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# Acoustic Dimensions of Functor Comprehension in Broca's Aphasia

by

Randy Allen Harris

A THESIS
SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH
IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE
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DATED 20 August 1985

*language is better analyzed by aphasia than by linguists.*

**—Jason W. Brown**

THE UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled Acoustic Dimensions of Functor Comprehension in Broca's Aphasia submitted by Randy Allen Harris in partial fulfilment of the requirements for the degree of Master of Science in Psycholinguistics.

Lois M. Stanford

Supervisor

Thomas Campbell

Date 15 ~~July~~ August 1985

# DEDICATION

This thesis is dedicated to the memory of Sephas Carey Harris, who lost his language, his strength, and his life, in a relentless series of strokes, and to his loving wife Gladys, who was his voice, his strength, and his reason to live. She remains an inspiration to everyone who knows her.

# ABSTRACT

This thesis is organized around Heilman and Scholes' (1976) elegant test of functor comprehension in aphasia, with the addition of a control on the acoustic dimensions of the key function word. Nine Broca patients heard four sentence pairs differing only in the postverb placement of *the* (and the argument structure cued by that placement), as illustrated by the following two sentences:

> The man showed her the baby pictures.
> The man showed her baby the pictures.

The task was a forced choice between four line drawings: one which depicted the correct action, one which depicted the action of the other member in the pair, and two which contained depictions of different figures and actions altogether. Each of the eight sentences was played in two conditions: one with NORMAL intonation, and another with an acoustically more distinct SALIENT *the* token in the postverb location.

Both of Heilman and Scholes' principal results were successfully replicated: the aphasic population was significantly less reliable overall than normals, and the difference between correct responses and function errors (choosing the depiction of the paired sentence) was not significantly greater than chance for the NORMAL sentences. Both of these results indicate that Broca patients have a peculiar deficit for some function words. However, a SALIENT effect was also discovered. The subjects were significantly more reliable with the acoustically boosted stimuli. This finding is used to suggest that there is a performance component to Broca syndrome functor difficulties, and therefore that proposals of lexical or syntactic or phonological incompetence are overzealous. A tentative explanation of the results is offered in terms of short term memory deficiencies.

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PAGES ix - xii OMITTED

## List of Tables

# List of Figures

Figure Page

## Table of Contents

Chapter Page

# 1. Introduction

The brain is a very mysterious organ and its functioning is far from clearly understood, but immeasurably more is known about it now than at any time in the past. To take a radical example, Aristotle saw the brain rather as a spongy radiator – a cooling device where blood, exited by muscular activity, could dissipate its heat. Herophilus thought it generated 'animal spirits', his medium of a hydraulic theory of muscle control. Th. Bartholinus, some centuries later, held it to be packing material, installed to "protect the cerebral vessels against the danger of violent movement, especially during the full moon when the brain swells in the skull" (Schiller [1979:168]). While some of us act now and again in a manner suggesting the accuracy of these proposals, in hindsight their only charm lies in absurdity. But they are not unreasonable hypotheses when evidence is drawn exclusively from autopsy of neurologically intact cadavers. Brains look a good deal more like radiators or packing material than "the most elegantly organized bundles of matter in the universe" (Calvin [1983:62]).

Fortunately for science, the misfortunes of a great many individuals have led to more soundly-based theories of the brain, and growing insight into the elegance of its organization. Cerebral pathology has afforded an irregular and winding, but functional, roadway from radiators to receptive fields. When damage to a localized region of the brain results consistently in a disruption of abilities present in people without such damage – vision, motion, calculation, language use – then it follows that the brain mediates the ability. It also follows that the specific site of damage mediates the ability. How the mediation occurs does not follow. For instance, the damaged region might be a knowledge store, or an access channel to a knowledge store, or it might subserve a largely independent mechanism incidentally employed in the access or utilization of knowledge. Or the damage might simply be running an interference pattern, diverting energy from processes necessary to the disrupted ability. Or some complex of these posibilities might be responsible for the impairment. None of this is clear from the injury-dysfunction correlation alone. But there are methods of getting at these questions, and an experiment with such a goal is at the heart of this thesis.

Neither the experiment, nor the specific question addressed, is difficult to summarize: the acoustic patterns of a small set of speech strings are digitally altered so that certain normally reduced elements (functors) are increased in duration, intensity, and stability of fundamental frequency ($f_0$); if reduced stress is a significant factor in the difficulty Broca's aphasics have comprehending function words during sentence processing, then they should demonstrate improved comprehension of those strings. The motivations and the significance of the experiment are not nearly so straightforward.

## 1.1 The Issues

### 1.1.1 Site and Syndrome

Aphasia is a language impairment consequent to neural insult, and location of insult makes a difference. Though there has been considerable debate between equipotential and modular theorists about site-specific deficits (see, e.g., Finger and Stein [1982:13-47]), this much is obvious. Damage to the peripheral nervous system, for instance, or the central nervous system below the medulla, does not result in prolonged linguistic interference. There is some interference, and this interference does say something interesting about the mechanisms of language use. But the problem is short term, and probably due to some incidental diversion of energy. There is no aphasia. Similarly, damage to the right hemisphere, even if quite severe, has minimal effects on language in nearly all cases. Damage to fairly large tracts of the left frontal lobe also leaves linguistic ability pretty much alone. Insult to the visual cortex, or to the upper stretches of the motor strip, does not directly affect language use. On the other hand, damage to the convolution adjacent and immediately anterior to the fissure of Sylvius, or to the posterior temporal operculum, results in aphasia very frequently. Damage to the bridge between these two areas, the arcuate fasciculus, results in aphasia. Recently there has even been evidence that thalamic lesions, subcortical, measureably interfere with linguistic ability (Mateer and Ojemann [1983]). Clearly the issue here is not localization, but relative localization.

The equipotentialist position is that the brain has no functional divisions, that all cortical material, *en bloc*, serves all human cognition. The modularists claim all interesting functions are locally distinct. They delight in diagrams, mapping the brain section by section, with the ultimate goal of labelling each individual neural circuit with the word or transformation or feature detector it subserves; their patron saint is Gall the Phrenologist. Patently, both sides are made of straw, and they have been fashioned by the groups most in need of straw theories, the opposition. Neither the tight pocketing of Gall nor the vagueries of equipotentialism are sensible, and sensible neuroscientists recognize this. Aside from random aberrations, common to any intellectual pursuit, radical equipotentialism exists only as a rhetorical device employed by theorists focusing on site-function correlation; and radical schematics of functional topography exist only as a rhetorical device employed by theorists with a healthy respect for the scatter and overlap of aphasic syndromes. One side claims language is too complex a phenomenon to be modular. The other side claims language is too systematic to be diffused throughout the brain. But neither side is stupid, and both sides have a wealth of support in aphasic data: bewildering diversity is there for the asking, as are over-riding patterns. More to the point, both diversity and patterning can be rather smoothly accommodated by either camp. Locationists can point out the manifold complications of aphasia data and marvel that recognizable trends of any sort emerge: if distinct shapes can be detected through the haze of so many confounding variables, they must be very distinct indeed. The equipotentialists, with numerous examples from sciences as diverse and pertinent as psycholinguistics and chemistry, can explain the patterns away as artifacts of the variables. Each side has a good deal of room to manoeuvre. The issue, again, is relative.

Nevertheless, there are patterns which emerge from the data, and this thesis takes the position that, theoretically if not clinically, they are better investigated than ignored. Like most such works it begins with two patterns, the "two most important and common forms of aphasia" (Kertesz [1982:43]) – Broca's aphasia and Wernicke's aphasia – though Kertesz' statement requires some qualifications he does not supply. In particular, it requires a modifying prepositional phrase on the order of 'in the linguistic literature'. The reason they are important and common is that they represent largely distinct clusters of symptoms, associated with damage to distinct cortical regions, and they get a lot of press. Even strong equipotential theorists, who would probably claim the disorders are distinct because they reflect different ends of a continuum, or of a vector, must concede that there is sufficient evidence to support at least this division. Convincing arguments exist that the distinction is valueless, even detrimental, for clinicians (e.g., Schuell [1965]), and it receives much less attention in the clinical literature. But there are probably convincing arguments that the physicist's distinction between mass and weight is not suited to structural engineers; that does not make the two properties one. In any event, it is the patterns, not the chaos, that allow linguists to form workable hypotheses about the psychological nature of language.

But the tenuous fabric that the patterns are imprinted on, the background of chaos, needs always to be kept in mind, and any extensive work in experimental aphasiology is obliged to include a list of riders and cautionary notes. The problem is not that others in the field, or in closely related disciplines, are unaware of how provisional most conclusions must be, but it is at once difficult to extrapolate beyond the highly constrained nature of the work, and discouraging to think its results can only bear on the small subject group tested. The reasonable procedure, then, is to establish a network of flags to identify areas where the ice is thinnest, and cross the lake with caution. It also seems reasonable to do the flagging at the outset, allowing readers the latitude to chose their own path, or to turn back. So, before offering a definition of the syndrome of concern and its primary foil, Broca's aphasia and Wernicke's aphasia, the troublesome nature of the data that support them must be addressed.

### 1.1.2 Complications of Aphasic Data

The most immediate problem, for theorists of either stripe, involves the matching of lesion sites. As many have observed, nature is a sloppy experimenter, at least in matters cognitive, and cortical damage to precisely the same region in two aphasia victims is very rare. Anatomy is largely the same, person to person, and it might be supposed that ruptures and blockages would occur in the same principal areas with reasonably high probability; that very similar damage would occur in large subgroups. Ultimately, a site-syndrome line of reasoning has to fall back on such a premise, but consider the variables. While gross anatomy is largely the same, there is much interesting variance in the details: height, eye, hair, and skin colour, facial bone pattern, sex, and even blood protein, differs person to person; some of the differences are inborn, some are environmental. Brains, and the probability of particular orders of brain damage, are subject to the same kinds of variability. To scratch only the surface: genetic factors (affecting, e.g., sex, development, handedness, and several classes of cerebral disorders), dietary habits (affecting, e.g., blood pressure and cholesterol count), and general lifestyle (middleweights having a different cortical make up than secretaries, alcoholics differing from teetotalers), all conspire to reduce the probability of precise damage match-ups to a much lower level than first blush would indicate.

And brains are malleable, dynamic organs. They learn, and hence reorganize. For example, the syndrome to be investigated below, Broca's aphasia, is defined in part as a symptom complex correlated with insult to the third prefrontal gyrus of the adult left hemisphere. Yet many features of this complex result from damage to tracts of the right hemisphere in children under six, and no language disorder is evident in many children with left third prefrontal gyrus injury. More dramatic examples are available, such as Smith's (1977) case of a linguistically (and intellectually) intact twenty-five year old who had undergone a left hemispherectomy at the age of five.[1] Obviously, at least one major reorganization of the language faculty (or access channels, or incidental processing mechanisms) can be charted as a function of age. The plasticity of young brains is phenomenal, and although there is no question that this plasticity decreases profoundly after young adulthood, it does not go away. Brains do not regenerate, but they do reorganize. They recover, and therefore, to brave a somewhat metaphysical image, it is not untoward to suggest that *minds* regenerate. Moreover, there is some evidence (from aphasiology) that mental reorganization is an ongoing process, which occurs even in the absence of brain damage (Brown [1977, 1979, 1982], Brown and Jaffe [1975], Obler *et al*. [1978]).

---

[1] Smith (1977) was presented at the fifth annual meeting of the International Neuropsychological Society, and has not to my knowledge been published. It is cited by Finger and Stein (1982:140f,152).

Brains differ, and they differ in manners not always matched easily to global properties like age, sex, or handedness. There have been, for instance, a few attested cases where damage to Broca's region in normal, adult, right-handed patients did not impair linguistic ability – including an instance of complete surgical "excision of Broca's area without persistent aphasia" (Zangwill [1975]). Types of damage, etiologies, also differ, and they have different consequents; all aphasia patients are not the victims of vascular rupture or blockage. Slow cortical damage (e.g., a tumour) allows the brain considerable time to reorganize.[2] Sudden damage (e.g., a trauma) allows no time at all for concurrent reorganization, though reorganization can and frequently does take place post-insult (c.f., Finger and Stein [1982]). Tumours also grow at different rates, depending on a multiplicity of poorly-understood factors, so two victims of neoplastic damage to the same general areas might display significantly different symptoms. Similarly, there are differences in sudden damage – trauma usually being more discrete, more focal, than hemorrhage or infarction.

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[2] The patient Zangwill reports on underwent tumour removal, and an argument designed to neutralize Zangwill's counter-evidence to site-symptom correlation has been advanced to the effect that the tumour displaced the 'real' Broca's area, which then settled back in once the imposter gray matter was excised (see the discussion appended to Zangwill's paper). If indeed Zangwill's case study is counter-evidence, as opposed to an exception, a more profitable answer seems to lie in the reorganization principle.

A further confounding variable, or class of variables, is implicated in the difficulties of isolating linguistic symptoms from impairments of another order, from motor problems or other cognitive deficits. It is, for instance, by no means obvious that the right side hemiplegia which so frequently attends Broca victims should be divorced from their language disturbances. In fact, there is an interesting neurobiological theory that speech evolved from the sequencing abilities necessitated by stone throwing, using that capacity as the "foundation for the language cortex" (Calvin [1983a]). And of course this difficulty of partitioning language and muscle disorders compounds when the motor dysfunctions involve direct control of articulation (dysarthria) or indirect, motor-plan controls of speech (apraxia), and the impairment of ostensibly nonlinguistic cognitive abilities, like calculation or memory, is even more problematic. Quite simply, an aphasia victim with hemiplegia might have a qualitatively different disorder than an aphasia victim with unimpaired movement. An aphasic with calculation or memory difficulties might have a different disorder than a classically 'pure' aphasic. Or it may be, as suggested in the final chapter, that at least some classically pure aphasias strongly implicate capacities not exclusive to language — like short term memory.

These complications come in addition to the standard battery of subject variables that can skew or mask results in nonpathological psycholinguistic experimentation – socioeconomic background, number and type of languages spoken or understood, education, I.Q., developmental, language or nonlanguage disorders (e.g., dyslexia or tinnitis), and a host of more subtle interferants (such as experimental attitude) – and all of these factors are somewhat more serious for pathological studies, since there is a much smaller population from which to choose. Often the experimenter is forced to work with subjects of widely different educational, social, or linguistic backgrounds, or even widely different pathological symptoms, because they are the only subjects available. Many of the experiments reported in the following chapter investigate ill-defined subject pools, carrying only the label "aphasics". Aphasia subtypes and severities are frequently not discussed, leaving the impression for an educated reader of a heterogeneity the experimenter prefers to ignore.

Still, there are controls. The same methodology available to responsible nonpathological psycholinguistic experimentation is available to responsible aphasia work. First, the population should be made as homogenous as possible, including such ostensibly unimportant factors as hemiplegia. Next, as many variables as possible should be statistically analyzed with respect to one another, to see if education or age or (premorbid) I.Q. or pathological symptoms, or some interaction(s), significantly accounts for any of the results' variance. Third, since neither of the first two are fully within the experimenter's control (information as to premorbid I.Q. is not often available, for example, and sample sizes are often skewed for variables like hemiplegia), more flagging should be done. Detailed subject descriptions should be included, to give the reader interpretive latitude. These controls are particularly important in a work of any scope, such as a thesis, and while statistical analysis of these variables was unfortunately not supported in my data set, every attempt has been made herein to regulate and flag all potential sources of variance. (Brookshire's [1983] very sensible guidelines have been adopted in this regard.)

One additional factor – experimental attitude – is particularly crucial when the subjects are aphasia victims, and it deserves special mention. For a number of reasons, varying from patient to patient, syndrome to syndrome, brain damage very frequently impinges on emotional stability; radical mood shifts are not uncommon. Severe depression, understandably, is often a consequent of aphasia, and Broca patients are the most susceptible – both in terms of frequency and of magnitude (Robinson and Benson [1981]). This is probably because they are the victims most aware of their communicative deficit, but there are also indications of chemical differences, of an increase in biogenic amines (Robinson and Benson [1981]). Overwhelming fatigue can also attend aphasia. Tasks that would have been trivial to the patient premorbidly can be completely litating. These variables potentially affect the way in which the subject views both experiment and experimenter; consequently, results can be badly skewed. There are two principal controls here. The task should be made as undemanding as possible, given the information sought. And the patients must be treated in a respectful, uncondescending manner, followed by a careful reporting of their performance during the task. Every effort has been made in these areas as well.

The crucial proviso here is that experimental control takes precedence over statistical control; indeed, statistics are treated with some suspicion in my analysis, and the experimental design was adopted to facilitate a brief series of *t*-tests.

### 1.1.3 Broca's Syndrome

The apparently glib designation above of Wernicke's aphasia as a foil to Broca's aphasia was not done lightly. The two syndromes involve very irregular looking symptom complexes, but in contraposition both begin to look far more regular. Isolated they appear chaotic; together they fall into recognizable patterns. Wernicke's aphasia is defined as a disorder signalled by fluent yet aimless production with intact functor and morphological distribution, by phonemic and semantic paraphasias, jargon, neologism, wordfinding difficulties, and by significantly impaired comprehension. This is not an appealing group of symptoms for a linguist. It indicates only that something profoundly wrong has happened to the victim's language capacity, but what that something might be is far from apparent: phonology, lexical access and semantics are all implicated. The same disarray is also evident in the symptom cluster commonly cited for Broca's aphasia: dysfluent yet pointed production, with a marked paucity of functors and inflectional morphemes, phonemic paraphasias, frequent misarticulations, word-finding difficulties, and relatively good comprehension. Syntax, morphology, phonology, and lexical access are all implicated.

However, as the somewhat biased phrasing indicates, if the two disorders are compared to one another both take on more definite form. In particular, the dimensions of production and perception are seen to be selectively impaired, in almost precisely opposite ways. Wernicke victims speak smoothly, with negligible content, and understand poorly; Broca victims speak haltingly, with content but negligible filler, and understand well, It is this dichotomy that generated Carl Wernicke's postulation of distinct aphasias, characterized by the interruption of sensory or motor capacities in language use, and it continues to fuel the division maintained by modern neurolinguists — though they tend to favour characterization in terms of semantics and syntax. In short, these syndromes are the primary focus for all theorists interested in promoting a central division in the aphasias. And of course there is anatomical support: Wernicke's aphasia is associated with damage to regions posterior to the Sylvian fissure; Broca's aphasia is associated with lesions immediately anterior to that fissure, and to the subcortical extentions of that region (Levine and Sweet [1982]). Clearly it is not requisite that injury to distinct areas results in distinct dysfunctions, nor that distinct dysfunctions be consequent to locally distinct lesions. Nevertheless, there is a certain formal elegance in site-symptom correlations, and elegance is always an important consideration in science.

On the other hand, it is obvious that a fair amount of overlap has been ignored for the sake of neat opposition, and the difference between the symptom complexes of the syndromes is far from binary. Phonemic paraphasias and word-finding difficulties are common to both disorders, and appear to pattern as a function of overall severity, not in terms of lesion site or of other symptoms. Such overlap, for theoretical if not clinical purposes, might best be viewed as the general result of introducing noise to the system – particularly as both slips of the tongue and temporary anomia are characteristics of normally functioning language users when the noise level goes up (due to fatigue, distraction, chemical agents, etc.). That is, not every symptom associated with a disorder need be considered a unique reflex of that specific disorder. Fever is a reaction to widely diverse bodily assaults, ranging from viruses to broken bones. It signals that something is awry, not that the right bimaleolar is fractured. In general, symptom complexes are meaningful in a way best captured by Wittgenstein's (1958) family resemblances: "a complicated network of similarities overlapping and criss-crossing; sometimes overall similarities, sometimes similarities of detail".[3] Again it is the overall pattern, not the individual details, that is of interest.

The overall pattern of Broca's aphasia just cited is the working definition of this thesis, and there will be occasion to invoke the Wernicke pattern just cited as well. One characteristic of Broca's syndrome in particular – agrammatism, the dysfluent, telegrammatic production symptom – is taken as criterial. There are two reasons for this: (1) agrammatism is unfailingly associated with aphasias consequent to Broca region insult; and (2) it has been the focus of much recent linguistic debate. Specifically, the claim that agrammatism is attended by a parallel comprehension deficit has become commonplace. Agrammatics are said to have the same difficulty understanding functors and inflections as they do producing them. These uniform productive and perceptive deficits are then, in turn, frequently taken in the literature as manifestations of a uniform competence deficit.

---

[3] "Ein kompliziertes Netz von Ähnlichkeiten, die einander übergreifen und kreuzen. Ähnlichkeiten im Großen und Kleinen", *Philosophische Untersuchungen* I.66. Translation by G. E. M. Anscombe. Marshall (1982:405), in a very good paper on the nature of aphasic symptom clusters, also uses Wittgenstein in this context.

### 1.1.4 Knowledge and Implementation

This buzzword, *competence*, introduces another issue that requires some attention. Along with its perennial companion, *performance*, it is at the centre of a principal controversy in linguistics generally, and aphasic studies particularly. They are labels, respectively, for the theoretical cognitive state, knowing language, and for the class of peripheral mechanisms required to implement that knowledge.

A simple dichotomy is most probably a gross underestimation of the links between knowing and doing, but at the very least it is reasonable to assume that: (1) a person who speaks and understands a language has an internal representation of the principles and procedures necessary to talk and understand; (2) there are mechanisms which differentially access and utilize that knowledge; and (3) the former, in normal adults, is relatively steady-state, while the latter is subject to numerous variables (fatigue, distraction, chemical interference). Points (1) - (3) are occasionally contested, but they seem uncontroversially straightforward to me and are accepted hereafter without further debate. In any event, the available literature is extensive enough to license a graceful bowing out.[4]

Once the distinction is accepted, the issue is localized to whether a competence or performance disruption

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[4] Cf. Watt's (1974) survey and discussion.

is responsible for a given aphasia syndrome, and what evidence bears on the matter. Consider first the rather crude analogy of a Tour de France athlete who loses the use of his legs through spinal damage. He would still have the knowledge of how to ride a bicycle, but his ability to implement that knowledge would be gone. For that matter, he would still have the motor programs for walking, but would be unable to walk. On the other hand, if he lost the ability to ride or walk through a blow to the head, it could no longer be legitimately claimed that his bicycle competence was gone or that his performance was intact. A neuronal relay to the middle ear might have been obstructed, for instance, incapacitating his ability to monitor balance. Access channels to the knowledge store might have been disrupted. In short, any number of disturbances aside from an obliteration of competence could account for the lost ability. Actual destruction of the knowledge, since it is only one link in a very long chain, is perhaps the least likely explanation; certainly it is the most difficult to confirm. The question becomes more dicey for a neurologically damaged cyclist who can walk but cannot ride, or ride, but not with his former proficiency. The conclusion that he has a selective deficit to his bicycle riding knowledge store is somewhat more easily justified here, but it is still only one alternative, and still very troublesome to demonstrate.

Language use is a far more complex activity than riding a bike, of course, and storage of the principles necessary to speak and comprehend probably occupy a good deal more cerebral space. Consider, then, another analogy. Consider the case of someone with a motor strip lesion which results in the lost control of one arm. It is functionally useless, rapidly atrophies, and remains clenched against one side. Yet, when she becomes tired, and yawns, her arm occasionally lifts, stretches out and flexes in a way she could not have willed. An exactly parallel situation occurs in language impairment. It is a clinical commonplace that aphasia victims who have much difficulty producing *dog* and *cat* can fluently and automatically turn the air blue with less polite monosyllables; in Hughlings Jackson's apt terminology, *propositional* language is disturbed, while *emotional* language is preserved (Jackson [1958:160, 161]). The damaged area subserves a facet of intellectual language production in a way that it does not subserve swearing. Yawning, a respiratory reflex, and cursing, an emotional reflex, are in both cases 'located' somewhere other than the damage site. Here is incontrovertible evidence that the motor knowledge for yawning, and for emotional outbursts, and all their performance mechanisms, remain neurologically intact. Clearly, the performance mechanisms shared by yawning and throwing a baseball, and those shared by speaking and swearing, are also intact. But there is still nothing obvious to be said about what is lost. Certainly there is a possibility that mental representations have been erased; yet it remains the least likely possibility, and the most difficult to verify. This introduces something of a truism in neurology: it is possible to demonstrate the presence of knowledge, but not its absence.

One more analogy, and the reader's patience, is required:

> Imagine a person who knows English and suffers cerebral damage that does not affect the language centers at all but prevents their use in speech, comprehension, or let us suppose, even in thought. Suppose that the effects of the injury recede and with no further experience or exposure the person recovers the original capacity to use the language. ... Suppose there is a second aphasic like the first, but because of some other and irrelevant problem (say, a circulatory disorder) he never recovers speech. Should we say in this case that the knowledge of English was lost? That would seem perverse. (Chomsky [1980:51-2]).

Indeed the claim would be perverse. No less perverse, for anyone schooled in the literature of aphasiology, is the proposed existence of two such abstractions. Chomsky goes on to suggest that "all sorts of evidence" might demonstrate retention of linguistic competence – for instance, "electrical activity or evidence from autopsy" (52) – and thereby reveals his lack of schooling in the area. But he does not have any empirical work to cite, using these methods or any others. And there is no mystery to the omission. No such cases have been documented.

The argument comes around, then, to why this section is so littered with analogies, of which Chomsky's is the *reductio ad absurdum*: there is no empirical support for competence models of language disorders. There are many that are not subject to disconfirmation by empirical means (indeed, most), but none that are uniquely supported by the data. Nor can there be until a much better understanding of neural circuitry develops. In the meantime, other hypotheses *are* open to testing, and factors like attention, short term memory, and temporal resolution can be fruitfully explored.

All this is by way of saying that competence is a valuable linguistic concept, and it is valuable for the reasons familiar from the arguments of its supporters: scientists need ideal, unattested constructs in their work. To use an example close to home, Fant's Source-Filter theory employs tube models with absolute rigidity and frictionless walls in order to understand the resonance properties of the vocal tract and predict the acoustic values of speech sounds. Grammatical models require the same distance from reality in order to explore rule-governed language behaviour and predict the grammaticality values of utterances. But the problems of aphasia are too immediate to be written off as irremediable knowledge deficits, interesting only by way of their implications for competence theories; that would be perverse. Since knowledge deficits cannot be demonstrated (even Chomsky's passage implies this), there is further perversion involved in their assumption, and insofar as the issue can be resolved, there is much aphasiological evidence of intact competence. Victims of Broca's syndrome, for instance, generally comprehend well and are very often painfully aware of grammatical deficiencies in their production. That is, they detect their productive deficiencies, and consequently can be said to have some knowledge of the correct output. But the crucial point here is simply that competence loss should be the last avenue explored. Ideal constructs are a luxury that aphasiology, and aphasia victims, cannot at present afford.

## 1.2 The Experiment

The experiment at the heart of this thesis, then, seeks to demonstrate the presence of knowledge and the impairment of implementation. The competence proposals for Broca's aphasia generally take this form: some intrinsic, definitional property of function words renders them unavailable to victims of the syndrome. The most common manifestation of this proposal is that the disorder is syntactic, and that Broca's region directly subserves a syntactic module. Presumably this bias is an outgrowth of the massive impact Transformational Grammar has had on linguistics, since TG analyzes sentences into *major lexical items* (nouns, verbs, adjectives, and adverbs) and *grammatical formatives* (everything else; see, e.g., Chomsky [1965:65]). That is, the theory considers all elements other than the (base form) four major categories to perform principally syntactic duties.

The evidence which is brought to bear on this functor deficit hypothesis comes primarily from experimental research into the comprehension difficulties of Broca victims. A particularly clear example of this evidence is Heilman and Scholes (1976), an experiment which managed to place an unusally heavy information load on *the* and found that Broca victims could not reliably detect that load. The argument from such data is that the function word in question is not consistently produced by victims of the syndrome, nor is it dependably perceived – therefore, it is unavailable to them. But, as above, reasoning along such lines requires a leap of faith. It is not possible to demonstrate the absence of knowledge.

Moreover, function words have properties other than syntactic ones. For instance, they generally have a much lower, more abstract, semantic value than content words, and there is some evidence that nonconcrete words are more problematic for aphasics than concrete words. Functors also receive sentential stress very rarely in normal production, while contentives are only rarely without stress in English, and there is a good deal of evidence that aphasics attend more closely to the stressed elements of a sentence. Either one of these factors, or a complex of both, might be responsible for the comprehension difficulties uncovered in work like that of Heilman and Scholes. My experiment tests the acoustic possibility, working with modified stress patterns and analyzing the affect those patterns have on comprehension.

### 1.2.1 Stress

However, modifying stress patterns raises some thorny theoretical issues and reintroduces the notion of competence. Prosody in general entails "a certain degree of vagueness" (Lehiste [1970:1]), and stress is the most mercuric of prosodic features. To start with, it has at least three manifestations: lexical stress, primary sentential stress, and specialty (contrastive or emphatic) stress. It also has three acoustic dimensions, each of which is a necessary property of any auditory communication. Every element of speech must have some value on a temporal metric, must have amplitude, and must occur at a characteristic frequency (even quiescent segments are defined in these terms, having a 0 on all scales). So stress is necessarily a relative phenomenon. Further, it is the clear product of a multilevel conspiracy. On the simple physiological level, there "is no single mechanism to which the production of stress can be attributed" (Lehiste 970:106]). But there are also obvious lexical, syntactic, and pragmatic factors, in addition to such general notions as rhythm and tempo.

These problems of definition compound somewhat in an experimental paradigm, since even with the impressive current technology of speech modifiers and synthesizers, there is no effective way to "automatically modify the intonation profile of pre-recorded speech" (Francis F. Lee, personal communication). That is, generating stimulus material, for theoretical reasons, is no easy task. Most aphasic studies of stress take the specialty route, recording stress and control stimuli separately and highlighting one or more elements in the stress condition by speaker-regulated "extra prosodic emphasis" (Pashek and Brookshire [1982:379). This method has its drawbacks: increasing the acoustic values of one word in a sentence by speaker regulation simultaneously reduces the values of other words, particularly those in the immediate vicinity. When the stress targets are functors (and the subjects victims of aphasia), this effect could run substantial interference, by reducing the intelligibility of content words, and the comprehensibility of the sentence.

Fortunately, most of these problems are neutralized in the present study, since stimulus production is by digital means and stress is involved solely as an incidental notion. No claims are advanced here with respect to the linguistic nature of stress. Stress is an abstract concept, and probably best explained in competence terms: there are principles of assignment that must have cognitive representation and must have reference to language specific features of phonology. But these facts are irrelevant to the present concerns. This thesis is only interested that the acoustic properties of stress effect a saliency that facilitates comprehension, and that items of relatively short duration, relatively low amplitude, and relatively indistinct $f_0$ (i.e., nonstressed sentence elements) are potentially more difficult for psychoacoustic analyzers to process. So a precise definition of stress is of very little consequence. Nor are the diverse factors operating on stress in normal production of concern. It is not even of particular interest that *salience* is as slippery a term in linguistics as *stress*. The only relevant point is that two conditions are employed with different acoustic values for the same lexical items. The manner in which those conditions correlate with stress – though one is an unnatural hybrid between primary and emphatic stress – is not at issue. Stress patterns are necessarily altered but the study is unconcerned with those patterns, especially as they might implicate suprasegmental phonology.

Some very interesting, and wholly independent, evidence that such things as precise definitions and mechanisms of assignment in production may be irrelevant to the function of stress in comprehension comes from the study reported in Woods (1982). Woods is involved in a quite extensive artificial intelligence research program on computer implemented speech recognition. The model his team uses, dubbed HWIM (Hear What I Mean), proceeds by way of rather conventional spectrographic representation: incoming waveforms are plotted in terms of frequency, amplitude, and duration. An 'acoustic phonetic analyzer' then processes this information to form a 'segment lattice', which is examined by the control centre in concert with lexical, syntactic, and pragmatic components. The output, deriving 'utterance level hypotheses' about the representation along a path laid out by nondeterministic strategies, is effectively translated into orthography. Rather than adopting a sequential policy, HWIM has proven very successful by scanning for 'anchors', for particularly reliable pattern clumps on the spectrogram, assigning structure to surrounding material as a function of the anchor's properties, and generating sentential hypotheses through comparison of one anchor to another.

There are two findings of this research which are particularly relevant to the Broca's syndrome comprehension problems:

> [1] We learned that small function words are highly unreliable anchors. For example, the sound in *a* is usually the same as that of the vowel in *the*, and it also occurs in many multisyllabic words.
>
> ...
>
> [2] We found that sequential left-to-right scanning has problems. It is often necessary to provide the ability to recover from a garbled word. The first word of the sentence is often garbled due to high subglottal pressure. But right-to-left scanning is not a viable alternative, as the last word of a sentence can be garbled due to low subglottal pressure that, for example, lengthens phonemes. We thus often find it expedient to work out from those "islands of reliability" provided by the stressed syllables away from the

> ends of the utterance. (98)

The implications here of HWIM for cognitive speech analysis are obvious: stress provides focus on the parts of the signal which are more crucial to the message, and unstressed material (like many functors) is secondary. A less efficient - damaged - analyzer might ignore unstressed material almost entirely.

Analogies from machines to minds are often very tenuous (see, e.g., Pylyshyn [1980], Calvin [1983b:53-62]). But in this case, the move is from an acoustic analyzer to an acoustic analyzer, not from computation to cognition, and consequently is far more concrete. The only important assumption required for the analogy to go through is that humans process speech signals in terms of frequency, amplitude and duration, an assumption made throughout this thesis and motivated by the entire discipline of phonetics. Further, the HWIM model simply affirms the widespread, common-sense notion of the function performed by stress: it "is used to indicate the most important word or words in a sentence or phrase" (Ainsworth [1976:90]); that is, stress is a tool of salience.

### 1.2.2 Summary

The primary objective of this thesis is to discover if functors can be made more salient acoustically for victims of Broca's aphasia, and to that end the stimulus modifications follow the lead of the primary agent of salience in language, stress. The hypothesis tested is that the comprehension difficulties Broca patients have with function words are, at least in part, a product of perception, signal analysis, or storage, and not strictly (if at all) of a competence disruption. If this hypothesis is correct, the performance of Broca victims on a task keyed to the comprehension of a functor should improve significantly. In turn, this would demonstrate that acoustic factors – performance variables – are to some extent responsible for the comprehension difficulties that follow from neural insult to Broca's area.

The paradigm for this test is that of Heilman and Scholes (1976), which is outlined in some detail in the following chapter, and very explicitly in Chapter 3. There are two principal reasons for this choice. The first should be self-evident: since it supplies some of the most compelling data in support of the functor deficit hypothesis, it requires, at absolute minimum, one replication to see if the results are stable. The second reason should become apparent when the paradigm is described in some depth: it is a very elegant design, and licenses a very direct test of the perceptual hypothesis. The subjects were played two versions of the Heilman and Scholes stimulus sentences, one which had normal stress assignment, and a version identical to that except for the substitution of a longer, louder *the* in the key location.

It might be argued that this replication is too safe: failure to reproduce Heilman and Scholes' results would compromise their competence hypothesis; reproducing them without a saliency effect would substantiate important work conducted a decade ago with a small subject pool, and it would support their hypothesis; and reproducing those results with a saliency effect would help circumscribe the Broca comprehension deficit, and compromise the competence hypothesis. But this surety of meaningful results, irrespective of the outcome, is a virtue of the design, not a flaw, and there remains a hierarchy of usefulness in the three possible outcomes.

The third result, replication with a saliency effect, is the most useful. If function words are difficult for Broca patients to understand because of their weak acoustic values, then speech therapy is clearly of value, and the established clinical practice of slower, louder, more careful enunciation makes sense. If, on the other hand, those difficulties follow from a deep-rooted competence disruption, therapy makes less sense, and clinical enunciation makes none. Fortunately, it was this result the experiment produced. Heilman and Scholes' findings held for the normal condition, but the patients were significantly more reliable when the key functors were acoustically boosted.

# 2. Literature Survey

This chapter observes one major division in its treatment of the relevant literature: experimental vs. theoretical. Adopting this distinction is not meant to imply that these two approaches are mutually exclusive, or even incompatible. Theory that does not rest on empirical research is no more scientifically compelling than, say, the Book of Genesis. Indeed, creationists are correct to point out that Genesis *is* theory; but it is not science. Similarly, experimentation is not of particular interest if it does not speak to theory, if it haphazardly generates information with no frame of reference.

But the two approaches are nonetheless distinct, and the contrast is sharper in aphasiology than in most fields of inquiry. In particular, theoretical linguistics which broaches aphasia is wont not to draw very heavily upon experimentation, or to do so only with suspicious selectivity. As that last sentence, and much foregoing discussion should indicate, the bent of this thesis is decidedly empirical. The experimental survey below is comprehensive: all the principal work, and some incidental work, on perception, discrimination, and comprehension of temporally and stress manipulated stimuli is addressed in detail, as is the work on the function word deficit in Broca's aphasia. The theoretical survey is more exclusive. It considers only two accounts of Broca's syndrome: Edgar B. Zurif's proposal of a syntactic deficiency, and

Mary-Louise Kean's proposal of phonological impairment. The first is chosen for its prominence, and for its attention to function word experimentation; the second is chosen because the experiment that motivated this thesis might, superficially, be seen to have some verificational power with respect to it. This is not the case.

## 2.1 Experimental

As with the overall organization of this chapter, there are also two principal divisions in this subsection - since there are two classes of experimental evidence which bear on the question at hand. First, there is a set of studies based on the physical manipulation of auditory signals. This group includes various methods of temporal alteration - such as slow speech, interpolated silences, and periodic repetition of brief signal samples - as well as direct controls of stress. The stress experiments, of course, are of the most immediate relevance, but stress is a much more difficult property to tame effectively than is duration. Consequently, there have been proportionately fewer studies. However, one of the features of stress - according to Fry's (1955) early experimental work, the single most important feature - is increased syllable duration; so the rather wide body of work done in this area, running the gamut from sinusoidals to poetry, is also of considerable interest.

There is some variance in the results, as is inevitable in language pathology experiments, but in general the physical manipulation work argues quite persuasively towards one conclusion, all the more compelling for the amount of data amassed: aphasia entails a breakdown of acoustic signal processing. Language comprehension is therefore facilitated for aphasia patients by exaggerating stress and by temporal expansion. Unfortunately for the purposes of this thesis, very little of the temporal alteration data are analyzed in terms of the symptom clusters outlined in the first chapter. The subtyping metric, if any, is usually a measure of total severity, graded with such tools as the Minnesota Test, the Sklar scale, the Porch Index of Communicative Ability (PICA), or the Token Test (TT). Consequently, it is rarely possible to discover whether or not clusters like Broca's or Wernicke's aphasia interact significantly in the results.

On the other hand, the second set of studies, investigating functor deficits, is virtually predicated on these clusters. Most of the experimenters have theoretical axes to grind – usually some form of the claim that Broca's aphasia is (or is not) a syntactic deficit – and the experiments serve as the grinding wheels. Still, motivations aside, lesion site and performance characteristics are very useful information to have for an aphasic subject pool; all the more so when they correlate. More importantly, the results of this work are also quite convincing. That is, victims of neural insult matching the symptom complex labelled *Broca's aphasia* in the first chapter evidence a comprehension deficit peculiarly implicating functors.

### 2.1.1 Perception and Discrimination of Temporal Domain Signal Characteristics

The first group of experiments concerning aphasic perception of temporally altered acoustic signals begins with the work of Robert Efron.

Efron (1963)

Efron's principal interest was in the hemispheric localization of the ability to sequence discrete events, but some of his efforts to this end involved the testing of aphasia patients, and his results show the key role played by duration in their perception. In particular, Efron (1963) demonstrates that increasing the interval between acoustically distinct signals facilitates aphasics' ability to correctly determine the sequence. That is, when subjects were exposed to two randomly ordered frequency pulses – one "a high-pitched 'beep'", the other "a low-pitched, somewhat rasping 'bop'" (405) – aphasics required a longer intervening period of silence than controls to accurately identify which came first. Neurologically damaged nonaphasics performed the task efficiently (100% correct identification) at a mean interval of 130 msec; the aphasics needed an average interval of 460.23 msec. This difference looks substantial, but two points must be noted: (1) homogeneity of variance is unsupported (Bartlett's test), and consequently standard tests of statistical significance are unavailable; and (2) one of the aphasics fell within the range of the control group.

However, much of the variance within the aphasic group is acounted for by the presence of three distinct syndromes. Once they are separated out, the homogeneity hypothesis is supported (Cochran's test), and the data are more amenable to statistical inquiry. The three syndromes, by Efron's taxonomy, are: *expressive aphasia* (6), *receptive aphasia* (4), and *unclassified* (1). The first two labels correspond to *Broca's aphasia* and *Wernicke's aphasia* respectively, as those terms are defined in the preceding chapter, and the third matches the Boston definition of *Global aphasia* (cf. Efron's clinical apraisals on p.410, and his lesion localization discussion on p.415). Since there was only one global aphasic, Efron does not include his/her data in subgroup analysis, but the remaining three groups fall into an interesting pattern: Broca's aphasics require a significantly longer duration than Wernicke's aphasics, who in turn require significantly longer than the controls. The results are summarized in Table 2.1. Two tailed *t*-tests show all the differences to be significant at the $\alpha=0.01$ level, and an expressive vs. control test is significant at $\alpha=0.001$. Further, as the distribution of means should make clear, the aphasic outlier mentioned above is a member of the receptive group. Broca's area appears to involve some dependency on temporal signal resolution.

Table 2.1

RESULTS OF EFRON (1963)

| | 75% | 100% |
|---|---|---|
| Control subjects | 75 | 130 |
| Receptive aphasics | 140 | 235 |
| Expressive aphasics | 400 | 575 |

Column 1 is the mean threshold for 75% correct responses, in msec. Column 2 is the 100% threshold. (Taken from pp. 409,410.)

Efron takes these findings to suggest that aphasia is the reflex of a general impairment of the ability to temporally organize the discrete elements of an input signal, explicitly rejecting a competence analysis:

> If this view is correct, we should not look upon the aphasias as unique disorders of *language* but rather as an inevitable consequence of a primary defect in temporal analysis. ... Aphasia, thus considered, would be an epiphenomenon. (418; Efron's italics)

A sequencing impairment is by no means necessary – a failure of discrimination, for instance, is just as likely a candidate – but the results do support a claim that extended duration plays a more substantial part in signal analysis for aphasics than nonaphasics, and this rôle may well be independent of linguistic competence. They also suggest that damage to Broca's area implicates a greater dependency on signal duration than other types of brain damage.

Efron's basic paradigm has since been replicated twice. In each case a different limitation of the original design was addressed.

### Edwards and Auger (1965)

The first of these replications, Edwards and Auger (1965), attempted to locate deficits in auditory perception which might be coincidental with, and consequently mitigate, Efron's results. They administered his test in concert with a battery of other auditory measures: "the modified Pitch, Tonal Memory, Loudness, Rhythm and Time subtests of the Seashore Form A (1939)" (207). The subject pool was also expanded – including 20 aphasics, 20 neurologically damaged and 20 neurologically sound nonaphasics – though unfortunately no aphasic subtype analysis was done on the data. Of these six tests, only the Efron sequencing task produced significantly different means for any two of the groups: at the 75% threshold level, the normals required an interstimulus interval of 67.49 msec, the neurologically damaged nonaphasics required only 50.79 msec, and the aphasics needed 141 msec. It is not clear from the discussion (since no standard deviations are supplied), whether these means are all significantly different, one from the other, or whether it is just the aphasics who differ from the two controls. But an analysis of variance yielded an F-ratio with $p<0.001$, and it is the aphasic results that are most prominent. The aphasic subjects required an interval substantially longer than that of the other two groups combined. Efron's findings hold, independent of pitch, tonal memory, loudness, rhythm, or time deficits.

Further, although no subtype analysis was performed on the aphasic data, there is some reason to believe that subjects meeting the symptoms of Broca's aphasia did less well than Edwards and Auger's counterparts on the sequencing task. A short digression on their evaluation tool, the Minnesota Test, is required; whatever its clinical merits, it has problematic areas. In particular, it is not designed to uncover the kind of symptom clusters of concern to most aphasia theorists. Instead, the test looks for functional language impairments and seeks a prognosis of readaption to society. Since comprehension is far more crucial to social integration than fluent output, the test's seven point *simple* to *irreversible* scale tends to run from productive to perceptive deficits. *Mild Aphasia with Persisting Dysfluency*, number 3 on the scale, meets most of the criteria set out in the first chapter for Broca's syndrome; *Aphasia with Intermittent Auditory Imperception*, number 6, meets most of the criteria set out for Wernicke's syndrome. All this is by way of pointing out that thresholds for the sequencing task had a relatively strong negative correlation (-0.56) with total severity of disorder, as measured by the Minnesota Test. That is, mild (Broca-like) aphasics required more time for the task than more impaired (Wernicke-like) aphasics.[5]

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[5] On the other hand, Edwards and Auger report that an "intense investigation of the unexpected sign reversal was conducted by a qualitative analysis of the neurological status of the aphasics. No orderly relationships could be

### 2.1.2 Perception and Discrimination of Temporal Domain Speech Signal Characteristics

Ebbin and Edwards (1967)

Ebbin and Edwards' (1967) replication attempted to discover if Efron's (1963) generalization from pure tones to speech sounds was justified. Consequently, they substituted syllables for frequency pulses and a discrimination task for sequencing. Again the subject pool was larger (24 aphasics, 24 neurologically damaged controls), and again no subtype analysis was done on the data.[6] The stimuli employed were CV structures consisting of either a stop [p, t, d, k] or a fricative [s] and "the vowel sound [ɔ] as in father" (121). Twenty-five combinations were generated under two conditions. In one condition (0 msec), there was virtually no interval: "the second syllable following the conclusion of the first syllable as closely as the physical limitations of splicing would permit" (122). The other condition included a 200 msec interval between stimuli. The number of errors per condition was measured, and the results fall into line with the earlier studies. Nonaphasics had some difficulty with the task, but their problems were independent of condition; in fact, they did marginally

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[5] (cont'd) detected" (208). The wording is muddy, but this passage may mean (depending on "qualitative analysis" and "neurological status") that lesion site and performance on the sequencing task showed no correlation.

[6] The Minnesota Test was once more the evaluation metric, and Ebbin and Edwards interpret its results as diagnosing their average aphasic subject as suffering "mild impairment" (121). Following the above logic, this indicates that most of their aphasics were Broca patients.

better on the 0 msec condition (20.7 vs. 21 mean errors). The aphasics had more difficulty overall, and there was a significant treatment effect. When the syllables were unseparated the aphasics averaged 34.15 errors, but with the 200 msec interval the mean dropped to 29.35. This is precisely the trend predicted by the Efron results – increasing the duration also increases accuracy of judgement – and the difference proved significant at $\alpha=0.001$.

In short, expanding the duration of a signal with interpolated silence makes a considerable difference in the reliability of aphasic perception, and at least one experiment (Efron's) shows that it makes more difference for Broca's aphasics.

### Carpenter and Rutherford (1973)

A similar, though far better controlled, consonant discrimination experiment, by Carpenter and Rutherford (1973), also tested aphasics against neurally intact and neurally insulted nonaphasics. The aphasic population was subtyped but of very uneven distribution (nine Broca's, two Wernicke's, two amnesic, and one unclassified), so group comparisons could not be profitably made. However, the high proportion of Broca patients among the subjects makes the study of particular interest.

The tests were also subtyped: three were classified as *spectral*, and concerned the frequency characteristics of the signal; three were classed *temporal*, and concerned cue duration (the lengths of stopgap [closure], frication, and vowel nuclei). The results, presented in Table 2.2, are very much in line with the earlier work.

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**Table 2.2**

RESULTS OF CARPENTER AND RUTHERFORD (1973)

| Subtests | Aphasic | Normal | Nonaphasic Brain-Damaged |
|---|---|---|---|
| <u>Spectral</u> | | | |
| tail/pail | 87.7 | 90 | 100 |
| fig/fib | 100 | 100 | 100 |
| shake/shape | 40 | 100 | 100 |
| <u>Temporal</u> | | | |
| stable/staple | 40 | 100 | 90 |
| base/bait | 20 | 80 | 80 |
| hid/hit | 13.3 | 100 | 70 |

Percent correct discrimination. (Taken from p. 538.)

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Both control groups did well on all the measures of spectral discrimination, and the aphasics did well on all but the *shake/shape* subtest. The control groups also did well on the discrimination of temporal cues, but the aphasics did very poorly here. Carpenter and Rutherford demonstrate statistical significance in two key dimensions. First, performance of the aphasics on the temporal discrimination tasks was significantly worse than either of the control groups ($p<0.005$). And second, aphasic discrimination of temporal differences in the signal was significantly worse than their discrimination of spectral cues ($p>0.001$). Further, there may well have been temporal contamination of the one spectral test aphasics scored poorly on. The principal frequency cue for the distinction of /ep/ and /ek/ is the second formant transition, and the authors admit (538) that their $f_2$ transitions on this task were very brief (<50 msec).

Sasanuma *et al.* (1973)

A convenient bridge between the temporal experiments using pure tone stimuli and speech sounds is provided by the work of two independent research teams. The first team, Sasanuma, Tatsumi, Kiritani, and Fujisaki (1973), studied the perception of both signal types by the same (Japanese) aphasic population. Unfortunately, they used a very small control group (n=4; against 29 aphasics), so the between-group findings, though they demonstrate the expected inferiority of aphasic discrimination, are statistically suspect and must be rejected. But a very useful result does surface: a high correlation for the aphasia within-group, between-task findings.

The subjects were required to discriminate (1) 200Hz pure tones of varying duration (100 - 400 msec); (two) a two vowel sequence which was manipulated for duration of the initial vowel (120 - 240 msec), and which corresponded to two Japanese words (oi/ooi); and (3) a VCV sequence which was manipulated for duration of closure (110 - 230 msec), and which also corresponded to two Japanese words (ita/itta). The linear regression figures – showing increased discrimination as a function of increased duration – are virtually identical for all three tasks.

### Tallal and Newcombe (1978)

The second 'bridge' study, by Tallal and Newcombe (1978), is considerably more detailed, and statistically more opaque, but produces the same practical results. They tested 10 aphasic patients on the perception of four synthesized acoustic pairs. One pair was "nonverbal": complex tones of identical harmonics but distinctive in fundamental frequency. The other three were "verbal": (1) steady state vowels /ɛ/ and /æ/; (2) CVs /ba/ and /da/, with 40 msec formant transitions; and (3) the same CVs with 80 msec formant transitions. All stimuli were 250 msec long, and the interstimulus interval varied from 8 to 428 msec.

The aphasic patients proved significantly worse in all tasks ($p<0.001$) than both the neurologically damaged and neurologically sound control groups (between whom there was no statistically relevant difference). As in the earlier studies, there was also a significant within-group difference for the aphasic population in the perception of sequences with a short interstimulus interval versus a long interval – performance being much better with increased duration ($p<0.001$). The effect of formant transition duration was less widespread, but some of the aphasics demonstrated improved performance with the 80 msec cues.

Sasanuma *et al*. (1973) provide a succinct statement of the importance of the temporal discrimination experiments with non-speech stimuli: they suggest "the presence of a certain kind of 'noise' or defect in the auditory system of aphasic patients even at a stage preceding speech comprehension" (72). That is, returning to the competence / performance distinction, there is clear evidence of a performance deficit and no evidence at all for a defect of competence (however that might be found) – a point stressed by Efron (1963). Further, there is a close correspondence between perceptual difficulties with dissociated frequency pulses and with phonologically valid strings.

### 2.1.3 Comprehension of Temporally Altered Speech

#### 2.1.3.1 General Tests

An additional factor in the Sasanuma *et al.* (1973) experiments, though not controlled for, is the presence of signification. Their phonological discrimination tasks employed words, meaningful elements of the subjects' language. Since only discrimination was tested, there is no way of knowing whether the subjects perceived these stimuli as lexical gestalts or just as distinct phoneme (or perhaps, sound) strings, but several other experiments suggest that there are semantic implications to the impaired temporal processing abilities of aphasics. Tallal and Newcombe (1978) supply some evidence of these implications. While they had no semantic elements in their study, they did use a comprehension test for screening purposes, and a *post hoc* analysis revealed a very high (Spearman's) correlation between their nonverbal task and test scores (r=0.83). As they point out, results such as this "strongly suggest that impairment in responding to rapidly changing acoustic information is, in most cases, concommitant with receptive language impairment" (22). Sequencing and discrimination, of pure tones and of complex speech sounds, improve with physical expansion of the signal. The same proves true of comprehension.

### Sheehan *et al.* (1973)

Sheehan, Aseltine, and Edwards (1973) applied Efron's (1963) technique of interpolated silences to meaningful linguistic strings. Their experiment is problematic, and in isolation provides little evidence that temporal expansion benefits aphasic comprehension. Specifically, neither the task nor its analysis is well defined. Still, the results are suggestive, particularly when viewed in concert with the other expanded signal work reviewed in this section.

Sheehan *et al.* made up tapes of "stories, poems, narratives, and so on" (652) under three conditions. The interpolated silences condition placed a noiseless gap of 150 msec between all "individual articulated phonemes" (652). The "accumulated time" condition left the words intact but separated them by stretches of silence, calculated as the sum of the potential silences of a given word (so that, e.g., a word with four internal silences under the first condition was separated by a 600, or 4 x 150, msec gap from the following word). The control tape contained the stimuli with "the experimenter normally enunciating every word" (652). Curiously, these tapes were then dubbed onto a videotape of the experimenter lip-synching the audio track. All subjects (n=30) heard all three conditions, and answered simple yes/no questions on the passage's content, recorded under the same conditions.

Subjects were subtyped solely by age, and the only interesting result was that patients under 50 showed significantly improved comprehension for the interpolated silences condition. The point cannot be pushed very far, but a number of studies have found that Broca patients tend to be younger than Wernicke patients (Brown and Jaffe [1975], Brown [1977, 1979, 1982], Obler *et al.* [1978]). The age of 50 is also important to these studies. For instance, Brown (1982:450f) reports on a study of 389 aphasics where the average "age of motor aphasics was 45.3, and fluent aphasics 56.5". However, age-performance may well be a correlation without causal connection here; the patients under 50 also evidenced substantially milder deficits (measured on the Sklar Aphasia Scale).

As above, the experiment was less than ideal, but this partially contributes to the significance of the findings: the test group was under quite severe handicaps in the interpolated silences condition, and would be expected not to understand it at all, yet the older subjects did no worse on it, and it was the best condition for the under 50 subjects. First, it is not at all clear how the 'individual articulated phonemes' were distinguished by Sheehan *et al.*, and the problems of mapping acoustic waveforms to discrete phonological entities is one of thorniest issues in phonetics.[7] Even more confounding is the authors' report that the interpolated silence condition for "normals ... is often incomprehensible until they learn recognition" (656); it is unnatural, and does not correspond to any familiar temporal alterations, like a slowed rate of speech or deliberate articulation. This makes the performance of both groups interesting: the older group's comprehension did not degenerate under the interpolated silences condition, as might be expected, and the younger group's comprehension improved. The younger group understood the interpolated silences condition better than normal enunciation, and better than the accumulated time condition, a more natural expansion. The difference is significant at $\alpha=0.02$. Further, both groups showed improvement upon second exposure. While the older group's improvement was marginal, the younger group's performance was significantly better: 55.6% correct responses on day 1, and 71.9% correct the following day ($\alpha=0.001$).

### Gardner *et al.* (1975)

An ambitious foray into aphasic comprehension difficulties was conducted by Gardner, Albert, and Weintraub (1975). They attempted to measure a number of different

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[7] For a recent review of the literature on this topic, cf. Blumstein and Stevens (1980). Notice that this lack of one-to-one mapping does not interfere with the Ebbin and Edwards (1965) experiment, since only discrimination and not comprehension was at issue.

factors in perceptive deficits, one being of particular interest here. Among their battery was a group of "neutrally worded" sentences containing "target nouns"; e.g., "You see a cat that is nice" (157). Presumably these were spoken at a normal rate with normal intonation, since nothing is mentioned to the contrary. The sentences were also presented at a rate of 60 words per minute. The subjects (46) were required to match the stimuli to a picture, from an array of seven, depicting the target noun. The slower rate of presentation yielded a highly significant improvement in performance on the matching task ($p<0.001$). The study also revealed a significant effect for site of lesion (no $\alpha$-levels given), with anterior patients showing better comprehension. But, unfortunately, no specific information is given as to improvement ratios. That is, it is not possible to know if either the anterior or the posterior aphasics benefited more from the reduced rate of presentation.

### Weidner and Lasky (1976), and Lasky *et al*. (1976)

Weidner and Lasky (1976) presented a group of 20 subjects with stimuli borrowed from the Minnesota Test, controlling for rate of speech. Four tasks were required: subtests IV, V, VI, and IX of the Auditory Disturbances section of the test, which comprise requests for simple actions, yes/no questions, and repetitions; factors of length and syntactic complexity are built into the stimulus sentences. All tests were carried out under two conditions:

(1) a 110 word per minute rate of presentation, and (2) a 150 wpm rate. The results pattern as the Minnesota Test predicts. Increasing length and complexity decreases the reliability of the patients' performance. But there was also a significant difference for rate of presentation, with by far the best performance under the 110 wpm condition; significance was beyond the 0.05 level.

Lasky, Weidner, and Johnson (1976) ran a slightly more detailed study of much the same order. In the Minnesota Test, syntactic complexity is not well-controlled – embeddings, conjunction, and adjunction are varied indiscriminately – but in this experiment only two dimensions were varied. The stimulus sentences differed only in voice and negativity; length also varied, since passives are longer than actives, negatives longer than affirmatives. There was also more control over presentation rate. Four temporal conditions were used: (1) a 150 wpm rate, with an interphrase pausetime of 1 sec (where phrase boundaries are defined as corresponding to the slash marks in sentences 1-3 below); (2) 150 wpm with no pauses; (3) 120 wpm with a 1 sec pause between phrases; and (4) 120 wpm with no pauses.

1. The grandfather / is kissing / the girl.
2. The player / is not hitting / the ball.
3. The dog / is chased / by the cat. (393)

The patients (15) again did uniformly better at the slower rate of presentation, and pause time also facilitated comprehension (though lack of control precludes saying anything about pause placement), so that the best condition was (3). Both effects - pause time and word rate - were significant beyond $\alpha$=0.05, as was syntactic complexity.

For both experiments aphasic subtyping was carried out by means of the PICA, so the only criterion was overall disability. In the first study subject results were analyzed in two groups, one consisting of all those subjects with a score above the 50th percentile, and the other group made up of those below. Not surprisingly, the group with the highest PICA scores also had the highest performance levels. Improvement as a function of decreased rate was likewise greater for this group than the under 50th% group. In the second experiment, the Porch Index appears to have been more of a screening tool, perhaps to boost overall results, since only those scoring above the 50th percentile were included, and no subanalysis was conducted.[a]

### Goldfarb and Halpern (1981)

Goldfarb and Halpern (1981) conducted a conventional word association test with aphasic and normal subjects, presenting the stimuli under two temporal conditions: a 'normal' rate of 10 phonemes per sec, and a reduced rate of five phonemes per sec. Only the aphasic subjects (32; mild to moderate impairment) provided interesting variance in

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[a] No figures are given for the two groups of Weidner and Lasky (1976), but if the same pool was used as for Lasky *et al.* (1976) then the *n*s would have been substantially unequal (15 vs. 5), making homogeneity of variance more difficult to support, and calling into question the significance of their *F*-statistic.

their response patterns. Under the normal rate, they produced a roughly even number of paradigmatic (same lexical category) and syntagmatic (related but different lexical category; e.g., an adjective for a noun stimuli) responses, with the edge going to the latter. But with increased signal duration, the difference became significant ($p<0.05$) and the majority of responses were paradigmatic (repetitious, anomalous, and unclassifiable responses remained relatively constant,, though the number of unclassified responses dropped somewhat in the slower condition).

There is some doubt as to whether word association tests require comprehension (cf. Goldstein [1948]), but at the very least they appear to implicate a recognition of lexical category, and this ability improves as a function of temporal expansion for aphasics. More to the point, under the reduced presentation rate the aphasic responses move in the direction of normal response patterns; Goldfarb and Halpern's controls supplied twice as many paradigmatic as syntagmatic responses in both conditions.

### Pashek and Brookshire (1982)

One of the few advantages Sheehan *et al*. has over the other experiments reviewed in this section is the inclusion of context, and their results are specifically validated by a better-controlled, recent run of a similar paradigm, Pashek and Brookshire (1982). Just as dissociated pure tones are further removed from natural language than are speech sounds, and speech sounds are further removed than sentences, sentences are less like natural language than are paragraphs. The argument here is not that people go around every day speaking in paragraphs. In fact, outside academia, we are more liable to speak in constituents shorter than sentences, not longer. But language is always subsumed by context. "The grandfather is kissing the girl" is a perfectly well-formed, comprehensible English sentence, but it is not likely to be heard unless that action is transpiring, and probably not then. The advantage of "stories, poems, narratives, and so on" is that they bring along their own context, a network of related propositions, so any given proposition is reinforced a number of ways, and is more likely to register with the hearer than if it were presented in isolation. There is some experimental work which establishes just this point for aphasics (cf., Wilcox, Davis, and Leonard [1978]).

Pashek and Brookshire (1982) used a much better defined stimulus set than Sheehan *et al.*, short paragraphs of 93 to 96 words that were gauged on the Dale-Chall Readability Formula to be at fifth and sixth grade reading levels. They also expanded these stimuli in a less artificial manner, having an experienced reader record them at rates of 120 and 150 wpm. The tapes were then tested for an overall accuracy of ±2 secs., and rerecorded as necessary. Comprehension was evaluated by eight pairs of yes/no questions, randomized, with each member testing the same proposition in a different format (truth value and/or wording; e.g., "Were Samuelson and Harbo fishermen by trade?" and "Were Samuelson and Harbo two famous doctors?"). There was no significant variance found in their (neurologically sound) nonaphasic data. But both groups of aphasics (20 overall; subtyped as high and low comprehension on the Token Test) performed markedly better on the slow rate of presentation than the normal rate ($p<0.01$). That is, the results are the same as those of Sheehan *et al.* – slowing the presentation rate of context-supported messages enhances aphasic comprehension – but it is a good deal easier to have confidence in them.

### 2.1.3.2 Token Tests

However, context is a double-edged blade in language studies. Its inclusion more closely approximates the way language is used daily; but language is rarely, if ever, employed independent of other cognitive abilities. Consequently, the inclusion of contextual information in a psycholinguistic study substantially restricts the certainty with which that study can be said to tap linguistic knowledge.

The Token Test of De Renzi and Vignolo (1962), used as a subtyping tool in the experiment just discussed, is a very elegant test for mild perceptual deficits, of the sort commonly associated with Broca's aphasia, and it is designed precisely to avoid these complications of context. It requires the patients only to manipulate on request a few simple geometric shapes of different sizes and colours. But the requests move from direct to quite subtle, necessitating comprehension of conditional clauses, word order, attribution, and a wide range of function words. The following examples should illustrate the ingenious simplicity of the test:

4. Pick up a circle.
5. Put the red circle on the green rectangle.
6. Pick up the rectangles, except the yellow one.
7. Instead of the white rectangle, take the yellow circle.

The advantage of geometric shapes is that they minimize the "involv[ment of] other intellectual functions than language" (665). They reduce the number of pragmatic constraints on the situation and place more of the information load on the linguistic string. For instance, if the task were to place a button in a cup, no matter how intricately worded the request, subjects would have a high probability of responding 'correctly' just by recognizing the nouns and surmising that some simple manipulation was required. A button and a cup limit the possible number of acceptable manipulations more than a circle and a rectangle.

De Renzi and Vignolo (1962:77-8) demonstrate the effectiveness of their test by using it to uncover the comprehension problems of "13 'pure' motor aphasics and six sensory aphasics at an advanced stage of recovery, none of whom had ever "shown any difficulty in understanding a normal conversation". Since everyday discourse is far more complex than a simple exchange of linguistically encoded information, the subjects could function adequately by drawing on their pragmatic resources. But they lacked full control of their language, and the Token Test located the areas of impairment.

Shortly after De Renzi and Vignolo's (1962) paper, Orgrass and Poeck (1962) published an independent evaluation of the Token Test, watching for correlations of score with age, sex, education level, or "behavioral defects in non-aphasic brain damaged patients" (242). None of these factors was found to significantly interact with the test, which demonstrates that it centres very well on language-specific deficits. A number of subsequent assessments have also been carried out (e.g., Boller and Vignolo [1966], Boller [1968], Swisher and Sarno [1969], and Poeck *et al*. [1972]), and all have returned the same favourable verdict. In brief, the test is short, well-controlled, effective, and investigates rather subtle deficits. This combination of features has made it a very attractive tool for experimental aphasiologists, and it has been employed in a number of paradigms. Of particular interest here are those experiments which control temporal aspects of the requests.

### Parkhurst (1970)

The first temporal comprehension experiment was that of Parkhurst (1970), reported to the Annual Convention of the American Speech and Hearing Association, but unfortunately not published. Though several subsequent experimenters cite Parkhurst's work (e.g., Liles and Brookshire [1975:222], Blanchard and Prescott [1980:116], Pashek and Brookshire [1982:377-8]), conditions, analyses, techniques, and subgroup performance differences are not given in any detail.

Principally, Parkhurst found that aphasic comprehension of the test's commands is significantly poorer than that of nonaphasics when the signal is electromechanically compressed by 35%. Within the aphasic population, significant differences occurred only for the more difficult test sections, which compression rendered very troublesome. Some of the aphasic subjects also showed improvement when the signal was expanded by 35%, but again only for the more difficult items.

### Liles and Brookshire (1975)

Trying a different tack than Parkhurst (1970), Liles and Brookshire (1975) ran a modified Token Test controlling temporally with the interpolation of five sec silent gaps. Normal token requests were matched against ones including a single gap in various locations, and the results proved quite interesting. First, a significant effect showed up between the expanded requests and their shorter, normal counterparts, just as earlier experiments predict. But location also played a role in the aphasia patients' comprehension. The subjects (20; all below the 90th% on the PICA) had a much easier time of it when the silences followed content words (adjectives or nouns) early in the sentence ($p<0.05$). Yet if the gaps followed functors (prepositions or disjunctions) anywhere in the request, or content words late in the sentence, interpolated silences improved comprehension only marginally (significant at the 0.25 level). This indicates that (1) increased processing time facilitates comprehension of semantic but not functional information, and (2) facilitation only occurs when the memory buffer is relatively unencumbered. The first indication is important here because it is functional information that gives Broca's aphasics the most trouble, though there is a good chance that interference occurred (functors are phrase initial and tend to cliticize, so there are very few natural gaps following function words in normal speech). The second is important because it implies a particular defect influencing aphasia, namely impaired short term memory; and both results show that simple overall signal duration has significant limits in its aid to aphasic comprehension. That is, there are other factors at work in signal expansion that improve aphasia victims' speech perception than increased length of utterance.

### Marckworth (1976)

More in line with Parkhurst (1970), both in technique and results, is Marckworth (1976).' She administered the test to 12 subjects with "mild to moderate receptive aphasia" (82); most were also hampered expressively and only

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' I should also note here that earlier sections of this survey are in debt to Marckworth (1976), which includes a rather succinct review of temporally manipulated signals in aphasia research.

one met the clinical description of "fluent", so the experiment is of particular interest here. The stimuli were presented under two recorded conditions: "a normal speech rate" (85), and an expanded version of the same signal (at a ratio of 1.96 to 1, almost six times Parkhurst's [1970] rate). Extended duration was accomplished by means of a signal expander, which periodically repeats brief samples of the signal. This results in a product that is more 'natural' than either a technique of interpolated silences or slowed dictation.

Marckworth's findings are not as clear cut as most of the work reported above, perhaps because of the expansion technique, or perhaps because the experimenter is more scrupulous statistically, and some subjects even showed degenerate performance on some of the expanded versions. But comprehension did improve as a function of signal duration, and the results are more encouraging than those of Liles and Brookshire (1975). The between-treatment variance was significant with a probability no greater than 0.05, and all but one subject (whose score was identical under both conditions) performed better with the temporally expanded signals. Further, the ambiguous results are mostly confined to the easier sections of the test. The harder the task, the more benefit is provided by increasing signal duration. This is clear from Table 2.3.

So the results, while not wholly uniform, are consonant with the findings reported above. As Marckworth says, they

Table 2.3

RESULTS OF MARCKWORTH (1976)

| | Token Test subsections (increasing complexity →) | | | | |
|---|---|---|---|---|---|
| Subjects' performance | I | II | III | IV | V |
| No Difference | 4 | 4 | 3 | 2 | 3 |
| Degraded performance | 4 | 3 | 1 | 0 | 2 |
| Enhanced performance | 4 | 5 | 8 | 10 | 7 |

Number of subjects by performance on Token Test subsections I-V. (Taken from p. 89.)

demonstrate that "temporal expansion of the natural language signal does facilitate improved comprehension in at least the subtype of aphasic patient tested" (90) – and the high proportion of expressively disabled subjects correlates her pool with the Broca patients this thesis is primarily concerned with.

### Blanchard and Prescott (1980)

A more recent study, employing the Revised Token Test (McNeil and Prescott [1978]), has produced essentially the same results, but its authors view it as "at variance with the findings of other researchers". Blanchard and Prescott (1980; quotation p.120) presented their stimulus sentences under four conditions: the control rate of 150 wpm, and three expansions of that signal by factors of 1.25, 1.50, and 1.75. Accuracy of response was measured and, as expected, correctness was both greater and far less variable for the control group (23; neurologically sound) in all conditions. And, as predicted by earlier work, aphasic comprehension improved with signal expansion. One mild surprise, however, was that the improvement was not linear: the test "means for aphasic subjects [23; above the 50th% on the PICA] were 12.59 at the no expansion factor; 12.76 at the expansion factor 1.25; 12.91 at the expansion factor 1.50; and 12.84 at the expansion factor 1.75" (119).

These differences look slight, but they are hardly at variance with earlier findings. The range of these means is 0.32, which contrasts significantly with the 0.03 control group range. More to the point, the results of Parkhurst (1970), Liles and Brookshire (1975), and Marckworth (1976) do not show across the board improvement. Expansion does not facilitate comprehension for all aphasics – there are substantial differences in degree and quality among aphasia deficits – and a *post hoc* factor analysis of Blanchard and Prescott's (1980) data uncovers a subgroup of 15 aphasia patients who evidence a marked increase of comprehension as a function of signal expansion: significant at the $p<0.01$ level of confidence.

### Poeck and Pietron (1981)

The largest study to date of a temporally manipulated Token Test is reported in a brief note by Poeck and Pietron (1981). They tested 42 aphasics (mostly non-fluent global patients, but not subtyped) and 42 right-damaged nonaphasics, at two rates of presentation: normal, and that signal expanded by a factor of 1.25. They found (1) there was a learning effect for the control group, but none for the aphasics; and (2) the aphasia victims' performance improved significantly in the longer condition ($\alpha=0.01$), while the controls responded no differently as a function of duration. The second result accords with all the other work reported in this review, and offers yet further evidence that aphasia involves some temporally dependent deficit. The first offers less direct support, by demonstrating the Token Test's power:

> the fact that even an immediate
> representation of the test –
> although in two acoustically
> different versions – did not lead to
> a learning process underscores the
> great specificity of the TT for
> tapping one or more basic factors in aphasia.

The experimental results of temporally altered Token Tests are all the more compelling when this absence of a learning effect is considered.

### Riensche, *et al.* (1983)

Another, more recent study – Riensche, Wohlert, and Porch (1983) – also claims, like Blanchard and Prescott (1980), to be at variance with earlier work; again, this is not quite the case. They administered the Revised Token Test to 15 subjects (mean PICA score=11;43) over four trials at four different rates of presentation: a base rate of 150 wpm, and expanded versions of 30%, 60%, and 100% more duration. The authors found no statistically important differences among these conditions and observed that the

> lack of a significant effect for rate upon comprehension scores ... is not particularly supportive of aphasics' improved performance by presenting speech at specified, unvaried TE [time-expanded] rates (46).

But the missing significance appears to be more a product of analysis than data. Riensche *et al*. only compared the performance averages over all subsections of their test: Parkhurst (1970) and Marckworth (1976) show that expansion is primarily effective in the difficult sections of the Token Test, a fact that would be obscured by averaging. Yet even working with overall averages, 11 of their 15 subjects had optimal comprehension rates in the expanded conditions. Further, of the four who performed best at 150 wpm, three had that rate as their last trial (43), and while there was no significant trial effect, a slight improving trend is evident from the trial means ($\bar{x}_1=10.66$, $\bar{x}_2=10.73$, $\bar{x}_3=10.90$, and $\bar{x}_4=11.02$).

### Summary: Brookshire and Nicholas (1984b)

Riensche *et al*. (1983) certainly have reason to be circumspect and to characterize their results with phrases like "not particularly supportive"; still, the study is not at radical odds with earlier research into aphasic comprehension of temporally expanded speech. Their study shows inconsistency – some improvement, some absence of change, even some regression. The earlier studies show inconsistency. And the significance findings between studies are inconsistent: most uncovered significant improvement (Sheehan *et al.* [1973], Garder *et al.* [1975], Weidner and Lasky [1976], Lasky *et al.* [1976], Goldfarb and Halpern [1981], Poeck and Pietron [1981], Pashek and Brookshire [1982]); but some reported ambiguity (Parkhurst [1970], Liles and Brookshire [1975], Marckworth [1976]); while others reported no meaningful significant differences (Blanchard and Prescott [1980], Riensche *et al.* [1983]). This inconsistency is the subject of Brookshire and Nicholas' (1984b) study. They administered the Revised Token Test to 10 aphasic subjects, employing three distinct temporal conditions and two levels of difficulty. More to the point, they tested each subject four times, one week apart, and attempted to locate some consistency in subject performance in correlation with three important aphasia variables. They found no consistency at all.

The four trials consisted of 10 Low Error and 10 High Error commands, each in the following conditions: a Standard condition, of 200wpm, with natural pauses; a Slow Rate, of 100wpm, with natural pauses; and a Pause condition, of 200wpm, with one 4 second pause inserted at a word boundary in the command. The order of presentation was controlled such that the commands were randomized within level and condition, the conditions were randomized within each trial, and the levels of difficulty were reversed between the first two and the last two trials. The patients did not perform reliably, either as a group or individually. Some improved as a function of expansion, some degraded with expansion, and some had improved performance for one condition and one level on one occasion and degraded performance for the same combination on another trial. Moreover, Brookshire and Nicholas correlated performance levels with severity, postonset time, and type of aphasia, and no correlation reached significance ($p<0.05$). These findings are quite cloudy, even by the necessarily relaxed standards of aphasiology, and while they do not vitiate the earlier temporal studies, they do indicate

> previous reports of the effects of pauses and slow rate upon aphasic listeners' comprehension should be interpreted with caution (327).

However, there is good reason to treat Brookshire and Nicholas (1984b) with some caution as well. For one thing, the sessions may have been quite taxing (60 demanded responses: 10 commands x 3 conditions x 2 levels). Since the presentation was randomized, this fact alone could account for inconsistent results: if the patients were systematically doing poorly in, say, the last third of the session, those performances would be distributed over all conditions, levels and trials. But their choice of location for the interpolated 4 sec pause also may not have been to the subjects' advantage. Recall that Liles and Brookshire (1975) found placing their (5 sec) silence early in the sentence improved performance significantly ($p<0.05$) over placement later in the sentence. Yet Brookshire and Nicholas (1984b) ignored that finding in their design and adopted a general strategy of interpolating "near the center of each command" (324). Further, the Low Error and High Error levels were established individually for each patient after a (live-voice, normal presentation) run of the RTT: a Low Error "subtest was one in which a subject made 2-4 errors (on 10 items) ... [a High Error] subtest was one on which a subject made 5-7 errors" (325). Given the highly variable nature of aphasic performance (a fact documented by Brookshire and Nicholas), setting the difficulty levels from one session – rather than from the average of several sessions, or by arbitrarily choosing two RTT subtests for all subjects – is a questionable decision.

But the really problematic factor in the experiment was the extreme heterogeneity of its pool. The subjects ranged in age from 46 to 86 years old, in postonset time from 1 month to 10 years, in RTT pretest percentile ranking from 1 to 95, in PICA percentile from 36 to 81, and consisted of three syndrome types (4 Broca's, 2 Wernicke's, and 4 conduction). While this diversity is required for the consistency questions the experiment attempts to answer, it is nonetheless troublesome in so small a pool. The possibility of interaction is too great to ignore, yet the paper never mentions it. Consider just the Broca group. Of the four subjects, one was 50 years old, 10 months postonset, in the 1st RTT percentile, and the 43rd PICA percentile; another was 51, one month postonset, in the 10th RTT percentile, and the 36th PICA percentile; a third was 46, five years postonset, and in the 79th percentile for both the RTT and the PICA; the fourth was 55, three years postonset, in the 95th RTT percentile, and the 50th PICA percentile. Only age is relatively constant within the group. Looking for reliability in such multivariate circumstances with only 10 subjects is perhaps too optimistic.

Nevertheless, despite a lack of statistically significant consistency and a multiplicity of variables, Brookshire and Nicholas (1984b) do uncover a trend (apparent from tabulated data but not commented upon): the most systematic result is an improvement of comprehension relative to the Standard condition, under both manipulations, for both difficulty levels. Of the 160 difference scores they generated (tabled on 326), 108 show improvement, and 57% of those are significant ($\alpha$=0.05). Only 10 difference scores indicate significant degradation of performance relative to the Standard condition, eight of which are the responses of two subjects and are quite systematic (for one subject, all four scores are in the Low Error/Pause condition; for the other, all are High Error and three are Pause).

In short, Brookshire and Nicholas (1984b) constitutes a synecdoche for all the temporal work reviewed above: little of it produces uniform results; all of it uncovers improved performance as a function of increased duration, to a greater or lesser extent. The other temporally manipulated comprehension studies are statistically more convincing on this second point than their Token Test counterparts – none of them failed to find significant improvement – but the generally more lax designs tend to compromise the statistics. The result is not remarkably robust, but it is there all the same: temporal expansion facilitates aphasic comprehension.

### 2.1.4 Aphasic Perception of Stress

Goodglass *et al*. (1967)

The earliest paper to examine systematically the role of stress in aphasia – Goodglass, Fodor, and Schulhoff (1967) – was interested in precisely the issues that motivate this thesis: the interaction of stress and function words in Broca's aphasia. Unfortunately, they did not test comprehension directly, but their work concerns peripheral processing mechanisms that impinge upon comprehension. They designed a number of simple repetition tasks controlling for rhythm and minimally implicating formal linguistic skills.

Drawing on two aphasic populations, fluent and nonfluent, in various combinations over several tasks, they found the clinical division to hold up experimentally. The groups had markedly different performance levels. The principal finding was that initial unstressed function words of three-word clauses were the most difficult for Broca's aphasics, but were quite easy for the Wernicke's. Further, there is some evidence that stress and not word class was the contributing factor, at least for the Broca victims.

First, the nonfluents demonstrated equal facility in repeating random three-word lists, independent of whether the items were content words or functors. Second, the best retained prosodic pattern was ´ ˘ ´, again irrespective of word class; in fact the tokens with initial functors were reproduced marginally better than those with initial content words ("Arén't thěy húngry" vs. "Dógs căn bárk"). The next best pattern (´ ´ ´) also contained an initial function word. The only crucial test remaining – an unstressed initial content word – is unavailable in English, and could not be tested. But initial unstressed function words were the worst condition and initial stressed function words were the best condition, with a significance probability beyond 0.01, and there was no significant difference between retention of stressed functors and stressed content words. Stress (or salience) is a far more likely candidate than word class. (The Wernicke's group showed significant interaction with prosody as well, and their performance was neither inverse nor parallel to the Broca's group. Stress clearly plays some nontrivial role in their language disability, but one that is outside the province of this thesis.)

### Kellar (1978)

Kellar (1978) is more of a theoretical paper than an experimental one. Although it centres on a replication of Zurif, Caramazza, and Myerson (1972), it adds little to their findings.[10] Zurif *et al*. (1972) observed that when Broca's aphasics were required to choose the words of a sentence (in pairs from random arrays of three) that 'go best together', the tendency was to group content words with one another and function words with one another. On the other hand, the normal subjects did just the opposite: they grouped words into phrasal constituents. For instance, with stimulus sentence 8, the strongest preference of Broca victims is to group *lawns* and *mowed* together; the strongest preference of normals is to pair *the* and *lawns*.

8. The lawns were mowed.

Kellar found exactly the same tendencies in her replication, but she expanded the subject pool to include Wernicke's aphasics and found that they also tend to group content words with content words and functors with functors. This is the only new empirical result of her work; the paper's merit lies elsewhere.

Zurif *et al*. (1972), and a plethora of subsequent papers by the same principals (discussed in some detail below), all hold this grouping tendency to evidence a specifically syntactic deficit. But Kellar (1978) notes that functors are not stressed sententially, while content words are, and suggests the aphasic is following "a simple

---

[10] Kellar's paper was delivered to the Academy of Aphasia, and has not been published. My principal access to her argument is by way of an abstract sent to me by Dr. Edgar Zurif, along with the enigmatic warning: "the work is somewhat problematic". It is also discussed briefly by Brown (1980, 1982), and Berndt, Caramazza and Zurif (1983).

heuristic: 'Whenever possible, cluster stressed words together'" (2). This interpretation of the data is at least as likely as the Zurif-Caramazza proposal. However, while her proposal is certainly tenable, and in some respects more attractive, it hardly amounts to a disconfirmation of the syntactic hypothesis. For the moment, neither is a clear winner.

### Laughlin *et al.* (1979)

Laughlin, Naeser,and Gordon (1979) provides another interface of sorts, this time between the temporal work of the previous section and the experimental manipulations of stress considered below. It accommodates this role for two reasons. First, the authors employ duration specifically as "the single most important factor in perception of stress in English" (312). Second, they control the temporal feature of syllables in an implementation of Melodic Intonation Therapy (Sparks, Helm, and Albert [1974], Sparks and Holland [1976], Sparks [1981]).

Melodic Intonation Therapy is a clinical program to treat the expressive difficulties of the nonfluent aphasias. It is comprised of five successive treatment levels, all of which pay very close attention to the suprasegmental characteristics of speech. First the therapist hums the intonational pattern of an utterance, requiring the patient to hum along. Then the utterance, retaining stylized intonation, is spoken in unison by therapist and patient. This continues, with the clinician gradually participating less, and the aphasic more, until the patient can produce intoned utterances independently. Laughlin *et al.* (1979) administered this therapy to five nonfluent aphasia victims (2 global, 2 mixed, 1 Broca's) under three conditions of syllable duration: (1) a 'normal' period of about 300 msec; (2) an expanded period of about 1.5 sec; and (3) a further expanded period of about two sec. (Times are approximate because, due to the necessarily flexible nature of the sessions – frequently requiring repetitions and returns to earlier stages of therapy – presentation was "with live voice" [315].) As Table 2.4 indicates, the results were dramatic.

---

Table 2.4

RESULTS OF LAUGHLIN *ET AL.* (1979).

| | Normal | | | | 1.5 sec | | | | | 2 sec | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | MIT Steps | | | | MIT Steps | | | | | MIT Steps | | | | |
| | 2 | 3 | 4 | 5 | 1 | 2 | 3 | 4 | 5 | 1 | 2 | 3 | 4 | 5 |
| *Subjects* | | | | | | | | | | | | | | |
| Global | 4 | 4 | 4 | 3 | 20 | 12 | 11 | 9 | 8 | 20 | 12 | 12 | 11 | 10 |
| Global | 8 | 8 | 6 | 6 | 20 | 13 | 11 | 11 | 10 | 20 | 17 | 17 | 17 | 17 |
| Mixed | 1 | 1 | 1 | 1 | 20 | 20 | 19 | 14 | 13 | 20 | 19 | 16 | 16 | 16 |
| Broca's | 3 | 3 | 3 | 3 | 20 | 20 | 20 | 17 | 14 | 20 | 20 | 20 | 19 | 19 |
| Mixed | 6 | 6 | 6 | 6 | 20 | 20 | 20 | 13 | 12 | 20 | 20 | 20 | 20 | 20 |

(Taken from p. 316; 20 is the highest possible score for any section.)

---

The order of the condition presentations "was counterbalanced" (316), which presumably means that each subject did not receive therapy in the same order for the three conditions. And while the most impressive improvements may have been partially a learning effect, it is clear that performance is enhanced by increased duration, across the board. The differences between the normal and the 1.5 sec condition proved statistically significant at $p<0.005$; between normal and two sec durations, improvement was significant at $p<0.001$; but no interesting variance was observed between the two expanded conditions.

This study says nothing specific about comprehension but, like Goodglass *et al.* (1967), it does address an essential prerequisite to comprehension: perception. It demonstrates that nonfluent aphasics can perceive segmental properties, such as "melodic line, rhythm, [illegible] points of stress" (311), and that this perception is facilitated by temporal expansion.

Swinney *et al.* (1980)

A more clearly experimental demonstration of stress perception in nonfluent aphasia is provided by the study of Swinney, Zurif, and Cutler (1980). Their paradigm affords the standard incontovertible experimental evidence of perception: a manipulated variable that results in a statistically interesting effect. They asked eight Broca's aphasics to push a button upon hearing a target word (e.g., *ball*) embedded in a sentence controlled for stress along the following lines:

9 a. The umpire said a new báll was necessary.
b. The umpire said a néw ball was necessary.

That is, in one token the target word received primary sentential stress; in the other, a nearby word received primary stress, necessarily reducing the target word. No subject heard both tokens of a sentence type. Response latencies were measured, and Broca victims reacted more quickly to those targets carrying stress than to those without it ($\bar{x}$=489.5 msec vs. 566.5 msec; significant at $\alpha$=0.025). A significant effect was observed, and perception was demonstrated. More interestingly, since the above studies also revealed stress perception, Swinney *et al.* (1980) also showed that this latency pattern is present in neurologically sound subjects, though at a higher significance level ($\alpha$=0.05) and with faster times overall. So, not only do Broca's aphasics perceive sentential stress, it facilitates lexical identification for them in roughly the same fashion it facilitates normal lexical decisions.

### 2.1.5 Stress and Aphasic Comprehension

Blumstein and Goodglass (1972)

Harold Goodglass' second venture into aphasic stress comprehension, Blumstein and Goodglass (1972), had the distinct benefit of a phonetician riding shotgun, but focusses specifically on lexical stress and consequently is only of indirect interest here. They tested a group of 17 aphasics on a picture-matching task. The stimulus set was comprised of lexical pairs distinctive solely by stress pattern (e.g., "sórehead" and "sore héad"). The matched items were chosen from an array of four conventional pictures, two of which depicted the conflicting meanings and the other two were distractors – e.g., pictures of (1) a boy, frowning, with a darkened 'thought ballon' over his head ("sorehead"); (2) a boy, grimacing in pain, with a bandage and a lump on his head ("sore head"); (3) a boy crying (lexical distractor for "sorehead"); and (4) a foot with illustrative symbols of pain 'radiating' out (lexical distractor for "sore head").

The aphasia victims made more stress errors (e.g., choosing 2 as a match for "sorehead") than 'random' errors (e.g., choosing 4 as a match to "sorehead"), and of course significantly more errors overall than a neurologically sound control group ($p<0.025$). But the between-error type variance proved statistically uninteresting. Stress did not cause the aphasics any specific trouble; precisely the expected result if, as Goodglass *et al.* (1967) indicates, aphasia does not significantly affect the victims' ability to perceive stress. Blumstein and Goodglass (1972) consider stress in their experiment to be a semantic cue, when a syntactic analysis is equally likely, but they draw the obvious conclusion: "the perception of stress is preserved in aphasia" (806).

### Baum *et al.* (1982)

Baum, Daniloff, and Daniloff (1982) pursued the answers to three clearly formulated questions, two of which are of immediate consequence to this thesis:

> [1] Can Broca's aphasics utilize lexical stress to disambiguate otherwise homonymous sentences? ...
> [2] Does raising the stress level of functor words in sentences increase their retrievability by Broca's aphasics? (264)

Unfortunately, the answers afforded by their paradigms are of no consequence whatsoever.

The answer they provide for [1] is a qualified "no". They arrive at this from the results of a sentence-picture matching task predicated on sentence pairs of the following sort:

10 a. That's a *hot* dog.
   b. That's a hot *dog*.

11 a. She is home *sick*.
   b. She is *home* sick.

(269; italicization represents primary stress)

Eight Broca victims and eight neurologically sound controls were required to select the correct picture for a given sentence from a vertical array of three, which included a depiction of each competing signification and a distractor. Not surprisingly, aphasic performance was significantly worse on the task, with an $\alpha$-level of 0.001. Ergo, conclude Baum *et al.*, "comprehension mediated by suprasegmental cues is somewhat impaired in this group of Broca's aphasics" (268). But there was insufficient experimental control to support even this modest conclusion. For instance, only one level of stress was used, and only one sentence type. If there was no interesting variance in performance on normal vs. emphatic stress for sentences like 10 and 11, or if Broca victims fared the same on lexically ambiguous sentences, the authors would have some substance for their claim. Similarly, if they had tested another aphasic subtype, or right-damaged patients, their conclusion could be given more credence. But aphasia victims, even mild expressive ones, will score worse on virtually any comprehension task, and a number of nonlinguistic variables are likely to be responsible; fatigue, inattention, or emotional difficulties, for example. There is no support for their contention that Broca's aphasics have a particularly suprasegmental impairment.

The answer [2] receives is less compelling yet. Baum *et al*. report "the failure of emphatic stress to enhance aphasics recall of functors" and suggest this supports the argument "that stress is not a salient feature in explaining retention and loss in Broca's aphasia" (269). But the functor test appears to have been very poorly designed: the only stimulus sentences they provide in the paper are the sentences of 12.

12 a. The spoon is in the glass.
   b. The spoon is *in* the glass.

(264; italicization represents emphatic stress)

That is, although two conditions were presented, the stimuli were perfectly transparent, irrespective of condition, irrespective even of the functors; as discussed in connection with the Token Test above, pragmatically obvious spatial relations can be resolved simply by understanding the content words. In fact, the subjects did very well on this task – 82% correct, as against 56% for the first task (significant at $p<0.001$), and even the controls found it easier – which indicates most of the sentences were at least as obvious as 12.

While the statistical analyses of Baum, Daniloff, and Daniloff (1982) support the claim that Broca victims are peculiarly insensitive to stress, their experimental methodology does not.

### Pashek and Brookshire (1982)

Using the subjects, methodology, and stimulus set outlined in the temporal section above, Pashek and Brookshire (1982) found counter-evidence to the claims of Baum *et al*. The control stimuli were read with "'normal' stress and intonation" and were compared with a reading "in which facts were given extra prosodic emphasis (e.g., Samuelson and Harbo were two *fishermen* who crossed the Atlantic Ocean alone)" (379). (They make no mention of whether the highlighted facts systematically corresponded to the yes/no questions used to assess comprehension, but their examples indicate that this was the case.) The findings were all but identical to the rate of presentation data reported earlier: there was no interesting nonaphasic variance, and aphasic performance was significantly better for the exaggerated stress condition than for normal stress ($p<0.001$).

Another, very intriguing, result also came out of these studies. In all, Pashek and Brookshire (1982) had 4 conditions: (1) slow rate, exaggerated stress; (2) slow rate, normal stress; (3) normal rate, exaggerated stress; and (4) normal rate, normal stress. As reported in the temporal section, 1 and 2 were significantly easier for aphasics as against 3 and 4; 1 and 3 also resulted in significantly fewer errors than 2 and 4. This means that condition 1 resulted in the best overall performance, while condition 4 resulted in the worst overall performance. But - and here is the curious part - they were best and worst respectively by only small margins. That is, the rate x stress interaction proved statistically insignificant.

A likely account for this is interference: since one of the components of stress is increased segment duration, it may well be the case that a temporal component is affecting performance in both situations. In effect, testing for a rate x stress interaction may be equivalent to testing a slow rate reader against a signal expander. Pashek and Brookshire (1982) briefly entertain this possibility, but rule it out on the basis of random sentence duration tests they conducted for corollary sentences in the different stress conditions. They found no interesting variance. There is a very good chance, however, that a similar test between words would produce significant figures; in particular, *fishermen* would probably be of markedly longer duration under the exaggerated stress condition, as perhaps factors adjacent to such stressed words would probably be shorter than under normal stress conditions.

### 2.1.6 Summary

Perhaps the most likely explanation for the Pashek and Brookshire results, however, is the operation of a ceiling effect; that is, decreased rate made the crucial items more salient, and exaggerated stress performed exactly the same function. So, the question remains: does stress facilitate comprehension because its increased temporal dimension provides for more processing time, or does increased duration facilitate comprehension because, like stress, it boosts the acoustic salience of the message.

### 2.1.7 Function Word Experiments

As early as Wernicke (1908) it was recognized that neurologically damaged people evidencing telegraphic, effortful, dysprosodic speech also have problems of speech perception, albeit on a subtler level than their productive difficulties:

> [in this disorder] there is almost invariably a certain inability to understand complicated constructions and finer differentiations of speech ... I am no longer of the opinion that in pure motor aphasia the ability to understand speech always remains unimpaired (quoted in Marshall [1982:399]).

In fact, discordant with his current depiction as a dogmatic locationist, there is evidence that Paul Broca was aware of the perceptual side of the disorder he identified (Caplan [1980:234]). Yet the syndrome is frequently discussed in linguistic literature, past and current, largely within the

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# Host plant discrimination and the evolution of feeding preference in the Colorado potato beetle *Leptinotarsa decemlineata* (Say)

by

Glenn D. Harrison

A THESIS

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Date 26 April 1985

# Abstract

Variations in plant sampling and feeding behaviour were used to examine mechanisms of host plant discrimination and the evolution of feeding preference in the Colorado potato beetle *Leptinotarsa decemlineata*. Beetles from three geographic populations were videotaped on four host plants, representing the three regional hosts and ancestral host of the species. Beetles were also tested on leaves treated with solanaceous alkaloids to determine whether these compounds act as sensory inhibitors of feeding.

On average, duration of sampling on the plant surface prior to biting systematically increased on plant species less preferred for feeding, indicating beetles were capable of discriminating among plant species based on olfaction and/or contact chemoreception. Sampling of plant fluids (gustatory sampling) also increased on less preferred species for those beetles that proceeded to feed. Movements of the antennae during gustatory sampling suggest one of the functions of this behaviour is to enhance the release of plant volatiles.

Host plants of *L. decemlineata* contain steroidal glycoalkaloids. The glycoalkaloids tomatine (from tomato) and solanine (from potato) did not affect first meal size or duration of plant sampling when tested at concentrations exceeding natural levels. These compounds are apparently not responsible for determining different patterns of initial host acceptance within regional populations of beetles.

Tropane alkaloids are found in solanaceous plants not used by *L. decemlineata* as hosts. When incorporated into potato, the tropane alkaloid, atropine, reduced meal size and increased gustatory sampling behaviour by beetles. However, tropane alkaloids may not restrict the beetles' host range, since plants containing these compounds may be discriminated against on the basis of olfaction before plant fluids containing the alkaloids are sampled.

Regional populations of *L. decemlineata* that have colonized new plants have not lost their preference for ancestral hosts. Relative to physiological adaptations, behavioural adaptations leading to acceptance of novel host plants may have developed slowly during colonization events. Other studies on insect herbivores are reviewed which support this

pattern. I conclude that for some insect species, host selection behaviour may represent a conservative force in insect-plant evolution. For these species, local selection pressures favoring altered patterns of host use may be the primary cause of host shifts.

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## Table of Contents

# List of Tables

Table Page

# List of Figures

Figure Page

# I. Introduction

The vast majority of phytophagous insect species restrict their host use to one plant species (monophagy) or a few related plant species (oligophagy). Within wide ranging species of insects especially, further specialization may lead to the formation of host adapted races or biotypes. Possible reasons for this specialization include the diversity and distribution patterns of host plants (Price 1980, and references therein), plant chemical defenses against herbivory (Feeny 1975, Rhoades and Cates 1976), and community properties such as competition or the local presence of predators or parasites (Fox and Morrow 1981). Host specialization may promote rapid speciation and has probably been a major factor in contributing to the enormous diversity of insect herbivores (Mayr 1963).

Studies of phytophagous insects have long been prominent in the evolutionary literature, and there are currently several active debates in this field of study. One controversy centers around claims that some species or host races have evolved under sympatric conditions (Bush 1969, 1975a, Guttman et al. 1981; but see Futuyma and Mayer 1980 for an opposing viewpoint). Another controversy concerns the extent to which individual insect and plant taxa have coevolved (engaged in adaptation and counter-adaptation through evolutionary time). Interest in this idea grew after publications by Fraenkel (1959) and Ehrlich and Raven (1964) which related host specificity and patterns of insect evolution to the defensive properties of secondary plant compounds. Recently however, the probability of strict reciprocal coevolution between insects and plants has been questioned (Futuyma 1983, Jermy 1984), as has the assumption that herbivore specialization is ordinarily a response to secondary plant chemistry (Fox and Morrow 1981).

Resolving questions about insect-plant evolution is often hampered by a poor understanding of host selection behaviour in insects, the mechanisms which control it, and their genetic basis. In the absence of real data, assumptions are often made regarding the flexibility of insect behaviour and its role in mediating host shifts. For example, most models of sympatric speciation assume that mutations at a single locus can lead to changes in host use (see Bush 1975b). Many of these assumptions are based on the notion that interactions between insects and plants are based on simple processes. However, mechanisms regulating host selection in insects are considerably more complex than first suspected. Traditional concepts that stressed single compound control of host choice have failed to account for the accumulated evidence, and new theories are gaining acceptance which emphasize the integration of total sensory input and the interaction of both pre- and post-ingestive mechanisms (Dethier 1982, review by Miller and Strickler 1984).

The present study was designed to clarify the role of behaviour in insect-plant evolution through analysis of evolutionary changes in the mechanisms which control host acceptability for feeding in the Colorado potato beetle *Leptinotarsa decemlineata* (Say). This oligophagous insect has recently undergone a host range expansion in North America induced by agricultural practices and therefore provides an opportunity to study behavioural phenomena associated with changes in host plant use. Adult food choice largely directs oviposition sites in this species, since females generally lay eggs where they settle to feed and do not fly when gravid (see Chapter four).

This thesis is organized around three chapters. Chapter two provides a detailed behavioural analysis of plant sampling and feeding behaviour and examines how beetles discriminate among potential host plants. The approach taken in this study is neuroethological, and is based on the rationale that mechanisms controlling host choice can be studied indirectly through variations in the insect's own behaviour patterns. As Fentress (1980) has stated, "Nervous systems do not simply build up a whole pattern through blind summation of the parts; they insist on the whole and adjust the parts accordingly." My objective was to identify "parts" of the the feeding sequence in beetles that vary in relation to plant preference, and use these relationships to suggest what mechanisms are responsible for allowing discrimination among plants. I also compare the behaviour of three recently evolved, host adapted populations of *L. decemlineata*, to determine how rapidly mechanisms controlling host plant recognition have evolved in this insect species.

Chapter three describes tests of the hypothesis that solanaceous alkaloids (secondary plant compounds) act as sensory inhibitors of feeding, and thereby function to regulate host choice in *L. decemlineata*. This possibility has been suggested from long term feeding studies, but these studies have not directly addressed mechanisms. In my experiments, variations in pre-ingestive sampling and feeding were used to directly observe the effects of alkaloids on behaviour.

In the final chapter, I review previous experiments on *L. decemlineata* and compare the behavioural and physiological adaptations that have evolved in this species during the formation of regional biotypes. I also review other studies in which both physiological and behavioural traits have been measured on the same insect species, in an attempt to assess the relative contribution of these adaptations in mediating host transfers.

**Study Organisms**

*Leptinotarsa decemlineata* is an oligophagous beetle which feeds exclusively on members of the Solanaceae, and primarily on plants of the genus *Solanum*. According to Tower (1906), *L. decemlineata* is descendant from *L. intermedia* Tower, an insect indigenous to Mexico where it feeds on Buffalo bur, *Solanum rostratum* Dunal. Tower suggests that movements of Spanish caravans into the United States in the seventeenth century allowed the northward expansion of both *S. rostratum* (the burs of the plant being carried by pack animals) and the insect. Sometime later *L. decemlineata* is presumed to have evolved from *L. intermedia* along the eastern foothills of the Rocky Mountains. However, in a revision of the genus Jacques (1972) regarded the two species as synonomous, and this treatment is now generally accepted.

During the mid-nineteenth century, potato (*Solanum tuberosum* L.) was introduced to the midwestern United States. *L. decemlineata* soon colonized potato and later dispersed across North America and Europe with the spread of potato agriculture (see Johnson 1969). Previous expansion of the beetles' range to the north or east had been prevented by the limited distribution of its primary *Solanum* hosts (see Fig. 1.1). *L. decemlineata* is now reported to feed on a number of wild and domestic solanaceous plants.

*L. decemlineata* reproduces by sex; there is no parthenogenesis in the species. Eggs are laid by females directly on the plant and larvae develop through four instars before burrowing into the soil to pupate. Depending on latitude, there may be from one to three generations per year. Although relatively large, adult beetles are reported to be good fliers and dispersal by flight may be common, especially where host availability is limited (Johnson 1969).

Collection sites for the three regional populations of *L. decemlineata* used in this study, and approximate distributions of the two primary wild host plants of the species are shown in Figure 1.1. In Arizona, beetles are isolated on one host plant, *Solanum elaeagnifolium* Cav., a perennial weed common along roadsides and other disturbed areas. In this region, however, beetles are rare and are normally found only in irrigated valleys, perhaps where moist soil conditions permit successful pupation and adult diapause. Tower (1906) made similar observations of the species' distribution in Mexico, noting that although *S. rostratum* grew on the open plains, beetles were only common near stream beds or other sources of water.

Potato, an occasional winter crop in Arizona, is grown only during the beetles natural diapause period (November to April) and is therefore not used as a host. During a week long search for the insects in southeastern Arizona in September 1983, I found no other *Solanum* species in the area, an observation consistent with those of Hsiao (1978) and the herbarium records at the University of Arizona in Tucson. Based on the records contained in Tower (1906), *L. decemlineata* has been isolated on *S. elaeagnifolium* in southern Arizona for at least 300 generations.

The Alberta population has been maintained as a breeding colony in the laboratory for several years. To avoid genetic drift and/or artificial selection, it is supplemented each year with wild insects collected from potato gardens in the Edmonton area. Potato is the

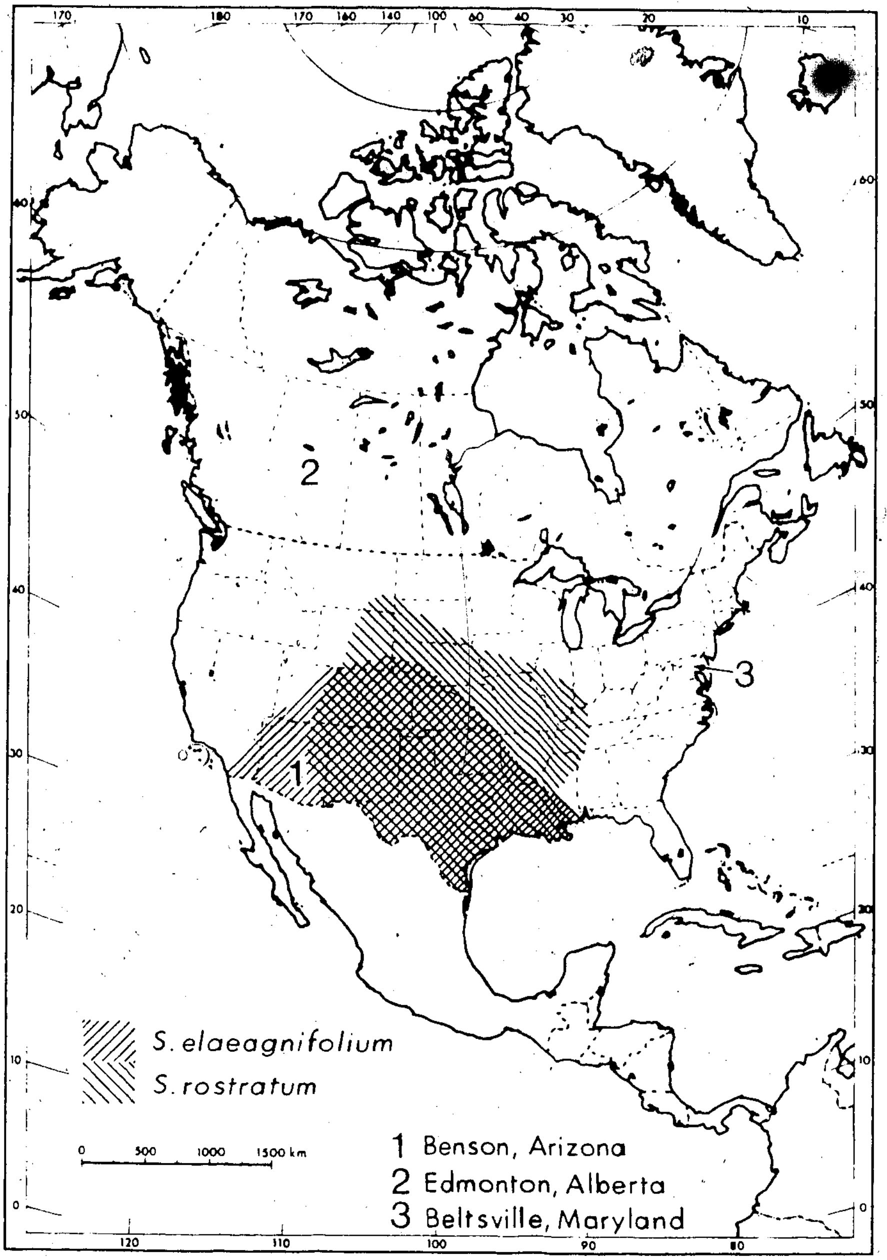

Figure 1.1. Origins of the three populations of *L. decemlineata* used in this study and estimated distributions of their two primary *Solanum* host plants in North America. (Sources: Whalen 1979, Rickett 1979).

primary host for *L. decemlineata* throughout western Canada; however beetles are occasionally reported feeding on both wild and domestic tomato. This population is a descendant from the original colonists on potato and has been largely isolated on potato for at least 150 generations.

An eastern population of Colorado potato beetles that feed on tomato (*Lycopersicon esculentum* Mill) was obtained from the Beltsville Agricultural Research Center in Beltsville, Maryland. Beetles from this area are collected from tomato fields and reared on the same plant in the laboratory. Although reports of *L. decemlineata* feeding on tomato date back to Tower (1906), the insect has only recently been elevated to "pest" status on this plant in areas of intense tomato cultivation in eastern North America. Other potential host plants in the region include potato and several species of wild *Solanum*.

Beetles were reared in active breeding colonies in the laboratory on their respective regional host plants as described in Appendix I. Procedures followed for the growth and maintenance of plants are given in Appendix II.

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# II. Host plant discrimination and its evolution in the Colorado potato beetle *Leptinotarsa decemlineata*

## Introduction

Host selection by phytophagous insects has traditionally been viewed as a sequential process involving the related phases of host finding and host recognition (Thorsteinson 1960, Miller and Strickler 1983). Due to the inherent problems associated with observing free-flying insects, analysis of long range orientation to a plant or its habitat has been somewhat neglected (but, see Ahmad 1983 for a recent review), with a resulting emphasis on more proximate interactions between insects and plants. The study of insect chemoreception (both taste and smell) has received special attention. It is with the aid of these senses that the "final decision" to accept a plant for feeding or oviposition is made.

In developing preliminary hypotheses concerning how insects identify their host plants, researchers drew from prevailing models in ethology and vertebrate neurobiology. The inital discovery that glucosinolates (mustard oil glycosides) in cruciferous plants acted as strong feeding stimulants for certain insects (Verschaffelt 1910) stimulated research into the effects of secondary plant compounds on insect behaviour. Summarizing the early literature, Fraenkel (1959) concluded that these compounds acted as a class of "token stimuli" (Tinbergen 1951) to insects. Evidence for the neurological correlate of token stimuli — "labelled lines"[1] — came later when Schoonhoven (1967) described a chemoreceptive cell in *Pieris brassicae* sensitive to glucosinolates.

Failure to extend the token stimulus concept far beyond the Cruciferae and their associated insects (see Dethier 1982) may have led, in part, to the hypothesis that secondary compounds defined host ranges by signalling to insects what *not* to eat (Jermy 1958, 1961). This idea was consistent with growing evidence that many secondary plant compounds (e.g. nicotine, strychnine, the pyrethroids) were toxic to insects. Although this hypothesis

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[1] labelled lines are thought to be hard-wired neural channels which respond to single classes of stimuli and result in specific behaviours.

proposed a different mode of action for secondary compounds, the concept of single factor regulation of plant choice remained, and numerous experiments followed that claimed to support Jermy's view (see Chapter 3, for a critique). Similarly, more detailed studies designed to investigate the control of food intake in insects (e.g., Hamamura et al. 1962) were modelled in simple linear, stimulus-response terms, as attempts were made to isolate from plants the appropriate "sign stimuli" (e.g., biting factors, swallowing factors) that were presumed to release each step in a behavioural sequence. Together, these approaches helped propagate a somewhat static and simplistic view of behaviour in phytophagous insects.

More recently, ideas concerning the control of host choice by insects have shifted to include more dynamic concepts involving the integration of patterned sensory input and the perception of total plant "Gestalts" (Dethier 1970, 1973, 1976, 1982). These ideas grew from the discovery that insect chemosensory neurons, like their vertebrate counterparts, are generally not highly specific, but instead have broad and overlapping response spectra (Schneider 1969, Dethier 1973, 1974, 1977; Blaney 1975; van Drongelen 1978 et al.). The current view is that sensory quality in these systems is coded not by individual labelled lines (although these may be a factor), but by large populations of interacting neurones which produce unique "across-fibre" (Pfaffman 1941, Erickson 1967) patterns of response.

Increasing understanding of how these complex systems function in discrimination among plants will require new directions in research. At the neurophysiological level, Dethier and Crnjar (1982) have attempted to determine how plants of varying quality are identified by insects through a detailed analysis of the patterns of sensory input produced across gustatory neurones exposed to plant saps. To date, no complementary approach has been taken at the behavioural level of analysis. Early ethological studies (Williams 1954, deWilde 1958, Zohren 1968) provided descriptions of preliminary behaviours (drumming plant with forlegs, palpating, nibbling, and so on) performed by phytophagous insects prior to feeding or oviposition. Later, when the functional significance of these behaviours in terms of plant sampling became apparent, more detailed analyses proved useful in exploring the effects of glucosinolates on plant acceptance in aphids (Nault and Styer 1972) and oviposition in the cabbage fly *D. brassicae* (Nair and McEwen 1976). However, studies of this kind have focused only on those species in which the behaviours are regulated largely by single compounds.

In this paper, I examine the broader question of perception of overall plant quality through analysis of entire sequences of plant assessment and feeding in the Colorado potato beetle *Leptinotarsa decemlineata* (Say). This insect is an appropriate model organism to use, since both olfactory discrimination based on complex mixtures of stimuli (Visser and Ave 1978, Ma and Visser 1978), and absolute discrimination based on gustatory inhibition by alkaloids (Hsiao and Fraenkel 1968, Bongers 1970), have been implicated from previous experiments. My first objective in this study was to determine whether measurable variations in behaviour patterns could be used to indicate how beetles discriminate among closely related plant species. My second objective was to use the behavioural data to gain insight into the role that underlying neural mechanisms play in the evolution of host choice by comparing three recently evolved geographic populations of insects which use different host plants (see Chapter 1, Study organisms).

## Materials and Methods

Insects used in this experiment were collected in the field at three different locations (see Chapter 1, Figure 1.1) and reared in the laboratory on their respective regional host plants. Twelve beetles from each geographic population were randomly assigned to each of four plant groups, *Solanum tuberosum* ("Norland" variety), *Solanum rostratum*, *Solanum elaeagnifolium*, and *Lycopersicon esculentum* ("Earliana" variety). These plants represent the three regional hosts and presumed ancestral host of the species (see Chapter 1, Study organisms). All beetles were tested as naive (no feeding experience) adults in their first day after emergence.

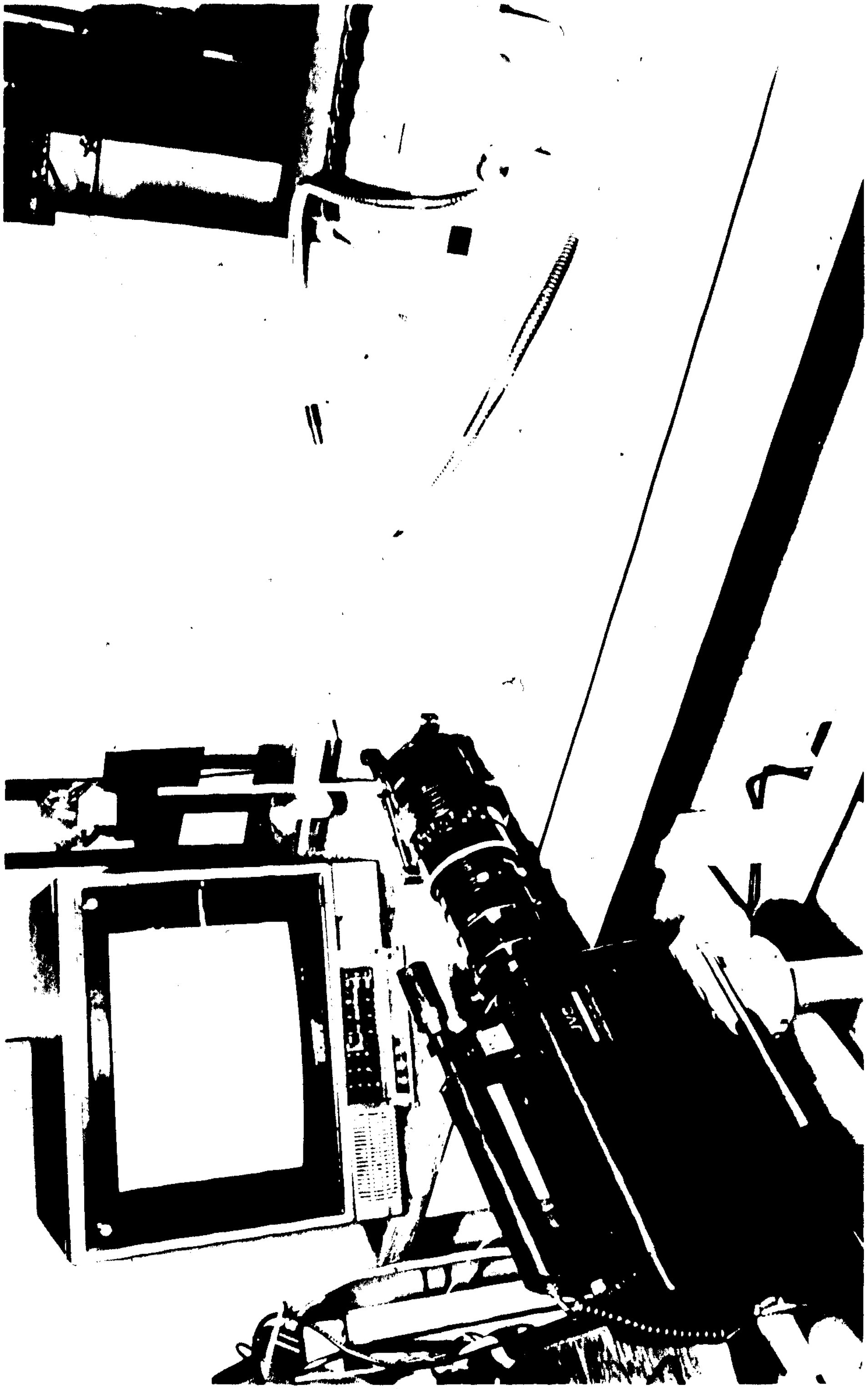
Each insect was tested individually with a single, separate leaf using a simple apparatus designed to allow videotape monitoring of behavioural events associated with feeding (see Figure 2.1). This apparatus consisted of a teflon rod held horizontally on a stand and split lengthways at one end to hold a leaf, whose petiole was placed in water. Beetles were transfered to the apparatus by inducing them to crawl up a second teflon rod which was then placed against the test rod as the insect walked. Leaf outlines were traced before and after feeding to provide a permanent record of leaf consumption.

Insect behaviour was recorded using a 0.5 inch format videotape system consisting of a JVC color video camera (model #HR7300U), a Panasonic cassette recorder (model #NV-8420), and a Sony CVM-1270 color monitor. Equipped with a C-mount, the camera could be adapted for use with standard photographic lenses. I used a Micro-Nikkor 105mm lens and two M-rings to achieve the desired level of magnification. Light was directed on the leaf using a Volpi Intralux 5000 fibre optic system. Unlike film units, video cameras require only moderate levels of lighting, well within the tolerance range of the insects, to achieve optimum resolution. Behaviour was videotaped for a minimum of three minutes from the time beetles first contacted the plant. This allowed repeated observations of the initial sampling behaviours on the leaf. Events that ocurred after the three minute videotape period were observed on the monitor and noted. Cumulative-time stopwatches were used to time all events.

Beetles were allowed free access to a leaf until three minutes without feeding elapsed. This period was previously determined as a minimum inter-meal interval time for this insect. Therefore, unlike long term feeding studies, this experiment focused on sensory aspects of plant discrimination by minimizing post ingestive effects on feeding.

In a preliminary study of beetles feeding on potato leaves in petri dishes, first meal size of females (Mean=27 mm$^2$, SD=12.0, n=10) and males (Mean=20 mm$^2$, SD=9.0, n=9) did not differ significantly (Kruskal-Wallis test, H=1.74, 1 d.f., P>0.10). Therefore, because supplies of new adults were limited, both sexes were used and assigned to

Figure 2.1. Equipment setup used for videotaping and monitoring insect behaviour during feeding experiments.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groups without knowledge of sex (sexes are indistinguishable unless examined with a microscope).

Plants used for both experiments and insect culture food were grown in a greenhouse under standard conditions (see Appendix II). *S. tuberosum* was grown from tubers, while *L. esculentum*, *S. rostratum*, and *S. elaeagnifolium* were all grown from seed. To minimize effects due to inter-plant variability, leaves from at least six plants of each species were used in the feeding tests for each population of beetles. All leaves were taken from healthy plants and only leaves from the second or third node below the apical tip (21 days to 42 days old) were used.

Leaf consumption was measured using a Licor Area Meter, model #3100 (accuracy=$1mm^2$). Since accurate estimates of leaf thickness could not be obtained, leaf areas consumed were corrected for differences in thickness using their weight:area ratios. Twenty-five leaf discs of equal size were cut from each of the four plant species and weighed. Leaf discs of *S. tuberosum* (mean=10.6 mg, SD=0.30), *S. rostratum* (mean=10.5 mg, SD=0.20), and *S. elaeagnifolium* (mean=10.4 mg, SD=0.20) were approximately equal in weight. Leaf discs of *L. esculentum* (mean=6.9 mg, SD=0.21) were on average 34% lighter than the three *Solanum* species. Therefore, each value for *L. esculentum* was reduced by 34% and values for the three other species were left unchanged.

## Data Handling

Because of small sample sizes, certain estimates of populations means were strongly biased by extreme scores. Since there was no *a priori* reason for discarding extreme values, I opted to *winsorize* them (see Sokal and Rohlf 1981). In this procedure, the extreme score is assigned the value of its nearest neighbour in rank. Potential outliers in each sample were first tested for statistical significance by the Dixon test. Outlier values, samples from which they came, Dixon test results, and assigned values are as follows:

(1)Alberta, *S. elaeagnifolium*/gustatory sample: score=20s (Dixon test r=.50, n=10,

$P<.05$); assigned value=11s.

(2)Arizona, *S. rostratum*/explore: score=32s (Dixon test $r=.79$, $n=12$, $P<.01$); assigned value=9.5s.

(3)Arizona, *L. esculentum*/explore: score=25s (Dixon test $r=.80$, $n=8$, $P<.01$); assigned value=12.5

All statistics were calculated using BMDP statistical software (Dixon 1983).

## Results

### Behaviour protocols

Sequences of adult *L. decemlineata* behaviour on primary host plants generally followed a stereotyped and ordered pattern of sampling, feeding, grooming and rest (Figure 2.2). With the exception of the "small bite phase", which is sometimes absent and tends to be indistinguishable from "sweep-feeding", the behavioural categories used could be reliably timed using clear beginning and end-points. For illustrations of categories A through D below, see Figure 2.3.

A. *Explore*: Duration on the leaf surface beginning with first physical contact with the leaf and ending with transition to *gustatory sampling*. Active movements include walking, palpating (repetitive contacts by the maxillary palpi on the leaf surface) and antennal waving. Sensory input, in addition to that from antennae, maxillary palps and labial palps, may also be received from sensilla situated on the tarsi.

B. *Gustatory sample:* Before feeding, exploring the leaf surface was followed by a period of "squeezing" the plant with repetitive movements of the mandibles. This typically occurred on the leaf edge, but beetles occasionally sampled leaf veins in a similar manner. On acceptable plants, this piercing action of the mandibles released visible droplets of plant fluid,

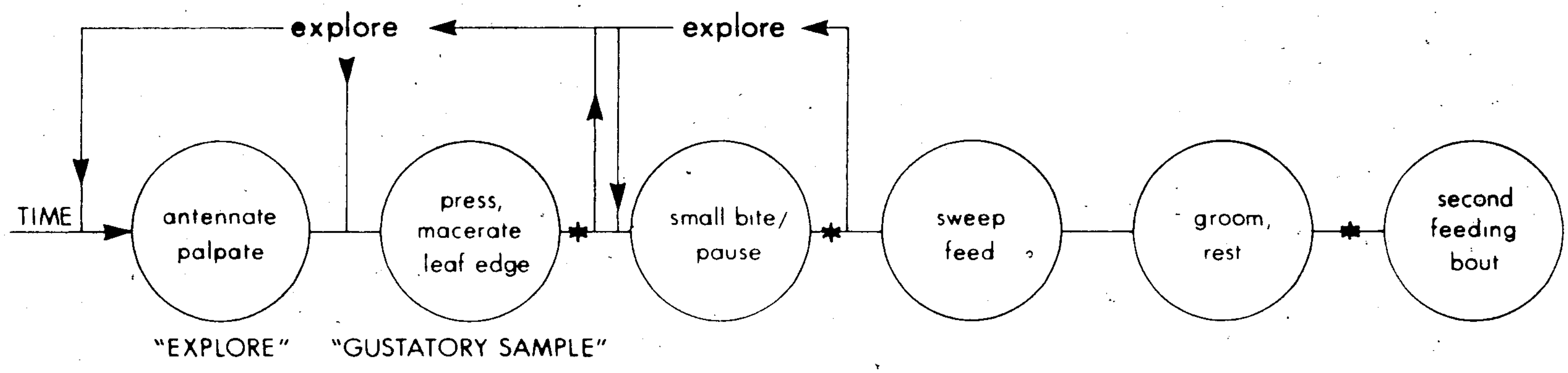
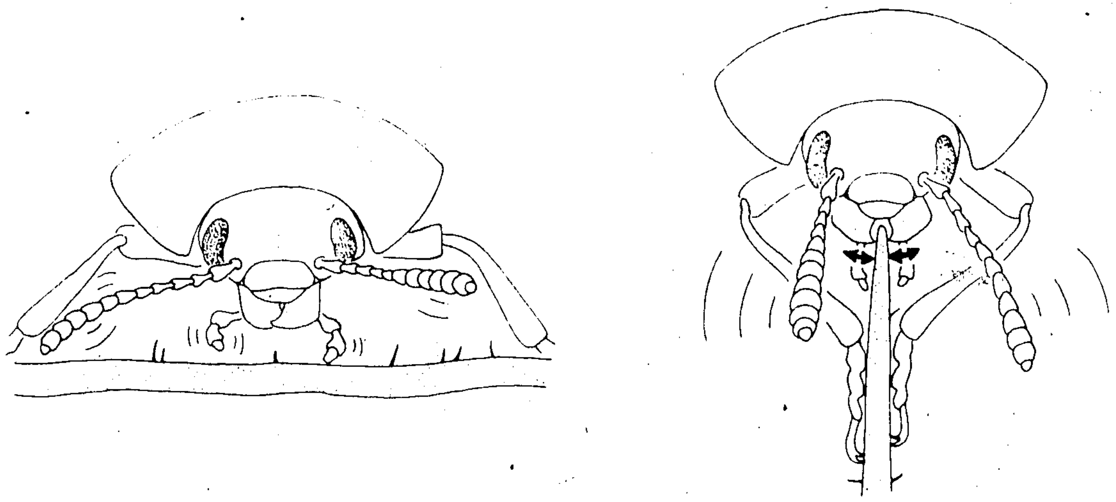
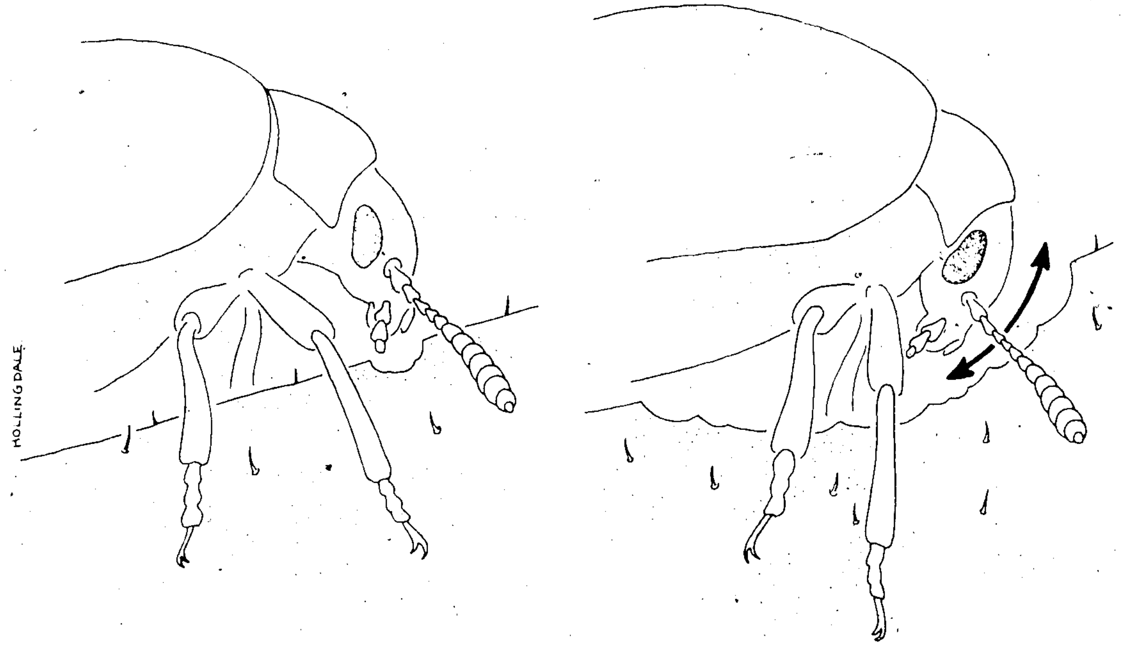


Figure 2.2. Plant sampling and feeding behaviour by *L. decemlineata* adults on a primary host. Ethogram illustrating a typical behavioural sequence from the time of initial plant contact through to the termination of first meal feeding.



A. Explore B. Gustatory sample



C. Small bite D. Sweep feed

Figure 2.3. Four component behaviours in the transition from plant assessment to feeding by *L. decemlineata* adults.

bringing gustatory sensilla on the insect's mouthparts into direct contact with leaf sap (thus the name gustatory sampling). On plants that were not eaten, however, action of the mandibles was often less vigorous, and gentle "pressing" of the leaf edge did not result in apparent breaks in leaf tissue. This behaviour is thus graded and depends on plant quality, but no attempt was made to quantitatively distinguish "pressing" from "macerating".

While I use the term gustatory sampling for convenience, it is not meant to imply that the only function of the behaviour is to stimulate gustatory sensilla on the mouthparts., As indicated in Figure 2.3(B) the antennae are actively drawn towards the sampling site during this phase. Thus, the movements of the mandibles may also serve to enhance the release of plant volatiles. The duration of the first gustatory sampling bout and the frequency of bouts during the test period were recorded.

C. *Small bite*: A bite was noted when a visible fragment of leaf was taken into the oral cavity. In most cases, biting involved distinct movements (bite through leaf with mandibles, lift head), and could therefore be easily distinguished from gustatory sampling. Beetles normally (but not always) took one or two small bites and paused while chewing the leaf fragments.

D. *Sweep feed:* Rapid feeding characterized by repetitive bites as the head is moved in a rhythmic, sweeping fashion. While small biting and sweep feeding are distinguished here to give the reader a "feel" for the gradual progression to full feeding, the two behaviours could not always be clearly separated. Subsequent use of the term "feeding" will therefore refer to both behaviours. Duration of feeding, measured from the time of first bite, was used to calculate feeding rate. The number of different feeding sites on the leaf was also recorded.

Feeding bouts were normally terminated by *grooming*, or *rest*, and occasionally by further examination of the plant surface. Rest was defined as a period of thirty or more seconds of motionlessness.

## Comparisons among plants: within insect populations

The relatively stereotyped sequences of *L. decemlineata* behaviour broke down on plants less preferred for feeding (for example, see Figure 2.4). On preferred host plants (plants eaten the most) beetles usually sampled and fed at a single site on the leaf before ending the feeding bout with a long (greater than 3 minutes) period of grooming. On plants that were eaten less however, fewer insects proceeded directly through the sequence, and many re-initiated sampling and feeding at numerous sites on the leaf before stopping to rest or groom.

In addition to these pattern differences, there were consistent trends in several of the single variables measured in relation to plant species preference. In Tables 2.1-2.3 behavioural data are arranged within each population by plant species ranked[2] in terms of consumption. On average, reduced feeding on a plant species was associated with increased exploration time prior to gustatory sampling and a longer gustatory sampling period for those insects that proceeded to feed. There was also an increase in the number of sampling and feeding sites on lower ranked plant species during a single feeding bout. However, when acceptance of a species by beetles from a population approached nil (e.g., *L. esculentum* for Arizona and Alberta groups), rejection of individual plants often occured after just one gustatory sampling event. Note that these trends were consistent although plant species were ranked differently by the insects within each population.

Not all differences in feeding and sampling behaviour were statistically significant. Where consumption differences among plant species were large, associated sampling behaviours also tended to vary significantly (e.g., the Alberta population, Table 2.1). However, variability in sampling behaviour was not statistically significant within the Maryland population, where differences in consumption among plant species was relatively

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[2] a plant's rank refers to consumption on that plant relative to the other species tested

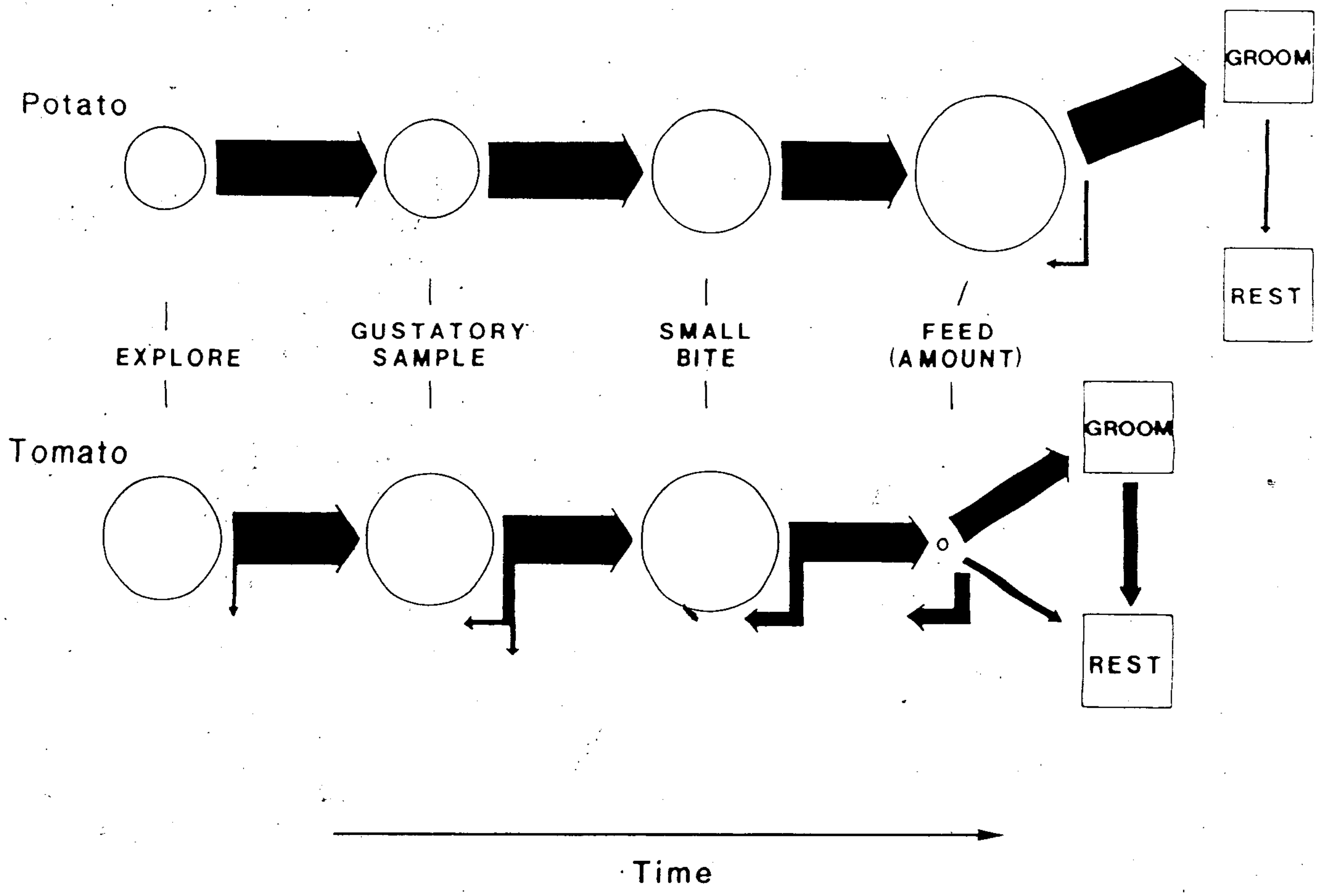

Figure 2.4. Kinematic graph depicting variable behaviour patterns by beetles from Alberta on their preferred regional host (potato) and a marginal host plant (tomato). Observations are from 12 beetles per plant. Areas of the circles are proportional to the time spent in each behaviour except Feed which is proportional to the amount of leaf consumed. Behaviours that typically terminated the first meal (in squares) were recorded for three minutes after feeding stopped. Width of the arrows is proportional to the number of animals in transition. Arrows pointing back refer to beetles which repeated an earlier behaviour in the sequence; arrrows pointing down to those that walked off the plant and did not return during the test period.

**Table 2.1.** First meal feeding and associated sampling behaviours by beetles from Alberta tested on four solanaceous plants ranked by consumption (Amount). Values given are means±standard errors or medians, range.

| | FEEDING | | | | SAMPLING | | |
|---|---|---|---|---|---|---|---|
| Plant | #Feed/n | Amount ($mm^2$) | Rate ($mm^2$/min) | #Sites | Exp[1]s | Prefeed GS[2](s) | #GS Sites |
| S.rostratum | 12/12 | 82±15 | 3.3±.33 | 1.0, 1-3 | 2.4±0.41 | 3.1±0.55 | 1.0, 1-2 |
| S.tuberosum | 12/12 | 72±11 | 9.0±.98 | 1.0, 1-1 | 3.3±0.33 | 3.7±0.43 | 1.0, 1-1 |
| S.elaeagnifolium | 10/12 | 43±10 | 3.1±.70 | 2.0, 1-6 | 3.4±0.50 | 5.5±1.20 | 2.5, 1-9 |
| L.esculentum | 10/12 | 5±2 | -- | 2.0, 1-3 | 4.9±0.95 | 5.5±0.84 | 1.5, 0-4 |
| | G=5.91[3]<br>3df<br>NS | F=8.26***<br>3, 18df | W=15.1***<br>2, 13df | G=8.20[4]*<br>3df | F=2.94*<br>3,43df | F=2.70[3]<br>3,40df<br>P=0.06 | G=16.6[4]***<br>3df |
| Levene's test (log transformed) | | F=2.15<br>3,39df<br>NS | F=3.66*<br>2,27df | | F=1.31<br>3,43df<br>NS | F=2.02<br>3,40df<br>NS | |

[1] Exp=duration *exploring* leaf surface prior to first *GS*.
[2] GS=duration *gustatory sampling* leaf prior to biting (note: feeders only included).
[3] calculated by grouping into feeders and non-feeders.
[4] calculated by grouping into categories of 1, and >1.
* P<.05, ** P<.01, *** P<.001

**Table 2.2.** First meal feeding and associated sampling behaviours by beetles from Arizona tested on four solanaceous plants ranked by consumption (Amount). Values given are means±standard errors or medians, range.

| | FEEDING | | | | SAMPLING[1] | | |
|---|---|---|---|---|---|---|---|
| Plant | #Feed/n | Amount ($mm^2$) | Rate ($mm^2$/min) | #Sites | Exp(s) | Prefeed GS(s) | #GS Sites |
| S.elaeagnifolium | 12/12 | 44±5.6 | 3.6±.74 | 1.0, 1-2 | 2.4±0.22 | 3.0±0.31 | 1.0, 1-2 |
| S.rostratum | 12/12 | 33±5.4 | 3.4±.43 | 1.0, 1-3 | 4.6±0.82 | 3.3±0.50 | 1.5, 1-3 |
| S.tuberosum | 2/12 | 12±6.0[2] | --- | 2.5, 1-4[2] | 14.3±3.78 | 12.4±1.10[2] | 6.5, 2-11 |
| L.esculentum | 1/12 | --- | --- | --- | 6.3±1.5[3] | --- | 1.0, 0-4 |
| | G=48.1*** 3df | | | | W=6.77** 3, 16df | | G=22.7*** 3df |
| Levene's test (log transformed) | | | | | F=10.57*** 3, 39df | | |

[1] Abbreviations as in Table 2.1.
[2] n=2 feeders only.
[3] n=8, four insects did not proceed to *GS* stage.
**P<.01, *** P<.001

**Table 2.3.** First meal feeding and associated sampling behaviours by beetles from Maryland tested on four solanaceous plants ranked by consumption (Amount). Values given are means±standard errors or medians, range.

| | FEEDING | | | | SAMPLING[1] | | |
|---|---|---|---|---|---|---|---|
| Plant | #Feed/n | Amount (mm²) | Rate (mm²/min) | #Sites | Exp(s) | Prefeed GS(s) | #GS Sites |
| S.tuberosum | 12/12 | 45±9.7 | 4.1±.54 | 1.0,1-6 | 3.4±.52 | 2.5±.38 | 1.0,1-2 |
| S.elaeagnifolium | 11/12 | 41±7.1 | 2.1±.28 | 1.0,1-3 | 3.5±.47 | 2.8±.46 | 1.0,1-2 |
| S.rostratum | 12/12 | 28±4.0 | 2.1±.22 | 1.0,1-3 | 3.9±.65 | 3.2±.30 | 1.0,1-3 |
| L.esculentum | 8/12 | 21±5.9 | 3.1±.74 | 1.5,1-4 | 4.9±1.34[2] | 3.7±.33 | 1.5,1-7 |
| | G=9.90*<br>3df | W=2.44<br>3,20df<br>NS | F=6.36**<br>3,34df | G=2.87<br>3df<br>NS | F=0.70<br>3,42df<br>NS | F=1.76<br>3,39df<br>NS | G=0.64<br>3df<br>NS |
| Levene's test (log transformed) | | F=5.78**<br>3,39df | F=0.88<br>3,34df<br>NS | | F=0.41<br>3,42df<br>NS | F=1.66<br>3,39df<br>NS | |

[1] Abbreviations as in Table 2.1.

[2] n=10, two beetles did not proceed to *GS* during test.

* P<.05, ** P<.01

small (Table 2.3).

Because most beetles from Arizona did not feed on *S. tuberosum* or *L. esculentum*, comparisons of measures related to feeding could not be made across all plant species within this population. Consumption of *S. elaeagnifolium* and *S. rostratum* by beetles from Arizona (F=1.71, d.f.=1,22, P=0.20), and duration of pre-feed gustatory sampling on these two plants (F=0.19, d.f.=1,21, P=0.67), were not significantly different.

Variability among beetles for acceptance of marginal plants also appeared to affect duration of the first gustatory sampling bout. On low ranked species at least, there is an indication that non-feeders reject plants after relatively short gustatory sampling bouts, while feeders tend to gustatory sample for a longer period before biting (Table 2.4). For this reason, only feeders are compared in Tables 2.1-2.3 with respect to the duration of the first gustatory sampling event. Non-feeders on the same plant also tended to explore longer than feeders, but the breakdown of animals into the two groups did not provide sufficient sample sizes to test this observation statistically.

To test for homogeneity of within group variances, I transformed the data to logarithms and applied Levene's test (Tables 2.1-2.3). This procedure is equivalent to testing for differences in coefficients of variation by correcting for relative changes in variance that may accompany samples with different sized means (Sokal and Braumann 1981). Where there was significant heterogeneity of within group variances, I used Welch's one-way analysis of variance test statistic **W** to test for differences in sample means. Welch's test statistic is recommended as a robust alternative to the ANOVA **F** statistic if sample variances are not homogeneous (Brown and Forsythe 1974).

Correlations between any single pair of variables within beetle populations were generally weak. The following values, taken from the Maryland population, are typical: feeding amount and exploration time (r= -0.19, d.f.=41, P>0.10); feeding amount and duration of gustatory sampling (r= -0.31, d.f.=41, P<0.05); explore time and duration of gustatory sampling (r=0.12, d.f.=41, P>0.10). These values varied among populations,

**Table 2.4.** Comparison of initial sampling behaviours by feeders and non-feeders on the same plant species. Values are means±standard errors and (n).

| | EXPLORE | | GUSTATORY SAMPLE | |
|---|---|---|---|---|
| Population / Plant[1] | Feeders | Non-feeders | Feeders | Non-feeders |
| Arizona / S.tuberosum | 3.4±1.65<br>(2) | 16.7±4.23<br>(9) | 12.4±1.10<br>(2) | 6.9±1.59<br>(10) |
| Arizona / L.esculentum | 1.0±----<br>(1) | 7.0±1.54<br>(7) | 8.4±-----<br>(1) | 3.9±1.35<br>(7) |
| Alberta / L.esculentum | 4.4±0.90<br>(10) | 9.8±-----<br>(1) | 5.5±0.84<br>(10) | 3.9±----<br>(1) |
| Maryland / L.esculentum | 3.2±0.60<br>(8) | 11.4±4.05<br>(2) | 3.7±0.33<br>(8) | 1.7±0.70<br>(2) |
| Maryland / S.eleaegnifolium | 3.4±0.51<br>(11) | 4.6±----<br>(1) | 2.8±0.46<br>(11) | 5.9±---<br>(1) |
| Alberta / S.eleaegnifolium | 3.4±0.61<br>(10) | 3.7±0.10<br>(2) | 6.0±1.50<br>(10) | 9.9±6.20<br>(2) |

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[1] on a population basis, first four plants listed are ranked low; the last two moderate.

and no single variable was a good predictor of plant preference.

Differences in feeding rate were not related to host preference, but reflected the physical characteristics of the plants. Both *S. rostratum* and *S. elaeagnifolium* have leaf surfaces covered by dense mats of trichomes which visibly interfered with feeding. As a result, feeding rates on these two plants were consistently lower than the other species tested. This physical interference did not seem to affect the size of the first meal however, since both plants were ranked highly in all populations.

Behaviours terminating feeding sequences generally did not vary in relation to host quality. Regardless of meal size, beetles normally ended feeding by grooming for several minutes and the sporadic occurrence of grooming during feeding bouts was not systematically related to plant type. Beetles from Alberta feeding on tomato were the one possible exception to this rule. Most of those insects initiated feeding, but stopped quickly and groomed for only a short period (if at all) before resting, perhaps indicating the operation of a post-ingestive mechanism affecting food intake.

### Comparisons between and across insect populations

Consistent trends within beetle populations between sampling behaviour and plant consumption suggested that combining population data to further investigate the nature of these relationships might be appropriate. However, first meal sizes (and feeding rates) of the Alberta population were considerably higher than those from Maryland and Arizona (see Tables 2.1-2.3). Also, I could not equalize the within group variance of all samples with transformations.

As an option to performing parametric regression analysis on the entire data set, mean sampling and feeding data were pooled from the Arizona and Maryland populations (which did not appear to be inherently different in terms of feeding behaviour) and analysed using Kendall's rank correlation test (suggested as a nonparametric test of trends on means by Sokal and Rohlf 1981). Both explore time and gustatory sampling were significantly negatively correlated with plant consumption using this analysis (Figs. 2.5 and 2.6). Data for the Alberta population are also provided in Figures 2.5-2.6 but correlation coefficients were not computed because at least five data points are needed for the analysis.

Two individual comparisons were of interest with respect to adaptation to novel hosts. Beetles from Alberta that have colonized potato and are descendant from a wild *Solanum* feeding stock (like the Arizona population), spent a shorter time in both kinds of pre-feed sampling behaviour on potato than beetles from Arizona. However, the Maryland population, which is descendant from a potato feeding stock (like beetles from Alberta) and is in an earlier phase of colonizing *L. esculentum*, explore on the new plant for an equal length of time as beetles from Alberta, but gustatory sample somewhat less (although not significantly less, t = 1.38, 16 df, P = .09; one-tailed test on log transformed data). This raises the possibility that adaptation to *L. esculentum* may first involve changes in sensitivity at the gustatory level.

## Discussion

### Mechanisms of Discrimination

My objective in this study was to investigate mechanisms of host plant discrimination in *L. decemlineata* adults by using a behavioural analysis. The results indicate that beetles are capable of graded, sensory-based discrimination of plants, over a range of species normally used by the insects in nature. This conclusion is based on the consistent inverse relationship between pre-ingestive sampling behaviour and food consumption across plant species. Previous electrophysiological and behavioural studies with *L. decemlineata* adults have shown that longer-range orientation to a host is dependent on precise ratios of green leaf volatiles which are coded by olfactory receptors on the antennae (Visser and Ave 1978, Ma and Visser 1978). In this study, beetles were apparently capable of recognizing different plants on the basis of olfactory and contact chemoreceptive input alone, without reference to

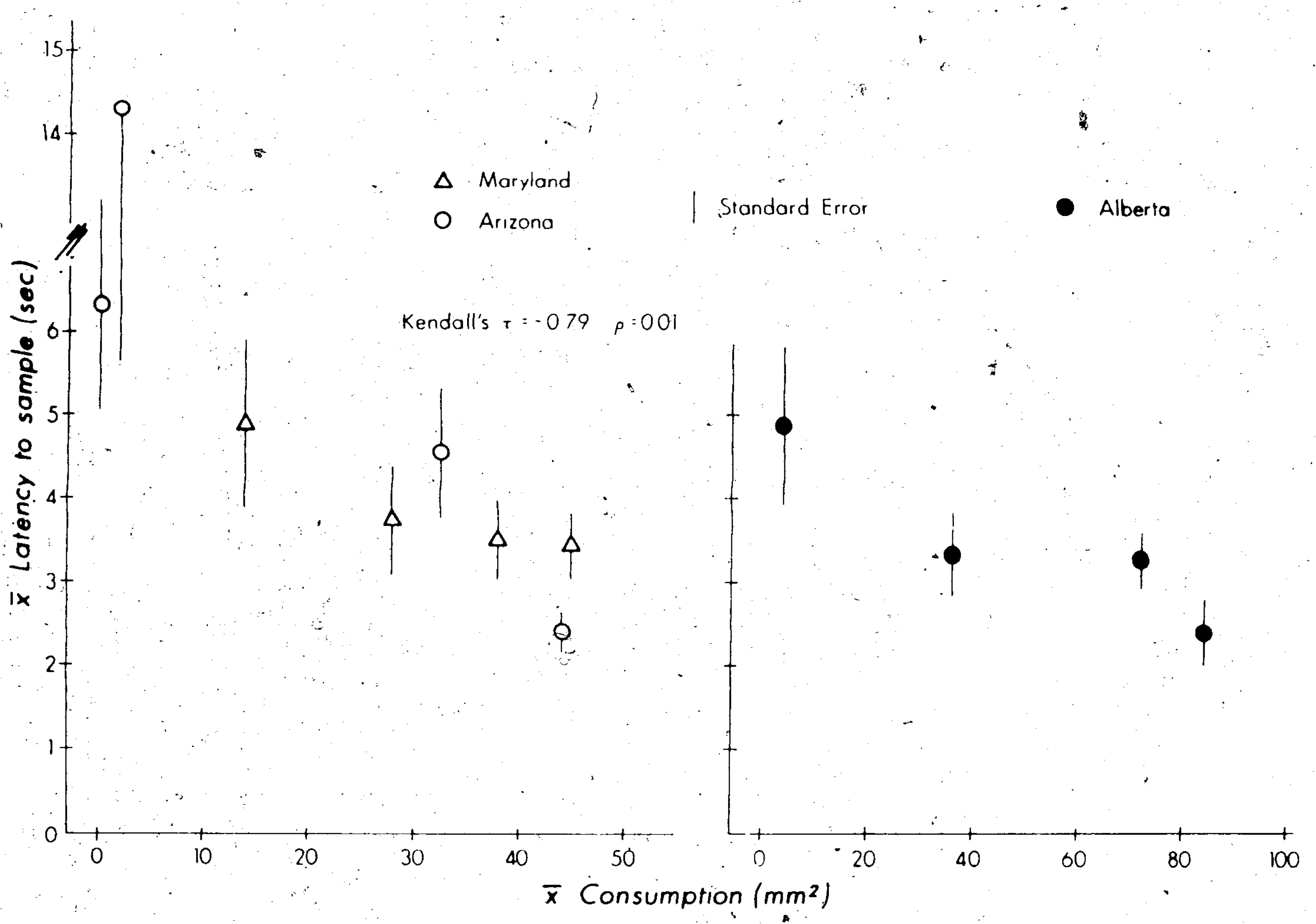

Figure 2.5. Mean latency to gustatory sample (exploration time) in relation to average food consumption on four species of plants for three beetle populations. Error bars for consumption omitted for clarity. N = 12 per plant.

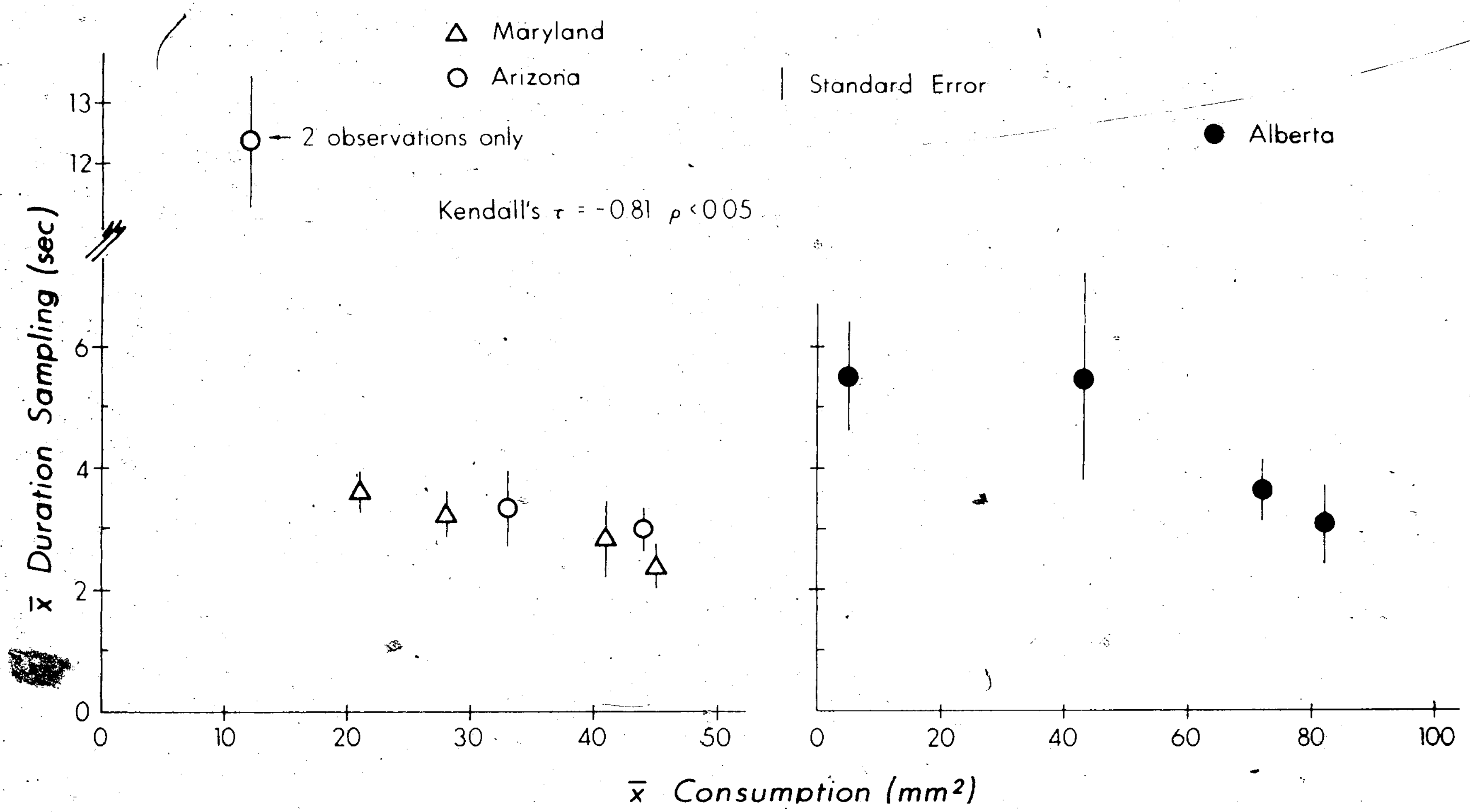

Figure 2.6. Relationship between mean gustatory sampling time and average consumption on four species of plants for three beetle populations. Error bars for consumption omitted for clarity. N=12 per plant.

internal plant saps. This finding plus the observation that the antennae are actively drawn towards the leaf during gustatory sampling suggest a dominant role for olfaction after the beetles contact the plant as well.

Although two categories of sampling behaviours (explore and gustatory sample) have been identified in this study, there is no reason to presume they involve separate underlying mechanisms. Input from mouthpart receptors in phytophagous insects typically converge with antennal input in the brain after only one synapse at the suboesophageal ganglion (Chapman 1982). And, as noted previously, antennal input is probably intensified by the same behaviour that initially exposes gustatory neurones to plant saps. Transition from "exploring" to "gustatory sampling" may involve a serial integration of sensory information to a single CNS site.

The additional sampling of plant fluids does, however, provide the opportunity for secondary plant compounds to act as feeding deterrents, perhaps by interfering with "normal" sensory messages (Schoonhoven 1982, Mitchell and Sutcliffe 1984). If this were the case, time spent by beetles in gustatory sampling might be expected to vary independently of exploration time on plant species less preferred for feeding. In this study, however, increased gustatory sampling time by feeders on low ranked species was consistently associated with longer initial exploration times (Tables 2.1-2.3). Also, non-feeders that reject individual plants after short gustatory sampling bouts tend to explore on the leaf surface first for much longer periods than feeders on the same plants (Table 2.4). These observations suggest that beetles discriminate among plants primarily on the basis of mixtures of plant volatiles and surface compounds, and not on the basis of inhibitory compounds (i.e., glycoalkaloids) in the plant saps.

A lower mean (but statistically insignificant) gustatory sampling period by Maryland beetles on *L. esculentum* as compared to Alberta beetles is the one notable exception to this pattern, and raises the possibility that adaptation by insects in Maryland to this plant involves a decreased sensitivity to the tomato alkaloid tomatine.

## Evolution of host choice

Evolutionary changes in host choice by phytophages have attracted considerable interest because of the potential for host-specific populations of insects (biotypes or host races) to develop into new species (Dethier 1954, 1970; Futuyma 1983, White 1978). In terms of underlying neurological mechanisms, colonization of new host plants by oligophagous insects may be associated with any combination of changes at the primary receptor level or in the CNS, such that new combinations of plant compounds are either detected, or interpreted differently, by the sensory system (Schoonhoven 1977).

To date, few attempts have been made to address this question. Best studied are a group of related moth species in the genus *Yponomeuta* which have evolved different host preferences (Herrebout et al. 1976, Schoonhoven et al. 1977, van Drongelen 1980, van Drongelen and van Loon 1980, review by Futuyma 1983). Correlations have been shown between the moths' electrophysiological and behavioural responses to certain host chemicals (secondary compounds and sugars) and patterns of host use in the field. While such functional changes in the sensory system will develop at some point during the speciation process (individual species do have unique response characteristics), they are unlikely to be factors which mediate initial rapid colonization of new plants.

An alternative scenario is suggested by the results of this study on more recently evolved biotypes of *L. decemlineata*. It is clear from the large differences in behaviour on marginal host plants, that considerable variability exists within populations in terms of host acceptability. Interestingly, individual insects that do feed on marginal plants have a tendency to sample these plants less prior to feeding (Table 2.4) i.e., they *perceive* the plants as more acceptable. As a new plant is colonized, it may be that these more catholic feeders are selected for, bringing about a temporary pool of generalist feeders which, after some longer period of association with the new plant, may undergo "fine-tuning" of the sensory system resulting in behavioural specificity for the new host.

Thus, the three geographic populations of *L. decemlineata* studied from North America have not totally lost their behavioural preference for the ancestral host, *S. rostratum*, despite being isolated[3] from the plant for up to several hundred generations (see Chapter 1). Figure 4.1 (Chapter 4) illustrates how populations in Alberta and Maryland have increasingly become generalists as new plants are added to the insects' repertoire of acceptable species during each colonization event. Other insect species that have been studied during the preliminary stages of plant colonization have also undergone expansion of feeding or oviposition preference, not direct behavioural shifts involving loss of preference for the old host (see Chapter 4).

Although not statistically significant, reduced feeding on *S. rostratum* by Arizona and Maryland beetles is associated with a slight increase in pre-ingestive sampling behaviour. This implies that functional changes in the chemosensory system are emerging within these populations that eventually may result in loss of preference for the ancestral host.

In summary, *L. decemlineata* beetles show graded preference for potential host plant species. A systematic increase in pre-ingestive sampling behaviour on less preferred species suggests a complex of stimuli is involved in plant discrimination. Olfactory input from plant volatiles and surface waxes may be especially important in this process. Colonization of novel host plants by regional populations of beetles has involved expansion of feeding preference. However, the fact that Maryland beetles rank their regional host (tomato) last of the four species tested, suggests adaptation to new plants may evolve relatively slowly, perhaps due to the complexity of mechanisms controlling host choice behaviour. This possibility is discussed in Chapter four.

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[3] Gene flow between the southern U.S. where *S. rostratum* occurs and the three regions sampled in this study is expected to be low. Large, dispersing populations of this insect develop only on agricultural crops.

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# III. Effects of solanaceous alkaloids on plant sampling and feeding behaviour by adult Colorado potato beetles

## Introduction

Secondary plant compounds are a diverse group of chemicals common to all vascular plants. Individual plant families, genera, or even species may be characterized by their own unique complement of these compounds (Robinson 1980, Harborne and Turner 1984). For example, Cruciferae contain mustard oil glycosides while the Solanaceae are known for their various alkaloids. Typically bitter tasting to humans, many secondary compounds are toxic or interfere with digestion in herbivores (see Rosenthal and Janzen 1979) and many act as feeding deterrents. However, others (especially the mustard oil glycosides) are known feeding stimulants for certain oligophagous insects (see Dethier 1982).

Current theory states that host specificity in plant feeding insects (and ultimately patterns of insect-plant evolution) is based on the defensive properties of secondary compounds which limit the number of plant species a given insect can use (Fraenkel 1959, Ehrlich and Raven 1964, Feeny 1975). Some authors have envisaged an evolutionary "arms-race", with plants adapting to herbivore selection pressure by developing new forms of toxic compounds, and insects counter-adapting physiologically through improved detoxification abilities, or behaviourally by evolving sensory recognition of the new compounds to aid them in identifying plants.

More recently, active roles in plant metabolism have been discovered for most secondary compounds investigated, and their function in terms of plant defense has been questioned (Robinson 1974, Seigler and Price 1976, Jones 1979). In addition, a new consensus is developing (following Jermy 1976) that insects have rarely coevolved with plants in a reciprocal gene-for-gene sense, but rather have adapted to existing plant chemistry which itself has evolved (and is evolving) in response to a multitude of selection pressures including non-insect herbivores and invading microorganisms (see Futuyma 1983). Nevertheless, there is ample evidence that secondary compounds are a factor, if not always the dominant one, in shaping patterns of host plant use by phytophagous insects.

Especially interesting in terms of insect behaviour are those plant chemicals that may act directly on the sensory system. Research in this area was stimulated by the discovery that certain mustard-oil glycosides in the Cruciferae act as strong feeding attractants for the cabbage butterfly *Pieris rapae* (Verschaffelt 1910). Since then the role of secondary compounds (both as stimulants and deterrents) have been predominant in theories of host plant recognition by insects (Fraenkel 1959, Dethier 1970, 1982, Schoonhoven 1982).

Studies on the Colorado beetle, *L. decemlineata* (Say), have played an important part in the development of these ideas. Early studies with this insect concentrated on demonstrating negative effects on larval fitness from the ingestion of alkaloids derived from marginal hosts or non-host plants (see Lipke and Fraenkel 1961, Hsiao 1974 for summaries of the early literature). Also, experiments with *L. decemlineata* adults demonstrated some reduction in feeding on natural plants with the addition of the tomato alkaloid tomatine (Stürckow and Löw 1961, Bongers 1970). None of the these studies directly investigated the mode of action of the alkaloids, yet in many of these papers and the reviews which followed (for example, Harborne 1982, Schoonhoven 1982), it is either implied, or explicitly stated, that the compounds exert their effects directly on the chemosensory system.

In the only direct electrophysiological investigation of this possibility, Stürckow (1959) reported that tarsal sensilla in *L. decemlineata* adults were more sensitive to tomatine than solanine (a potato derived alkaloid). However, in a recent re-investigation of this topic, Mitchell and Harrison (1985) discovered the bursting type "responses" reported by Stürckow were actually injury effects which only developed after long periods of contact with pure compounds. There was no evidence of alkaloid receptors on the tarsi or the galea, nor were there different sensitivities, in terms of injury, across alkaloids tested (including tomatine and solanine).

While the above study suggests alkaloids may not function at the sensory level in *L. decemlineata*, it is not conclusive. There are epipharyngeal sensilla in this insect which are not accessable with current electrophysiological techniques. In addition, more subtle effects on the gustatory system, including inhibition of stimulant compounds at the receptor sites, are possible (Schoonhoven 1982, Mitchell and Sutcliffe 1984).

The experiments reported in this paper were designed to test the hypothesis that solanaceous alkaloids act as sensory inhibitors of feeding in *L. decemlineata* adults. Using videotape, direct observations were made on the beetles' behaviour during pre-ingestive sampling and first meal feeding on plants treated with alkaloids. It has previously been demonstrated that sampling of plant fluids ("gustatory sampling") by *L. decemlineata* beetles increases on plants less preferred for feeding (see Chapter 2). My objective in this study was to determine whether any reduction in feeding on alkaloid treated leaves was associated with similar changes in gustatory sampling behaviour; thereby demonstrating effects by the compounds at the sensory level.

## Materials and Methods

Insects used in these experiments were collected in the field and reared in the laboratory on their respective regional host plants (see Chapter 1, Study organisms). All were first day, naive (no feeding experience) adults. In a preliminary study of Alberta beetles feeding on potato, first meal size of females (mean=27 $mm^2$ SD=12.0, n=10), and males (mean=20 $mm^2$, SD=9.0, n=9) did not differ significantly (Kruskall-Wallis test H=1.74, d.f.=1, $p>0.10$). Therefore, both males and females were used and assigned randomly (sexes are indistinguishable by eye) to treatment groups.

Plant sampling and feeding behaviour was recorded for each insect individually using an apparatus designed to allow videotape monitoring of behaviour (see Chapter 2, for details). Beetles were allowed free access to a leaf until three minutes without feeding elapsed. This period was previously determined by observation as a minimum inter-meal interval time for this insect. Leaf area consumed was measured using a Licor Area Meter, Model 3100 (accuracy = $1mm^2$).

Plant leaves were treated chemically by passive transpiration. Leaf petioles were cut with a sharp razor blade, weighed, emersed in a narrow test tube containing the alkaloid solution, and sealed with Parafilm. Since alkaloids are non-volatile they accumulate in the leaf as transpiration occurs. From a knowledge of the percent water content of leaves, (Appendix III) and the concentration of the test solution, I was able to determine the approximate concentration of alkaloid accumulating in a leaf by weight loss of the solution in the test tube. Control leaves were placed in deionized water for a comparable length of time as treated leaves before being used. Throughout the course of the experiments, control and treatment leaves were interspersed randomly in time. All alkaloids used were obtained from Sigma Chemical Co.

To determine whether alkaloids were being distributed throughout the leaf and accumulating at the desired concentration, I conducted two tests. In the first, leaf petioles were placed in a water soluble flourescent dye and at periodic intervals photographed under UV light (which illuminated the dye in the leaf). After fifteen minutes, dye was visible throughout most of the leaf. Since treatment of plants with alkaloids took at least two hours, I am confident that test solutions were distributed evenly within the leaves.

In a second test, I attempted to directly measure the total glycoalkaloid content (TGA) of a group of alkaloid treated leaves. However, problems with the technique used (Fitzpatrick and Osman 1974, Fitzpatrick et al. 1978) when high concentrations of alkaloid were present (a precipitate formed in a separation phase) resulted in a TGA value of only 70% of that predicted. Since the time this test was carried out, Coxon (1984) has reviewed several studies that tested Fitzpatrick and Osman's technique and found recovery rates of standards highly variable and ranging from 46% to 78%. Given a minimum 22% loss, my analysis of treated leaves therefore accounted for at least (70 + 22) = 92% of the predicted alkaloid content.

In order to treat leaves to a desired TGA level, I also measured the resident glycoalkaloid levels in the three *Solanum* species used in these experiments (Appendix III). Levels of glycoalkaloid in *L. esculentum* were approximated by using values reported by Sinden et al. (1978).

Using the methods described above, three experiments were performed, each using a different insect population and plant combination.

**Experiment 1**

In this experiment I asked whether the initial rejection of *S. tuberosum* by Arizona beetles (see Chapter 2) was due in part to the presence of solanine in the leaves of this plant. A concentration of 1 mM solanine (at least twice the normal level found in potato) was infused into *S. elaeagnifolium* leaves and tested on seven beetles. An equal number were also tested on control leaves treated with distilled water. *S. elaeagnifolium* is the natural host of beetles in Arizona.

**Experiment 2**

This experiment served as a direct test of the hypothesis that reduced feeding on *L. esculentum* is caused by the alkaloid tomatine acting as a sensory deterrent. A total of twenty Maryland beetles were tested with either 2mM tomatine or water treated *L. esculentum* leaves. In this experiment the background level of positive stimulus input from the tomato leaves was presumably much lower than that from a primary host plant (Maryland beetles ranked *L. esculentum* fourth of four plants tested in Chapter 2). Since the control of food intake is thought to result from the balance of positive and negative stimulus input, any sensory based inhibition due to tomatine should have been readily detected.

### Experiment 3

This study was designed to investigate the comparative effects of three alkaloids within a single beetle population. In addition to a control group, twelve Alberta beetles were individually videotape [illegible] potato (*S. tuberosum*) leaves treated with a 2mM solution of solanine, tomatine, or atropine. Atropine is a tropane alkaloid with a different molecular structure than the steroidal alkaloids tomatine and solanine (Robinson 1980). Tropane alkaloids are common in several Solanaceae genera such as *Atropa* and *Datura* (Evans 1979) which are not hosts of *L. decemlineata*.

## Results

### Experiment 1

Sampling and feeding behaviour by Arizona beetles did not change with the addition of 1mM solanine to their regional host plant *S. elaeagnifolium* (Table 3.1). This alkaloid concentration represents twice that normally found in potato (which the insects largely reject) and several times the amount estimated in their regional host *S. elaeagnifolium*.

### Experiment 2

Increasing the existing tomatine content in *L. esculentum* leaves by 2mM to yield an estimated TGA level of 2.5mM had no detectable effect on the behaviour of Maryland beetles (Table 3.2). Having one beetle reject a tomatine treated leaf was not unusual since one-third of the beetles tested on untreated leaves in an earlier experiment (Chapter 2) did the same. The slight reduction in feeding on tomatine treated leaves was not significant and there were no consistent trends in other variables measured.

**Table 3.1.** First meal feeding and associated sampling behaviours by beetles from Arizona tested on *S.elaeagnifolium* leaves treated with 1mM solanine or water (control). Values given are means±standard errors or medians, range. N=7 per treatment.

| | | FEEDING | | | SAMPLING | | |
|---|---|---|---|---|---|---|---|
| Treatment | #Reject | Amount ($\text{mm}^2$) | Rate ($\text{mm}^2$/min) | #Sites | Exp(s) | GS(s) | #GS Sites |
| Control | 0 | 21±3.8 | 2.4±.40 | 1.0,1-2 | 2.3±.63 | 3.3±.42 | 1.0,1-2 |
| Solanine | 0 | 24±2.4 | 2.8±.29 | 1.0,1-1 | 2.7±.27 | 2.6±.52 | 1.0,1-1 |
| | | F=0.54<br>df=1,12<br>NS | F=0.62<br>df=1,12<br>NS | | F=0.17<br>df=1,12<br>NS | F=1.06<br>df=1,12<br>NS | |

Exp=duration *exploring* on leaf surface prior to first GS
GS=duration of first *gustatory sampling* event prior to feeding

**Table 3.2.** First meal feeding and associated sampling behaviours by beetles from Maryland tested on tomato leaves treated with 2mM tomatine or water (control). Values given are means±standard errors or medians, range. N=10 per treatment.

| | | FEEDING | | | SAMPLING[1] | | |
|---|---|---|---|---|---|---|---|
| Treatment | #Reject | Amount (mm²) | Rate (mm²/min) | #Sites | Exp(s) | GS(s) | #GS Sites |
| Control | 0 | 18±6.2 | 4.6±.73 | 1.0, 1-2 | 1.8±.26 | 7.5±1.6 | 1.0, 1-3 |
| Tomatine | 1 | 13±3.5 | 6.2±.81 | 1.0,0-3 | 3.7±.85 | 5.8±1.1 | 1.0, 1-2 |
| | G=1.44<br>df=1<br>NS | F=0.41<br>df=1,17<br>NS | F=2.09<br>df=1,16<br>NS | | F=4.01<br>df=1,17<br>NS | F=0.75<br>df=1,17<br>NS | |

[1] Abbreviations as in Table 3.1

## Experiment 3

The addition of alkaloids to *S. tuberosum* leaves increased variability of meal size among Alberta beetles (Levene's equal variance test, F=2.97, d.f.=3, 36; P=0.045) but not overall food consumption (Table 3.3). Relative to controls, atropine had the most pronounced effect on feeding behaviour as four of the ten animals tested did not feed (likelihood-ratio test G=12.5, d.f.=3, P<0.01).

Within group variability in pre-feed gustatory sampling increased with the addition of alkaloids (Levene's equal variance test, F=9.55; d.f.=3, 36; P<0.0001). When variances were equalized among treatment groups using square root transformation, ANOVA yielded a significant effect on gustatory sampling (F=4.29; d.f.=1, 36; P=0.01). However, only atropine treated leaves (F=7.94, d.f.=1, P<0.01 using experiment wise error rate) and not tomatine treated leaves (F= .177, d.f.=1, NS) differed from the control group. Not shown in Table 3.3 is the difference in gustatory sampling time between non-feeders (mean=11.2s) and feeders (mean=6.7s) in the atropine treatment group.

Both the number of sampling and feeding sites tended to increase with the addition of foreign alkaloids, a pattern similar to that observed with feeding behaviour on marginal host plants (see Chapter 2).

## Discussion

The purpose of this investigation was to determine whether solanaceous alkaloids added to plants would induce a sensory-based reduction of feeding in *L. decemlineata* adults. Detailed behavioural analysis of plant sampling and feeding behaviour provide no evidence for such inhibitory effects for the steroidal glycoalkaloids tomatine and solanine, but reveal a clear effect due to the tropane alkaloid atropine.

It has often been implied in the literature that resistance of *L. esculentum* to *L. decemlineata* is due to the action of tomatine on the insect's sensory system (see Bongers 1970, Schoonhoven 1982). However, in the present experiments, increasing the tomatine

**Table 3.3.** First meal feeding and associated sampling behaviours by beetles from Alberta tested with alkaloid treated potato leaves (concn.=2mM). Sampling data include both feeders and non-feeders if present in treatment group. Values given are means±standard errors or medians, range. N=10 per teatment.

| | | FEEDING | | | SAMPLING[1] | | |
|---|---|---|---|---|---|---|---|
| Treatment | #Reject | Amount ($mm^2$) | Rate ($mm^2$/min) | #Sites | Exp(s) | GS(s) | #GS Sites |
| Control | 0 | 31±2.2 | 6.2±.71 | 1.0, 1-4 | 3.3±.62 | 3.2±.41 | 1.0, 1-5 |
| Solanine | 0 | 37±5.2 | 6.0±.75 | 2.0, 1-3 | 3.6±.50 | 2.8±.65 | 1.0, 1-2 |
| Tomatine | 0 | 31±4.8 | 5.8±.49 | 1.5, 1-2 | 3.3±.59 | 4.1±1.04 | 2.0, 1-5 |
| Atropine | 4 | 31±6.1 | 3.9±.61 | 3.5, 1-4 | 3.5±.47 | 8.4±1.95 | 4.0, 1-8 |
| | G=12.5**<br>df=3 | F=0.45<br>df=3,32<br>NS | F=1.83<br>df=3,32<br>NS | G=5.80<br>df=3<br>NS | F=0.06<br>df=3,34<br>NS | F=4.29*[2]<br>df=3,36 | G=11.6**<br>df=3 |

[1] Abbreviations as in Table 3.1.

[2] after square root transformation

* $p<0.05$, ** $p<0.01$

concentration to levels characteristic of "resistant" tomato varieties (Sinden et al. 1978) had no significant effect on the beetles' behaviour that would indicate a chemosensory based mode of action for the alkaloid. The reduced feeding previously reported from long-term experiments with this compound may have been due to post-ingestive effects (e.g., anorexia or intoxication).

Atropine is a non-steroidal alkaloid found in several solanaceous plants not used as hosts by *L. decemlineata*. Kogan (1976) has suggested *L. decemlineata* may be physiologically adapted to steroidal alkaloids but not to tropane alkaloids, thereby allowing expansion of the species' host range to include tomato but not to include *Datura* or *Atropa* species. The strong inhibition of feeding due to atropine tends to support this hypothesis. However, the results must be interpreted with caution. Atropine is not normally found in high concentrations in solanaceous plants. Hyoscyamine, the dominant tropane alkaloid in many *Datura* species, is found in leaves up to 0.4% dry weight, or approximately 1.5mM (Avery et al. 1959). However, this concentration is somewhat less than that used in my experiment.

Also, beetles may reject plants on the basis of olfactory input before proceeding to the gustatory sampling stage where alkaloids are first contacted. Therefore, testing a foreign alkaloid in a primary host may lead to erroneous conclusions. My own results (see Chapter 2) and those of Visser and Ave (1978) have shown that *L. decemlineata* adults are capable of fine, olfactory-based discrimination of plants. Thus, beetles may not be attracted to plants containing tropane alkaloids in the field, and if they do contact them, the beetles may not sample the plant fluids.

For several reasons, interpreting the evidence for secondary plant compounds acting as behavioural deterrents is difficult based on present data (reviews by Chapman 1974, Schoonhoven 1982, and several chapters in Rothensal and Janzen 1979). First, both electrophysiological and behavioural studies have relied largely on the use of pure chemicals tested out of context with natural plant stimuli. Feeding bioassays typically use secondary compounds incorporated into artificial diets or media such as filter paper with perhaps only one feeding stimulant present. For example, Bernays and Chapman (1977) tested over one-hundred secondary compounds for their effects on feeding in *Locusata migratoria* by incorporating the chemicals in wheat flour discs. As Dethier (1977) has noted, these experiments by design tend to overemphasize the importance of the compound in question because most of the positive sensory input used by the insect to recognize plants is removed. In the above-mentioned study, the authors actually provide data showing that the addition of a single positive stimulus (sugar) to a wafer containing one of their most effective deterrents (tomatine) completely neutralized the feeding inhibition, yet the authors go on to conclude that "the failure to eat most plants results from the presence of one or more chemicals in amounts which inhibit feeding."

Second, most experiments have been conducted on the larval stage, yet it is adults who usually do the host selecting in holometabolous insects. Larvae are generally poorly equipped to seek out new hosts and are therefore usually less discriminating in their feeding. Studies demonstrating negative effects on larval fitness due to secondary compounds may be valid in their own right; however these results should not be intepreted in terms of host selection processes.

Third, many of the compounds which are tested on insects come from plant families never used, or perhaps never even encountered, by the insects in nature. Since those insect species which have been carefully studied are capable of discriminating among plants on the basis of other sensory modalities (vision, smell) in addition to taste (see Chapter 2), the relevance of these kinds of experiments must be questioned.

'Wherever possible, future studies using secondary plant compounds should use the insect's natural plant as the feeding substrate; this will avoid biasing the experiments in favor of positive results. Also, ecologically relevant combinations of plants and compounds should be used if results are going to be interpreted in terms of host selection mechanisms and evolutionary processes. The results of the present study suggest the role of alkaloids in affecting host choice in *L. decemlineata* has been overemphasized by the nature of experimental methods used.

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# IV. Regional differences in host plant preference in the Colorado potato beetle and the role of behaviour in insect-plant evolution

## Introduction

Many wide ranging species of herbivorous insects are actually composed of regional populations of dietary specialists variously refered to as biotypes, ecotypes or host races.[4] Populations may become geographically isolated on one host plant, and subsequently evolve as obligate monophages; but, species may also develop regional differences in host use where there is no apparent restriction in plant availability (Gilbert 1979, Cates 1981). The adaptive response of a host-adapted race may be physiological, resulting in increased larval digestive efficiency (Rausher 1982, Scriber 1983), or behavioural, leading to altered oviposition preference (Singer 1971, Tabashnik et al. 1981, Jaenike and Grimaldi 1983) or both.

Studies of host-adapted populations of insect herbivores have been prominent in the evolutionary literature for over a century (Walsh 1864, Thorpe 1930, Mayr 1942, Dethier 1954, White 1978). Recently, a number of authors have claimed to document sympatric host race formation and speciation in herbivorous insects (Bush 1975, review by Strong et al. 1984) and have challenged the traditional view of allopatric speciation via geographically isolated populations (Mayr 1963, Dobzhansky 1970, Futuyma and Mayer 1980). Despite their theoretical importance, however, there have been relatively few detailed studies of the properties of insects that facilitate host plant specialization.

Inadvertently, human agricultural practices have given us an opportunity for studying evolutionary interactions between insects and plants in the field. Rapid colonization of introduced crops has been documented for a variety of insects (see reviews by Price and Waldbauer 1982, Gould 1983). A well known example is the Colorado Potato Beetle *L. decemlineata*. Once confined to the western United States and Mexico where it fed primarily on buffalo bur, *Solanum rostratum*, *L. decemlineata* colonized the potato plant (*S.*

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[4] I will follow recent convention and restrict use of the term "host race" to sympatric populations of host adapted insects (Jaenike 1981).

*tuberosum*) soon after the plant was introduced to the United States, and later dispersed throughout most of North America and Europe with the expansion of potato agriculture (see Tower 1906, and Johnson 1969, for historical summaries). *L. decemlineata* is now reported to use a number of native and introduced plants as hosts, most in the family Solanaceae.

Hsiao (1978) has studied larval adaptations of several geographic populations of *L. decemlineata* in North America, and found local specialization (probably in digestive efficiency) where populations are isolated largely on one plant; for example in Arizona where *S. elaeagnifolium* is the only available host plant. In this study, I report on regional differences in feeding behaviour by adults of the same species from three North American populations in different states of evolutionary transition with respect to host plant use (see Chapter 1).

Adult food choice is often ignored as a factor in insect-plant evolution, with emphasis instead being placed on female oviposition behaviour, larval feeding behaviour and larval digestive physiology. Yet, like many other holometabolous insects, *L.decemlineata* adults require a period of feeding on a suitable host both for the development of ovaries (deWilde and deLoof 1973) and wing muscles (see reviews by Johnson 1969, 1974). Subsequent migration or dispersal may occur, but only by females with incompletely developed ovaries (gravid females do not fly) which then undergo a period of maturation feeding prior to egg-laying. For these species, the distribution of females on plants, and therefore their oviposition sites, is directed largely by adult food choice.

Laboratory oviposition studies have shown that *L. decemlineata* females lay large numbers of eggs on non-host plants that are toxic to developing larvae (Bongers 1970, Hsiao and Fraenkel 1968). However, these studies are probably meaningless, since having no food preference for these plants, the ovipositing female will not normally settle on these plants in nature. Bongers (1970, p.63) concludes "... oviposition normally will occur on the preferred food plant on which the females complete their maturation feeding. It is, therefore not to be expected that oviposition preference will interfere with food preference". In fact, *L.decemlineata* may not have an "oviposition preference" at all in terms of a discrete behavioural mechanism; eggs are simply deposited where the gravid female settles to feed.

In this paper, adult feeding preference will be considered crucial in determining patterns of host plant use by *L. decemlineata*. New data on regional differences in feeding behaviour are reported and discussed in relation to a wealth of information currently available for this species. Specifically, I compare and contrast the evolutionary response of larval fitness (physiological) and adult behavioural (host selection) characteristics and assess the relative contributions of each in facilitating the host range expansion that has occurred in this insect.

It has been suggested by Futuyma (1983) that genetically labile host selection behaviour may be responsible for mediating rapid host shifts in phytophagous insects. However, I conclude that for *L. decemlineata*, colonization of new hosts has been aided by the broad physiological tolerances of the larvae and their rapid evolutionary response to new host use. Adult feeding behaviour, rather than promoting host transfers, appears to act as a conservative force in the absence of ecological constraints on primary host availability. Previous studies are reviewed which support this conclusion for severa[illegible]ther species of insect herbivores.

## Materials and Methods

Insects used in this experiment were collected in the field and reared in the laboratory on their respective regional host plant (see Chapter 1, Study organisms). All were first day, naive (no feeding experience) ad[illegible]

Feeding behaviour was [illegible]ed from a total of one-hundred and forty-four beetles, forty-eight from each geographic population. From these, an equal number were randomly assigned to each of four plant groups, *S. tuberosum* ("Norland" variety), *S. rostratum*, *S. elaeagnifolium*, or *L. esculentum* ("Earliana" variety).

Each insect was tested individually with a separate leaf using a simple apparatus designed to allow videotape monitoring of behavioural events associated with feeding (see Chapter 2 for details). Beetles were allowed free access to a leaf until three minutes without feeding elapsed. This period was previously determined as a minimum inter-meal interval time for this insect. Therefore, unlike conventional studies, this experiment was designed to measure only first meal consumption to avoid possible long term effects on feeding from induction of food preference. However, what I have defined as first feeding bouts are actually quite long feeding episodes that may take over thirty minutes to complete. This is ample time for sensory mechanisms regulating food intake to operate.

Further details of the methods used in this experiment are given in Chapter 2.

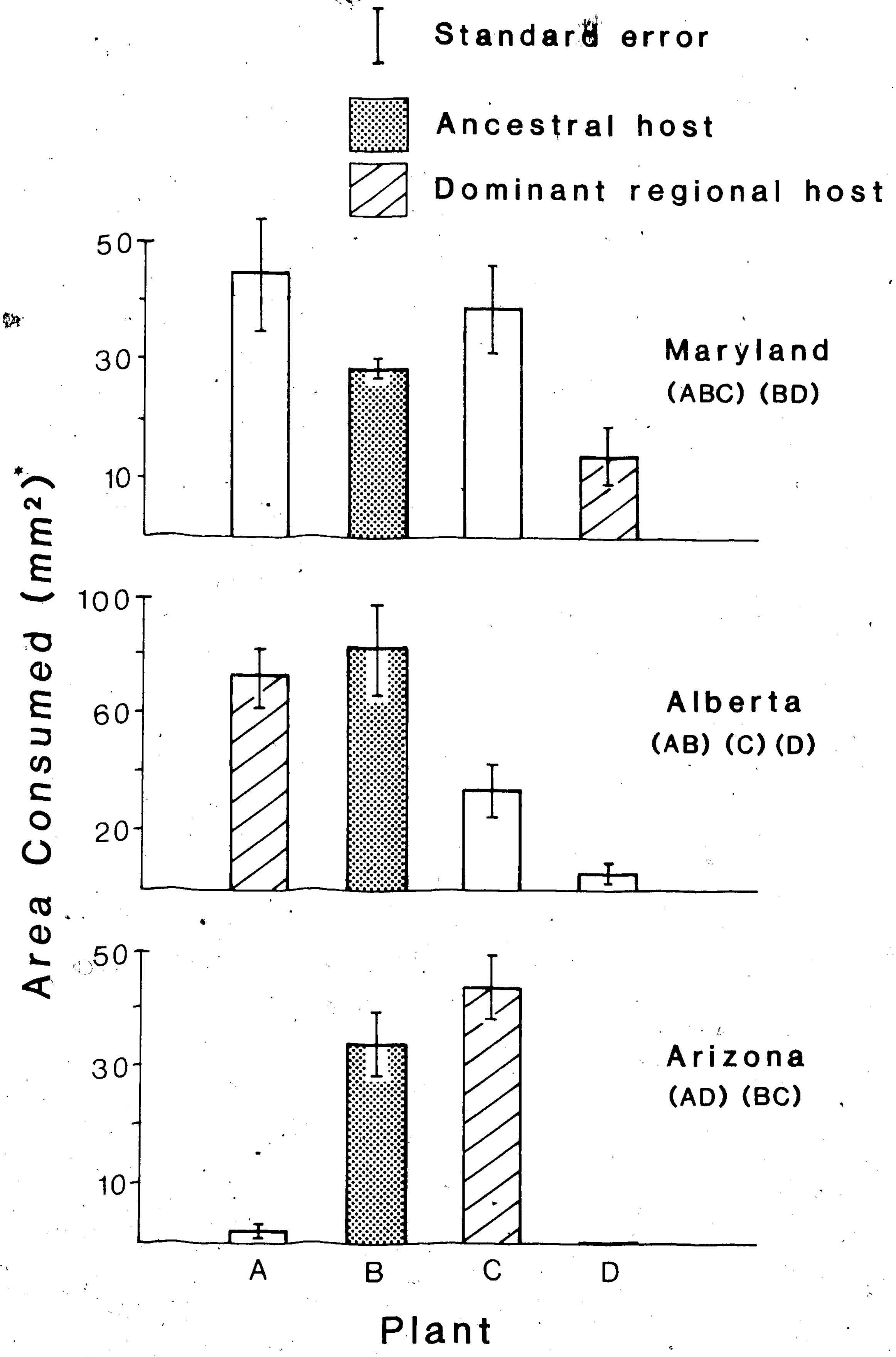
### Statistical analysis

This experiment was originally outlined as a two-way factorial design (Population X Plant). However, analysis of the feeding rates of each population (reported in Chapter 2) revealed inherent differences in feeding under laboratory conditions regardless of plant type (Alberta beetles fed on average twice as fast and consumed approximately twice as much as beetles from Arizona and Maryland). Therefore, between population comparisons of food consumption were abandoned, and each population was treated separately for within group differences by Kruskal-Wallis tests and non-parametric multiple comparisons (Conover 1980). Between population comparisons of rejection and acceptance patterns, which should not have been affected by a differential response to laboratory conditions, were treated by contingency table analysis.

### Results

Patterns of host plant acceptance and first meal consumption varied considerably among the three geographic *L. decemlineata* populations (Fig 4.1). Only *S. rostratum*, the ancestral host, was accepted for feeding by all beetles regardless of their origin. Beetles from

Figure 4.1. First meal consumption by naive, first-day beetles from three geographic populations. Means enclosed by parenthesis are not significantly different at $p=0.05$. Plant A = *S. tuberosum* (potato); B = *S. rostratum*; C = *S. elaeagnifolium*; D = *L. esculentum* (tomato). N=48 per population. *Area corrected for differences in leaf thickness.


Standard error
Ancestral host
Dominant regional host
Area Consumed (mm²)*
50
30
10
Maryland
(ABC) (BD)
100
60
20
Alberta
(AB) (C) (D)
50
30
10
Arizona
(AD) (BC)
A
B
C
D
Plant

Arizona preferred *S. rostratum* and their regional host plant *S. elaeagnifolium* to *S. tuberosum* and *L. esculentum* (H=38.1, d.f.=3, $P<0.001$) which were largely rejected (only two of twelve beetles fed on potato, while one nibbled briefly on tomato). Similarly, the Alberta population prefered *S. rostratum* and their most abundant regional host *S. tuberosum* to *S. elaeagnifolium* which in turn was eaten more than *L. esculentum* (H=21.1, d.f.=3, $P<0.01$).

Despite being reared on *L. esculentum* as larvae, fewer adult beetles from Maryland fed on this plant than the two preferred hosts *S. tuberosum* and *S. elaeagnifolium* ($X^2=4.8$, d.f.=1, $P<0.05$), resulting in significantly lower food consumption (H=10.9, d.f.=3, $P<0.05$). Feeding on *S. rostratum* by Maryland beetles was intermediate, and did not differ statistically from any other plant by pair-wise comparisons.

## Discussion

The comparative analysis of feeding using naive adult beetles from several geographic populations provides a clear example of regional differences in host preference with an apparent genetic basis. With regard to evolution of host choice in *L. decemlineata*, there are three important points to be derived from this study: (1) Initial host acceptance by adults is relatively conservative or "fine-tuned". The almost total rejection of *S. tuberosum* by Arizona beetles was unexpected given the close taxonomic affinity of this plant to both *S. elaeagnifolium* and *S. rostratum* within the genus *Solanum* (Whalen 1979, and references therein). (2) Colonization of a new host has not been associated with absolute shifts in feeding preference. Instead, new plants are added to the insects' repertoire of acceptable species as populations evolve in association with them. Thus *S. rostratum*, the ancestral host, is still preferred by more recently evolved populations which have not used the plant locally for at least one-hundred and fifty generations (see Chapter 1). (3) There may be a lag time in the evolution of behavioural mechanism(s) regulating acceptance of novel hosts. Although this insect has recently reached "pest" status on *L. esculentum* in Maryland, beetles from that area ranked the plant fourth of the four solanaceous hosts tested in this study. One-third of the beetles rejected the plant outright on first contact.

The implication of these observations is that constraints on the availability of primary hosts should be crucial in allowing colonization of new plants. If that is true, one would not predict multiple host use and population differentiation in areas where the ancestral host is common. My own observations and those of Neck (1983) and Hsiao (1978) in the Southwestern United States confirm this prediction. *L. decemlineata* has been recorded from this area for several hundred years (Tower 1906) and *S. rostratum* is still the most frequently used host plant by far, despite the local presence of several *Solanum* species, including *S. elaeagnifolium*. Directional selection for new host use has only been effective in this species at the periphery of its range where some degree of isolation on one plant (Arizona) or one very dominant local plant (Maryland, Alberta) has existed. Under these allopatric conditions, conservative host selection behaviour by adults has not prevented colonization events simply because there has been no choice available but to use the marginal plant.

### The role of behaviour in insect-plant evolution

Distinctions are often made in the literature between larval fitness traits (metabolic efficiency) and adult host selection characteristics (usually oviposition) with respect to their relative contributions in promoting phytophagous insect diversity. Some authors downplay the role of physiological specialization and argue that genetically labile behavioural mechanisms promote insect diversity by mediating rapid host shifts (for example, see Futuyma 1983, Futuyma et al. 1984).

The data for *L. decemlineata* do not support this hypothesis. While complete acceptance of *L. esculentum* by Maryland beetles has not yet evolved (see above), larvae reared in the laboratory on this plant show no apparent increase in mortality or protracted development time (Harrison, unpublished data). In addition, Hsiao (1978) has demonstrated that larvae from populations in Arizona and Utah (equivalent to the Alberta insects used in this study) are physiologically more efficient on their regional hosts than other plants (including *S. rostratum*), whereas adults from these populations show no corresponding degree of behavioural preference for their new hosts. Colonization of novel plants by *L. decemlineata* appears to first involve physiological adaptation (which may lead to physiological specialization) followed in time by the evolution of behavioural mechanisms regulating host selection in adults.

Is this scenario for *L. decemlineata* evolution a special case, or is it true for other phytophagous insect species? Table 4.1 lists all the examples I could find for which both larval fitness and adult host selection trai[illegible]ave been studied within the same species of sexually reproducing insect. A similar table, including many examples of parthenogenetic species of crop pests, was compiled recently by Gould (1983, pp. 627-630). Note that with the exception of Wasserman and Futuyma (1981) (who used an insect that was reared in the laboratory for 300 generations and who did not measure oviposition directly) there are no examples (nor are there in Gould's table) where genetic differentiation of behavioural traits have evolved independently of metabolic changes. There are, however, several examples where metabolic efficiency for a new host has evolved without a concomitant change in oviposition or feeding behaviour, including those species in which the characters were measured soon after the host shift ocurred (i.e. *C. philodice*, *M. destructor*, and *L. decemlineata*).

On theoretical grounds, these results are not suprising. A related question to how much genetic variability is resident within populations for a given trait, is how complex the traits are in terms of their organization. Phytophagous insects are infamous for their abilities to rapidly adapt (physiologically) to resistant crop strains (Maxwell and Jennings 1980) and to insecticides (Georghiou and Saito 1983) and some of these adaptations have been traced to single gene effects (see Gould 1983). In contrast, a new consensus is developing that mechanisms underlying host selection processes in insects are not simple, but complex and interactive (see Chapter Two). This complexity might account for the relatively

**Table 4.1.** *Comparison of between population variability in behavioural and physiological traits with a reported genetic* basis. Included are studies in which both types of characteristics have been measured on the same sexually reproducing insect species.

| | | Characters measured and genetic variability found? (Yes/No) | | |
|---|---|---|---|---|
| Insect | Hosts tested | Behavioural | Physiological | Reference |
| Colias philodice<br>(Lepidoptera) | *wild and domestic*<br>Leguminosae | oviposition<br>preference (No) | larval Gr,DT,Sv (Yes)<br>larval PW (No) | Tabashnik (1983) |
| Euphydryas editha<br>(Lepidoptera) | Scrophulariaceae<br>Plantaginaceae | oviposition<br>preference (Yes) | larval Gr,GE,Sv (Yes) | Singer (1971),<br>Rausher (1982) |
| Deloyala guttata<br>(Coleoptera) | Convolvulaceae | oviposition<br>preference (No) | larval DT,PW (No)<br>*fecundity (Yes)* | Rausher (1983),<br>*Rausher (1984)* |
| Mayetiola destructor<br>(Diptera) | varieties of wheat | oviposition<br>preference (No) | larval Sv (Yes) | review by<br>Gould (1983) |
| C. maculatus<br>(Coleoptera) | azuki beans,<br>pigeon peas | oviposition<br>preference (Yes)[1] | larval DT,Sv (No) | Wasserman and<br>Futuyma (1981) |
| L. decemlineata<br>(Coleoptera) | wild and domestic<br>Solanaceae | adult feeding<br>preference (Y/N)[2] | larval PW,Sv (Yes) | Hsiao (1978),<br>this study |

DT=development time; GE=growth efficiency; Gr=growth; PW=pupal weight; Sv=survivorship

[1] measured indirectly as part of a complex trait called "realized fecundity/oviposition preference"

[2] Three populations tested:two have evolved feeding preference to match ancestral host, a third has not; however, anecdotal evidence suggests larvae from this population are physiologically adapted.

slow evolution of behavioural traits indicated by present data.

One of the basic assumptions of theories of sympatric speciation is that simple genetic changes can mediate rapid changes in host preference (see Bush 1975). This assumption may have been influenced by the conventional belief that mechanisms of host recognition in insects are simple, and by the traditional view that shifts into new adaptive zones or niches are initiated by behaviour (Mayr 1963). With regard to insect-plant evolution, both these premises deserve re-evaluation. First, as stated above, there is growing evidence that mechanisms underlying host choice in insects are complex, and relatively slow to respond to evolutionary changes in host use. There is no convincing example in the literature of a gene mutation spontaneously giving rise to a new population of host-adapted genotypes. This does not mean that such an event is impossible, but it has yet to be demonstrated.

Second, the idea that changes in behaviour ultimately drive colonization events (see Futuyma 1983, Parsons 1983) perhaps has been applied too loosely to phytophagous insects. The majority of these insects can rightly be considered parasitic (Price 1980), and most are highly specialized in terms of their physiological adaptation to plants (see Introduction). Unlike non-parasitic organisms whose foraging tactics may uncover new resources or habitats, changes in host (i.e. habitat) use by insects may result in a significant loss of fitness through decreased fecundity or larval mortality. Therefore, if other factors are not considered, evolutionary theory would predict selection against, not for, lability of host selection behaviour.

A reconsideration of the role of behaviour as potentially representing a conservative force in insect-plant evolution affects the way we percieve causation in these systems. Frequent references in the literature to behavioural changes initiating, or causing host shifts implies a role for behaviour not substantiated by present data. Fox and Morrow (1981) have warned that host plant specialization may not be an inherent property of insects, but may be imposed by a complex of ecological factors in the insects' local environment including microclimate, variable host phenology, presence of predators, parasites, and so on. If there are "causes" of host specialization and host shifts in phytophagous insects, they may lie in the varied nature of these selection regimes, as well as in properties intrinsic to the organisms.

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## V. Concluding Discussion

In a recent review of the mechanisms of host plant recognition in insects, Dethier (1982) warned that much of the evidence supporting a dominant role for secondary plant compounds was correlative. Stressing the need for demonstrating causal relationships, the author noted "Since the acceptance or rejection of a plant depends in the final analysis on the ability of the herbivore to assess some characteristics of the plant, the fundamental question is whether the compounds under discussion affect individual behavior in any way."

In this study, I used an analysis of individual insect behaviour to investigate the sensory basis of host recognition in adult Colorado potato beetles, *L. decemlineata*. The results indicate that these beetles are capable of graded discrimination of potential host plants, perhaps based on their total "Gestalt" or flavour. Moreover, variable acceptance of plants among regional populations of insects is not related to the presence of glycoalkaloids acting as feeding deterrents. For this species, it appears that the primary constraint on host acceptability is set by the beetles' finely tuned sensory system which functions independent of secondary plant compounds.

For this reason, it is unlikely that non-steroidal alkaloids (e.g. atropine) have been a major factor in preventing colonization of plants in more distant Solanaceae genera, since the beetles are probably not attracted to these plants in the field. Theoretically, if *L. decemlineata* were to continue with a host range expansion such that individual beetles developed generalist feeding habits, then certain plants containing behavioural deterrents would eventually undergo attempted colonization. However, it appears that regional populations of *L. decemlineata* are beginning to evolve behavioural specificity for their new hosts — a pattern typical of many phytophagous species. Within these differentiating populations, choice of plants will continue to be constrained by sensory systems tuned to the total chemical make-up of their hosts. This may effectively limit future host range expansion by *L. decemlineata* to plants with chemical profiles similar to those of *Solanum* species, except where agricultural practices induce selection for more distantly related plants (as in Maryland, on tomato).

Clearly, other factors are shaping behavioural specificity in *L. decemlineata* besides secondary plant compounds. Future research will be needed to determine how widespread this phenomenon is in plant feeding insects, but it is unlikely that *L. decemlineata* represents a special case. Most insects probably choose plants on the basis of complex patterns of sensory information gathered across several sensory modalities including smell, taste, and vision (Dethier 1982, Miller and Strickler 1984); an ability which endows them with the potential for perceiving, and responding to, subtle variations in plant quality. While many of these interactions involve secondary compounds, it is becoming clear that these chemicals rarely act as single, dominant factors in regulating host choice behaviour. Even among Cruciferae feeding insects, glucosinolates acting as stimulants are not entirely responsible for host discrimination as was originally supposed (Nielsen et al. 1979, Chew 1980, Feeny et al. 1983).

Perception of host plant quality based on variations in complex patterns of sensory stimuli is a fundamentally different concept than single compound, single neural pathway models (see Chapter two). The existence of an intervening control mechanism in the CNS which acts to integrate sensory input both within and across sensory modalities, and whose own state (and therefore outputs) is modifiable through ontogeny, has been almost totally ignored in classic input-output studies of insect feeding behaviour which treated the organism as a "black box" (see, for example, Blom 1978).

Attempts are now being made, however, to incorporate CNS mechanisms in models of host plant discrimination in insects. For example, Rausher (1983) has borrowed the sensory template concept originally developed to account for species-specific responses to auditory communications (Marler 1976, Hoy et al. 1977). But, sensory templates are assumed to represent precise neural networks in the brain which respond only to very specific patterns of sensory input. Application of this concept to plant perception by insects becomes awkward, because it leads to postulating separate templates for each individual plant species an insect might encounter. It is perhaps more economical (in terms of nervous system function) to think of a single CNS reference state (probably represented by neural networks) whose characteristics are determined genetically, but are modifiable by experience. Schoonhoven's (1977) analogy of a lock and key mechanism is useful in this context — the lock representing the CNS reference state and the key, patterns of sensory input. Individual insects that have broader acceptance thresholds for marginal host plants may have a "broadly tuned" lock and key mechanism. Selection for these animals within colonizing populations of insects may represent a first step in the evolution of new insect-plant associations.

At this time it is not clear how mechanisms underlying host selection behaviour affect the evolution of feeding preferences in insects. Current opinion seems to favour an active role for behaviour based on the assumption that it may be genetically labile (Bush 1975, Futuyma 1983, Futuyma et al. 1984). However, in this study I present evidence that indicates host selection behaviour may be a conservative trait in insect-plant evolution (see Chapter Four). Although data are limited, behavioural adaptations in some species appear to evolve slowly during colonization events; an observation that may be attributed to the complexity of the sensory systems involved (see above). Unfortunately, we know virtually nothing about the genetic basis of host selection in insects. But, it would be surprising if only single loci were involved, since even relatively simple behaviour patterns in animals usually have a polygenic basis (Frank 1974).

For insect species with conservative host selection behaviour, the importance of local selection pressures in maintaining altered patterns of host use over successive generations cannot be overstated. Phytophagous insects harbour considerable within population genetic variability for both physiological and behavioural traits related to host use (see review by Gould 1983, and recent papers by Jaenike and Grimaldi 1983, Via 1984). Therefore, all but strictly monophagous species are to some degree preadapted for feeding on other plant species. Directional selection for using these novel hosts will depend on the nature of local selection regimes (relative plant abundance, variable host phenology, microclimate, soil conditions and so on; see Fox and Morrow 1981) which can affect both the probability of ovipostion on a given plant and the viability of developing larvae.

During the recent host range expansion by *L. decemlineata*, some degree of isolation on a dominant regional host appears to have been critical in allowing local specialization to develop. Given strong enough selection pressures however, populations may diverge on different plants in close proximity and in spite of some gene flow (Ehrlich and Raven 1969, Endler 1977, Templeton 1981). The potential for ecological factors to interact in unique ways to affect patterns of host plant use by insects stresses the need for future studies to examine in detail the behaviour and ecology of individual species at the population level.

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# VI. Appendix I: Beetle cultures

Beetle larvae were reared in 6 liter glass aquaria containing approximately 2cm of gravel, covered by 8cm of loose sand. A glass tube inserted through the sand and into the gravel layer allowed adding water as needed to provide a moisture gradient for pupating larvae. Adult colonies were reared in larger (68 liter) aquaria prepared in a similar fashion. All insects were maintained at 16L:8D, 25°C ± 3° under a combination flourescent and incandescent light fixture.

Fresh food was provided as needed in the form of potted plants or leaves placed in water. Egg batches were collected from adult colonies and stored in petri dishes until they hatched. Typically, larvae were kept in these dishes with food before being transfered to aquaria at the second instar stage. At room temperature, larvae passed through four instars and pupated in about three weeks. Pupation time averaged seven to ten days.

By rotating larvae between two or more aquaria and timing the emergence of adults, beetles with no feeding experience as adults were available for experiments.

## VII. Appendix II: Plant growth conditions

Plants were grown year round in a heated, outdoor greenhouse. Daylength was maintained at a minimum of 16 hours using flourescent fixtures or Sonline high-intensity sodium lamps as supplemental lighting. Nightime temperatures were kept at about 15°C. Daytime temperatures in the greenhouse varied from 20°C to 30°C.

Potato plants ("Norland" variety) were grown from tubers seeded in a large bed. All other plants including tomato ("Earliana" variety) were grown from seed. Germination of *S. elaeagnifolium* and *S. rostratum* seeds (which possess a hard seed coat) was improved by soaking the seeds for twenty-four hours in 2000ppm gibberellic acid before planting. Standard soil mixtures were used for all plants. Plants were fed regularly (once a week in summer, once a month in winter) with 20-20-20 or 28-14-14 fertilizer.

Since one of the objectives of this study was to record sequences of insect behaviour on unaltered plants, no insecticides were used which might have left detectable residues on the plant surface. Greenhouse pests were controlled by pruning infested plants, washing them with water, or applying soap solutions. To remove any soap residue, plants were routinely washed with water before being used in experiments or as culture food.

## VIII. Appendix III: Total glycoalkaloid levels (TGA) and percent water content from leaves of four solanaceous host plants of *Leptinotarsa decemlineata*

| Plant | % Water[1] | TGA[2](mg/g dry wt) |
|---|---|---|
| S. tuberosum | 91 | 5.2 |
| S. rostratum | 84 | 0.53 |
| S. elaeagnifolium | 86 | 0.85 |
| L. esculentum | 88 | 7.8[3] |

[1] Calculated by subtracting dry weight from wet weight. Dry weight determined by oven drying ten leaves at 100°C for twenty-four hours.
[2] Following methods of Fitzpatrick and Osman (1974), and Fitzpatrick et al. (1978).
[3] from Sinden et al. (1978); flowering plants (60 days) grown under long days (16 hr).