

Oxford  
LINGUISTICS

# The TRANSITION to LANGUAGE

EDITED BY  
ALISON WRAY

STUDIES IN THE EVOLUTION OF LANGUAGE

# The Transition to Language

---

Edited by  
Alison Wray

**OXFORD**  
UNIVERSITY PRESS

# OXFORD

UNIVERSITY PRESS

Great Clarendon Street, Oxford OX2 6DP

Oxford University Press is a department of the University of Oxford.  
It furthers the University's objective of excellence in research, scholarship,  
and education by publishing worldwide in

Oxford New York

Auckland Bangkok Bogotá Buenos Aires Cape Town Chennai  
Dar es Salaam Delhi Hong Kong Istanbul Karachi Kolkata  
Kuala Lumpur Madrid Melbourne Mexico City Mumbai Nairobi  
São Paulo Shanghai Singapore Taipei Tokyo Toronto  
and associated companies in Berlin Ibadan

Oxford is a registered trade mark of Oxford University Press  
in the UK and in certain other countries

Published in the United States

by Oxford University Press Inc., New York

© The several contributors and in this collection Dr Alison Wray 2002

The moral rights of the author have been asserted

Database right Oxford University Press (maker)

First published 2002

All rights reserved. No part of this publication may be reproduced,  
stored in a retrieval system, or transmitted, in any form or by any means,  
without the prior permission in writing of Oxford University Press,  
or as expressly permitted by law, or under terms agreed with the appropriate  
reprographics rights organization. Enquiries concerning reproduction  
outside the scope of the above should be sent to the Rights Department,  
Oxford University Press, at the address above

You must not circulate this book in any other binding or cover  
and you must impose the same condition on any acquirer

British Library Cataloguing in Publication Data

Data available

Library of Congress Cataloging in Publication Data

Data applied for

ISBN 0-19-925065-0

ISBN 0-19-925066-9 (Pbk.)

10 9 8 7 6 5 4 3 2 1

Typeset in Minion

by Peter Kahrel

Printed in Great Britain

on acid-free paper by

Biddles Ltd., Guildford & King's Lynn

## Preface and Acknowledgements

---

The aim of this book is to examine the theme of transition from a number of different angles, and to raise issues and new challenges regarding the ways in which we, as researchers in the field, perceive our evolving task. As my introductory chapter makes clear, I view the future as one of cross-disciplinary collaboration, and the reconciliation of individual scenarios within a larger, consistent picture. The book includes contributions from the fields of anthropology, archaeology, artificial intelligence, biology, genetics, linguistics, primatology, and psychology. I hope that this broad range of perspectives will contribute to a fuller recognition of what seems to me an undoubted fact about this field of enquiry: none of us has purchase on the whole of the answer to the question, 'How did language evolve?'

The chapters of this book are a small sample of the papers presented at the Third International Conference on the Evolution of Language, held in April 2000 at the École Nationale Supérieure des Télécommunications in Paris. The organizing team for the conference was led by Jean-Louis Dessalles and Laleh Ghadakpour, and it was generously sponsored by the École Nationale Supérieure des Télécommunications, the Sony Computer Science Laboratory, France Telecom R&D, the Centre Nationale de la Recherche Scientifique, the Department of Sociology and Anthropology at the University of East London, and the Fondation Louis Leprince-Ringuet.

The various rounds of anonymous refereeing, for the conference and for the book, relied on the generosity of the individuals who gave their time to read and comment on the proposals and papers. A particular debt of gratitude is owed to the referees who participated in the final stage, providing detailed and insightful notes on the papers short-listed for inclusion in the book. I should also like to thank the authors themselves, who stuck to some tough deadlines and indulged me as I pestered them over fiddly bits of detail.

The book owes much of its identity, and perhaps its very existence, to the efforts of Jean-Louis Dessalles, whom I particularly thank for his invaluable contribution in the months after the conference. The series editors,

Jim Hurford and Fritz Newmeyer, have been a strong support to me, as has John Davey of Oxford University Press. I should also like to extend my heartfelt thanks to Chris Knight for his thoughtful advice, support, and example. Finally, my own work on the book would not have been possible without the time afforded by my Senior Research Fellowship at Cardiff University, and the patience and encouragement of my partner, Mike Wallace.

A.W.

*Cardiff*  
*July 2001*

# List of Figures

---

|      |                                                                                                                         |     |
|------|-------------------------------------------------------------------------------------------------------------------------|-----|
| 2.1  | Midsagittal MRI images of chimpanzee and human                                                                          | 22  |
| 2.2  | Cineradiographic still images of dog barking                                                                            | 33  |
| 3.1  | Transition diagrams obtained from songs of Bengalese finch and white-backed munia                                       | 49  |
| 3.2  | Hypothetical neuro-anatomical substrates for syntax and semantics                                                       | 52  |
| 3.3  | Independent evolution of semantics and syntax                                                                           | 59  |
| 4.1  | Simultaneous chaining paradigm                                                                                          | 68  |
| 4.2  | Types of responses and their consequences on a 4-item list                                                              | 70  |
| 4.3  | Number of possible errors and the probability of guessing the correct sequence on simultaneous chains of varying length | 72  |
| 4.4  | Learning curves for 3-, 4-, and 7-item lists                                                                            | 74  |
| 4.5  | Serial position functions                                                                                               | 75  |
| 4.6  | Accuracy and reaction times on subset test                                                                              | 79  |
| 5.1  | The diaspora of modern <i>Homo sapiens</i>                                                                              | 96  |
| 5.2  | Hand preference in chimpanzees and <i>Homo sapiens</i> compared                                                         | 97  |
| 5.3  | The anatomical 'torque' in the human brain from right frontal to left occipital                                         | 98  |
| 5.4  | Regions of homology between the X and the Y chromosome                                                                  | 100 |
| 5.5  | The sex difference in the rate of brain growth                                                                          | 103 |
| 5.6  | Hypothetical trajectories of growth of the cerebral hemispheres in humans                                               | 104 |
| 5.7  | The structure of ProtocadherinXY                                                                                        | 106 |
| 6.1  | Mappings of meanings to words and word strings                                                                          | 119 |
| 9.1  | Hand-axe from Tabun                                                                                                     | 184 |
| 9.2  | Tula adze slug from Glenormiston Station, Queensland                                                                    | 185 |
| 9.3a | Scatter plot of 100 pairs of random numbers                                                                             | 191 |
| 9.3b | Scatter plot of pairs of random numbers from Fig. 9.3a adjusted                                                         | 191 |
| 9.3c | Histogram of correlation coefficients for 100 examples of process illustrated in Figs. 9.3a and 9.3b                    | 192 |
| 9.3d | Histogram of ratios of width/length for samples in Fig. 9.3c                                                            | 193 |

|      |                                                                                                                                  |     |
|------|----------------------------------------------------------------------------------------------------------------------------------|-----|
| 9.4  | Core from Tabun with three flakes removed                                                                                        | 194 |
| 9.5  | Acute and obtuse angle platforms on core from Tabun                                                                              | 196 |
| 9.6a | Flake scars on margin of flake from Tabun                                                                                        | 196 |
| 9.6b | Flake scars on margin of flake from Tabun<br>after one-flip rotation                                                             | 196 |
| 9.7  | Tip of hand-axe from Tabun                                                                                                       | 198 |
| 11.1 | A population of communicating agents                                                                                             | 232 |
| 11.2 | Communicative error over time for a population of ten,<br>using ten examples to train new individuals                            | 236 |
| 11.3 | Communicative error over time for a population of ten,<br>using twenty examples to train new individuals                         | 237 |
| 11.4 | Communicative error over time for a population of twenty,<br>using ten examples to train new individuals                         | 238 |
| 11.5 | Communicative error of populations over time when<br>new individuals always start from the same initial weights                  | 243 |
| 11.6 | Communicative error of populations over time when new<br>individuals are always trained on the same set of meanings              | 244 |
| 11.7 | Communicative error of populations over time when new<br>individuals are taught by the better communicators in the<br>population | 245 |
| 12.1 | Example of a typical Talking Heads set-up                                                                                        | 255 |
| 12.2 | Evolution of word–meaning relations for the same meaning<br>over a period of 90,000 games                                        | 256 |
| 12.3 | Evolution of word–meaning relations for the same word,<br><i>bozopite</i> , over a period of 250,000 games                       | 257 |
| 12.4 | Evolution of word diversity                                                                                                      | 258 |
| 12.5 | Simulation experiments with 20 agents and 10 meanings<br>for 20,000 games                                                        | 261 |
| 12.6 | Example of a part of the conceptual repertoires<br>of a single agent                                                             | 262 |
| 12.7 | Communicative success measured over number of games                                                                              | 264 |
| 12.8 | Communicative success of the emergent lexicon and the<br>lexicon change over time                                                | 267 |
| 15.1 | Three dimensions squashed into two                                                                                               | 315 |
| 15.2 | Three dimensions squashed into one                                                                                               | 316 |
| 15.3 | The 6-dimensional space of Agenthood and Patienthood                                                                             | 317 |
| 15.4 | Two grammatical polar points of a transitive clause                                                                              | 318 |

---

|      |                                                                                                                                                          |     |
|------|----------------------------------------------------------------------------------------------------------------------------------------------------------|-----|
| 15.5 | Language as a system of mappings between meanings and external forms                                                                                     | 319 |
| 15.6 | Phonological structure, what's in it?                                                                                                                    | 321 |
| 15.7 | Typical hierarchical tree structure                                                                                                                      | 326 |
| 15.8 | Movement in English question forms                                                                                                                       | 330 |
| 15.9 | Agreement ('concord') in English                                                                                                                         | 331 |
| 16.1 | Finite-state grammar used to generate stimuli                                                                                                            | 341 |
| 16.2 | Overall classification performance for aphasic and normal control subjects                                                                               | 342 |
| 16.3 | Syntactic trees for a consistent head-first, right-branching NP, a consistent head-last, left-branching NP, and an inconsistent NP with centre-embedding | 345 |
| 16.4 | An illustration of the Simple Recurrent Networks used in simulations                                                                                     | 346 |
| 16.5 | Overall classification performance for subjects trained on consistent and inconsistent languages                                                         | 348 |
| 16.6 | A syntactic tree showing ungrammatical Wh-movement                                                                                                       | 349 |
| 16.7 | A syntactic tree showing ungrammatical Wh-movement                                                                                                       | 350 |
| 16.8 | The classification performance on subadjacency and general items for subjects trained on natural and unnatural languages                                 | 352 |
| 18.1 | Principle of reconstruction                                                                                                                              | 380 |
| 18.2 | Some salient paths of categorial shift in grammaticalization                                                                                             | 383 |
| 18.3 | The main source domains of spatial orientation                                                                                                           | 386 |
| 18.4 | The main source and target domains of predicative possession                                                                                             | 387 |

# List of Tables

---

|      |                                                                                          |     |
|------|------------------------------------------------------------------------------------------|-----|
| 11.1 | The utterances used by a neighbourhood of a population for a subset of the meaning space | 239 |
| 13.1 | Communities from which an indigenous signed system of communication emerged              | 276 |
| 16.1 | The two grammars used for stimuli generation in Christiansen (2000)                      | 347 |
| 16.2 | The structure of the natural and unnatural languages in Ellefson and Christiansen (2000) | 351 |
| 18.1 | Mechanisms of the grammaticalization process                                             | 378 |

# Contents

---

|                                                                                                                                                        |     |
|--------------------------------------------------------------------------------------------------------------------------------------------------------|-----|
| <i>Preface and Acknowledgements</i>                                                                                                                    | vii |
| <i>List of Figures</i>                                                                                                                                 | ix  |
| <i>List of Tables</i>                                                                                                                                  | xii |
| 1. Introduction: Conceptualizing Transition in an Evolving Field<br><i>Alison Wray</i>                                                                 | 1   |
| <b>Part I</b>                                                                                                                                          |     |
| <b>Making Ready for Language:<br/>Necessary, but not Sufficient</b>                                                                                    |     |
| 2. Comparative Vocal Production and the Evolution of Speech:<br>Reinterpreting the Descent of the Larynx<br><i>W. Tecumseh Fitch</i>                   | 21  |
| 3. Sexual Display as a Syntactical Vehicle: The Evolution of Syntax<br>in Birdsong and Human Language through Sexual Selection<br><i>Kazuo Okanoya</i> | 46  |
| 4. Serial Expertise and the Evolution of Language<br><i>H. S. Terrace</i>                                                                              | 64  |
| <b>Part II</b>                                                                                                                                         |     |
| <b>Internal Triggers to Transition:<br/>Genes, Processing, Culture, Gesture, and Technology</b>                                                        |     |
| 5. ProtocadherinXY: A Candidate Gene for Cerebral Asymmetry<br>and Language<br><i>T. J. Crow</i>                                                       | 93  |
| 6. Dual Processing in Protolanguage: Performance without Competence<br><i>Alison Wray</i>                                                              | 113 |
| 7. Language and Revolutionary Consciousness<br><i>Chris Knight</i>                                                                                     | 138 |
| 8. Did Language Evolve from Manual Gestures?<br><i>Michael C. Corballis</i>                                                                            | 161 |
| 9. The Finished Artefact Fallacy: Acheulean Hand-axes<br>and Language Origins<br><i>Iain Davidson</i>                                                  | 180 |

**Part III**  
**External Triggers to Transition:**  
**Environment, Population, and Social Context**

|                                                                                                                                   |     |
|-----------------------------------------------------------------------------------------------------------------------------------|-----|
| 10. Foraging versus Social Intelligence in the Evolution of Protolanguage<br><i>Derek Bickerton</i>                               | 207 |
| 11. Methodological Issues in Simulating the Emergence of Language<br><i>Bradley Tonkes and Janet Wiles</i>                        | 226 |
| 12. Crucial Factors in the Origins of Word-Meaning<br><i>L. Steels, F. Kaplan, A. McIntyre, and J. Van Looveren</i>               | 252 |
| 13. Constraints on Communities with Indigenous Sign Languages:<br>Clues to the Dynamics of Language Genesis<br><i>Sonia Ragir</i> | 272 |

**Part IV**  
**The Onward Journey:**  
**Determining the Shape of Language**

|                                                                                                                                                                              |     |
|------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|-----|
| 14. The Slow Growth of Language in Children<br><i>Robbins Burling</i>                                                                                                        | 297 |
| 15. The Roles of Expression and Representation in Language Evolution<br><i>James R. Hurford</i>                                                                              | 311 |
| 16. Linguistic Adaptation without Linguistic Constraints:<br>The Role of Sequential Learning in Language Evolution<br><i>Morten H. Christiansen and Michelle R. Ellefson</i> | 335 |
| 17. Uniformitarian Assumptions and Language Evolution Research<br><i>Frederick J. Newmeyer</i>                                                                               | 359 |
| 18. On the Evolution of Grammatical Forms<br><i>Bernd Heine and Tania Kuteva</i>                                                                                             | 376 |
| <i>List of Contributors</i>                                                                                                                                                  | 399 |
| <i>Index</i>                                                                                                                                                                 | 407 |

# 1 Introduction: Conceptualizing Transition in an Evolving Field

---

ALISON WRAY

## 1.1 Transition and Transitions

A book entitled *The Transition to Language* could give the impression that there was a single event at some point in prehistory before which there was no language and after which there was language. But that is far from the case. The constituent properties of human language—its mediums of transmission, its micro- and macro-structure, the mechanisms that process it, the manner in which it is used to convey messages—all entail independent, or partially independent, developments of physical, mental, and/or social configurations. Each such development can be conceptualized in terms of a transition. A transition may be sudden or gradual. That is, it may be the result of one event with major consequences for the species, or a slow accumulation of relatively unimportant small changes that ultimately effect a combined impact.

### 1.1.1 *The Challenge of Complexity*

The evolution of language as a whole must, in either case, be construed as a complex event-sequence essentially driven by the dynamics of chance. It behoves us to remember that there was no advance plan, and we should not impose upon our accounts too strong an impression of our retrospective standpoint. We do not know how else language might have turned out, and how different our conception of grammar, words, or effective communication might have been if some other combination of factors had taken our ancestors down a slightly different path. We do not know how many times one or another component of language *nearly* emerged, or emerged briefly

but died out. We do not know which, if any, components emerged more than once and survive to this day as separate routes to the same outcome. Our aim as researchers is to trace a continuous line of events that culminates in our use of syntactic language for a range of interactive purposes, but in the course of our backwards reconstruction, the line may cross or tangle with others, or become obscured so that we can no longer be sure of where it goes next.

Some indication of the intrinsic complexity and the role of chance is evident in the computer simulations reported by Tonkes and Wiles and by Steels *et al.* in this volume, as also elsewhere, by Kirby (e.g. 1998, 2000), Batali (e.g. 1998) and others. When effective language-like systems emerge in these trials, each is a macro-pattern arising, after many iterations, out of a soup of random and semi-random events. This kind of modelling takes for granted the 'noise', whereby pretty well any configuration may occur once or many times, without ultimately prevailing. A coherent story emerges only out of a very large body of data. For those using other investigatory means it is, in general, extremely difficult to accommodate the full scope of the likely complications of the original scenario. Yet, unless we are careful in our visualizations of the events about which we hypothesize, we risk making over-precipitous assumptions, which may have far-reaching implications. This is what Davidson's chapter warns us of, as he reveals the potential dangers of too readily imposing onto data *post-hoc* rationales which then discount the residue of evidence.

### 1.1.2 *The Challenge to Open-Mindedness*

It is unquestionably necessary to locate any proposal within a solid context of existing theory. However, this presents us with a further, and difficult, challenge, because it means that a coherent account of how a given part of the linguistic package evolved can only be developed in relation to a particular hypothesis about the 'before' and 'after' states. In other words, answering the question of *how* and *why* a change occurred depends entirely on your position regarding *what* changed into *what*. The problem is that, as a result, each stage in the construction of a model of complex transition becomes, itself, a variable within the model as a whole. That is, it feeds into the investigator's perception of the transition event, determining the directions in which the account can evolve, and excluding other routes as incompatible. The risk is that assumptions made too readily at one point will deflect atten-

tion from lines of investigation that, in the final count, turn out to be of considerable significance.

The remedy is the continual reappraisal of the assumptions we make about language, but that is harder than it sounds, because the assumptions run so deep. The very conceptualization of what constitutes a transition event in the first place is dependent on adopting a committed position regarding the overall nature of language and, in particular, the order in which various components of the language 'package' evolved. A fundamental transition within one model of language evolution may simply evaporate in another. For instance, a model such as Bickerton's (e.g. 1996, 1998, this volume; Calvin and Bickerton 2000), in which full syntax developed out of a simpler spoken protolanguage, automatically entails that a previous transition also occurred, whereby agrammatical semantic representation became united with controlled phonetic vocalization. In contrast, the model that Corballis (this volume) proposes sees fully syntactic messages delivered through the medium of sign, long before speech was adopted. Such a view does not entail a transition to phonetic words without grammar, and envisages the unification of vocal delivery with an already fully-fledged grammatical language system.

Even the apparently fundamental assumption that the 'word' existed before the complex message can be challenged, when one asks just what the function of the 'word' could have been before there was syntax. If, as Terrace and Wray both propose in this book, the basic unit of expression was not referential but manipulative, then the 'translation' of so-called simple one-word messages reveals them not to be so simple after all. Just as the vervet's alarm call (Cheney and Seyfarth 1990) is more usefully glossed not as *eagle* but as *behave in a manner appropriate to my having seen an eagle*, so, in our ancestors, we might be forced to gloss a 'one-word' utterance not as *meat*, so much as *behave in some appropriate way in relation to me and the meat*. That, in turn, challenges our view on just what kind of expressive complexity syntax delivered for the first time, and what complexity it just repackaged.

### 1.1.3 *Types of Evidence*

If, from our perspective as adept users of an integrated linguistic system, it is very difficult to ascertain which parts of the language package came before others, it is even harder to work out whether a precursor should be viewed as prerequisite. Each assumption about the order in which our

ancestors developed the various capacities necessary for language needs to be scrutinized and evaluated in the light of at least two types of evidence. One is internal consistency. From what we understand of language as a system, is it possible, or likely, that there was syntax before there were words, as Okanoya proposes? Is the apparatus of speech more likely to be the foundation of linguistic expression, or a response to it? Just how mentally adept at problem-solving could we have become *without* developing language? The other kind of evidence is comparative. Do other species, whether closely or not so closely related to our own, display skills and behavioural patterns that belie common assumptions about the order in which the constituent parts of language evolved, and why they did? Since there are in principle so many different position statements, each of which will support a different account of the events, the major challenge to any researcher of language evolution is to find independent support for the assumptions underpinning the given hypothesis. Without it, a model is little more than idle speculation.

## 1.2 Themes in Researching Transition

Since, as already pointed out, there is no single story of transition, or transitions, to tell, there is inevitably no entirely simple way to allocate a set of studies to thematic sections. The structure chosen for this book reflects three aspects of transition, without directly imposing a chronological ordering on them. These aspects may be characterized as the run-up to transition, the immediate triggers of transition, and their aftermath. But in each case, it is not necessarily the same transition that is under discussion. In other words, rather than attempting to map out, through the sequencing of chapters in the book, the story of how language might have evolved, the sections aim to focus on the issues arising out of these three faces of transition as a phenomenon.

### 1.2.1 *Part I. Making Ready for Language: Necessary, but not Sufficient*

Human language primarily uses the *vocal-auditory channel* (Hockett 1960), though as Ragir's account of sign languages (in Ch. 13) makes plain, it does not need to. Of course, humans are far from the only creatures to use this channel, but the units transmitted in human language are phonetic. Pho-

netic production requires a particular configuration of the vocal tract and this is the focus of Ch. 2, as Fitch seeks to separate out fundamental from non-fundamental features of that configuration. Fitch challenges some long-held beliefs about the uniqueness of the human vocal tract, beliefs that have led to associations between physical attributes and linguistic capabilities. He demonstrates, for instance, that although humans differ from apes in possessing a low larynx, the significance of this fact has been exaggerated. He draws on evidence from several species to argue that our unusual laryngeal arrangement is likely to have evolved for reasons other than the articulation of linguistic forms. Similarly, he shows that other animals can perceive formant patterns comparable with those characterizing human vowels, which suggests that language harnessed this channel because we could already discriminate within it, rather than the reverse.

The study of finch song, Okanoya argues in Ch. 3, can give us important insights into another aspect of language evolution, the relationship between syntax and semantics. The standard assumption, and one that is made in several chapters in this volume, is that syntax subserves the expression of meaning, so that semantics is assumed to predate and underpin the evolution of grammar. Okanoya's work on the song of the Bengalese finch demonstrates that syntax, albeit less complex than that in human language, can evolve independently of meaning. Moreover, the peculiar circumstances under which this finch has developed complexity in its song are such that it is possible to make direct links between syntactic prowess and sexual selection. Okanoya shows that while complexity in the male song correlates with increased female reproductive activity, in the wild the effects of preferential selection by females of mates with complex songs are countermanded by the increased vulnerability of good singers to predation. Only in a captive species, where predation no longer affects survival patterns, does sexual selection override natural selection, leading to the evolution of ever more complex song. Okanoya proposes that syntax might have evolved in a similar manner in humans, independently of message meanings, for the purpose of sexual display.

One of the characteristics of the human capacity for interacting with the world is a clear distinction between procedural knowledge (knowing *how*) and declarative knowledge (knowing *that*). Since declarative knowledge is so closely tied into information exchange, and information exchange is most efficiently achieved using language, there has been a tendency to assume that non-human animals do not possess it. All animal behaviour has been

assumed to be grounded in procedural knowledge. Terrace (Ch. 4) directly challenges this assumption. He reports an experiment in which monkeys were trained to select sequences of images in a particular order, even though the images were differently positioned on the screen in different trials. The only way for them to achieve success—which they did—was to learn the sequence of images independently of their position in presentation, thus ruling out an automatic procedural response based on physical movements. They had to know *that* a particular image came in a particular place in the sequence, and tests demonstrated that they did indeed know the serial positions of the items, both relative to each other and in absolute terms. Terrace uses this evidence to conclude that declarative knowledge is independent of linguistic expression, and that we must look elsewhere to explain why humans are the only species to have developed language. In his view, the key difference between humans and other animals is that animals only ever use symbols manipulatively, in pursuit of a reward. In contrast, humans are also capable of using symbols referentially, that is, to talk about the world for its own sake.

### 1.2.2 *Part II. Internal Triggers to Transition: Genes, Processing, Culture, Gesture, and Technology*

If one assumes a general level of stability for a species in its environment, it is as well to look for both internal and external triggers when accounting for a transition. Stability will tend to impose the biological equivalent of the maxim ‘if it ain’t broken, don’t fix it’, so that most random genetic changes, even if they might be construed as beneficial, will not be necessary, and so will not be favoured by natural selection. Only when the organism lives within a sufficiently challenging environment will a small change to its physical or mental capabilities make a real difference to its survival chances. Meanwhile, a change in external factors, if it does not coincide with relevant variation within the species, will exert the same pressure on all individuals, and so will not precipitate selective survival. In the case of natural selection, then, transition will come about when the internal stage is set for certain individuals to respond better to new external circumstances, or vice versa. Alongside natural selection, however, operates sexual selection (cf. Okanoya, Ch. 3), whereby a genetic pattern is successful because its carriers are preferred as mates. There are undoubtedly some strong correlations between sexually selected traits and the overall capacity to survive—not least because