

The Implications of Adaptability

R.J. Robinson

10 London Road, Alton, Hampshire, GU34 4EG, United Kingdom

☎ +44 7962 227886

rj.robinson@prometheus.org.uk

Running head: Implications of adaptability

Keywords: adaptability; development; environment of evolutionary adaptation; fitness landscapes

Word count: 6495 words

Abstract

Many key evolutionary concepts such as 'fitness landscapes' or 'environment of evolutionary adaptation' assume that the adaptiveness of species evolves incrementally and that, on the developmental plane, that plasticity is limited to adjustments to existing patterns. A capacity for radical reconfiguration of the structure of activity within a single lifetime, or indeed within a single act, would equally radically undermine the logic of these concepts. However, as evolution approaches intelligence (most notably in the case of human beings), this capacity to apply the same structure to indefinitely many functions or to construct the same function out of many combinations of structure, and moreover to do so in the course of each act, seems to be increasingly the norm. In such conditions, functional and developmental activity is likely to supersede evolution as the primary basis for adaptation, and many key evolutionary concepts will require substantial revision.

1. Introduction

This essay is about the consequences for evolutionary theory of radical levels of adaptability. These consequences are substantial and serious, especially for the application to highly adaptable organisms such as human beings of basic evolutionary concepts such as 'environment of evolutionary adaptation' and 'fitness landscape', and probably many others.

2. Defining adaptability

What then do I mean by adaptability? Given the number of similar concepts of plasticity available to evolutionary theory – facultativeness, exaptation, learning, and so on - adaptability is perhaps most easily explained by contrasting it with its inverse, adaptedness.

2.1. Adaptedness

J.T. Bonner once observed that 'successive lifecycles allow the accumulated information of millions of years to be used at a moment's notice' (Bonner 1974: 156-157). Thus a stickleback builds its nest without having to first learn the necessary skills, the archer fish performs its extraordinary tricks without being required (as were Henry V's bowmen) to spend every Sunday morning in target practice, and so on. In that respect Bonner's remark appears to be a claim about the pre-adaptedness of organisms to their niches.

Although such an extreme is seldom (if ever) reached, a perfectly adapted organism would be one that dealt with its evolutionary niche exclusively by means of obligate specialisations. Its functioning would be determined directly by a discrete suite of pre-determined structures, which would be tied exclusively to those functions. These structures might be modifiable in the light of activity and experience (e.g., the facultative variability that probably accompanies all real obligate adaptations), but there is no general freedom of deployment or re-combination. Thus, nephrons and only nephrons are used for a certain kind of human kidney function, and they are not used for much else.

The advantages of adaptedness are clear enough: to each contingency there corresponds a predetermined functional response, efficiently elicited and executed via pre-established and evolutionarily tested structures. Such pre-adaptedness minimises the demand for, and risk of relying on, experience, development or creativity – the young organism hits the ground running. But adaptedness exacts a price: tactical facility means strategic narrowness, the inability to operate ‘outside the box’ (other than by the serendipitous byways of exaptation – Gould and Vrba 1982) and a limited ability to respond directly to a changing environment. Hence adaptedness’s immediate strength is also its potential long-term weakness.

For example, the bees’ familiar system for communicating about food sources seems extraordinarily intelligent until one realises that bees are completely incapable of generalising it to other topics, that the only flexibility of which this ‘language’ is capable is a kind of internal ‘recalibration’ (Rozin 1976), and that bees never sit around reminiscing about how much sweeter honey was in the old days. As a result, they will never be able to use this pseudo-symbolism to broaden the reality with which they are able to engage, as true language has allowed human beings to do. Conversely, the limits on the language of the bees all reflect its real adaptedness, whereas a truly intelligent language is massively, if not infinitely, adaptable. Equally clear-cut instances of adaptedness can be found in the relationship between many parasites and their hosts, especially where a single host supports all stages of the parasite’s lifecycle (Thompson 1994: Chapter 7).

Different models of how adaptedness works have emerged in the history of biology – for example, fixed genes or obligate neural circuits for very specific functions, and so on. But whatever the exact mechanism invoked, certain key principles recur. For example, Fodor’s description of modules as ‘domain-specific, innately specified, hardwired, autonomous, and not assembled’ (Fodor 1983: 37) could also be applied to many other forms of adaptedness, as could Atran’s suggestion that a true module manifests ‘cross-cultural universality, early and rapid ontogenetic acquisition, ease and rapidity of cultural transmission, hyperactivity

and difficulty in inhibiting operation even in the face of contrary instruction, selective cerebral localization or impairment, evolutionary analogies, functional phylogenetic homologies, imperfect but ecologically performative design' (Atran 2001). In short, adaptedness assumes that the functional correlation between environmental conditions, the organism's current state and that organism's response to this situation are founded on specific, pre-assigned systems and executed through unavoidable, pre-programmed structural links.

2.2. Adaptability

If the radically adapted corresponds closely to the obligate, the adaptable is by no means identical with the facultative. The latter vary from the way certain bacteria and yeasts can switch between aerobic and anaerobic production of ATP in different atmospheric conditions, to various kinds of maternal effect on embryonic development (Bernardo 1996), to the female spadefoot toad's choice of a heterospecific mate when circumstances favour hybridisation (Pfennig 2007), to the formation of calluses on the human hand. However, facultativeness as such neither requires nor entails the ability to do this via freely varying the structures applied to perform a given function, or *vice versa*. Likewise adaptability's specific difference from the idea of generalised structures supporting a wide range of functions (e.g., Tooby and DeVore 1987) or other kinds of organismic plasticity, which include to the ability to exploit memory, learning, habituation, and so on in the interests of refining and optimising an already established relationship between structure and function.

In short, other forms of plasticity lack the organisational flexibility - the 'mix-and-match' approach – adaptability exhibits when linking structures and functions to one another, and to do so in the very course of activity. As least as defined here, adaptability consists of just this dissociation of the organism's available structures from *any* particular type of functioning, and *vice versa*. As a result, the highly adaptable organism can perform many different kinds of functioning with a relatively small repertoire of general-purpose tools (Lorenz 1977: 142-146), without the link between structure and function being given (programmed, encoded, or otherwise determined) in advance. Conversely, the adaptable organism can execute the

same function via a range of structures that is limited only by the objective appropriateness of the structures at its disposal to the objective requirements of that function – an option that is simply not open to the adapted organism. In other words, for an adaptable organism, the structures at its disposal are elicited *by* the situation according to functional relevance, not imposed *upon* the situation by evolutionary *fiat*.

That is not to say the adaptable organism needs to be aware of the objective suitability of structure to function or *vice versa*) – adaptability is not equivalent to intelligence (Robinson 2005) - but it is to say relevance predominates over programming in direct proportion to how adaptability predominates over adaptedness. In short, so although all adaptable adaptations are necessarily plastic, the plastic is not necessarily adaptable.

This is not an absolute distinction, of course. It is very likely that, evolutionarily speaking, adaptability is closely related to other forms of plasticity, if only because it is difficult to imagine how a fully developed dissociation between structure and function could have appeared without facultative and generalised precursors, or without being oiled on the developmental plane by learning and memory. However, once it has been established, it seems equally likely that it permits development as such to move to centre stage as far as adaptation is concerned, and for the importance of evolution as such to be highly qualified, if not actually displaced, as its principal mechanism. From an evolutionary point of view, adaptability endows the individual organism with the power to introduce radical structural variations into its functioning without waiting for the improbabilities of variation and selection on which a more adapted organism would be obliged to attend. If a particular approach does not suit a particular situation, the adaptable organism may be able to create the same outcome by a different route. Nor, once it has constructed a given structure, is an adaptable organism obliged to persisting with that structure in future. On the contrary, as evolution moves towards the more adaptable end of the spectrum, not only ontogeny but each particular act tends to be constructed rather than simply elicited from a pre-existing repertoire.

2.3. Aspects of adaptability

Short of its obvious presence among human beings, it can be difficult to demonstrate that adaptability is a significant (or even a real) phenomenon. It is not especially obvious in modestly adaptable organisms such as reptiles or most mammals and birds. However, there are conditions where the alternatives seem inadequate. These generally arise where the relationship between organism and environment undergoes radical change, be it through the organism's adoption of a radically new approach to an existing problem or by the organism being thrust into a new environment in which no plausible facultative adaptation is likely to exist and the normal forces of variation and selection would be too slow to provide solutions to the pressing problems of survival and reproduction.

For example, behavioural flexibility and innovation are closely aligned with the ability to deal with a wider and richer range of sources of nutrition, to respond to seasonal changes or to occupy new regions in genuinely innovative ways (Lefebvre, Reader, and Sol 2004). Indeed, highly adaptable organisms can create forms of activity that are astonishingly novel. For example, rats can compensate for surgically excised pancreas, parathyroid, thyroid and adrenal glands by changes in their behaviour – literally life-saving accomplishments, yet hardly contingencies for which they could have previously evolved strictly adapted responses, even as facultative adaptations (Richter, quoted in McFarland 1985: 276-277; on the general role of behavioural and physiological plasticity in resolving conflicts, see Mrosovsky 1990: Chapter 2).

On the other hand, it may also be adaptability (rather than, for example, exaptation - Anderson 2007) that explains why, though many species fail when introduced into a new environment, others sweep all before them, even though they are far less directly adapted to local conditions than native competitors. Hence the extraordinarily swift destruction of innumerable once-thriving oceanic island populations when confronted by rats and cats for the first time – holocausts whose rapidity make it hard to believe that, say, learning could explain them. Hence - perhaps (Barnosky *et al.* 2002) - the extinction of almost every large

mammal in Australia and the Americas shortly after the first human hunters – the ultimate in adaptability – appeared on the scene. In each case the invaders seem to have needed genuine adaptability to prevail in conditions to which they had no relevant forms of adaptedness.

In fact among *Homo sapiens* the dynamism and versatility adaptability bestows can scarcely be ignored. To take a very simple example: callusing. As in other organisms, human calluses are *formed* by a facultative adaptation that assumes little or no adaptability (in the present sense), which is to say, through the normal functioning of very specific structures, which cannot in turn be used for much else. However, calluses can be both *prevented* and actively *removed* by virtue of our adaptability. As far as prevention is concerned, human beings have developed a variety of devices, from gloves to hand creams to servants to machines, that prevent calluses from forming. Likewise, when we remove them with anything from warm water and a pumice stone to skin surgery, this is clearly not a facultative adaptation in the usual sense. Not only does using a pumice stone not seem to be the product of any pre-adapted structures but if we were to discover another method of removing calluses tomorrow (e.g., Robinson 2007: 96), we could equally well use that. Likewise, if we find another use for the pumice stone (as we certainly have for warm water), that too could be instantly put to other purposes. This is very different from the strictly facultative process by which the callus appeared in the first place.

There are many more general circumstances in which the ability to recombine, substitute and interpolate new components more or less freely into old routines or to synthesise new routines from established structures would plainly be a useful alternative to specific facultative variants or the limited refinements we are offered by learning. Many of the most dramatic events an organism can face, be it a volcanic eruption or a novel infection, operate on timescales that are too short for learning, let alone for the reproductive cycle of the organism (and therefore evolution) to address. On the other hand, one of the major evolutionary lifecycle strategies, namely lengthening the organism's lifespan, increases both

the likelihood of particular organisms being confronted by eventualities to which they have no facultative response. Likewise a second adaptive strategy - migration to new niches (Plotkin and Odling-Smee 1979, 1981; Levins and Lewontin 1985; Lewontin 1991: 107-123; Waddington 1969: 106-128) is almost designed to spring unprecedented surprises on the migrating population. And in all these cases, it is perhaps above all the sheer number and variety of occasions on which something genuinely unpredictable (by evolution, at least) may arise that creates a selective pressure for adaptability as such.

All in all, the problem adaptability helps solve is simple and, for any but the most adapted species, all but universal: the problem of 'uncertain futures' (Waddington 1969, 'Paradigm for an evolutionary process'). As Oyama has put it: 'We live in *many* worlds, all different from the ones that existed many thousands of years ago, and each world, even if reduced to the unique world of the individual, is not unitary. It is composed of roles and settings that may overlap, conflict, and impinge on other complex worlds; it changes, sometimes rapidly and not necessarily in synchrony with others' (Oyama 2000: 104; see also Gray 2000 or Oyama *et al.* 2001). In such conditions, genuine adaptability may not only be advantageous: it may be the only game in town.

3. Adaptability and development

One direct corollary of the reciprocity of adaptability and adaptedness is the changing balance between evolution and development. Explanation in terms of adaptability rather than adaptedness focuses not on structural end-points such as fixed genes or neural structures but on the operational and developmental pathways through which a functional solution is reached. Conversely, the role of pre-adapted structures in developmentally oriented explanations is to provide a global platform and generic resources out of which a multiplicity of *transient* and *reversible* adaptations can be dynamically constructed, as determined by the demands of the individual organism's current activity, through which activity the *process* of adaptation actually takes place. In other words, for adaptability, adaptations are actively

synthesised in the course of performing the required function – which is to say, in the course of development, not evolution.

So the balance between evolution and development shifts as adaptability comes to predominate over adaptedness. At the pre-adapted extreme, although all development takes place in interaction with a definite environment even when most canalised by heredity or experience (Gottlieb 1991a, 1991b; Moore 2001; Waddington 1957), it would be hard to demonstrate that development plays much active part in the life of the nematode or the common housefly. After all, how different can one fly be from another, not matter how diverse their environments? Even among altricial species, parental nesting and brooding practices such as viviparity and building hives often tend to minimise the variation their neonates face in the ante- and perinatal environments, and so minimise the need for adaptability.

A little further along the continuum (if that is the right metaphor), adaptability may do no more than expand the organism's developmental options, providing a more flexible route by which the mature organism may come to possess essentially the same structures, talents and propensities as all other members of its species. In such cases, where the possible effects of adaptability (and other form of flexibility) are still quite narrowly prescribed, evolution continues to predominate, with development simply tuning the body, selecting and adapting it to that particular organism's niche, and so on. Even here, it is still adaptedness that explains *what* the organism is, with adaptability serving only to refine how it gets that way. Development is still tactical, not strategic: it may help to determine exactly how the organism operates, so to speak, but not its nature or 'goals'.

But in yet more adaptable species, adaptability may itself be the developmental strategy, with no final laying down of any very narrowly fixed nature. Hence perhaps the more or less open-ended malleability of some aspects of the human central nervous system. For example, many neural mappings maintain a considerable degree of adaptability well into adulthood (Bruehlmeier *et al.* 1998; Edelman 1987; Jenkins *et al.* 1984; Kaas *et al.* 1983). On that level, development and evolution must be regarded as partners, with ontogeny the partner of

phylogeny in the definition of at least some aspects of the organism, and epigenesis capable of throwing up genuine surprises.

Finally, a radically adaptable structure such as intelligence may possess the ability not only to match structures to functions more or less freely but also to adapt still further to the products of its own adaptability, to the products of its neighbours' activity, and so on. Once that is possible, it is hard to avoid concluding that development is capable of inventing unprecedented realities of the kind that litter human history. Although there is no space here to make the point in any detail, there are grounds for believing that it is this very adaptability that set *Homo sapiens* off on its unique odyssey and led to the creation of the true wonders of the human world, such as true political and economic systems, science, ideological forms such as art, religion and philosophy, and so on (Robinson 2004, 2005).

But whatever the exact trajectory of human nature, there seem to be few significant biological differences between the inhabitants of Cro-Magnon or Lascaux and modern-day London, Bangalore or Kinshasa, or even California, so we are obliged to conclude that these are all strictly developmental productions – which, I believe, could only have come to the fore by virtue of our radical adaptability. Yet they are as novel to life in general as the functions introduced by life itself – including evolution, adaptation and epigenesis - were novel to non-living matter (Robinson 2005). Indeed, the change from savannah scavenger to office worker is so great that in any less adaptable organism it would raise doubts about whether we and our forebears were even members of the same species. Yet this same change is readily accommodated once it is accepted that adaptability may achieve a radical ascendancy over adaptedness, and so liberate the powers of development to the point where it throws the very notion of a determinate 'human nature' into question.

Indeed, we have a term for the vast leeway radical adaptability creates for development, within which evolution plays practically no role: it is called 'history'.

4. The evolutionary implications of adaptability

This argument will probably seem straightforward to most biologists. Yet the distinction between adaptedness and adaptability has consequences that have not, as far as I am aware, been integrated into our model of evolution. These consequences bear on many of the mostly widely used concepts in evolutionary theory, of which two are especially important: the 'environment of evolutionary adaptation' (EEA), and the 'fitness landscape.

Such concepts are applied not only by evolutionary biologists and physical anthropologists but also (sometimes with alarming casualness) by social anthropologists, psychologists, economists, sociologists, philosophers and even the occasional historian. Nevertheless, broadly speaking, none of these concepts can be applied without a good deal of qualification to any species that exhibits a high level of adaptability. To the extent that human beings – who have so often been analysed in terms of their adaptedness to this or that (generally pre-historic) environment – are the acme of adaptability, they are of such doubtful value as to be not only almost wholly irrelevant but also profoundly misleading.

4.1. The environment of evolutionary adaptation

That adaptation fits a species to its specific niche through the selection of equally specific modifications is scarcely open to doubt. There is, as I have already noted, generally an element of local plasticity that allows a particular adaptation to be better attuned and re-attuned to the exact details of any particular organism's unique circumstances, especially where the species' niche is somewhat complex or dynamic, but to a very large extent the main dimensions of such adaptation have demonstrably been laid down in pre-adapted form. But in any case where adaptability is present and reaches a high level and the various adapted organs and skills at the organism's disposal can be applied in highly configurable and reversible ways – as in many primates, aquatic mammals and quite a few birds - then adaptability carries precisely the opposite message: that whatever the original function of a

given structure or the particular niche in which it originally evolved, it cannot sensibly be regarded as uniquely, or even especially well, specified for either.

To invoke the computer analogy generally much admired by the scientifically inclined, the fact that the innards of my computer are highly structured doesn't prevent them from carrying out a remarkably diverse set of tasks. And the fact that much of the underlying technology was developed with military applications in mind doesn't entail that my computer is constantly on the verge of planning a nuclear attack, or designing some instrument of mass destruction. (Dupré 2001: 58)

Indeed, our current extraordinary level of adaptability renders a huge range of environments more or less equivalent from *Homo sapiens sapiens'* point of view, however diverse the practical problems of coping with each might be. So, if human beings evolved in some kind of hunter-gatherer society inhabiting the savannahs of east Africa, does that make those savannahs our 'environment of evolutionary adaptation'? If this question means, Was that the particular niche in which we happen to have developed our extraordinary capabilities, then Yes, it was. However, if it means, Are those same savannahs the niche to which we are peculiarly adapted, and if we stray too far from them (or something equivalent) we are likely to find ourselves out of tune with our environment, then No, it does not. For an organism as radically adaptable as a human being, no environment is its EEA in this latter, more technically precise sense. We had to emerge somewhere, of course, but the same forms of adaptability might easily have emerged from any number of other, biologically quite distinct environments. Conversely, having evolved these adaptations in one environment, we should still find any number of other environments just as congenial as that original Eden. Indeed, the 'norm of reaction' for radical adaptability is increasingly defined not by any particular environmental content or context or by the empirical or functional features defined by a particular niche (current, ancestral, or otherwise), but by the organism's ability to transcend *any* concrete condition or circumstance.

Where does this leave the idea of a hypothetical ancestral environment to which modern human beings are allegedly optimised? Where does it leave the view that the cause of many

a contemporary malaise is the lack of resemblance between the modern world and *Homo sapiens'* environment or evolutionary adaptation? Where does it leave any notion of that most adaptable of human adaptations, namely our intelligence, as an adaptation to *something in particular*? Nowhere, it would seem.

Read in the light (if that is the word) of contemporary evolutionary thinking, this may seem an implausible, not to say absurd claim. How can any adaptation be an adaptation to everything in general? Plainly it cannot, and I am not suggesting that there could ever be an omniscient adaptation that allowed us to thrive in literally any niche. But it is perfectly plausible that an adaptation should be a response to the diversity, complexity and dynamism of life rather than the demands of any particular shopping list of necessary functions or any particular property of our original niche. Conversely, such an adaptation, not being definable in advance, could consist only of the organisational liberty of adaptability as defined here, which is to say, as the twin freedoms to apply one structure to many different functions and to construct a given function out of many different structures.

And this is indeed the path that human evolution has taken: we have preferred flexibility and versatility to specialisation, and have (so to speak) taken a capacity for abstract capabilities such as reason, norms and principles at least as seriously as any particular concrete skills. As a result, human beings are equally 'adapted' not only to savannah, jungle, desert and tundra but also to farmstead, office block, monastery and space craft. Making ourselves at home in any and all of the latter did not require the formation of yet more adaptations; rather, once we possessed the adaptability needed to deal with the former 'niches', human beings could take (and indeed make) the latter in our stride. Our adaptability enables the same human being to be monarch, farmer, stock market speculator, prostitute, industrial worker, miner, housewife, pastoralist, artist, soldier, student, bureaucrat, slave, priest and evolutionary theorist just as readily as hunter, fisher, scavenger or gatherer. And if modern human beings are not obviously an especially contented lot, there are many more

obvious (and proximate and manageable) contributing factors than global biological maladaptation.

Conversely, one might legitimately assume that the *future* development of a radically adaptable organism is equally unconstrained by the nature of both the environment from which it originally emerged and the environment in which it finds itself right now. For the nature of radically adaptable organisms such as human beings liberates them from any particular environment – not only from the rich, diverse but still quite specific environment of the savannahs but from any environment whatsoever. This is no doubt why the highest accomplishments of human cognition, including not only logic and mathematics and scientific method but also the illimitable *potential* undergirded by human culture and technology, are transferable to the fullest possible range of new conditions.

4.2. Fitness landscapes

An analogous critique can be applied to any concept that expects – implicitly or explicitly – the adaptiveness of highly adaptable organisms to be explained by its ‘adaptedness’, which is to say, by the close linkage between the structures and functions through which it adapts. For example, it is debatable to what extent any highly adaptable organism has a ‘fitness landscape’ in the usual sense of this otherwise invaluable term.

A fitness landscape is a multi-dimensional graph showing how variations along different dimensions of adaptation combine to generate an overall level of adaptiveness. Typically the graph shows a number of local peaks or optima at which a given combination of features would normally out-perform any competitor operating on the surrounding slopes and troughs. Sometimes there is also a clear-cut global optimum, which shows the combination of attributes that would defeat all comers anywhere else on the landscape. Although the basic concept of a fitness landscape is complicated by issues such as identifying the graph’s dimensions, testing their orthogonality, quantifying the ruggedness of the landscape, and so on, it offers a simple, powerful tool for reasoning about adaptiveness.

There are various aspects of fitness landscapes that are important here. Firstly, evolution itself can be thought of as a 'walk' across the landscape, with species marching up and down local peaks as they become more or less fit. Secondly, a fitness landscape is a logical model, not a physical one: the same empirical niche or environment may represent a different fitness landscape for each of the species, organisms and variations that occupy it. Likewise, as each species evolves, changes its distribution or invades new niches, the fitness landscape changes not only for that species but also for all the other species inhabiting the same fitness 'space'. Finally, species that successfully reach a local optimum may find themselves trapped on what are, from the global perspective, sub-optimal hillocks well below the global peak. For if moving to a higher pinnacle requires the species to traverse a dangerously deep trough, and so fall victim to competition with locally fitter variants and competitors, then no such change is likely to take place. In such a situation, the only hope of further advancement really is a 'hopeful monster'.

Not only individual species but also general developments in life as a whole tend to alter what kinds of fitness landscapes are likely to exist and how they behave. The increases in complexity and variability that flow from the emergence of, say, sexual reproduction or central nervous systems will also tend both to destabilise fitness landscapes and to amplify the contrast between adapted and adaptable species' respective ability to deal with change. On the other hand, to the extent that direct inter-species competition dominates a species' landscape, highly adapted species will be increasingly hard-pressed to reach even local optima, which will not only be relatively 'sharp' (and so hard to find) but also highly unstable (and so hard to keep track of). What is more, not only is a relatively adaptable species inherently better equipped to meet these demands but its greater versatility and dynamism will actively raise the local optimum, which in turn exacerbates the plight of its adapted competitors. As a result, the adaptable species will have far less difficulty in sustaining its position at or near the local optimum. For example, the stability of landscapes will be reduced by the increased directness and dynamism of competition that arises between animals, as

opposed to the indirectness and static nature of competition between plants. On the other hand, where direct competition of this kind is relatively weak, adaptedness is likely to have the upper hand.

Nor is navigating the fitness landscape the same for adapted and adaptable species. Far from requiring the evolutionary push of inter-generational variation to move from optimum to optimum, for adaptable species such leaps will be increasingly at its individual disposal and can be deployed within the lifetimes of particular organisms. That is not to guarantee that any given optimum is necessarily within reach, but the mere fact of being able to move across the landscape by self-reconfiguration, and so without having to painstakingly traverse the intervening plains and chasms variation by variation, and moreover to be able to do so within the lifetime of a single organism, is obviously a significant advantage.

Indeed, the more adaptable the species the more likely it is, in different expressions, to occupy *multiple* local optima at the same time, with each single optimum representing just one of the many combinations of capabilities at its disposal. This may even extend to the point where, as well as occupying a single local peak, the adaptable organism could colonise *all* the local optima simultaneously – and ultimately, the global optimum. What is more, to achieve this the adaptable organism is not required to *cross* the troughs that separate optima (and so, improbably, surrender its current adaptive advantages). Rather, its ability to reconfigure its activity dynamically allows a highly adaptable organism to exit Optimum A and re-emerge at Optimum Z without having passed through sub-optimal points B, C, D, and all the rest. So what are to more adapted organisms radically different regions of the landscape, separated by obstacles of every kind, will be, to the adaptable organism, essentially the same place, because the same combination of adaptable elements may be actively recombined to deal with quite different contexts and contents.

Whether these differences have any effect on the evolutionary process depends on the same issues as the relative effectiveness of adaptability generally. A rugged fitness landscape is fine for the specifically adapted organism as long as the local optimum is quite

close by, the troughs that shield it from competitors deep, and its local region does not change too quickly or too drastically to be tracked by routine variation and selection. But when conditions begin to close in on such a species, its days are very likely numbered. An adaptable species, by contrast, is likely to be relatively successful in an unstable landscape, but far less so in a stable, clearly delineated niche where adapted organisms can achieve a comparable level of adaptation without expending as much energy on 'expensive' tissues (Aiello and Wheeler 1995) or elegant but useless sophistication. But generally speaking, as the adaptable organism's fitness landscape changes and local optima rise, fall and migrate across the landscape as a whole, not only will it find tracking these changes easier but, in proportion to its adaptability, these will not *be* changes from that organism's point of view. The same adaptable organism (and so, *a fortiori*, species) may be just as capable of elaborating the newly required competence as the old one without undergoing any further evolution.

In summary, where adaptability predominates to the extent that we observe among human beings, of what value or meaning is the concept of a fitness landscape? If a single species can move through its fitness landscape at will, leaping from one optimum to the another without passing through any intervening space, this is tantamount to abolishing the very geometry that gives the landscape metaphor – and the technical model - its meaning. If the same species can leap from peak to peak then the landscape is reduced to a completely flat surface, if not a single point. In other words, when it approaches the extremes that characterise human intelligence, adaptability effectively annihilates the very landscape onto which evolutionary theory would map it.

5. Conclusions

Of course, whatever qualifications this account of adaptability may suggest, concepts like 'fitness landscape' and 'environment of evolutionary adaptation' remain as valuable as ever to evolutionary theory as a whole. However, the more adaptable the species to which they

are applied the more closely their use needs to be scrutinised. Quite a few other evolutionary concepts, notably homology by common descent (Robinson, in preparation), life history strategy and modularity, would probably benefit from similar scrutiny.

A more general evolutionary corollary of high levels of adaptability is that, for a highly adaptable organism, very little about what it actually does can be said to have 'evolved'. In an indirect sense all its capabilities can be said to have evolved, of course, but to the extent that its concrete actions and experience reflect the adaptable configuration and reconfiguration of these or those structures as the situation changes and different threats and opportunities emerge, to say that any particular configuration itself evolved would be misleading. Indeed, given how central adaptability seems to be to most of the central features of a specifically human existence, it is increasingly difficult to speak of the 'evolution' of anything about human beings beyond their most general features.

6. References

- Aiello, L.C. and Wheeler, P. (1995). The expensive-tissue hypothesis: The brain and the digestive system in human and primate evolution. *Current Anthropology*. Vol. 36, No. 2, 199–221.
- Anderson, M.L. (2007). Evolution of cognitive function via redeployment of brain areas. *The Neuroscientist*, 13(1): 13-21. DOI: 10.1177/1073858406294706
- Atran, S. (2001). A cheater-detection module? Dubious interpretations of the Wason selection task and logic. *Evolution and Cognition* 1(2): 1-7.
- Barnosky, A.D., Koch, P.L., Feranec, R.S., Wing, S.L., Shabel, A.L. (2004). Assessing the causes of late Pleistocene extinctions on the continents. *Science* Vol. 306, no. 5693: 70-75.
- Bernardo, J. (1996). Maternal effects in animal ecology. *Am. Zool.* 36: 83–105.
- Bonner, J.T. (1974). *On Development*. Cambridge: Harvard University Press.
- Bruehlmeier, M., Dietz, V., Leenders, K. L., Roelcke, U., Missimer, J., and Curt, A. (1998). How does the human brain deal with a spinal cord injury? *European Journal of Neuroscience* 10 (12), 3918–3922.
- Dupré, J. (2001). *Human Nature and the Limits of Science*. Oxford: Oxford University Press.
- Edelman, G.M. (1987). *Neural Darwinism: Theory of Neuronal Group Selection*. New York: Basic Books.
- Fodor, J.A. (1983). *The Modularity of Mind*. Cambridge, Massachusetts: MIT Press.
- Gottlieb, G.(1991). Experimental canalization of behavioral development: Theory. *Developmental Psychology* 27: 4-13.

- Gottlieb, G.(1991). Experimental canalization of behavioral development: Results. *Developmental Psychology* 27: 35-39.
- Gould, S.J., and Vrba, E.S. (1982). Exaptation - a missing term in the science of form. *Paleobiology* 8: 4-15.
- Gray, R.D. (2000). Selfish genes or developmental systems? In Singh *et al.* (2000: 184-207).
- Jenkins, W.M., Merzenich, M.M., Ochs, M.T. (1984) Behaviorally controlled differential use of restricted hand surfaces induces changes in the cortical representation of the hand in area 3b of adult owl monkeys. *Soc. Neurosci. Abstr.*, 10:665
- Kaas, J.H., Merzenich, M.M., Killackey, H.P. (1983) The reorganization of somatosensory cortex following peripheral nerve damage in adult and developing mammals. *Ann. Rev. Neurosci.*, 6:325{56.}
- Lefebvre, L., Reader, S.M. and Sol, D. (2004). Brain, innovation and evolution in birds and primates. *Brain, Behavior and Evolution*, 63: 233-246
- Levins, R. and Lewontin, R. (1985). *The Dialectical Biologist*. London: Harvard University Press.
- Lorenz, K. (1977). *Behind the Mirror: A Search for a Natural History of Human Knowledge*. London: Methuen.
- McFarland, D. (1985). *Animal Behaviour: Psychobiology, Ethology and Evolution*. London: Longman Scientific and Technical.
- Moore, D.S. (2001). *The Dependent Gene. The Fallacy of 'Nature vs Nurture'*. New York: W.H. Freeman.
- Mrosovsky, N. (1990) *Rheostasis. The Physiology of Change*. Oxford: Oxford University Press.
- Oyama, S. (2000). *The Ontogeny of Information. Developmental Systems and Evolution*. Second edition. Durham, N.C.: Duke University Press.
- Oyama, S., Griffiths, P.E., and Gray, R.D. (2001). *Cycles of Contingency. Developmental Systems and Evolution*. Cambridge, Mass.: MIT Press.
- Pfennig, K.S. (2007). Facultative mate choice drives adaptive hybridization. *Science*, 318 (5852): 965 – 967.
- Plotkin, H.C. and Odling-Smee, F.J. (1981). A multiple-level model of evolution and its implications for sociobiology. *Behavioral and Brain Sciences*, 4: 225–268.
- Robinson, H. (2007). *Contraptions*. London: Duckworth Overlook.
- Robinson, R.J. (2004). *The History of Human Reason*. Prometheus Research Group: www.prometheus.org.uk.
- Robinson, R.J. (2005). *The Birth of Reason*. Prometheus Research Group. Electronic document: <http://www.prometheus.org.uk>.
- Robinson, R.J. (in preparation). Homology without common descent.
- Rozin, P. (1976). The evolution of intelligence and access to the cognitive unconsciousness. *Progress in Psychology and Physiological Psychology*, 6: 245-280.
- Thompson, J.N. (1994). *The Coevolutionary Process*. Chicago: Chicago University Press.
- Tooby, J., and DeVore, I. (1987). The reconstruction of hominid behavioral evolution through strategic modelling. In Kinzey (1987: 183-237).
- Waddington, C.H. (1957). *The Strategy of the Genes*. London: Allen and Unwin.

Waddington, C.H. (ed.) (1969). *Towards a Theoretical Biology*, vol. 2. Edinburgh: Edinburgh University Press.