functional neuroimaging techniques currently available. Our findings are provocative, for, in addition to showing the contributions of classical left-hemisphere-parsylvia language areas in sign language comprehension in native signers, they also reveal considerable right-hemisphere (RH) activation.

This RH activity was not predicted by studies of aphasia in deaf signers, which have argued for an exclusive role of the left hemisphere in ASL processing. We maintain that this RH activity reflects language processing requirements of a signal condition which are not observed in the processing of written English. The Hickok et al. critique raises two main issues about this study: (1) What is the source of the RH activation? (2) How do the activation patterns of the left hemisphere help address issues related to the neurobiology of linguistic processing? The issues of left-hemisphere processing are complex and cannot be adequately addressed in this brief forum. Rather, we focus here on a discussion of the RH involvement observed in our study.

Examining the patterns of activations for sign-gibberish, we have argued that the early acquisition of a natural language is important in the expression of the strong bias for left-hemisphere areas to mediate language, independent of the form of the language. In addition, the extensive activation of the right hemisphere reflects that the specific processing requirements of a language also, in part, determine the organization of the language systems of the brain.

We therefore agree with Hickok et al. with respect to the importance of left-hemisphere structures in the mediation of signed languages. We differ, however, with respect to the relative importance of the extensive RH activation observed in the fMRI study of ASL processing. It is important to note that several groups using PET and fMRI techniques have reported RH activation of temporal and frontal areas in response to spoken language processing tasks (see Box 1). Thus, findings of RH activity in language studies should not be come as a complete surprise to Hickok et al.

However, we do believe that the RH activity observed when native signers process ASL is qualitatively different. Several observations support this claim. First, in these spoken language experiments the RH activity is never as statistically robust as the left-hemisphere activity. In our study, the RH activation of native signers in the ASL condition was as robust as that observed for the left hemisphere. Second, the RH regions identified in spoken language studies tend to be restricted to small portions of the temporal lobe and, less frequently to the frontal lobe. The RH activation observed in the signers processing ASL is extensive, and extends to frontal, temporal and parietal sites. Finally, it is particularly interesting that only in deaf native signers do we find reliable activity of a right-hemisphere Broca’s area homologue and dorsolateral prefrontal cortex. This suggests that specialization of these frontal areas for language processing may be dependent upon difference in sensory input at formative points in development. Taken together, the differences in degree and extent of activation observed in the ASL studies and the within group comparisons between native signers versus deaf native signers (leads us to believe that no single factor will sufficiently account for the RH activity observed when native signers process ASL.

In their discussion of this work, Hickok et al. suggest that the robust RH activation observed in the ASL study is an artifact of the comparisons of these data with a condition of written English and the comparison of these data with a condition of written English. They note that the presence of information such as facial expression, and non-linguistic gesture in the signing conditions may account for the observed differences in RH activation. As noted, in our experiment, facial information and non-linguistic gesture are common in both the ASL and sign-gibberish stimuli and thus cannot be responsible for the RH activity observed. This point is made clear in the comparison of the hearing non-signers who showed no consistent activation when viewing the alternation between ASL and non-sign gibberish. This finding provides evidence that a language specific processing is revealed by electric and magnetic brain responses.

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Evidence that the non-sign gibberish provides a good control for the ASL condition, as any spurious systematic differences between these conditions would have led to significant activation in hearing persons unfamiliar with the linguistic content of the stimuli. Prosodic information is present in the naturalistic ASL stimuli and may contribute to some of the RH activation that has been attributed to prosody in studies of spoken language. However, based on the very limited RH activity reported by Bavelier et al.1 when English native speakers read well-formed sentences comprised of CRH during the reading of syntactically complex sentences. Significant activation was observed in right middle temporal gyrus when subjects read syntactically complex sentences compared to less complex constructions. In a related finding, Jur et al.1 reported both left and RH activity in a task requiring reading of sentences with increasing syntactic complexity. They proposed activity in both left and RH sites (corresponding to Broca’s and Wernicke’s areas) to be modulated by sentence complexity, though the RH activity was approximately 25% of the amount of activity observed in the left-hemisphere sites. These authors speculate that while the left hemisphere is usually the primary site of language comprehension, the right hemisphere may be recruited in times of high demand.

**Box 1. Right-hemisphere activation in spoken language tasks**

Maayar et al.1 contrived passive listening of French (the subject native language) to passive listening to an unfamiliar language, Tamil. While overall left posterior sites showed greater activation, RH activation was observed in left and right superior temporal lobes and right temporal pole. Price et al. (Ref. 10; experiment 3) reported limited RH activation in a condition contrasting naming of single words with naming to backward words. In several reading tasks, RH activity has also been observed. Activity in the middle portion of the superior temporal sulcus of the RH has been reported by Bavelier et al.11,12 when English native speakers read well-formed sentences comprised of CRH during the reading of syntactically complex sentences. Significant activation was observed in right middle temporal gyrus when subjects read syntactically complex sentences compared to less complex constructions. In a related finding, Jur et al.1 reported both left and RH activity in a task requiring reading of sentences with increasing syntactic complexity. They proposed activity in both left and RH sites (corresponding to Broca’s and Wernicke’s areas) to be modulated by sentence complexity, though the RH activity was approximately 25% of the amount of activity observed in the left-hemisphere sites. These authors speculate that while the left hemisphere is usually the primary site of language comprehension, the right hemisphere may be recruited in times of high demand.

**References**


**Production versus comprehension**

One explanation for the differences between the lesion studies and the fMRI study concerns an issue that until recently has been largely unaddressed: namely, the differences in the neural systems underlying language production versus comprehension. This basic difference has broad implications not only for the interpretation of these data, but also for the many neuroimaging reports which look to studies of aphasia for guidance in interpreting imaging results.

Our initial study purposely cast a broad net in this first phase of this amnestic syndrome study analyses reported by Hickok et al.1 (which is cited in Ref. 3 as ‘confirm[ing] the hypothesis... that the left hemisphere is dominant for sign language’, p. 132), we again see that the production studies are weighted most heavily. Here, four out of the six comparisons are measures of language production. Moreover, of all the comprehension measures available, the scores of only two tests (the BDAE command test and the Boston Diagnostic Aphasia Examination [BDAE] command test) were obtained. In a previous paper (below) we discuss a possible explanation for the omission of an important test of syntax comprehension in this analysis. As is evident, the weight of the assessment of sign language aphasia (as in the case of spoken language aphasia) falls upon measures of language production. It may be the case that the discrepancy we observe in the lesion studies and the fMRI results reflects a language system in which production is highly lateralized, while comprehension appears to be more modality independent. Regardless of the ability of our study to support this claim, in recent neuroimaging studies of ASL production, activation appears to be more lateralized to classic left-hemisphere perisylvian language areas13,14. This stands in contrast to the robust bilateral activity observed in our comprehension study of ASL.

In light of the discussion of production versus comprehension, we briefly entertain a very specific hypothesis. It is possible that some of the RH activation found in our study reflects processes underlying syntactic comprehension in ASL. Though not widely reported, disturbances in syntactic processing in American Sign Language have been attested to after both left-hemisphere and right-hemisphere damage. Two of the RH-damaged subjects tested by Pozniak et al.15 showed performance well below controls on two tests of ASL syntax. Indeed, as pointed out in their paper,
A second important issue in comparing comprehension in ASL (Ref. 12) is consistency with results of our study and rate performance. This observation is consistent with results of our study and with recent ERP studies of sentence comprehension in ASL (Ref. 12).

Heterogeneity of the deaf population
A second important issue in comparing results of the Neville et al. (1997) study and lesion studies of deaf signers concerns differences in subject groups. To date, the great majority of aphasia studies of deaf signers have involved deaf subjects who have not learned ASL as a native language. In contrast, in our fMRI studies, all subjects were congenitally deaf because of genetic factors, and all were native signers (i.e. acquired ASL at an age that is typical for primary language acquisition). Lesion studies involving the deaf community need to acknowledge the many factors that may influence language and cognitive development in the deaf: age of sign language acquisition, degree and nature of hearing loss, competence in English, etc. Indeed, when we examine the multitude of factors that may shape functional architecture of the cognitive systems in exceptional populations, we must seriously consider whether group studies of these brain damaged individuals are appropriate at all. A recent group study analysis reported in Hickok et al. (1998) is critical in the problem of whether or not differences between LH- and RH-damaged signers do not vary as a factor of age of onset of deafness and age of exposure to sign language. However, careful examination of these group data reveals significant methodological flaws, which severely limit the strong conclusions drawn from the data presented. Moreover, at most, only three native learners of ASL who sustained RH dam- age were included in these group comparisons, and no detailed case studies from these subjects have been published. The careful assessment of comprehension deficits in these three cases will be very informative.

The problems of subject group variability are far less serious in the case of studies of non-brain-injured deaf individuals, where one can carefully control for variables such as etiology of deafness, age of onset of deafness, and age of acquisition of ASL. This important homogeneity of critical factors is never obtained in group studies of brain damaged patients. The significance of these factors is underscored by recent reports that individuals who acquire ASL after the normal age for primary language acquisition do not display the same degree of RH activation during ASL sentence comprehension as do native signers (12,17). Thus, as is the case for spoken language, where delayed exposure results in a reduction of the normally left-lateralized pattern, late learners of ASL may fail to develop the normal, bi- lateral pattern of activation for sign comprehension (12,17).

Conclusion
Much research remains to be conducted on the question of the neurobi- ology of signed language. At present, most of the evidence from patient studies concerns ASL production and most neuroimaging studies focus on comprehension. Complementary stud- ies are needed. It will be critical for future group studies of brain-damaged signers to control for factors such as etiology of deafness, age of onset of deafness, and age of acquisition of ASL, as each of these variables has been shown in (neuroimaging studies of non-brain-damaged signers) to affect cerebral organization for both lan- guage and non-language processing (12,17). Once this homogeneity of task demands and subject variables has been attained, it will still be important to study the neurobiology of ASL by employing lesion studies, event-related-potential (ERP) and magneto-encephalographic (MEG) studies, and blood flow measures, as each method yields different information and per- spectives on the issues. Lesion studies, if properly controlled, can point to brain regions that may be necessary and sufficient for different processes. Neuromaging studies index, either directly (e.g. in the case of ERP, MEG) or indirectly (in blood flow methods), neuronal activity that co- occurs with the normal processing of ASL. Information from each of these different perspectives will help to ensure that a multidimensional view of the neural basis of ASL processing is obtained.