Second Language Acquisition Research: Theoretical and Methodological Issues Susan Gass and Jacquelyn Schachter, Editors

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Second Language Acquisition and the Critical Period Hypothesis

Edited by

David Birdsong *University of Texas*



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Lawrence Erlbaum Associates, Inc., Publishers 10 Industrial Avenue Mahwah, NJ 07430

Cover design by Kathryn Houghtaling Lacey

Library of Congress Cataloging-in-Publication Data

Second language acquisition and the critical period hypothesis / edited by David Birdsong.

p. cm. — (Second language acquisition research)
Chiefly papers presented at a conference held Aug. 1996,
Jyväskylä, Finland.
Includes bibliographical references and index.
ISBN 0-8058-3084-7 (alk. paper)
1. Second language acquisition—Congresses. J. Service.

1. Second language acquisition—Congresses. I. Series. P118.2.5428 1998 401'.93---dc21

> 98-42609 CIP

Books published by Lawrence Erlbaum Associates are printed on acid-free paper, and their bindings are chosen for strength and

Printed in the United States of America 10 9 8 7 6 5 4 3 2 1

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White, L., & Genesee, F. (1996). How native is near-native? The issue of ultimate attainment in adult second language acquisition. Second Language Research, 12, 238–265.

White, L., & Juffs, A. (1997). Constraints on wh-movement in two different contexts of non-native language acquisition: Competence and processing. In S. Flynn, G. Martohardhono, & W. O'Neil (Eds.), The generative study of second language acquisition (pp. 111–129). Mahwah, NJ: Lawrence Erlbaum Associates.

CHAPTER TWO

Functional Neural Subsystems
Are Differentially Affected
by Delays in Second Language Immersion:
ERP and Behavioral Evidence in Bilinguals

Christine M. Weber-Fox
Purdue University
Helen J. Neville
University of Oregon

AGE OF IMMERSION AND NEURAL SUBSYSTEMS IN L2A

Our aim has been to test the hypothesis that the age of immersion in a second language has differential effects on the neural subsystems involved in language processing. This hypothesis arises from consideration of studies of the development and organization of visual, auditory, and somatosensory systems. Within these systems, the nature of sensory input significantly affects the development of specific neurophysiological and behavioral processes (Freeman & Thibos, 1973; Kaas, 1991; Knudsen, 1988; Patkowski, 1980; Wiesel & Hubel, 1963, 1965). Morever, different functions within a system display distinct vulnerabilities to altered timing of input during development. For example, within the visual system, the timing of abnormal visual experience differentially affects the development of stereopsis, monocular spatial resolution, and spectral sensitivity (Harwerth, Smith, Duncan, Crawford & von Noorden, 1986). Although plasticity has been shown to characterize sensory and motor maps even in adult mammalian brains (Kaas, 1991; Kaas, Merzenich, & Killackey, 1983),

many such experience-dependent changes occur only during specific critical or sensitive periods. A general principle that emerges from a variety of studies is that the impact of altered sensory experience for many functions diminishes with maturation.

Lenneberg (1967) hypothesized that maturational processes similar to those that govern sensory and motor development may also constrain capabilities for normal language acquisition. Results from a variety of behavioral studies indicated that for primary and secondary language learning, the age of immersion is the best predictive variable for the ultimate linguistic proficiency (Johnson & Newport, 1989; Mayberry & Eichen, 1991; Newport, 1988; Oyama, 1982). Further, particular aspects of language have been found to be more profoundly impacted by delays, for example, grammatical functions of language. Other aspects such as vocabulary are relatively unaffected by delays in language immersion. Recent evidence from a study utilizing functional magnetic resonance imaging (fMRI) raises the hypothesis that different cortical areas associated with first and second languages may be differentially affected by delays in language immersion (Kim, Relkin, Lee, & Hirsch, 1997). The fMRI findings indicated that, within anterior language areas, the cortical locations for some aspects of first and second language functions do not overlap in late learners of a second language. In contrast, the fMRI results for early second language learners indicated that their native and second language were represented in common cortical areas within these regions. The behavioral and fMRI findings indicate that different aspects of language function and neural representation show distinct effects attributable to variations in delays in second language immersion. We hypothesized that the relevant functional cerebral subsystems specialized for semantic and grammatical processing are differentially impacted by delays in second language immersion.

Utilizing a bilingual model, we investigated this hypothesis using a combined behavioral–electrophysiological approach. A large group of Chinese–English bilinguals was tested. These participants were divided into groups based on the age at which they were immersed in English: 1 to 3, 4 to 6, 7 to 10, 11 to 13, and greater than 16 years of age (Weber-Fox & Neville, 1994, 1996, 1998). All participants were immersed in English for at least 5 years. And, it should be noted that the years of experience with English were similar for the participants in the 11 to 13 and greater than 16 groups. Measures of self-rated proficiency and standardized tests of knowledge of English grammar were used to help determine linguistic knowledge for these groups of participants. Relevant results are displayed in Fig. 2.1 and Fig. 2.2.

Self-Rated Proficiency

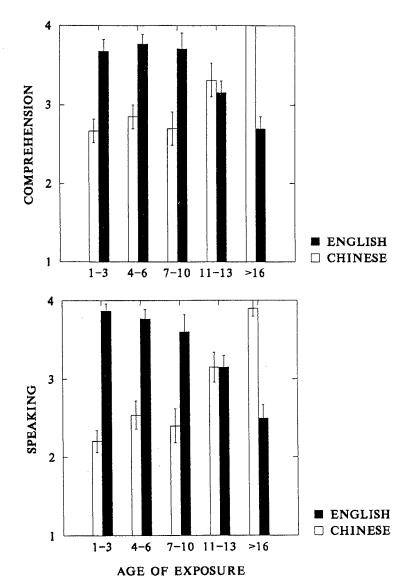


FIG. 2.1. Self-rated proficiency for comprehension and speaking in Chinese (white bars) and English (black bars). Scores are grouped according to age of exposure to English. Proficiency scale used: 1 = scarcely; 2 = sufficiently; 3 = well; 4 = perfectly. (From Weber-Fox & Neville, 1996).

Standardized Tests

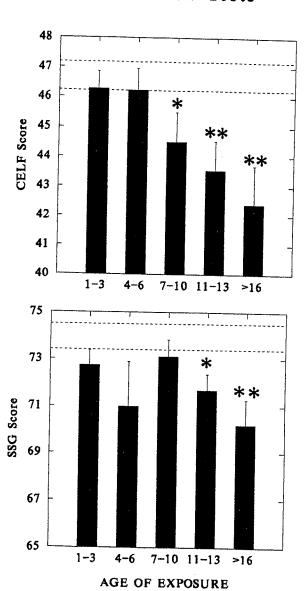


FIG. 2.2. Performance on standardized tests: Clinical Evaluation of Language Function (CELF–Word and Sentence Structure Subtest) and Saffran & Schwartz Grammaticality Judgment Test (SSG). Scores are grouped according to age of exposure to English. (From Weber-Fox & Neville, 1996).

Note: In Fig. 2.2, double dashed lines indicate the performance of monolinguals (mean scores +/- standard error). Scores of bilinguals which differed from those of monolinguals are asterisked (** p < .01; * p < .05).

Consistent with previous behavioral studies (Johnson & Newport, 1989; Newport, 1988), the findings shown in Fig. 2.1 and Fig. 2.2 indicated that the age of immersion in a second language is an important variable for predicting linguistic competence.

EFFECTS OF DELAYS ON PROCESSING SYNTACTIC VERSUS SEMANTIC ANOMALIES

The linguistic stimuli that allowed careful comparison between semantic and syntactic processing were previously developed for an ERP (Event-Related Brain Potential) study in English monolinguals (Neville, Nicol, Barss, Forster, & Garrett, 1991). The randomized sentence stimuli were presented one word at a time on a monitor (1 word per 500 msec). After each trial, participants were required to judge whether or not the sentence was "a good English sentence." Half of the 240 sentences included violations in semantic expectations (e.g., "The boys heard Joe's orange about Africa") or one of three syntactic rules: (1) phrase structure (e.g., "The boys heard Joe's about stories Africa"), (2) specificity constraint (e.g., "What did the boys hear Joe's stories about?"), or (3) subjacency constraint (e.g., "What were stories about heard by the boys?"). The remaining sentences served as semantically and syntactically appropriate controls. The underlined words in the anomalous sentence examples indicate the point of linguistic deviation and the ERP comparison points between the violation and their control sentences.

The effects of age of second language immersion on grammatical judgment accuracy in detecting syntactic and semantic anomalies in these stimuli sentences were investigated (Weber-Fox & Neville, 1996). As in previous studies, the relation between age of immersion and linguistic judgment accuracy was not uniform across different types of language constructs; namely, syntactic proficiency was more profoundly impacted than lexical (or semantic) judgment accuracy. Judgment accuracies for syntactic structures were reduced in bilinguals with delays of only 7 to 10 years. In contrast, judgment accuracy for semantic processing was decreased only for bilinguals with delays in second language immersion greater than 16 years. These findings are displayed graphically in Fig. 2.3 and Fig. 2.4.

Note: In Fig. 2.3 and Fig. 2.4, double dashed lines indicate the performance of monolinguals (mean scores +/- standard error). Scores of bilinguals which differed from those of monolinguals are asterisked (*** p < .001; ** p < .01; * p < .05).

Experimental Sentences

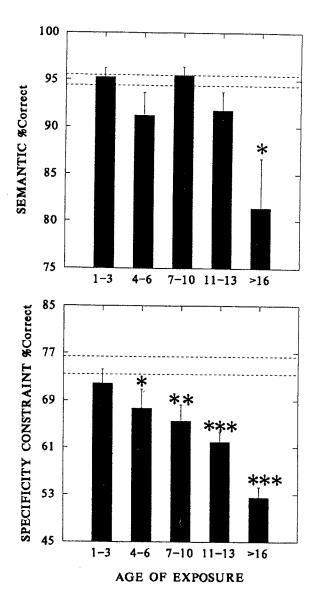


FIG. 2.3. Performance accuracy on judgments of experimental sentences: Semantic and Specificity Constraint. 100% is based on a possible 60 items correct (30 control and 30 violation sentences). Scores are grouped according to age of exposure to English. (From Weber-Fox & Neville, 1996).

Experimental Sentences

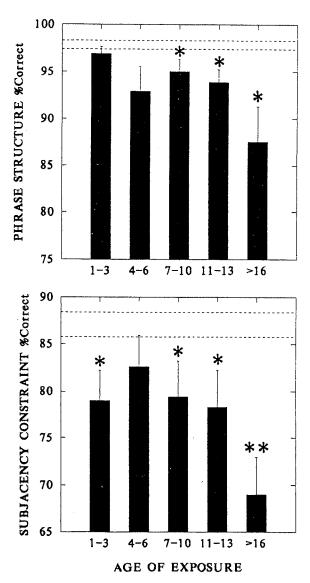


FIG. 2.4. Performance accuracy on judgments of experimental sentences: Phrase Structure and Subjacency Constraint. 100% is based on a possible 60 items correct (30 control and 30 violation sentences). Scores are grouped according to age of exposure to English. (From Weber-Fox & Neville, 1996).

Turning now to another source of evidence, electrophysiological findings in monolingual English speakers indicated that the ERPs elicited by semantic violations are distinct in timing and distribution from ERPs elicited by syntactic violations, and further, that different types of syntactic processing (e.g., phrase structure vs. specificity constraint) are associated with distinct neural subsystems (Neville et al., 1991).

Figure 2.5 displays averaged ERP waveforms over left and right parietal sites for monolinguals and each of the bilingual groups; Fig. 2.6 relates to anterior temporal sites. Traces in solid lines indicate responses to control words. Negativity is plotted upward. Dashed lines represent responses to violations: In Fig. 2.5, responses indicated by dashed lines were elicited by violations of semantic expectation; in Fig. 2.6, responses indicated by dashed lines were elicited by phrase structure violations.

As was the case with other evidence, ERPs showed differential vulnerabilities to delays in second language immersion. The amplitude and distribution of the N400 response to violations in semantic expectations were not affected by alterations in the timing of second language experience (Fig. 2.5). However, the latency of the N400 was longer (approximately 20 msec) for delays in immersion greater than 11 years, suggesting a slight slowing in processing. In contrast, ERP responses to each of the syntactic violations showed changes in amplitude and distribution, as well as actual presence of ERP components that were related to increased age of second language immersion. For example, for phrase structure violations, the distribution of the negativity increase between 300 and 500 msec poststimulus onset showed increased bilateral distribution with increased second language immersion. That is, with increasing delays of immersion in English, the asymmetry was diminished and increased negativity was observed over both the left and right hemispheres. ERP results for phrase structure violations are shown in Fig. 2.6.

The phrase structure violations also elicited a syntactic positive shift (SPS), as described by Osterhout and Holcomb (1992, 1996), in the latency range of 500 to 700 msec poststimulus onset. The SPS has been thought to index attempts to recover, or "patchup," syntactically anomalous sentences (Canseco et al., 1997). The SPS was observed in the ERPs of unilinguals (Neville et al., 1991) and the bilinguals who were immersed in their second language before the age of 11 (Weber-Fox & Neville, 1996). The mean amplitudes between 500 and 700 msec of the phrase structure difference ERPs (calculated by subtracting the waveforms for the control sentences from those elicited by violations in phrase structure) indicated that for bilinguals immersed in English after 11 years of age, there was no SPS within this latency range (Fig.

SEMANTIC ANOMALY

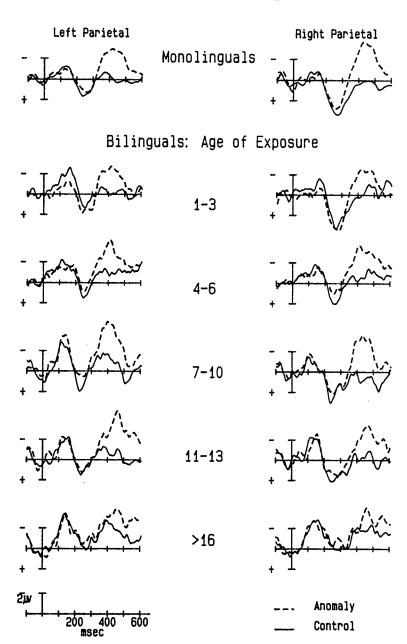


FIG. 2.5. Averaged ERP waveforms, violations of semantic expectation.

PHRASE STRUCTURE VIOLATION

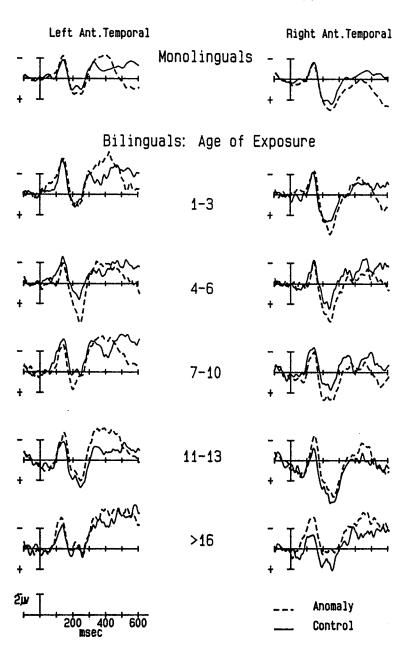


FIG. 2.6. Averaged ERP waveforms, violations of phrase structure expectation.

2.4). Analyses of a later latency window (700 to 900 msec) revealed that the 11 to 13 bilingual group did show an SPS in this later window; however, an SPS was still not evident in the ERPs of the bilingual group with the longest delays in second language learning. So, despite similar years of experience with English, the latest learning bilingual group members appeared to be much slower in their attempts to recover the sentence or perhaps utilized different strategies in interpreting the syntactic anomaly.

2. ERP AND BEHAVIORAL EVIDENCE

In summary, the N400 indices of semantic processing were relatively stable for each of the bilingual groups in terms of amplitude and distribution. However, a latency shift (approximately 20 msec) was noted for the bilingual groups who were immersed in English after 11 years of age, suggesting a slight slowing in processing. In contrast, our results suggested that for syntactic (grammatical) aspects of language, the actual presence and distribution of ERPs may be altered by delays in second language immersion. These results suggested that for processing syntactic anomalies, the ERPs of later learning bilinguals are associated with reduced specialization in the left hemisphere and include increased right hemisphere involvement, in some cases may reflect much slower processing, and overall may reveal differences in the strategies that later learners of English may utilize in the interpretation or recovery of violations of English syntax or grammar.

EFFECTS OF DELAYS ON PROCESSING OPEN- VERSUS CLOSED-CLASS WORDS

In a second ERP experiment, the EEG was recorded and averaged separately for word types that occurred correctly in read sentences (Weber-Fox & Neville, 1994, 1998). The word types were open- and closed-class words. The open-class words—such as nouns, verbs, and adjectives—convey referential meaning. They are dependent on vocabulary knowledge and primarily related to the semantic content of a sentence. In contrast, the closed-class words—such as articles, conjunctions, and determiners—primarily provide structural or grammatical information in a sentence. Based on behavioral evidence and the ERP results reported earlier, we hypothesized that the neural subsystems postulated to mediate the processing of these two different word classes may be differentially affected by delays in second language immersion.

In normal-hearing adults, the ERP response to open-class words is characterized by a negative component that peaks at 350 msec post word onset (Neville, Mills, & Lawson, 1992). The distribution of this component is bilateral and is largest over posterior areas. In contrast, the ERPs elicited by closed-class words are characterized by a negative peak that occurs earlier (280 msec post word onset) and is lateralized

over anterior temporal regions of the left hemisphere. Studies of deaf individuals and children have provided further evidence for the distinctness that characterizes the neural subsystems mediating the processing of open- and closed-class words (Neville, 1994; Neville, Coffey, Holcomb, & Tallal, 1993; Neville et al., 1992). These studies have shown further that the organization of neural subsystems associated with grammatical processing may be more vulnerable to alterations in early language experience, whereas the N350 elicited by open-class words is very similar in deaf and hearing adults. The N280 component is absent or small in deaf individuals who learn English late and imperfectly (Neville et al., 1992). Grammatical subsystems have

We utilized the same linguistic stimuli employed in the study of monolingual speakers in pursuing the hypothesis that the neural subsystems associated with processing closed-class words (N280) and open-class words (N350) would be differentially affected by alterations in the timing of second language immersion (Weber-Fox & Neville, 1994, 1998). The bilinguals who participated in this second experiment were similar in characteristics to the groups described previously. These were adult Chinese–English bilinguals who were grouped according to the age at which they were immersed in their second language, English.

been found to display a longer developmental time course in children compared with the ERPs for semantic processing (Neville, 1994). It has also been found that the neural subsystems associated with grammatical processing are more vulnerable in language developmental

disorders (Neville et al., 1993).

The ERP results in all groups of bilinguals supported the previous findings that the neural subsystems for processing open- and closed-class words are distinct in timing and distribution. The amplitudes, distributions, and latencies of the N350 elicited by open-class words were similar for all bilingual groups, regardless of age of immersion in their second language. The amplitudes and distributions of the N280 were also similar for all bilingual groups. All bilingual groups showed a similar left-anterior temporal negativity associated with processing closed-class words (Table 2.1). However, increases in delays of second language immersion of as little as 7 years were associated with increases in the peak latency of the N280 response, suggesting a slowing in the processing for these groups of bilinguals. For a detailed description of these findings, see Weber-Fox & Neville (1998).

These additional ERP findings for processing open- and closed-class words are consistent with the previous findings that grammatical or syntactic aspects of language processing appear to be more vulnerable to alterations in the timing of language experience compared to more semantic or lexical processing. These findings also indicate that even later learners of English display lert-hemispheric specialization for at

TABLE 2.1 Closed-Class Words: Peak Amplitude (Mean Microvolts and Standard Error) in the 215 to 375 Msec Windows.

	Left Temporal Site	Right Temporal Site	
Group			
Monolinguals	-1.803 (.47)	-1.054 (.32)	
Bilinguals 1–3 4–6 7–10 11–13 >16	-1.544 (.54) -1.928 (.57) -1.120 (.53) -2.143 (.45) -2.503 (.65)	913 (.45) 986 (.71) 050 (.56) 925 (.61) -1.211 (.57)	

Note: Measures are shown for the Event-Related Brain Potentials (ERPs) over the left and right temporal sites for monolinguals and each of the bilingual groups.

least some aspects of their second language, including the response to closed-class words. However, the results of the syntactic anomaly processing studies suggest that for some types of grammatical or syntactic processing, this left-hemispheric specialization may be reduced and increased right-hemisphere involvement may occur. Together, these findings suggest that later learners utilize altered neural systems and processing of English syntax.

Our ERP findings suggest a similar anterior left-hemisphere distribution for processing closed-class words for the bilingual groups (with a slight shift in latency noted). Because of the relatively poor spatial resolution of the ERP technique when employed with the number of electrodes in this study (16), it is not possible to determine whether the localization of the N280 within the left-anterior hemisphere differed among the groups. However, based on the recent fMRI and PET (Positron Emission Tomography) data (Kim et al., 1997; Perani et al., 1996), it could be hypothesized that for the later learner (>7 years), there may exist nonoverlapping cortical areas involved in the processing of closed-class word information in their two languages.

In conclusion, converging evidence from behavioral, electrophysiological, and fMRI studies suggests that specialized systems that mediate different aspects of language may be distinct in their susceptibilities to alterations in the timing of second language learning. Our findings are consistent with the hypothesis that the development of at least some neural subsystems for language processing

is constrained by maturational changes, even in early childhood. Additionally, our results are compatible, at least in part, with aspects of Lenneberg's (1967) original hypothesis that puberty may mark a significant point in language learning capacity and neural reorganizational capabilities. The maturational constraints we observed were most profound for the bilinguals who learned their second language after puberty. These findings contribute to our understanding of the dynamics of the development of functional neural subsystems for language and carry implications for the design and timing of programs for language education and habilitation.

REFERENCES

- Canseco, E., Love, T., Ahrens, K., Walenski, M., Swinney, D., & Neville, H. (1997). Processing of grammatical information in jabberwocky sentences: An ERP study. [Abstract]. Cognitive Neuroscience Society, 4.
- Freeman, R. D., & Thibos, L. N. (1973). Electrophysiological evidence that abnormal early visual experience can modify the human brain. *Science*, 180, 876–878.
- Harwerth, R., Smith, E. Crawford, M., & von Noorden, G. (1986). Multiple sensitive periods in the development of the primate visual system. *Science*, 232, 235–238.
- Johnson, J. S., & Newport, E. L. (1989). Critical period effects in second language learning: The influence of maturational state on the acquisition of English as a second language. *Cognitive Psychology*, 21, 60–99.
- Kaas, J. H. (1991). Plasticity of sensory and motor maps in adult mammals. *Annual Review of Neuroscience*, 14, 137–167.
- Kaas, J. H., Merzenich, M. M., & Killackey, H. P. (1983). The reorganization of somatosensory cortex following peripheral nerve damage in adult and developing mammals. *Annual Review of Neuroscience*, 6, 325–356.
- Kim, K. H. S., Relkin, N. R., Lee, K-M., & Hirsch, J. (1997). Distinct cortical areas associated with native and second languages. *Nature*, 388 (10), 171–174.
- Knudsen, E. (1988). Sensitive and critical periods in the development of sound localization. In S. S. Easter, Jr., K. F. Barald, & B. M. Carlson (Eds.), From message to mind: Directions in developmental neurobiology (pp. 303–318). Sunderland, MA: Sinauer Associates.
- Lenneberg, E. H. (1967). Biological foundations of language. New York: Wiley.
- Mayberry, R. I., & Eichen, E. B. (1991). The long-lasting advantage of learning sign language in childhood: Another look at the critical

- period in language acquisition. *Journal of Memory and Language*, 30, 486–512.
- Neville, H. J. (1994), Developmental specificity in neurocognitive development in humans. In M. Gazaniga (Ed.), *The cognitive neurosciences*, (pp. 219–231). Cambridge, MA: MIT Press.
- Neville, H. J., Coffey, S. A., Holcomb, P. J., & Tallal, P. (1993). The neurobiology of sensory and language processing in language impaired children. *Journal of Cognitive Neuroscience*, 5, 235–253.
- Neville, H. J., Mills, D. L., & Lawson, D. S. (1992). Fractionating language: Different neural subsystems with different sensitive periods. *Cerebral Cortex*, 2, 244–258.
- Neville, H. J., Nicol, J. L., Barss, A., Forster, K. I., & Garrett, M. F. (1991). Syntactically based sentence processing classes: Evidence from event-related brain potentials. *Journal of Cognitive Neuroscience*, 3, 151–165.
- Newport, E. L. (1988). Constraints on learning and their role in language acquisition: Studies of the acquisition of American Sign Language. *Language Sciences*, 10, 147–172.
- Osterhout, L., & Holcomb, P. J. (1992). Event-related brain potentials elicited by syntactic anomaly. *Journal of Memory and Language*, 31, 1–22.
- Osterhout, L., & Holcomb, P. J. (1996). Event-related potentials and syntactic anomaly: Evidence of anomaly detection during the perception of continuous speech. *Language and Cognitive Processes*, 8, 413–438.
- Oyama, S. (1982). The sensitive period and comprehension of speech. In S. D. Krashen, R. C. Scarcella, & M. H. Long (Eds.), Child-adult differences in second language acquisition (pp. 39–51) Rowley, MA: Newbury House.
- Patkowski, M. S. (1980). The sensitive period for the acquisition of syntax in a second language. *Language Learning*, 30, 449–472.
- Perani, D., Dehaene, S., Grassi, F., Cohen, L., Cappa, S. F., Dupoux, E., Fazio, F., & Mehler, J. (1996). Brain processing of native and foreign languages. Cognitive Neuroscience and Neurophysiology, 7, 2439–2444.
- Weber-Fox, C. M., & Neville, H. J. (1994). Sensitive periods differentiate neural systems for grammatical and semantic processing: ERP evidence in bilingual speakers. [Abstract]. *Cognitive Neuroscience Society*, 18, 89.
- Weber-Fox, C. M. & Neville, H. J. (1996). Maturational constraints on functional specializations for language processing: ERP and behavioral evidence in bilingual speakers. *Journal of Cognitive Neuroscience*, 8, 231–256.
- Weber-Fox, C. M. & Neville, H. J. (1998). Neural subsystems for open and closed class words differentially impacted by delays in

second-language immersion: ERP evidence in bilingual speakers. Unpublished manuscript, Purdue University.

Wiesel, T., & Hubel, D. (1963). Effects of visual deprivation on morphology and physiology of cells in the cat's lateral geniculate body. *Journal of Neurophysiology*, 26, 978–993.

Wiesel, T., & Hubel, D. (1965). Comparison of the effects of unilateral and bilateral eye closure on cortical unit responses in kittens. *Journal of Neurophysiology*, 28, 1029–1040.

Co-Evolution of Language Size and the Critical Period

James R. Hurford Simon Kirby University of Edinburgh

INTRODUCTION: GENE-LANGUAGE CO-EVOLUTION

Species evolve, very slowly, through selection of genes that give rise to phenotypes well adapted to their environments. The cultures, including the languages, of human communities evolve much faster, maintaining at least a minimum level of adaptedness to the external, noncultural environment. In the phylogenetic evolution of species, the transmission of information across generations is via copying of molecules, and innovation is by mutation and sexual recombination. In cultural evolution, the transmission of information across generations is by learning, and innovation is by sporadic invention or borrowing from other cultures. This much is the foundational bedrock of evolutionary theory.

But things get more complicated; there can be gene-culture coevolution.² Prior to the rise of culture, the physical environment is the only force shaping biological evolution from outside the organism, and cultures themselves are clearly constrained by the evolved biological characteristics of their members. But cultures become part of the external environment and influence the course of biological evolution. For example, altruistic cultures with developed medical knowledge reduce the cost to the individual of carrying genes disposing to certain

¹Not every property of an organism is adaptive, of course; spandrels do exist.

²Although not uncontroversial, the idea of gene–culture co-evolution has been developed in a variety of models, including Lumsden and Wilson (1981) and Boyd and Richerson (1985); Dawkins and Krebs (1984) proposed a co-evolutionary mechanism at the root of the evolution of signaling systems, and Deacon (1992) discussed human brain–language co-evolution in detail.