European Review, Vol. 18, No. 3, 287–296
doi:10.1017/S1062798710000049

The Evolution of Evolutionary Theory

PATRICK BATESON

Sub-Department of Animal Behaviour, University of Cambridge, Madingley Road, Cambridge CB23 8AA, UK. Email: ppgb@cam.ac.uk

Charles Darwin has had an extraordinary impact on many aspects of human affairs apart from revolutionizing biology. On the 200th anniversary of his birth, the Cambridge Darwin Festival in July 2009 celebrated these contributions to the humanities, philosophy and religion and the approach to medicine, economics and the social sciences. He is a man to revere. It is no discredit to him that the science of evolutionary biology should continue to evolve. In this article I shall consider some of the ways in which this has happened since his day.

In 1859, Darwin published his great book *On the Origin of Species by means of Natural Selection*.[1] He proposed a blind process for biological evolution that started with variation in characteristics between competitors, followed by differential survival and reproductive success and finally some means by which descendents of the successful organisms inherited their characteristics.

Darwin knew nothing of genetics. Gregor Mendel's experiments only became well known at the beginning of the 20th century, long after Darwin's death. By the 1930s it was possible to put together Darwin's evolutionary mechanism with what was by then the understanding of the mechanisms of inheritance. This gave rise to what was known at the time as 'The Modern Synthesis'. On this view, differences between organisms in their genes gave rise to differences in their expressed characteristics. The successful organism then left its genes to its descendents. So, it was argued, biological evolution involves changes in gene frequencies. This form of Neo-Darwinism has held sway until the present and only recently has it begun to show its years.

The 1930s' Neo-Darwinist orthodoxy asserts that speciation results from a slow process of Natural Selection, that mutations in genes drive evolution with the organism passively playing no role, and that developmental processes are irrelevant to an understanding of evolution. In this article I shall examine all three assertions

Is Speciation Slow and Gradual?

Even as Darwin's thinking hit the headlines in 1859, many of his friends doubted whether he had produced a theory that explained the transmutation of species. Natural Selection provided a wonderful mechanism to explain adaptation and, as it happened, to discredit the Natural Theology of William Paley, which had been so popular with the intelligentsia since the beginning of the 19th century. But did this postulated slow process of adaptation explain the formation of a new species? Even Darwin's cousin, Francis Galton, imagined that speciation might be discontinuous. He wrote:

> The mechanical conception would be that of a rough stone, having, in consequence of its roughness, a vast number of natural facets, on any one of which it might rest in 'stable' equilibrium. That is to say, when pushed it would somewhat yield, when pushed much harder it would again yield, but in a less degree; in either case, on the pressure being withdrawn it would fall back into its first position. But, if by a powerful effort the stone is compelled to overpass the limits of the facet on which it has hitherto found rest, it will tumble over into a new position of stability, whence just the same proceedings must be gone through as before, before it can be dislodged and rolled another step onwards. (Ref. 2, pp. 354–355)

Darwin's mentor when Darwin was an undergraduate at Cambridge was John Henslow. He was fascinated by 'monstrosities', the appearance of 'sports' markedly different from their lineages. Homoeotic changes in organisms were also the concern of William Bateson, a kinsman of mine. He coined the term 'genetics' after the rediscovery of Mendel's papers, but several years before that he had published a book, *Materials for the Study of Variation Treated with Special Regard to Discontinuities in the Origin of Species*.[3] The second part of his title was regarded as a direct challenge to Darwinism and was much criticized by Darwin's supporters, although Bateson was not a critic of Natural Selection as a driver of adaptedness.

Despite the attacks on Bateson, many modern thinkers have been inclined to support his views that discontinuities do arise in evolution. Hosts of examples of big events having no effect and small events leading to big changes are to be found and many of these are now formalised by the non-linear mathematical techniques derived from Catastrophe Theory and Chaos. Recently, a biography of William Bateson has been published by the late Alan Cock and Donald Forsdyke.[4] They used for the title of their book a splendid piece of Bateson's advice to biologists: 'Treasure your exceptions.'

Discontinuities in evolution have been given especial prominence by some modern palaeontologists who have been impressed by periods of stasis and sudden change in the fossil record.[5,6] They suggested that after periods of stasis in evolution, sudden changes can occur in the fossil record and these may represent the appearance of new species. This idea of discontinuity has recurred periodically and, notably, was foreshadowed in the writings of Goldschmidt[7] who, in a memorable phrase, referred to a fresh arrival that might give rise to a new species as a 'Hopeful Monster'.

Even though the discontinuities in natural variation, which Bateson had documented so carefully, no longer pose a problem in developmental biology, Hopeful Monsters are disparaged to this day on the grounds that even if a big change in the phenotype could occur as a result of mutation, the Hopeful Monster would be a novelty on its own with no possibility of finding a mate. Without a mate it could never found a new species. However, if somehow or other, enough Hopeful Monsters sprang into existence simultaneously and thus were able to breed successfully with each other, the possibility exists of competition between the Hopeful Monsters and the stock from which they sprang. It is not at all difficult to suppose that, by the process of natural selection, Hopeful Monsters could quickly replace their competitors if they were better adapted to the environment. No new fancy principles of evolution are involved here. The critical question for an understanding of biological evolution is how could a whole group of individuals, founders of a new species, suddenly arise at the same time?

Suppose that a population splits into two sub-groups as the result, say, of migration. The sub-groups remain separated for many generations and a different mutation goes to fixation in each of them. Then, the populations merge again. The combination of the mutated genes in the two previously separated sub-groups interacts to produce a radically new phenotype that is sufficiently frequent in the population to allow breeding to occur. Now the conditions are in place for a competition between the phenotypes. If the new phenotype is more successful than the old, the historical record would show a discontinuity in evolution.[8]

Another model for speciation also suggests that post-zygotic isolation results from an interaction between two or more genes.[9] Suppose the initial genotype is *aabb*, the population splits and in one population an *A* mutation appears and goes to fixation and in the other population a *B* mutation appears and also goes to fixation. If *A* and *B* do not function well together, then hybrids between the two populations will be less viable or infertile. As Orr and Presgraves[9] point out, this model highlights the role of epistasis in evolution. Although credit is usually given to Dobzhansky[10] and Muller[11] for the idea, as Orr[12] noted, the problem was first solved by William Bateson[13]. Population geneticists have typically not liked to contemplate interactions between genes because it complicates their mathematics, but the empirical evidence for such effects is strong. One example is to be found in one of William Bateson's experiments on chickens. When a white silky hen and a white Dorking cockerel were mated, the offspring were all brown.

These conjectures about the sudden emergence of discontinuous change in evolution do not necessarily imply speciation. However, they would do so if hybrids between old and the new phenotypes were less viable. A plausible case would be a change in chromosome number that could prohibit the formation of gametes in hybrids. Examples of closely related species with different numbers of chromosomes are well known. In horses, the chromosome number ranges from 32 in *Equus zebra hartmannae* and 46 in *Equus grevyi*, to 62 in *Equus assinus* and 66 in *Equus przewalski*; all but two of the horse hybrids are sterile,[14] therefore the differences between the species must have occurred in jumps.

Active Role of Organisms in Evolution

A second challenge to the orthodoxies of Neo-Darwinism comes from the evidence that organisms play important roles in the evolution of their descendants. The evidence is of four types: choice, control of the environment, adaptability and mobility. I shall consider these in turn.

Choice

Charles Darwin[15] himself suggested that choice of a mate could drive evolution. He called the evolutionary process 'sexual selection'. Alfred Russell Wallace, although the co-author with Darwin of the first clear statement about the role of Natural Selection, did not like the new idea. Indeed, for many years most biologists did not take sexual selection seriously. I well remember when I was an undergraduate being confidently told that even if it were possible in theory, the process probably played little part in biological evolution. In recent years, however, many experiments have supported Darwin's thinking. A famous experiment by Andersson[16] involved lengthening the tail of male long-tailed widow birds. He found that the males with extra-long tails attracted more mates. The reason why longer tails are not found in nature is probably because it carries a big cost for the male – in rainy weather, a bird with an extra long tail cannot drag the great encumbrance off the ground when attacked by a predator.

Another example of choice is that involved in predators' choice of prey.

Gazelle that have seen a predator, jump into the air. The behaviour pattern is called 'stotting'. A suggested evolutionary mechanism is that, first, some gazelle jump after noticing cheetah.[17] Cheetah learn not to chase jumping gazelle. The next step is that all gazelle jump after noticing cheetah. Some gazelle gain advantage by giving an exaggerated jump – a stott – after noticing cheetah. This is because cheetah learn not to chase stotting gazelle.

Control of the Environment

The environment does not simply set a problem to which the organism has to find a solution. The organism can do a great deal to create an environment to which it is best suited. This should give pause if evolution is considered purely in terms of selection by external forces.[18] By leaving an impact on their physical and social environment, organisms may affect the evolution of their own descendents, quite apart from changing the conditions for themselves. Some of the impact is subtle, such as when a plant sheds its leaves which fall to the ground and change the characteristics of the soil in which its own roots and those of its descendents grow. These ideas have been developed extensively and are now referred to as 'niche construction'.[19] One example is provided by beavers, which change their environment by building dams and creating lakes for themselves. This sets up conditions that affect subsequent evolution. The artificially created aquatic environment led the beavers to evolve adaptations such as webbed feet that facilitated swimming.

The effect of behavioural control on evolutionary change could be especially great when a major component of the environmental conditions with which animals have to cope is provided by their social environment. A similar type of positive feedback to that flowing from the effects of mate choice could operate in such circumstances.[20] If individuals compete with each other within a social group and the outcome of the competition depends in part on each individual's capacity to predict what the other will do, the evolutionary outcome might easily acquire a runaway property. In discussing the social function of intelligence,[21] Humphrey expressed the idea as follows:

> An evolutionary 'ratchet' has been set up, acting like a self-winding watch to increase the general intellectual standing of the species. In principle the process might be expected to continue until either the physiological mainspring of intelligence is full-wound or else intelligence itself becomes a burden. The latter seems most likely to be the limiting factor; there must surely come a point where the time required to resolve a social 'argument' becomes insupportable. (Ref. 21, p. 311)

As Humphrey noted, such an explanation makes sense of the astonishing rate of increase in the cranial capacity of humans, if it is assumed (reasonably) that cranial capacity and intellectual ability are correlated. Here again the ideas have been developed extensively in recent years.[22]

The Adaptability Driver

The adaptability of the organism is likely to play an important role in initiating evolutionary change. This effect is often called the Baldwin effect after Baldwin.[23] Two others published the same idea in the same year, namely Lloyd Morgan[24] and Osborne[25]. However, 23 years before, Spalding[26] had published the same hypothesis in *Macmillan's Magazine*. It was not an obscure publication – it was the predecessor of *Nature*, which continues to be published by Macmillan.

Given Spalding's[26] precedence and the simultaneous appearance in 1896 of the ideas about 'organic selection', it seems inappropriate to term the evolutionary process the 'Baldwin effect'. The trouble is that calling the proposed process the 'Spalding effect' is not descriptive of what initiates the hypothetical evolutionary process. As will already be apparent, I have a strong preference for a term that captures the active role of the organism in the evolutionary process. The notion of a behavioural driver in evolution was introduced by Wyles *et al.*,[27] but they laid primary emphasis on imitation and, of course, other active behavioural processes, such as mate choice, had already been recognised by Darwin.[15] That is how I come to my preferred term, namely the 'adaptability driver'.[28]

Many changes in the environment and/or in the expression of the genome may require adaptability on the part of the organism; if the same phenotypic effect can be generated at lower cost, Darwinian evolution can lead to a change in the underlying developmental mechanism. Adaptability may save the organism from extinction and thereafter promote a new direction in evolution. Simpson[29] disputed its importance in biological evolution. He believed that if a new phenotype were valuable to the organism, it would evolve along traditional Darwinian lines. Secondly, he argued that, if plasticity were a pre-requisite for the evolutionary process and was generally beneficial, it would be disadvantageous to get rid of it.

On Simpson's first point, if learning (as an example of one form of adaptability in animals) involves several sub-processes or steps as in operant chaining, then the chances against an unlearned equivalent appearing in one step in the course of evolution are very small. However, with the learned phenotype as the standard, every small step that cuts out some of the plasticity with a simultaneous increase in efficiency is an improvement. As an example, consider the Galapagos woodpecker finch, which pokes sharp cactus spines into holes thereby obtaining insect larvae as food. Suppose it does so without much learning but that an ancestor did so by trial and error. In the first stage of the evolutionary process, a naive variant of the ancestral finch, when in foraging mode, might, for example, have been more inclined to pick up cactus spines than other birds. This habit spread in the population by Darwinian evolution because those behaving in this fashion obtained food more quickly. At this stage the birds still learned the second part of the sequence. The second step would have been that a naive new variant, when in foraging mode, was more inclined to poke cactus spines into holes. Again this second habit spread in the population by Darwinian evolution. The end result is a finch that uses a tool without having to learn how to do so. Simultaneous mutations increasing the probability of two quite distinct acts (taking cactus spines and poking them into holes in the case of the woodpecker finch) would be very unlikely. Learning makes it possible for the mutations to occur at different times and in any order. Without learning processes, having one act but not the other has no value. As a matter of great interest, it seems to be the case that the Woodpecker finch is half way down the evolutionary road from fully learned to fully spontaneous because naive birds readily pick up small sticks but then still have to learn how to use them.[30]

As far as learning is concerned, Simpson's second point of criticism is based on an inadequate understanding of how behaviour is changed and controlled. Learning in complex organisms consists of a series of sub-processes. If an array of feature detectors is linked directly to an array of executive mechanisms as well as indirectly through an intermediate layer and all connections are plastic, then a particular feature detector can become non-plastically linked to an executive system in the course of evolution without any further loss of plasticity. Whether these replies to Simpson's objections can be applied as cogently to plants or less complex animals requires arguments that have, as far as I know, not yet been developed.

Mobility

Development depends on the constancy of many genetic and environmental conditions. If any of these change, as can happen to environmental conditions when organisms are mobile, the characteristics of the organism can change. High mobility by animals, such as that involved in active exploration or migration, would have frequently placed them in conditions that revealed heritable variation not previously apparent in the population.

When discussing his results of experiments on what he called 'genetic assimilation', Waddington[31] suggested that the heat shock, applied to the larvae of fruit flies, led to the expression of genes that were carried in only a part of the population. Waddington bred from the flies that had developed a particular character (lack of a cross-vein in the wings) as a result of their larval experience. He continued to apply heat shock in each generation and to breed selectively from the flies with cross-veinless wings. After many generations of heat shock and selective breeding, cross-veinless wings developed spontaneously in the absence of the external triggering condition of heat shock.

Waddington's finding involved expression of a novel character in a new environment, but the character was not an adaptation to the triggering condition. Because of artificial selection, however, it did confer some advantage on its possessor. Cross-veinless wings do not bear any functional relation to the environment that supplied a heat-shock when the flies were larvae. Nor need there be such a relationship under natural conditions. All that is required initially is that the environmental conditions trigger the expression of a phenotype that can be repeated generation after generation so long as the environmental conditions persist.

Waddington's fruit fly experiment is just one illustration of innumerable possible scenarios. The developmental break-out may provide radically new opportunities for those individuals equipped with the new phenotype.[32] For that reason, behaviour, along with other forms of dispersion, was likely to be important in initiating evolutionary change. In addition, behavioural adaptability of the animals would have helped buffer them against extinction in new conditions.

Conclusion

The 'Modern Synthesis' of the 1930s no longer looks modern and some of its premises have been seriously challenged by fresh evidence. Species may form suddenly, organisms (particularly animals) play an active role in the evolution of their descendents and genes often follow rather than lead evolutionary change. The evidence suggests that the conditions of development can radically affect an organism's characteristics, thereby challenging the third prop of Neo-Darwinist orthodoxy that development is irrelevant to an understanding of evolution. The orthodoxy was already under threat from the evo-devo movement that show how developmental tool-kits can profoundly influence the course of evolution.[33] Further support for the importance of development in evolution is provided by the rapidly expanding field of epigenetics.[34] Acquired information can be passed to progeny without changing DNA sequences and information can be inherited for a period in the absence of the initial environmental trigger.[35]

In other words evolutionary theory is evolving. Would Charles Darwin have been concerned if he had lived to see his 200th birthday? I doubt it. At the end of *The Origin of Species* Charles Darwin wrote:

> … contemplate an entangled bank, clothed with many plants of many kinds, with birds singing on the bushes, with various insects flitting about, and with worms crawling through the damp earth … so different from each other, and dependent on each other in so complex a manner, have been produced by laws acting around us.

The sense of wonder he expressed here and his strong commitment to evidence would have equipped him for the richness of evolutionary processes. One of his great strengths was his willingness to test his ideas by observation and experiment and to change his thinking when the findings told him to do so. We should all continue to revere him and be delighted that the science of evolutionary biology, which he transformed, remains in such a healthy state.

References

1. C. Darwin (1859) *On the Origin of Species by means of Natural Selection* (London: Macmillan).
2. F. Galton (1892) *Hereditary Genius: An Inquiry into its Laws and Consequences*, 2nd edn (London: Watts).
3. W. Bateson (1894) *Materials for the Study of Variation: Treated with especial regard to Discontinuity in the Origin of Species* (London: Macmillan).

4. A. G. Cock and D. R. Forsdyke (2008) *Treasure your Exceptions: The Science and Life of William Bateson* (New York: Springer).
5. N. Eldredge (1995) *Reinventing Darwin* (London: Weidenfeld & Nicolson).
6. S. J. Gould (2002) *The Structure of Evolutionary Theory* (Cambridge, MA: Harvard University Press).
7. R. Goldschmidt (1940) *The Material Basis of Evolution* (New Haven, Conn: Yale University Press).
8. P. Bateson (2002) William Bateson: a biologist ahead of his time. *Journal of Genetics*, **81**, 49–58.
9. H. A. Orr and D. C. Presgraves (2000) Speciation by postzygotic isolation: forces, genes and molecules. *BioEssays*, **22**, pp. 1085–1094.
10. T. Dobzhansky (1937) *Genetics and Origin of Species* (New York: Columbia University Press).
11. H. J. Muller (1940) Bearing of the Drosophila work on systematics. In J. S. Huxley (ed.) *The New Systematics* (Oxford: Oxford University Press) pp. 125–268.
12. H. A. Orr (1998) The population genetics of adaptation: the distribution of factors fixed during adaptive evolution. *Evolution*, **52**, 935–949.
13. W. Bateson (1909) Heredity and variation in modern lights. In A. C. Seward (ed.) *Darwin and Modern Science* (Cambridge: Cambridge University Press) pp. 85–101.
14. M. King (1993) *Species Evolution: The Role Chromosome Change* (Cambridge: Cambridge University Press).
15. C. Darwin (1871) *The Descent of Man, and Selection in Relation to Sex* (London: Murray).
16. M. Andersson (1994) *Sexual Selection* (Princeton: Princeton University Press).
17. C. D. Fitzgibbon and J. H. Fanshawe (1988) Stotting in Thomson gazelles – an honest signal of condition. *Behavioral Ecology & Sociobiology*, **23**, pp. 69–74.
18. R. C. Lewontin (1983) Gene, organism and environment. In D. S. Bendall (ed.) *Evolution from Molecules to Men* (Cambridge: Cambridge University Press) pp. 273–285.
19. F. J. Odling-Smee, K. N. Laland and M. W. Feldman (2003) *Niche Construction: The Neglected Process of Evolution* (Princeton, NJ: Princeton University Press).
20. A. Jolly (1966) Lemur social behavior and primate intelligence. *Science*, **153**, pp. 501–506.
21. N. K. Humphrey (1976) The social function of intellect. In P. P. G. Bateson and R. A. Hinde (ed.) *Growing Points in Ethology* (Cambridge: Cambridge University Press) pp. 303–317.
22. R. W. Byrne (2000) Evolution of primate cognition. *Cognitive Science*, **24**, pp. 543–570.
23. J. M. Baldwin (1896) A new factor in evolution. *American Naturalist*, **30**, pp. 441–451, 536–553.
24. C. Lloyd Morgan (1896) On modification and variation. *Science*, **4**, pp. 733–740.

25. H. F. Osborn (1896) Ontogenic and phylogenic variation. *Science*, **4**, pp. 786–789.
26. D. Spalding (1873) Instinct with original observations on young animals. *Macmillan's Magazine*, **27**, pp. 282–293.
27. J. S. Wyles, J. G. Kunkel and A. C. Wilson (1983) Birds, behavior, and anatomical evolution. *Proceedings of the National Academy of Sciences, USA*, **80**, pp. 4394–4397.
28. P. Bateson (2005) The return of the whole organism. *Journal of Biosciences*, **30**, 31–39.
29. G. G. Simpson (1953) The Baldwin effect. *Evolution*, **7**, pp. 110–117.
30. S. Tebbich, M. Taborsky, B. Fessl and D. Blomquist (2001) Do woodpecker finches acquire tool-use by social learning? *Proceedings of the Royal Society B: Biological Sciences*, **268**, pp. 2189–2193.
31. C. H. Waddington (1953) Genetic assimilation of an acquired character. *Evolution*, **7**, pp. 118–126.
32. M. J. West-Eberhard (2003) *Developmental Plasticity and Evolution* (New York: Oxford University Press).
33. S. B. Carroll (2005) *'Endless Forms Most Beautiful' The New Science of Evo Devo* (New York: Norton).
34. S. F. Gilbert and D. Epel (2009) *Ecological Developmental Biology* (Sunderland, MA: Sinauer).
35. M. D. Anway, A. S. Cupp, M. Uzumcu and M. K. Skinner (2005) Epigenetic transgenerational actions of endocrine disruptors and male fertility. *Science*, **308**, pp. 1466–1469.

About the Author

Patrick Bateson was Professor of Ethology, the biological study of behaviour, at the University of Cambridge (1984–2005). He was Provost of King's College, Cambridge (1988 to 2003). He was formerly Director of the Sub-Department of Animal Behaviour at Cambridge and later Head of the Department of Zoology. He was Vice-Chairman of the Museums and Galleries Commission and, in 2004, was elected President of the Zoological Society of London. He was elected a Fellow of the Royal Society of London in 1983 and was its Biological Secretary and Vice-President from 1998 to 2003. He was knighted in 2003. He is a foreign member of the American Philosophical Society. He has edited 15 books and is co-author (with Paul Martin) of *Measuring Behaviour* (Cambridge: Cambridge University Press, 3rd edn, 2007), and *Design for a Life: How Behaviour Develops* (London: Cape, 1999).