The return of the whole organism

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The long trend towards analysis at lower and lower levels is starting to reverse. The new integrative studies must make use of the resources uncovered by molecular biology but should also use the characteristics of whole organisms to measure the outcomes of developmental processes. Two examples are given of how movement between levels of analysis is being used with increasing power and promise. The first is the study of behavioural imprinting in birds where many of the molecular and neural mechanisms involved have been uncovered and are now being integrated to explain the behaviour of the whole animal. The second is the triggering during sensitive periods in early life by environmental events of one of several alternative modes of development leading to different phenotypes. A renewed focus on the whole organism is also starting to change the face of evolutionary biology. The decision-making and adaptability of the organism is recognized an important driver of evolution and is increasingly seen as an alternative to the gene-focused views.

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1. Introduction

The sheer excitement of uncovering the molecular biology of the gene has provided a powerful incentive for young biologists entering the field. Moreover, as the possibilities for biotechnology opened up, this new generation could look forward to certain employment. These opportunities have had their down side. Anybody working in a biology department of a university over the last quarter of a century must have been aware of the way in which whole areas of comparative physiology and behaviour have been steadily depleted of active research workers.

Two changes in thought are bringing this long trend to halt. First, it has become obvious that reductionism has its limits. Eventually, the mass of detail from yet lower levels of analysis provides no more explanatory power. An appropriate base for understanding the whole organism will be the gene at the lowest level and, in the case of an animal's behaviour, it will usually be at the level of its nervous system. The point is well illustrated in many essays in the book edited by Bock and Goode (1998). Secondly, my own sense is that the drive to understand the molecular mechanisms of inheritance has reached its apogee, though much detailed work doubtless remains to be done.

The ability to sequence genomes was a great scientific achievement. The much-heralded publication of the human genome does not and cannot provide the hoped for "Book of Life" that would enable us to understand all aspects of human nature. Numerous post-genomic projects are based on the assumption that, if clever enough mathematics and sufficient informatics were applied to the problem, somehow the code for the characteristics of whole human beings would be laid bare. The problem for biology in the post-genomic era is not, however, one of cryptography. Genes code for proteins not people. If we want to understand what happens in the life-long process from conception to death, we must study the process by which an embryo becomes a child and a child becomes an adult. Moreover, the nexus of interactions between gene expression and behaviour of the individual must be related to the current utility of behaviour and its evolutionary origins.

As developmental biology has come of age, the links with evolutionary theory have grown in the so-called "Evo-Devo" movement (Akam *et al* 1994; Raff 1996). In the

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thinking about the origin of species, increasing emphasis has been placed on the importance of gene-gene interaction (epistasis). Post-zygotic isolation is thought to result from an interaction between two or more genes. As Orr and Presgraves (2000) point out, this model highlights the importance of epistasis in evolution. Though credit is usually given to Dobzhansky (1937) and Muller (1940), Orr and Presgraves (2000) note that the problem was first solved by William Bateson (1909). Once epistasis was recognized as important in the developmental process, the factors influencing phenotypic characters were less profitably thought about in terms of the genes as units but in terms of the factors that are generated downstream. Even in the simplest case, the physical interplay is not strictly between genes but between the products of genes.

At one time a commonly expressed view in the behaviour genetics literature was that genes usually interact in additive fashion (Broadhurst 1979). In part this may have arisen because the biometrical advice was to rescale data until a way has been found to minimize the non-additive interactions (Mather and Jinks 1971). This procedure made for simple genetic models but did not in itself provide evidence for the absence of interplay between the different factors affecting development. Equally important, epistasis could easily be missed if only first generation of hybrids between two pure bred lines were examined. The first generation of hybrids carry an almost complete set of alleles from each relatively homozygous parent. Consequently, when relevant genes are not suppressed, the hybrid phenotype is influenced by and benefits from either or both sets of genes from their parents. In such circumstances the possibility of statistical interactions between genes at different loci only becomes apparent after resegregation in the second generation of hybrids (Bateson and D'Udine 1986). These general issues raise the question of what precisely happens in an individual's development.

An important synthesis, sometimes described as Developmental Systems Theory, has been assembled by Oyama *et al* (2001) and their edited book provides an invaluable modern source (see also Gottloeb 1997). Lehrman (1970) set the scene for this approach when he argued that the interaction out of which the organism develops is between organism and environment as opposed to heredity and environment. His wise point has been accepted in the literature on behavioural development for a long time. The importance becomes obvious when examining specific examples and I shall give two here.

2. Behavioural imprinting

Imprinting in birds is an example of tightly constrained learning occurring at a particular stage in the life-cycle. The predispositions to respond to particular features and give particular responses to the stimulus are central to understanding the process. Perhaps the most important conclusion from the behavioural work is the need to think of a given phenomenon in terms of a series of sub-processes. Bateson and Horn (1994), who developed a neural net model, referred to these sub-processes as "modules". The work on imprinting has focused on the analysis of the features of the stimuli that start off the formation of the social attachment, the establishment of a representation of that combination of features and the linking of such a representation to the system controlling social behaviour (Bateson 1990; Hollis *et al* 1991). Different sub-processes have different underlying rules for plastic change. Contiguity of the various elements is likely to be important in forming a category, whereas contingency is crucial in learning that is dependent on external reward (Bateson 2000).

Inferences about the sub-processes involved in an overall transaction with its environment are being examined at the neural level. The intermediate and medial part of the hyperstriatum ventrale (IMHV) has been implicated as the site of a neural representation of the imprinting object by an array of different neurobiological techniques (Horn 1985, 2000). In locating the neural seat of imprinting located, it was not good enough simply to show that a particular part of the brain is active when the bird is learning about the imprinting object. This is because lots of other things happen during the imprinting process: the young bird is visually stimulated and aroused by the imprinting object and it also tries to approach and follow the object. All these processes produce their own changes in brain activity. When experimental evidence is open to a variety of different interpretations, greater confidence in one particular explanation can be attained by tackling the problem from a number of different angles.

In the case of imprinting, the first approach took advantage of the fact that, in birds, all the sensory input to the brain from one eye can be restricted to one hemisphere of the brain by cutting a bundle of nerve fibres running between the two hemispheres. After this had been done, one of the chick's eyes was covered with a patch, so that it could only see the imprinting object (a flashing rotating light) through one eye. This procedure meant that only one side of the chick's brain was exposed to sensory information about the imprinting object. When this was done, a difference in brain activity between the exposed and unexposed sides of the chick's brain was found only in the forebrain roof. No differences between the two sides were observed in other regions of the brain. This 'split brain' technique eliminated the possibility that both sides of the brain were affected equally by training (Horn *et al* 1973). However, it did not exclude the possibility that the enhanced brain activity was due to greater visual stimulation of the trained side. Other procedures were therefore needed.

Another set of experiments exploited individual variation in the chicks. Various aspects of the chicks' behaviour were measured while the chicks were being trained, and their preferences for the familiar object were then tested. This procedure opened up to examination the relationships between behavioural measures of imprinting and neural activity in different parts of the brain. Only one behavioural measure was positively correlated with biochemical activity in the roof of the anterior forebrain – namely, how much the chicks preferred the familiar object to a novel object when given a choice between the two. This index of learning was not correlated with biochemical activity in any other region of the brain and, equally important, was only weakly linked with other behavioural measures such as the birds' overall activity and responsiveness (Bateson *et al* 1975). The analysis therefore revealed a specific link between a behavioural measure of imprinting and biochemical activity in a part of the brain that had already been implicated as the seat of imprinting in other experiments.

The final component in narrowing down the range of explanations was to exploit the asymptotic character of learning: a phase of rapid change is followed by one of much slower change. Therefore, animals that are at the rapid phase will be likely to show greater activity in brain sites that are specifically involved in learning than those that have moved onto the slower phase, even though many other aspects of the animals' experience and activity are matched. Animals may be prepared in advance by under-training them or over-training them on the task in question. This technique was successfully exploited when identifying the role of IMHV as a site for the neural representation of the imprinting object in imprinting (Bateson *et al* 1973; Horn *et al* 1979).

Each piece of evidence obtained by the different approaches was ambiguous, but the ambiguities were different in each case. When the whole body of evidence was considered, therefore, much greater confidence could be placed on a particular meaning. An analogy is trying to locate on a map the position of a visible mountain top. One compass bearing is rarely enough. Two bearings from different angles provide a much better fix and three bearings give the most reliable position for the top. The strong inference from the triangulation studies of the neural basis of imprinting was that the IMHV did, indeed, represent the site where a representation of the imprinting object was formed.

Chicks that have had both left and right IMHV removed surgically are unable to imprint and if bilateral lesions are placed immediately after imprinting, the birds show no recognition of the imprinting object (Horn 1985). Nevertheless, these lesioned chicks will show a preference for a stimulus that has a head and neck feature over one that does not, thereby dissociating the analysis component of the imprinting process from the recognition component. The lesioning experiments also dissociated recognition learning from learning involving external reward. Chicks will learn a visual discrimination rewarded with heat after bilateral removal of IMHV (Cipolla-Neto *et al* 1982; Honey *et al* 1995). They will also learn to press a pedal rewarded by the view of an imprinting stimulus even though they do not go on to learn the characteristics of that stimulus (Johnson and Horn 1986).

Many of the detailed cellular and molecular events occurring in IMHV are beginning to be worked out (Solomonia et al 2000) and the physiology of the system is described (Horn 1998, 2000). However, the links between imprinting and other learning processes occurring in parallel with it are still poorly understood. The behavioural theories undoubtedly make assumptions about the nervous system and these assumptions may prove to be false. As the neural understanding grows, the inquiry has to return to the behavioural level so that the parts may be reassembled and, if necessary, new behavioural experiments may have to be done. This is a very different picture from that of a classical reductionist approach in which the behavioural people hand a problem to the neural people who, having made their contribution, hand it on to the molecular people. The return flow of ideas from lower to higher levels of analysis now seems a much more attractive and plausible picture of collaboration between disciplines (Johnston and Edwards 2002).

3. Environmental triggers

Behavioural imprinting provides one of the classic examples of sensitive periods in development where a given input from the environment is much more effective at one stage in the life-cycle, usually an early one, than at others. Gradually, it has been appreciated how widespread sensitive periods are and, when the development of a range of phenotypes can be triggered during these periods, how important they can be to the life history of the organism. Many species of both plants and animals have the capacity to develop in a variety of different ways (Caro and Bateson 1986; Lott 1991; Schlichting and Pigliucci 1998; West-Eberhard 2003). These alternative modes of development are often referred to as "reaction norms" (Schmalhausen 1949) or "polyphenisms" (Mayr 1963). The castes of the social insects and solitary/migratory phases of locusts have been known for many years. Another striking insect example is provided by the alternative phenotypes of grasshoppers. After a fire on the high grassland planes of East Africa, the recently hatched grasshoppers of the eggs that survive are black instead of being the normal grey or yellowish-green. Something has switched the course of their development onto a different track. The grasshopper's colour makes a big difference to the risk

that it will be spotted and eaten by a bird, and the scorched grassland may remain black for many months after a fire. So matching its body colour to the blackened background is important for its survival. The developmental mechanism for making this switch in body colour is automatic and depends on the amount of light reflected from the ground. If the young grasshoppers are placed on black paper they are black when they moult to the next stage (Rowell 1971). If they are placed on pale paper, however, the moulting grasshoppers are the normal grey or green colour. The grasshoppers actively select habitats with colours which match their own. If the colour of the background changes they can also change their colour at the next moult to match the background, but they are committed to a colour once they reach adulthood.

Each grasshopper starts life with the capacity to take one of two distinctly different developmental routes – becoming green or black. A particular feature of the environment determined the path taken by the individual for the rest of its life. And once committed, the individual cannot switch to the other route. Once black as an adult, the grasshopper cannot subsequently change its colour to green.

The implication of such phenomena is that environmental induction involves a prediction about the conditions of the world that the individual will subsequently inhabit. In mammals the best route for such a forecast is often via the mother. Vole pups born in the autumn have much thicker coats than those born in spring; the cue to produce a thicker coat is provided by the mother before birth (Lee and Zucker 1988). The value of preparing in this way for colder weather is obvious.

Weaning represents a period of major transition for young mammals, marking a change from complete dependence on parental care to partial or complete independence. This transition, which is shown most obviously by the change in food source, involves a whole range of behavioural and physiological changes on the part of both mother and offspring (Martin 1984). If, as is likely for a variety of reasons, the time of weaning may vary according to factors such as maternal food supply, then the developing offspring must be able to adapt by altering its behaviour accordingly (Bateson 1981). Domestic cats do so (Bateson *et al* 1981, 1990; Bateson and Young 1981; Martin and Bateson 1985; Tan and Counsilman 1985) exhibiting a higher rate of play after early weaning. This may mark a conditional response by the kitten to enforced early independence, boosting the benefits of play before complete independence. Similar contingent development is found in the rat (Smith 1991; Gomendio *et al* 1995).

Human development may also involve environmental cues that prepare the individual for the sort of environment in which it is likely to live. Men who had had the lowest body-weights at birth and at one year of age were most likely to die from cardiovascular disease later in life (Barker 1998). Those born as the heaviest babies and brought up in affluent environments enjoyed a much reduced risk of dying from cardiovascular disease or developing many other diseases such as non-insulin-dependent diabetes. These ill-effects of low birth weight are usually treated as yet another pathological consequence of poverty. However, a functional and evolutionary approach suggests that possibly the pregnant woman in poor nutritional condition unwittingly signals to her unborn baby that the environment which her child is about enter is likely to be harsh. If so, this weather forecast from the mother's body may result in her baby being born with adaptations, such as a small body and a modified metabolism, helping the child to cope with a shortage of food. This hypothetical set of adaptations has been called the 'thrifty phenotype' (Hales and Barker 1992; Hales *et al* 1997). Perhaps these individuals with a thrifty phenotype, having small bodies and specialized metabolisms adapted to cope with meagre diets, run into problems if, instead, they find themselves growing up in an affluent industrialized society to which they are poorly adapted (Bateson *et al* 2004).

If the functional explanation is correct, why don't individuals adapt continuously to changes in their local conditions during their own life-times? The image of the adaptive landscape used by Wright (1963) in evolutionary biology may be helpful here. His thought was that in the same environment individuals with different gene combinations might be equally well adapted (on equally high mountains using his image), but that going from one mountain to another entailed a loss of fitness. Engineers and economists dealing with optimization problems often find local optima, knowing full well that better solutions can be found. In the context of the evolutionary adaptive landscape, an organism may reach the top of one mountain. While it might be beneficial to cross over to a higher mountain, getting from a low mountaintop to a higher one involves going downhill before climbing once again. The same image may be used in development. Once a phenotype is fully formed, it may be difficult to switch to another phenotype that has become more beneficial because of a change in local conditions. A body, once built, is difficult to alter. Making fundamental changes to mature behaviour patterns or personality traits will similarly take time, resources and quite possibly support from others. Adults have important tasks to carry out, such as feeding and caring for their family, and cannot readily dissolve themselves and re-construct their behaviour without others to care for them during the transition phase (Bateson 2001).

The general point is that humans and many other plants and animals, are capable of developing in different ways and, in stable conditions, their characteristics are well

adapted to the environmental conditions in which they find themselves (Moran 1992; McNamara and Houston 1996; Bateson *et al* 2004). Generally such systems of developmental plasticity work well, but in a changing environment they generate poorly adapted phenotypes because the environmental forecast proved to be incorrect. Little is known about the mechanisms involved when the environment triggers a developmental response that is appropriate to those conditions. A powerful hint has provided by a study of the honey bee (Evans and Wheeler 2001). Here the reproductive queen has been shown to express different genes from the sterile workers (Evans and Wheeler 2000). Use of such genomic techniques holds much promise for uncovering the developmental mechanisms. However, different processes will also need to be disentangled. Sometimes the organism makes the best of a bad job in sub-optimal conditions. Sometimes the buffering processes of development may not cope with what has been thrown at the organism (such as thalidomide taken by the human mother to relieve sickness penetrating the placental wall) and a bizarre, maladapted phenotype is generated. Whatever the adaptedness of the phenotype, integration between the different levels of organization is required.

4. The adaptability driver

The various ways in which the behaviour of animals might have changed the course of evolution have become serious areas of inquiry (Bateson 2004; Gottlieb 1992; Weber and Depew 2003). Four major proposals have been made for the ways in which an animal's behaviour could affect subsequent evolution (Bateson 1988; Wcislo 1989). First, animals make active choices and the results of their choices have consequences for subsequent evolution. Second, by their behaviour, animals change the physical or the social conditions with which they and their descendants have to cope and thereby affect the subsequent course of evolution. Third, animals are able to modify their behaviour in response to changed conditions; this allows evolutionary change that otherwise would probably have been prevented by the death of the animals exposed to those conditions. Finally, by their behaviour animals often expose themselves to new conditions that may reveal heritable variability and open up possibilities for evolutionary changes that would not otherwise have taken place. I shall focus here particularly on the third point.

Modern thinking about the importance of adaptability in evolution is usually thought to stem from Baldwin (1896), but Lloyd Morgan (1896) and Osborn (1896) independently developed ideas about "organic selection", as the subject was called at the time. However, Spalding (1873) had raised the idea more than 20 years before. Lloyd Morgan's (1896) account of the postulated process was particularly clear and may be paraphrased as follows:

(i) Suppose that a group of organisms that are capable of change in their own lifetimes are exposed to new environmental conditions.
(ii) Those whose ability to change is equal to the occasion survive. They are modified. Those whose ability is not equal to the occasion are eliminated.
(iii) The modification takes place generation after generation in the changed environmental conditions, but the modification is not inherited. The effects of modification are not transmitted through the genes.
(iv) Any variation in the ease of expression of the modified character which is due to genetic differences is liable to act in favour of those individuals that express the character most readily.
(v) As a consequence, an inherited predisposition to express the modifications in question will tend to evolve. The longer the evolutionary process continues, the more marked will be such a predisposition.
(vi) Thus plastic modification within individuals might lead the process and a change in genes that influence the character would follow; the one paves the way for the other.

It is obvious from this outline of the proposed process, that Lloyd Morgan (1896) was not suggesting genetic inheritance of acquired characters as a mechanism. The crucial postulate is a cost of operating the original process of phenotypic adaptation, a cost that can be subsequently reduced by genotypic change enabling Darwinian evolution to occur. Adaptability to new conditions might be physiological, such as coping with high altitudes by enhancing the oxygen carrying capacity of the blood or it might be by learning.

The great child psychologist Jean Piaget, who began his career as a biologist and was much influenced by Baldwin, provided an early example of how the process might work. He studied pond snails in different Swiss lakes that differed in how much wave action occurred; however, his work did not come out in book form until the end of his life (Piaget 1979). When he transferred snails from one lake to another, the morphology of the shell was changed in response to the musculature required for the wave action of that lake. The descendants of the transferred snails eventually inherited the changed morphology without needing to be exposed to the wave action of that lake. In the terms used by Lloyd Morgan, the initial change could involve adaptability by the individual snail; the adaptability is won at some cost so that descendants expressing the character more efficiently would be more likely to survive.

George Gaylord Simpson (1953) and many others who forged the new synthesis did not think that behaviour

played an important role in evolution. This became the standard line of neo-Darwinists. The dispute is about whether individual adaptability provided the leading edge for evolutionary change or whether it was both unimportant and, if it occurred, involved no new principles. Simpson asked if learning is so useful, why dispose of it? He went on, if the character generated is so important, Darwinian evolution would be sufficient. The first criticism is based on an impoverished understanding of how behaviour is changed and controlled. The answer to those who think that the proposed evolutionary change would lead to a generalized loss of ability to learn is to state quite simply that it wouldn't. Learning in complex organisms consists of a series of sub-processes (Heyes and Huber 2000). If an array of feature of detectors are linked directly to an array of executive mechanisms as well as indirectly through an intermediate layer and all connections are plastic (Bateson and Horn 1994), 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 (Bateson 2004).

What does adaptability add? The existence of a phenotype, acquired by learning, sets an end-point against which phenotypes that develop in other ways must be compared. The chances that all the necessary mutations and genetic recombinations would arise at the same time are very small indeed. In the natural world, if a spontaneously expressed phenotype is not as good as the learned one in the sense that it is not acquired more quickly or at less cost, then nothing will happen. If it is better, evolutionary change is possible. The question is whether the spontaneously expressed phenotype could evolve without the comparison. If learning involves several sub-processes, as well as many opportunities for chaining (the discriminative stimulus for one action becomes the secondary reinforcer that can strengthen another) then the chances against a spontaneously expressed equivalent appearing in one step 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 of how the setting of an end-point might work, suppose that the ancestor of the Galapagos woodpecker finch (*Cactospiza pallida*), that pokes sharp sticks into holes containing insect larvae did so by trial and error and its modern form does so without much learning. In the first stage of the change, a naïve variant of the ancestral finch, when in foraging mode, was more inclined to pick up sharp sticks 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 learn the second part of the sequence. The next step is that a naïve new variant, when in foraging mode, was more inclined to poke sharp sticks 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 (picking up sticks and poking them into holes in the case of the woodpecker finch) would be very unlikely. Learning makes it possible for them to occur at different times. Without learning, having one act but not the other has no value.

How does the adaptability driver relate to what Waddington (1953) called "genetic assimilation". Frequent references are made in the literature to learned behaviour becoming an instinct by genetic assimilation. The claims are made casually and without thought being given to how a usually implicit reference to Waddington might explain what was being proposed. Most of the explanations for Waddington's results seem either vague or incoherent. How is it supposed that a shake-up of development in one generation leaves the developmental process more likely to be shaken up in the next? What is the nature of this cumulative process? Appeals to re-canalization or alterations in threshold don't seem to answer this question. In fact evidence provided by Waddington and others for genetic assimilation seems very different from that needed for the evolutionary process of an adaptability driver.

The adaptability driver involves necessary compensation for the effects of a new set of conditions and immediate response by the individual to the challenge. The accommodation is not inherited and differential survival of different genotypes may arise from subsequent differences in the ease with which the new adaptation is expressed. The evidence for genetic assimilation also involves expression of a novel character in a new environment, but the character is not necessarily an adaptation to the triggering condition, even though it may confer some advantage on its possessor. Cross-veinless wings of *Drosophila* adults do not bear any functional relation to the environment which supplied a heat-shock when the flies were larvae. 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. The initial response of the adaptable animal is fast whereas the developmental effects of exposing fruit fly larvae to heat shock were not seen until they were adult. In the adaptability process, most individual's will survive in the initial stages. In Waddington's experiment those expressing the cross-veinless character, a subset of the total population, were artificially selected for further breeding. Finally, in the case of organic selection described by Lloyd Morgan, though not Baldwin, fresh phenotypic variation presumably arises by mutation which allows the adapted character to be expressed more easily and thence leads to differen-

tial survival. In Waddington's experiment mutation was neither postulated nor needed. Admittedly, all these dimensions of difference are continua and many cases might lie in an intermediary position on one or more of them. This allows for plenty of room for confusion in any attempt at categorization of examples. Nevertheless, I think it is both helpful and important to recognize the differences between the extreme examples.

The most important conclusion here is that the adaptability driver provides a ladder in evolution. Clearly complex structures can develop without such a process, but the driver is important when intermediates provide no benefit and a combination of simultaneous mutations needed to provide a functional whole is improbable.

5. Conclusions

Asking what something is for is never going to reveal directly the way in which it works. But the functional approach does help to distinguish between independent mechanisms underlying behaviour and can lead fruitfully to the important controlling variables of each system. This is important in the design of experiments in which, inevitably, only a small number of independent variables are manipulated while the others are held constant or randomized. The experiment is a waste of time if important conditions that are going to be held constant are badly arranged. A functional approach can provide the knowledge that prevents expensive and time-consuming mistakes. In behavioural development, functionally inspired approaches have played a useful role in making sense of what otherwise seemed a confused area. Asking what might be the current use of behaviour helps to distinguish juvenile specializations from emerging adult behaviour and helps to understand the developmental scaffolding used in the assembly process. Functional assembly rules are important, for instance, in determining when an animal gathers crucial information from its environment. With attention focused on the problem, attempts can be made to analyse the mechanisms. As in other areas, the optimal design approach frames and stimulates research on the processes of development (Bateson and Martin 2000).

The streams of ideas between "how" and "why" approaches flow both ways. The need for knowledge of the mechanisms to address functional and evolutionary questions is also being recognized. It has been important in understanding behavioural imprinting. It is happening in areas of work generally lumped under the heading of "life-history strategies", which raise important issues to do with conditional responses to environmental conditions (Moran 1992; McNamara and Houston 1996; West-Eberhard 2003). A given genotype will express itself very differently in different environmental conditions. The growing body of evidence shows how important it is to keep track of what happens to the whole organism as it develops.

In general, these changes in thought are occurring because what animals do is being seen as important in stimulating (as well as constraining) ideas about function and evolution. Finally, the mechanisms involved in the development and control of an organism may often generate ratchets or drivers in evolutionary processes, as seems likely to be the case with the phenomenon of adaptability (Bateson 1988). The decoupling of development from evolutionary biology and the attribution of intentions to genes could not hold sway for ever. Whole organisms survive and reproduce differentially and the winners drag their genotypes with them. This is the engine of Darwinian evolution and the reason why it is so important to understand how whole organisms behave and develop.

In this much changed intellectual environment, the time seems right to rebuild an integrated approach to biology. With a whole array of promising new research areas and techniques emerging, integrative biologists have a lot to be excited about. This matters in a highly competitive world in which determined and well-placed people can, in a remarkably short time, change what is and what is not funded, close research institutes and radically alter the departmental structure of universities. It is important, therefore, to offer to the new generation of young scientists who are coming into the field a sense of what is becoming once again one the most exciting areas in biology.

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