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A history of embryology

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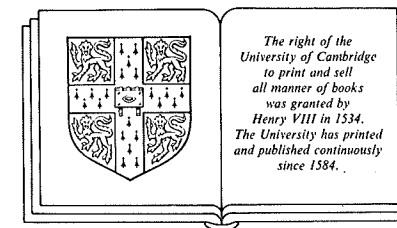## T. J. HORDER

Department of Human Anatomy, University of Oxford

J. A. WITKOWSKI

Royal Postgraduate Medical School, London

C. C. WYLIE

St George's Hospital Medical School, London

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Reductionism and holism in biology

NEIL W. TENNANT

Department of Philosophy, University of Stirling, Scotland, UK

I

The modern science of embryology is a fascinating one for the philosopher of science, lying as it does between the 'hard core' sciences, like physics or chemistry, and the 'softer' or less strongly predictive ones, like evolutionary biology and psychology. Embryology is a discipline which highlights various problems with which the philosopher of science is engaged:

-   the problem of whether there is an ultimate level of reality (such as that described by fundamental particle physics) which – in a sense to be clarified – *determines* all other levels;
-   the problem of whether scientific laws are deterministic and strongly predictive, or at best statistical in character;
-   the problem of whether science is a mere sophisticated continuation of commonsense or whether it involves radical departures from our everyday modes of thought and conceptual scheme;
-   the problem of whether some entities (such as electrons) must forever be regarded as theoretical or whether they might one day be rendered observational by progress in instrumentation and investigative techniques;
-   the problem of whether observational vocabulary, even for middle-sized objects of moderate duration is 'theory laden', so that the observational/theoretical dichotomy is not licit;
-   the problem of holism *vs* methodological individualism, i.e. whether complex systems may have emergent properties that cannot be predicted from the properties of their constituent parts; and finally, intimately connected with this problem of emergent properties,
-   the problem of whether higher level theories, such as biology,

psychology and sociology, could, in principle, be *reduced* to a chosen lower level theory such as fundamental particle physics. The first problem on this list is known as the problem of physical determinationism; the last one is known as the problem of reductionism. I intend to examine embryology with these problems in mind, in the hope that I might engage the interest of embryologists in philosophical and methodological problems that are, unfortunately in my view, all too often the exclusive concern of professional philosophers of science.

My main focus will be on the first and last problems on the list. I shall explain the significance of a result in mathematical logic that bears importantly on the connection between these two problems. The result is Beth's Theorem on definability. It has the form of an implication

if A then B

in which it is arguable that A could be interpreted as the thesis of physical determinationism and B could be interpreted as the claim that all theories are reducible to physics.

Beth's Theorem is therefore of special significance for the anti-vitalist embryologist who wishes to maintain *logically* privileged autonomy for his discipline. If the interpretation that I have intimated of Beth's Theorem can be sustained, then the anti-vitalist embryologist would have to accept the consequence that his discipline is, *in principle*, reducible to physics.

Of course, whether or not it is reducible *in practice* is quite another question. Perhaps the *practical* impossibility of such reduction – despite its logical possibility – is sufficient to ensure the embryologist his theoretical autonomy and security of employment even under the harshest of selective regimes!

Although my examples and illustrations of general points are thus directed to embryologists, it is worth noting that what I have to say would apply, in principle, to any other 'higher-order' science whose relationship to physics is similarly in question. I shall share the prevailing assumption among modern scientists that if any theory has a claim to be describing the determining level, it is first and foremost physics. Curiously enough, the logical investigations to be described would apply even if the determination were – outrageously – the other way round: even if, say, a theory of social individuals and group minds were taken as describing the determining level, on the bizarre metaphysical conviction that the 'level of reality' whereof it

spoke – namely collective unconsciousness, interanimation etc. – determined what was the case even at the level of fundamental particles.

II

Embryologists can number one of the most accomplished methodologists and philosophers of science of modern times among their company. It was J. H. Woodger who translated the great works of the mathematical logician Alfred Tarski into English, and he was one of the first scientists to absorb the significance of Popper's falsificationist philosophy of the empirical sciences and communicate it effectively to his scientific colleagues. Woodger recommended in 1948 that embryologists engage in a program of conceptual and logical analysis and organisation of their data and theoretical hypotheses. This would require attention to the *language* of embryology:

Language is one tool which is common to all the sciences and without which no science would be possible. And yet very little attention is paid to it compared with the care and research which are lavished upon microscopes and all other scientific instruments . . . From time to time, of course, both in genetics and embryology, muddles of a linguistic origin have become sufficiently acute to demand attention . . . It is difficult to persuade anyone of this who has not felt it himself. It is like persuading a man who does not feel toothache to go to the dentist. The only science which has seriously studied its own language is mathematics and the outcome of these studies has important bearings on the other sciences.

Woodger complained that the data gathering of the day was badly in need of higher-order explanatory hypotheses. Higher-order hypotheses would explain lower-order generalisations by logically implying them (and also the data that they in turn implied); and they would be empirically testable by going beyond the data to make new predictions that were in principle falsifiable by observation and experiment. Embryology had an impressive record of observations of both normal and pathological growth. Much of the pathological growth is at the investigative instigation of the embryologist: grafting, transplantation between species, suturing, irradiating, amputating, homogenising. What end is to justify these means? Woodger's answer was: new explanatory hypotheses. These would, it was hoped and expected, open up new fields of (more humane?) experimentation and provide further impetus to *link* embryology with neighbouring disciplines – expecially biochemistry – and thus to

consolidate and broaden its empirical range. But of especial interest, from the point of view of a mathematical logician, is that Woodger was at pains to emphasise how important it was to arrive at a clear understanding of language as a theoretical tool. He urged upon his fellow embryologists the task of classifying their observational and theoretical terms (or predicates) with a view to discovering which of these were basic and indefinable when formalising their data and laws and hypotheses. In this way the logical structure of the discipline would be better understood; and the newly clarified logical structure would suggest theoretical ways forward from the existing data base and current explanatory hypotheses.

It is easy to scoff at the utility – or futility – of pursuing such a program. It may look like nothing more than formalisation for formalisation's sake. A glance at the results of such attempts for theoretical physics itself (Suppes, McKinsey & Sugar, 1953; Suppes & Rubin, 1954; Sneed, 1971) should give the enterprising formalising biologist pause: for biology promises to offer greater complication in the project of formalisation than does physics. Even before its formalisation physics was already a highly mathematical discipline with but a few fundamental notions to be orchestrated in a set of axioms that would allow the derivation of all its laws. But on the other hand the results of such an investigation in the case of embryology could enable philosophical assessment of the claim, say, that modern gradient theory is just as 'metaphysical' and untestable as was Driesch's theory of entelechies. One can command a clear view of the matter and be in a position to answer such a philosophical charge, only by understanding the logical connections between theoretical talk of progress zones, thresholds, gradients and positional values, and observational results in the laboratory and in the wild.

The time may be ripe for a re-assessment of the recommendations Woodger made in 1948. His program was not prosecuted with the vigour it deserved: probably because there were not the skilled, trained analytical minds with sufficient interest in the subject to do the hard work he called for. One mild exception I have found to this claim is Mary Williams' work, aimed at formalising the theory of natural selection. It is wrong on important details: for example, she regards overproduction in a world of limited resources as logically *necessary* for evolution to take place. And it is written in an over-numerical idiom ill-suited to the description of the *qualitative* relationships at issue. But despite these drawbacks, it was interesting work, and ought

to be improved upon to the benefit of both evolutionary biologists and philosophers of science.

I shall not offer, with regard to embryology, anything like a definitive 'formalisation' of its theoretical claims. There is enough variety in its terminology for one to be content, at this stage, with only the most tentative classification or categorisation. It is instructive to approach the writings of some leading contemporary embryologists with this task of logical classification in mind. The happy indications are that Woodger's promissory note is being fulfilled by his scientific successors. Wolpert's work (Wolpert, 1978) provides an example of the kind of methodological awareness that could be sharpened and refined by the kind of analysis Woodger recommended. There we find a conspectus of lower-order empirical and higher-order theoretical claims, and of the logical relations among them; as well as a case not only for linking embryology downwards with those disciplines, such as molecular biology, which can clarify mechanisms, but also for linking it upwards with evolutionary biology, by offering the latter grosser mechanisms or models of morphological change.

I have classified terms from the language that embryologists use into the following categories: biochemical terms; natural kind terms from organismic biology; anatomical terms; phase sortals; event and process terms; topological/morphological terms; and theoretical terms. The best explanations are always by way of example, so several representatives for each category are shown in Table 1.

There may be disagreements over entries in these lists. The reader will observe that I have not attempted to 'subordinate' any of these terms to any others. But obviously 'mouse' is subordinate to 'vertebrate', for example. There are some puzzles that I have not been able to resolve to my own satisfaction, concerning where a given term should go. Is 'cell cycle' an observational term, or a theoretical term? Was I right in regarding 'blastoderm' as an anatomical term – denoting a spatial part of something – or is it really, in the mouths of embryologists, a phase sortal term? Where would 'proliferative zone' go? It sounds a touch more observational than 'progress zone', which, in the context of Wolpert's writings, I regard as most definitely theoretical. Is the notion of 'developmental history' strictly theoretical, on the grounds that it applies to all events in an organism's life up to a given point, and therefore concerns events that are unobservable, or that involve entities that are unobservable? Is 'cytoplasm' an anatomical or biochemical term?

Table 1. *Classification of technical terms*

Biochemical terms	Organismic kinds	Anatomical terms
macromolecule	amphibian	organ
gene	vertebrate	skeleton
protein	insect	dermis
enzyme	*Escherichia coli*	cell (200 types)
haemoglobin	nematode worm	connective tissue
	sea urchin	limb
	fruit fly	dorsal mass
Phase sortals	newt	ventral mass
	chick	antenna
egg	mouse	gut
sperm	guinea pig	wing
zygote	chimpanzee	muscle
morula	human	nerve
blastula		tendon
embryo		cartilage
larva		bone
pupa		blood
		digit
Theoretical terms	*Topological/*	epiphyseal growth plate
vegetal pole	*morphological*	mesoderm
co-ordinate system	proximo–distal axis	notochord
boundary region	antero–posterior axis	somite
threshold	dorso–ventral axis	apical ectodermal ridge
classical gradient		imaginal discs
classical organiser		blastoderm
contractile forces		
allometric relationship	*Terms for events and*	
generative program	*processes*	
positional information	meiosis	fertilisation
response selection	mitosis	cytodifferentiation
equivalence (of cells)	pattern formation	change in form
autonomy (of growth)	gastrulation	invagination
progress zone	cell aggregation	cell migration
polarising region	cell-to-cell interaction	regeneration
developmental history	morphallaxis	epimorphosis
diffusible morphogen	induction	heterochrony
	abortion	death

It is interesting to note also that many terms in the jargon of the professional embryologist, which are not current in everyday speech, can be explained easily to a lay person with no detailed knowledge of histology or biochemistry or organismic biology. Among these, for example, are 'morula', 'blastula', 'notochord' and 'somite'.

III

Latinate impenetrability is one thing; genuine theoreticity is another. Some of the terms I have categorised as theoretical seem very 'removed' from those under other headings. The contrast with any supposed observational/theoretical demarcation in Newtonian physics is quite marked. There the theoretical term 'point mass' is an abstraction rooted in the everyday notion of physical object. The notion of mass is cognate to that of weight, of which we have immediate experiential grasp. The same can be said also of forces. The picture of the physical world that Newtonian physics offers is a skeletal, austere one, which nevertheless enjoys conceptual congruence with the familiar everyday world. In quantum physics and in relativistic physics this conceptual congruence is ruptured, although we are left with scar tissue in the form of preservation theorems such as Ehrenfest's. Ehrenfest's theorem says, roughly, that in the large the predictions of quantum physics coincide with those of Newtonian physics. But the recondite terms of modern physics – such as 'quark', 'charm', and 'spin' – can only be understood by someone who has gained familiarity with the mathematical framework in which they feature. The theoretical terms of quantum physics are at a great remove from conceptual extrapolations within the reach of a lay person. He can grasp them only by ceasing to be lay, and becoming a competent theorist in that area.

Can the same be said of embryology? If not, that is still no criticism of embryology as a scientific discipline. For one must be mindful of the Aristotelian dictum that the level of precision (and one might add: abstraction, or abstruseness, or theoreticity) that we are trying to achieve should be appropriate for the chosen area. When we try to describe growth and development in manifold species of organism, and to discern regularities of pattern, correlations of measurable quantities, and successions of different types of event, we might – in order to be faithful to the phenomena and not pretend to be able to predict and explain more than we can – have to

confine ourselves to a much more 'humdrum' vocabulary than does the theoretical physicist. This is a constraint working counter to some of the theoretical directions that, after Woodger, embryologists might have followed. As one seeks new higher-order explanatory hypotheses for embryology, to unify and subsume all that has been observed and hypothesised at lower levels, one must anchor one's new theoretical notions suitably to the observable by various logical links. These links are all important. The Aristotelian caution is that the higher conceptual hatches must be well battened down if we are to show that we can weather experimental tests. The modern notions of gradient, positional value, threshold, and co-ordinate system are cases in point. They must be seen to issue in predictions open to confirmation or refutation by observation and experiment. Woodger himself was keenly aware of this:

... simply to assert that gradients exist in embryos does not help at all. The gradient concept will only be really useful when it enters genuine explanatory hypotheses.

In this respect Wolpert's later work represents progress, but with a curious twist given by Wolpert himself. Not only does he agree implicitly with Woodger's claim that

In order to take further steps in embryology we are *compelled* to invent hypotheses concerning submicroscopical cell structure which will be explanatory of the behaviour of cells during development.

but he sees also linkage upwards, just as much as linkage downwards, as representing further progress. For he offers the prospect of explaining evolutionary change as change in pattern formation; while at the same time offering a 'downward looking' account of what this latter change consists in. The crucial mechanisms for Wolpert will be submicroscopical and biochemical in nature: he suggests there is at least one mechanism by means of which a cell may measure time spent in a 'progress zone', and one other by means of which a cell measures its position, within the organism and according to an organically intrinsic coordinate system, by monitoring levels of a 'diffusible morphogen'. In this regard, says Wolpert (1978, p. 164).

those of us who work on such problems are in the situation of genetics long before DNA was identified as the genetic material: ...

But now comes the twist:

we have rules governing the phenomenology but the molecular basis of the phenomena is completely unknown. (My emphasis)

Wolpert may be unfair to himself in saying this. For even pending a molecular mechanism for cell measurement of positional value and of time spent in a progress zone, he has taken an important theoretical leap by importing the last two notions. He may have got more than just the phenomenology right by postulating these notions-in-need-of-a-mechanism. The notion of *gene* was one in need of a mechanism for several decades, yet it helped geneticists during that time to do more than just *describe* the phenomena. The Mendelian laws helped theorists to see the phenomena in a new light, and to search for results that would confirm or deny the existence of a particulate mechanism of heredity. Similarly, in the embryological case, I for one was struck after my first acquaintance with the notion of positional value by the question 'What empirical tests would show that this was the right way to organise the results of our observations?' and had the immediate subsequent gratification of reading such passages as

This model suggests that if there are no long-range interactions between mesenchymal cells, a progress zone should continue to develop autonomously when it is excised and grafted to another site ... Our experimental grafts conform rather well to the theory.

The experiments prompted by the model afford a good example of what Woodger had in mind when he spoke of key hypotheses setting in motion new lines of investigation. Progress in this regard will only be consolidated, however, when we have successfully 'battened down' the new theoretical terms that Wolpert has introduced. Here are some of his key 'upward linking' generalisations that may help to do so (Wolpert & Stein, 1982):

In the evolution of vertebrates the histological cell types have probably not changed much either in quality or quantity ... The difference between (man) and (chimpanzee) may be attributed to pattern formation. (ibid, p. 332)

(I have bracketted their terms to highlight the possibility of other substitutions.)

... the genome provides a generative programme not a descriptive one. There are no genes describing the arm, only genes involved in specifying the processes for making it. (ibid, p. 333).

It is far more difficult to generate new functional proteins that would characterize a new cell-type than to generate new plans for rearranging existing cell types. (idem)

. . . the basic cellular processes have probably not changed their nature during evolution of multicellular organisms. Differences in form result not from the differences in these cellular activities, but from their spatial and temporal organization. (idem)

. . . the same set of positional values can be used to generate quite different patterns. This means that there could be a universal coordinate system which is used again and again, both within the same embryo as well as in other embryos. The main change in evolution would thus be in interpretation. (ibid, p. 334)

Non-equivalence enriches the repertoire of evolution, letting small parts of the body change independently of the rest. (ibid, p. 338)

These are representative of the claims 'linking upward' with evolutionary biology and using the new theoretical notions introduced by Wolpert. Like all claims of evolutionary biology itself, they cannot be expected to yield firm predictions. Their function is rather to point to ways of seeing the evidence, of understanding how the pieces of a jigsaw puzzle fit together. This is characteristic of all 'inference to the best explanation'. What, then, of 'downward' linkages involving the new theoretical terms? We have the following:

Differences in positional value can make cells nonequivalent even though they differentiate into a similar cell type. The principle of nonequivalence says that cells of the same differentiation class may have intrinsically different internal states, such as positional value. (ibid, p. 334).

. . . the pattern of the muscle and tendons uses the same positional field . . . (ibid, p. 337)

. . . positional information is initially specified in a two-dimensional cell sheet, the mesoderm in vertebrates, and . . . when this mesoderm comes to underlie the ectoderm, positional information in the ectoderm is specified by transfer of positional values from mesoderm to ectoderm. (ibid, p. 338)

. . . pattern formation can be viewed as a two-step process: first the cells are assigned positional information and then they interpret that information according to their genetic programme. (Wolpert, 1978, p. 154)

. . . positional information . . . is the same in the antenna as in the leg: it is the interpretation that is different. (idem)

One general feature of positional fields is that they are always small and another feature is that the time required to establish them is long. (ibid, p. 156)

However . . . a gradient is established, it can be interpreted by cells if their genetic programme is specified in terms of thresholds: if above a certain concentration the cells differentiate as one type and below it they differentiate as another type. (idem)

. . . the positional values imparted to the cartilage lead to different growth programs in different regions . . . (ibid, p. 158)

Unlike cartilage cells, muscle cells are 'equivalent'. (ibid, p. 161)

. . . gradients can control the earliest patterning in a developing insect egg. (ibid, p. 162)

Both the posterior cytoplasm of the egg and the zone of polarizing activity of the wing bud appear to act as boundary regions that provide a positional signal. (idem)

Morphallaxis can now be understood as the establishment of a new boundary region at the cut surface and the specification of new positional values with respect to that boundary. In epimorphosis . . . (new) positional values are generated in the new tissue. (ibid, p. 164)

. . . intercalary, or interpolated, regeneration takes place whenever discordant positional values come to the adjacent to each other: new positional values are generated in the growing tissue until the discordance is eliminated. (idem)

This second list of illustrative claims concerning positional value, gradients etc. seems to have genuine empirical import. Whatever mechanism may one day be proposed as underlying Wolpert's theoretical notions, one will be able to return to the claims above and see which ones were *wrong* as descriptions of reality *even pending* specification of the mechanisms. Convinced one day as to the nature of the mechanism to whose existence these claims pointed, we shall be able to re-assess some of them as over-hasty or only approximately true. We surely cannot dismiss *all* of them as on a par with the well known 'dormitive virtues' explanation of why a certain drug can put one to sleep. Wolpert is closer (as in his own estimation) to something more like the gene concept than he is to dormitive virtue. It is hard to read all the claims above as involving only allegedly theoretical cogs that whir but do not engage: as involving something analogous to claiming that when one has described line A being parallel to line B by saying that the direction of A is identical to the direction of B, one has thereby hit upon a new theoretical notion – direction – without which geometry as a science cannot progress. Wolpert's theoretical notions appear not to be of this kind. *Pace* Wolpert, he is not just doing phenomenology (by which I understand the description of what everyone agrees appears to be the case, rather than the more rarified philosophical doctrine of Husserl or the sense-data theorists). He is, rather, going importantly beyond the description of appearances, and even beyond the statement of objective

regularities in things and events observed, by importing theoretical notions linked both upwards and downwards to neighbouring disciplines. These at once constrain the search for a mechanism and open up new fields of application: good science by anyone's lights.

Wolpert, like Woodger, believes that the 'lower' levels determine the 'upper' levels. Woodger had written

... we have reached a stage where the *changes* in cells are to be explained, and we can only explain change in a thing by hypotheses that speak about its parts.

And Wolpert wishes to

view development in terms of a generative programme contained within the fertilized egg's DNA.

Thus one can describe each of them as a *physical determinationist*; but whether either would wish to be described as a *reductionist*, is another matter. In what follows I shall explain the difference between these positions, and reflect on arguments for the autonomy of embryology as a scientific discipline.

IV

Quine (1960) describes physics as limning the ultimate traits of reality. It is commonly held that biological traits are not ultimate. The development of an embryo may be constrained, and ultimately determined by, the underlying physical processes studied in, say, thermodynamics and quantum mechanics. But embryological development as such, so one such view further holds, is not one of the 'ultimate' processes in reality. Laws governing embryological processes – should any exist – do not possess the 'ultimate' character of the laws of physics: not, that is, if they deal directly with specifically embryological concepts such as invagination, gastrulation and the like.

Wherein lies this 'ultimacy' of the laws of physics? And if laws of embryological development are essentially supplementary to the laws of physics, might it nevertheless be essential to supplement the latter with the former? These are the two main questions I shall attempt to answer. More pithily, they can be posed as follows:

What level determines what others?
Can all laws of the levels described be reduced to the laws of the determining level?

Note now the generality of the question schemata. For the purposes of illustration, I have chosen physics and embryology. But, as noted above, the question concerns determination and reduction in

general: determination as a relation between different levels of reality, and reduction as a relation between different levels of theoretical description. Physics is the commonest choice of determining theory, concerned with the supposedly 'ultimate' level of reality. Various other 'higher level' sciences (in our example, embryology) may then be contrasted with physics, as being concerned with supposedly 'higher', 'derivative' or 'less basic' levels of reality. In our example, we could have replaced embryology with chemistry, psychology or sociology in order to generate the questions of determination and reduction. The last two choices, however, could be regarded as slightly far-fetched or strained: physics lies 'too far below' psychology and sociology. One can think of the 'levels' of reality, and of corresponding scientific theories, as falling in a rough partial order as given in the following diagram (Fig. 1), with theories arguably

		History of nations
Evolutionary biology		Anthropology
Ecology and population genetics	Sociobiology	Sociology
Organismic biology –	Behavioural genetics	Group psychology
embryology, immunology	Neurology, etc.	Individual psychology
Cell biology		
Genetics		
Molecular biology		
Chemistry		
Physics		

Size of system ↑

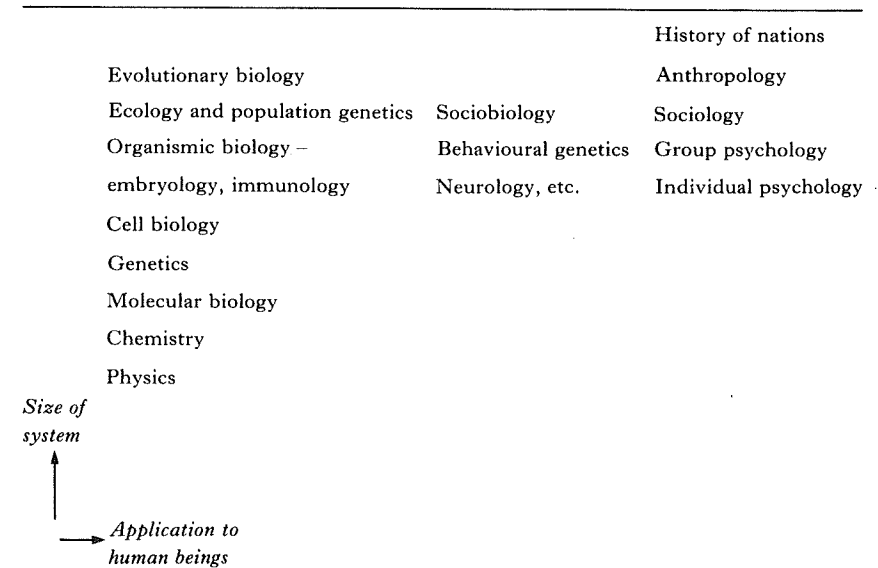→ *Application to human beings*

Fig. 1.

becoming less and less scientific as it peters out at the history of nations (compare Riedl, 1979). The diagram reflects both our concern to order systems by containment or size, and our special interest in ourselves. The determination–reduction question is most engagingly posed with respect to close neighbours in the list. Thus we can generate such problems of the past and present as:

the problem of whether evolution is incompatible with thermo-

dynamics (via the pair 'physics–evolutionary biology');

the problem of methodological individualism (via the pair '(individual) human psychology – sociology'); and

the mind–body problem (via the pair 'human neurology–human psychology').

If one believes in the determining strength of a lower level with regard to its next highest neighbour in the list, then by transitivity one would conclude that the relation of determination straddles the list from one end to the other. Likewise, if one believes that one can reduce each higher theory to the one immediately below it, then by transitivity one would conclude also that the relation of reduction straddles the list from top to bottom. Determination concerns *levels of reality* (as described by their theories); reduction concerns *theories* (as they describe their levels). Determination and reduction most plausibly hold, however, with choices of closely neighbouring levels and scientific disciplines within something like the scheme above.

The foregoing talk of levels acquiesces in a convenient intellectual fiction in order to set up the problem of reduction in its stark essentials. But the various levels are never completely insulated from each other, via corresponding theories with no terms in common, like layers of an intellectual onion. Scientists in any discipline borrow from and trespass into others, and must do so as the scope of their 'how' and 'why' questions widen. Their background concepts, laws and theories straddle all available levels. When talking about cell division, there is talk of thermodynamics too; when explaining gross morphological change, one profitably invokes findings of molecular biology; when treating schizophrenia, one would be advised to heed what pharmacology and neurology have to offer. We have seen above how at least one embryologist – Wolpert – envisages bridge laws linking embryology upwards with evolutionary theories of morphological change, as well as laws linking it downwards with molecular biology and biochemistry, once the mechanism of diffusible morphogen (among possibly others) has been specified. So the tapestry of science is a criss-cross affair. The 'levels' inter-animate via multifarious bridge laws, including (*pace* Davidson, 1970) laws connecting mental with neurological phenomena.

Quine (1960) has advanced a 'network model' of language and theory, according to which those statements most sensitively attuned to sensory experience lie at the periphery, and fundamental

scientific laws and laws of logic at the heart, of an interconnected network of sentences. In his account there is no mention of the sorts of levels that we have been discussing. If one allowed for them in Quine's metaphor, one would obtain what I shall call a 'banded network'. Most vividly, think of Miss Havisham's wedding cake shrouded in dusty webs joining layer to layer. Each layer of the cake on its own is like a Quinean network, with an interior/periphery distinction to be made, on the basis of how liable statements are to revision in the light of experience. The icing consists of observation reports with so-called 'stimulus meaning'. The marzipan consists of Quine's 'standing sentences'. The more fruity interior consists of those higher-order explanatory hypotheses, and those laws of mathematics involved in the discipline (such as embryology) corresponding to that layer. Thus each layer corresponds to one of the main scientific disciplines mentioned above, bringing with it, as just indicated, a rough observational/theoretical distinction as well. Now the webs joining adjacent layers of the cake represent theoretical connections – 'bridge laws' – between neighbouring theoretical levels. And as Needham said about D'Arcy Thompson's theory of growth and form

(u)ntil we can find the links between the superimposed levels of organisation, there remains a certain meaninglessness about the genetics of size and shape or the mathematics of spirals and polyhedra. A unified science of life must inevitably seek to know how one level is connected with the others. (Needham, 1900)

V

What is reduction? It is common for practitioners in one branch of science to hold out the possibility of reducing the concepts and laws in another to those of the former. For example, (some) physicists think that they can reduce the concepts and laws of chemistry, possibly even biology, to physics. Since Crick and Watson's discovery of the genetic code, evolutionary biology has started to simmer in the reducing heat given off by molecular biology below. Genes have been defined as double-helical structures, whose constituents are of known chemical structure. A biochemical theory of replication, coupled with a biochemical theory of cellular pattern formation, might one day displace evolutionary biology by reformulating all the main claims of the latter in biochemical terms. Yet higher, at another level in the diagram above, materialistically minded philosophers of mind have sought to establish mentality as

mere epiphenomenal fog generated by the real processes 'below', namely the neurological ones. Pain-states, for example, might one day be *defined* theoretically as states of the central nervous system: perhaps concentrations of known chemicals are responsible for lowered synaptic thresholds in certain patterns (who knows? – I merely conjecture for the sake of argument). Pain-avoidance behaviour might then be predictable from knowledge of what characteristic stimuli to the motor system would ensue when that physical basis for pain obtains. So the neurological-cum-biochemical theory might one day displace our ordinary predictive apparatus that involves talk of sensation and bodily actions (or reactions).

Let us now move away from these particular examples, away from the inadequate metaphors and contrived reductions with which I have given them. Let us ask, quite generally, what it *means* when one says one can reduce one theory to another. What it means for the logician is this: *one can take the terms expressing concepts of the theory to be reduced and provide explicit definitions of them using only terms for concepts in the reducing theory. Then, using these definitions, and one's reducing theory, one can derive within the reducing theory the laws of the theory to be reduced.*

A fine example of reduction comes from the foundations of mathematics. Von Neumann (1923) gave an analysis of the notion of *natural number*, or in general *ordinal number*, in terms of *set*. The reducing theory in this case was set theory – and the theory to be reduced was arithmetic. Von Neumann defined 0 as the empty set, the set which contains no members (the set of all x such that x is not identical to x). He then defined each ordinal as the set that consisted of all preceding ordinals. So, for example, the number 1 was the set whose sole member was the empty set; 2 was the set whose sole members were the empty set and 1, which in turn was the set whose sole member was the empty set; and so on. With this ingenious reduction of the objects of arithmetic, he was able to replace arithmetical talk by set theoretical talk. And by reducing, or reformulating, the axioms of *arithmetic* via these definitions, he was able to derive those axioms as theorems of *set theory*. It is in this sense, the one just defined in a general way, that arithmetic is now regarded as reducible to set theory.

VI

What is determinationism? *Physical* determinationism is the view that the physical facts determine all the facts. The principle of physi-

cal determinationism has been nicely expressed within a mereological framework by Hellman & Thompson (1975). Space–time and the distribution of matter therein is taken as the basic substrate of existence. Then bundles of it, and bundles of bundles, and so on, are available as the only entities one may talk about. (The rest is not there even to be passed over in silence!) The principle of physical exhaustion is then just the thesis that there are no objects, or entities to be talked about by any science, which are not contained in this cumulative hierarchy erected on matter-in-space-time. It rules out vitalism: there are no entelechies, or *vires vitales*, in addition to the basic physicochemical processes in the organism. There are no special mental entities in addition to brains; all mental events are physical events. I take the principle of physical exhaustion to be a working hypothesis of modern science. Just as no mathematician bothers to assert that numbers exist, but proceeds to prove interesting results about them, so too does the modern scientist proceed to formulate and test theories on the implicit assumption that there is, indeed, nothing but the physical.

The thesis of *physical determinationism* goes one step further than the principle of physical exhaustion. There are many 'ways of looking' at the physical systems just granted exhaustive tenure. Some are genes that replicate; some are embryos that invaginate; some are human beings that talk to each other; some are nation states that trade and war with one another. We discuss these systems using the language of genetics, embryological development, everyday psychology and sociology respectively. We ascertain and express genetic, embryological, psychological and sociological *facts* in doing so. Now the principle of physical determinationism simply says that these latter 'higher level' facts about these various (physical) systems, systems identified by 'higher level' concepts (such as 'gene', 'embryo', 'human being', 'nation state'), are nevertheless *fully determined* by the 'low level' *physical* facts concerning them.

Another way of putting the thesis is to say that the 'higher level' in question (say, the mental) is *supervenient upon* the physical. The thesis of supervenience in the philosophy of mind, for example, maintains that there is no change in a mental state without a corresponding change in physical state. Put another way, the physical state of an organism – including perhaps part of its environment, and not just its brain – uniquely determines what its mental state is. If the mental properties vary – say upon satiation or persuasion – then

underlying the changed desire or changed belief there must be some alteration of physical state: a change, perhaps, in the pattern of neuronal excitation, or a change in the physical environment. The physical story fixes the mental story: the physical facts determine the mental facts, and indeed *all* the facts there are. This is *not* to say that physical processes are *deterministic*: physical determinationism, as just explained, is compatible with anti-determinism within physics.

Nor is this thesis of *physical* determinationism a way of saying that the world – *pace* Wittgenstein (1922) – *is* all that is *physically* the case. It is rather to say that the world – after Wittgenstein, all that is the case – is *determined* by all that is *physically* the case. One can be a physical determinationist and still grant the existence of, say, mental and social facts; and grant the licitness of mental and social vocabulary in describing these facts. Indeed, a physical determinationist (or supervenience theorist) can even grant the existence of *irreducibly* mental and social facts, and grant the *indispensability* of the idioms that bring them out as such. In short, a physical determinationist need not be a reductionist. This is the philosophical position that I believe modern embryologists to occupy; and that they would wish to see defended.

Physical scientists of this philosophical persuasion often draw comfort and support for their view from some form of *holism* or from an acknowledgement of *emergent properties*. Indeed, I think it fair to say that holism and emergent properties have even been cited as evidence against determinationism. This, however, I think to be misguided, and I shall consider only how, once granted the thesis of physical determinationism, holism and emergent properties have been applied as brakes in the slide to reductionism. But I shall argue that they have been *wrongly* so applied: and that, insofar as the philosophical position above (determinationism with anti-reductionism) can be defended, it is neither correctly nor most effectively defended by appeal to holism and emergence.

VII

What is holism? Very roughly, it is the idea of global dependence. One can illustrate the idea from branches of enquiry besides physics and biology. In linguistics and semantics, holism is the doctrine that one cannot grasp the meaning of a word in isolation before one understands the whole language to which the word belongs (for a

fuller discussion of which, see Tennant, in press (*a*)). In the philosophy of science, one also speaks of holism with respect to the evidence. This is the view that our theories 'face the tribunal of experience as wholes' – every theory must address itself to *all* the evidence, not just evidence selectively presented or emphasised; and as a corollary, should theoretical predictions be at odds with the data, it can prove to be difficult to pinpoint exactly which statements of the theory should be revised. Another holistic view is expressed by Mach's principle in physics. Mach maintained that the inertial mass of a body was determined by the distribution of matter in the universe as a whole.

But the sense of holism which will engage the biologist most acutely is that of 'the whole being greater than the sum of its parts'. This is a difficult idea to make precise, and I shall not attempt to do so. Suffice it here to say that it will not be enough to maintain that

Perhaps the most important aspect of holism is that it emphasises relationships. I, myself, have always felt that relationships are not given sufficient weight. (Mayr, 1982)

For the same could be said of computer dating bureaux.

The main task in explicating the idea of a whole being greater than the sum of its parts will, I think, be to isolate a sense in which the *causal powers* of the whole cannot be predicted on the basis of the causal powers of its parts. Causally interactive ensembles will have to be shown by the holist to display regularities of interaction that are not to be obtained by any method of superposition or aggregation of the causal interactions of their constituents. Here the anti-holistic trend in modern embryological writing is worth noting: for example, Wolpert's insistence that cell-to-cell interactions, and small changes in their modes, can effect both the bodily growth of individual organisms and gross evolutionary changes in morphology, respectively. Moreover, the causal interactions of the ensembles could still be described by the holist in strictly physicalist language. The version of holism I am canvassing here is quite compatible with physical determinationism, provided only that the 'determining level' of physical reality is amenable to theoretical description at the corresponding 'lowest level' of physical theorising. This may require certain terms in the language of physical theorising to be taken, *primitively*, as applying to physical ensembles, or wholes, that are quite 'high up' in the cumulative hierarchy of Hellman and Thompson described above. For example,

'cell' or 'organism' might be such a term, and be reckoned to the determining level of theory. But this would already be to avoid the problems posed to the would-be reductionist by the phenomenon of holism. *Of course* one can avoid being unable to reduce, say, biological theory to what is commonly regarded as physics, by simply subsuming the former to the latter and regarding biology-cum-physics as the determining theory! But what this devious move in effect amounts to is an acknowledgement, on the part of the holist physical determinationist, of his inability to reduce biological theory to what is commonly regarded as physics.

The holism that thus stands in the way of reductionism can, of course, have even more far-reaching effects. We have thus far imagined wholes to display new causal powers not predictable from the causal powers of their parts. The causation in question has still been easy to regard as *physical* causation. (Lorenz's well known example of the capacitor comes to mind here, Lorenz, 1973.) But what now if the *emergent properties* of the whole started registering themselves, or making themselves felt, in ways that we were forced to describe in terms that we could not regard as belonging to the language of physical theorising? For some collections of cells are so complicated in their aggregative behaviour that they are dignified as *persons*, as having thoughts, beliefs and desires, and as engaging in *social* interactions. The complexity of these ensembles was produced by evolution, as of course was their very own cognitive apparatus for dealing efficiently with the gross overall effects of the highly complex physical processes going on inside and around them – processes which, according to the physical determinationist, do nevertheless still determine what is happening at what we like to call the mental and social levels.

Holism thus goes in hand with the doctrine of emergent properties. The more drastically different in kind the emergent properties of wholes are from those properties of their parts that we imagine ourselves exhaustively to have characterised, the more grave the problems facing the would-be reductionist. Emergent properties are those that arise (and we can think in a temporal or evolutionary sense when we say this) when constituents come together and join up, to produce a new whole that has dramatically different properties from those of the constituents that went to make up the whole. A standard illustration here is the way sodium and chlorine combine to give common salt, whose sharp taste cannot be predicted from knowledge of the chemical

properties of sodium and chlorine alone. Here I can only endorse the following extended remark of Waddington (1981):

> If we could observe the behaviour of sodium and chlorine only when each is in isolation, and if we regarded these two substances as made up of atoms, we might be able to discover something about these atoms but not very much. There is no reason why we should expect to become aware of the properties which allow them to combine with each other and form common salt. When this compound is formed, it is not that some new emergent properties appear, it is simply that a new avenue is opened to us for discovering a little more about sodium and chlorine atoms.

Even so, the 'little more' discovered by this 'new avenue' concerns the *psychological* effect (sharp taste) of salt on sentient organisms (us). So even if, with Waddington, we refuse to be unruffled as *physical determinationists* by the emergent properties of common salt, those properties might nevertheless give us pause as *reductionists*. It is the same problem to which Mayr alerts us when he denies that

> ... it is part of emergentism to believe that organisms can only be studied as wholes ... All (that emergentists) claim is that *explanatory reduction* is incomplete since new, and previously unpredictable, characters emerge at higher levels of complexity in hierarchical systems.
>
>   (Mayr, 1982)

Still, the would-be reductionist could refuse to be impressed by this justification of emergentism, the observation that new and previously unpredictable characters emerge at higher levels of complexity in hierarchical systems. For the reductionist could argue as follows:

> What the discovery of these so-called emergent properties shows you is that there would have been a very complex linguistic predicate made up of the terms of the reducing theory which is of special interest at this new level. If, indeed, the emergent property *can* be reduced to something before, its novelty lies simply in its unpredictable complexity. Among all the very complex formulae that one might have devised using terms of the reducing theory, it is highly unlikely that *this particular* complex formula (the one that successfully achieves the sought reduction of the emergent property) would have been hit upon, before the fact of emergence, as one peculiarly germane in the envisaged circumstances.

This is a cogent defence by the reductionist. He undermines the emergentist's opposition to reduction by pointing to a logical possibility. This is the possibility that, *should* there be a reduction, the complex predicate that captures the emergent property is likely to be so complex in its construction out of the reducing notions that one is

not liable to identify it as theoretically relevant (in conveying truths about the world) *before* the emergent property has, so to speak, hit one in the eye.

VIII

It may only be after a rigorous program of logical analysis, such as was advocated by Woodger, that philosophers of biology will be able to give content to the notion that a given theory treats its objects holistically, or gets to grips with emergent properties, or is irreducible to any lower level theory. The contributions of Frege (1903), Russell & Whitehead (1910–13) and Gödel (1931) eventually provided a definitive answer to the question whether arithmetic was reducible to logic. Likewise Montague (1974) has attempted a rigorous analysis of what it means to say that a theory is *deterministic*. Bealer has similarly tried to show that, upon rigorous analysis, the philosophy of mind known as *functionalism* collapses to plain old physicalist reductionism.

In all this work, various philosophical or intuitive notions are clarified upon analysis of logical and syntactical properties of the theoretical systems themselves. The question whether a given theory is reducible to another is a deep and difficult metamathematical question. So much so, that I think it safe to say that one cannot simply *see* that reduction is impossible on mere acquaintance with the two theories concerned. We need detailed argument to support any intuition that we ought to be content to operate at the higher level, and not seek to reduce it to the lower level. Any strong and immediate intuitions to such effect could be expected to be grounded in logical workings of the theories that are not so complicated as those involved in a detailed metamathematical proof that reduction is impossible: otherwise, whence their strength and immediacy? For this reason, I think that logical analysis might succeed in revealing whatever it is about the internal structure of theories that prompts anti-reductionist convictions. Beyond this, I cannot, at this stage, offer any more detailed suggestions; I can only point out a direction research might follow, and a goal that it might thereby reach. Prescinding, however, from details of particular theories, there is another more powerful and more general method of attack on the problem. It has been used independently to date by Hellman & Thompson (1975) and by Bealer (1978). It invokes Beth's theorem (Beth 1953) which states that if a new concept Q can be defined *implicitly* by means of a theory T using

concepts $P_1, \ldots, P_n$, then it can be defined *explicitly* in terms of $P_1, \ldots, P_n$, relative to T. Explanation of these notions is required. First, *implicit definability*:

Suppose one understands the concepts $P_1, \ldots, P_n$. One develops a theory using them, and one can identify what count as P_i in the domain to which the theory addresses itself. Suppose further that a new concept Q is imported, and a grasp of it conveyed by means of a set T of statements involving *both Q and $P_1, \ldots, P_n$*. Suppose finally, on the assumption that T is a true account of what is the case in the domain, and that you have settled what, in the domain, count as P_i, that there turns out to be *but one* way of understanding what Q applies to. Then we say that we have *implicitly* defined Q in terms of $P_1, \ldots, P_n$ relative to T.

Secondly, *explicit definability*:

Suppose there is a complex concept R built up from $P_1, \ldots, P_n$ but *not* involving Q and that it follows as a logical consequence of T that R and Q apply to exactly the same things. Then we say that R provides an *explicit* definition of Q relative to the theory T.

Beth's theorem, to repeat, states that if Q is *implicitly* defined in terms of $P_1, \ldots, P_n$ relative to T then there is some such R that *explicitly* defines Q in terms of $P_1, \ldots, P_n$ relative to T. Why is it important in the present context? For the following reason: Suppose one is a physical determinationist working with concepts $P_1, \ldots, P_n$ from the determining level (say physics) and with various concepts from a higher level (say embryology). Let T be one's full story *concerning both levels. The claim that the lower level determines the higher level is exactly the hypothesis of Beth's theorem*, namely that each concept Q is implicitly defined in terms of $P_1, \ldots, P_n$ relative to T. Put another way, we may say that in the statement

　　if A then B

of Beth's theorem, the antecedent A can be interpreted as the thesis of physical determinationism. So now the implication that is Beth's theorem guarantees an explicit definition of each higher level concept Q in terms of the lower level concepts $P_1, \ldots, P_n$. The consequent B of Beth's theorem, in other words, is the thesis of reductionism. For now replace in T each occurrence of a higher level concept Q by its defining formula $R(P_1, \ldots, P_n)$. The result is a theory that operates at the lower level and yet covers all the higher level phenomena, albeit by the complex defining formulae $R(P_1, \ldots, P_n)$.

Beth's theorem, then, according to the determinationist, *implies*

reductionism. It appears to render uninhabitable the intellectual niche sought by the physical determinationist who, prompted by considerations of holism and emergent properties, was a would-be anti-reductionist. It threatens to demolish the philosophical position that I described above as the one most likely to be adopted by modern embryologists (and biologists generally). In vain would Mayr be able to protest that

The claim that genetics has been reduced to chemistry after the discovery of the structure of DNA, RNA, and certain enzymes cannot be justified. To be sure, the chemical nature of a number of black boxes in the classical genetic theory was filled in, but this did not affect in any way the nature of the theory of transmission genetics. As gratifying as it is to be able to supplement the classical genetic theory by a chemical analysis, this does not in the least reduce genetics to chemistry. The essential concepts of genetics, like gene, genotype, mutation, diploidy, heterozygosity, segregation, recombination, and so on, are not chemical concepts at all and one would look for them in vain in a textbook on chemistry. (Mayr, 1982).

For Mayr has come nowhere near establishing the *logical* impossibility of achieving a chemical definitional reduction of the notions of genetics. Just because they are not to be found in any extant textbook on chemistry does not show that it is not, in principle, possible to devise such a reduction. Beth's theorem would ensure that the reducing formulae R exist. They might be fiendishly complex: but they would be there.

   If this possibility cannot be foreclosed then we have to live with it. What value would then remain in the insistence that there will always be a place for the holistic, a place for the emergent, as our minds grapple with reality? Terms such as the embryological ones that I categorised above would probably defy *workable* definition in strictly physicochemical terms. The details of such definitions would be elusive, and the definitions themselves would be tiresomely, if not monstrously, cumbersome. What would such a definition of 'blastula' look like? of 'pupa'? of 'mesoderm'? In these definitions one would have (at the very least) to talk of cells of certain types lying in various topological configurations. Then the reference to cells would have in turn to be replaced by strictly physicochemical terminology: so cells would be defined as certain topological configurations of cytoplasm and nuclear substance within a protein-fibre wall; then the cytoplasm, nuclear substance and wall themselves would in turn be defined as ... and so on. Then there is the further

problem that each species' gastrula has a characteristic number of cell types, and possibly also a characteristic rate at which these differentiate further. So 'gastrula' *tout court* as a non-species-specific term in embryology, would probably have to have built into it a disjunction, across species, of these characteristic cell types. The details are too awesome to contemplate. Nor does the resulting definiens capture the open-textured *meaning* of the word 'gastrula'. This meaning can be mastered pre-theoretically after ostensive training. One who has thus grasped it can characteristically recognise a gastrula of a newly discovered species without having to know anything about its characteristic number of cell types. So the physico-chemical definition of *gastrula* served up by Beth's theorem would not be meaning-preserving. The complex predicate F serving in this role would not be in what the philosopher calls *intensional* agreement with the ordinary term *gastrula*. For in some possible world (perhaps even one compatible with the underlying laws of physics that hold in the actual world) the extensions of the term *gastrula* and the complex predicate F may not coincide. This, however, is not fatal to scientific practice in the actual world, so long as extensional agreement there between the terms is guaranteed. But would such agreement ever be *reached*? The practising reductionist would be referring to an entity in incubation not as 'this gastrula here', but as 'this (instance here of the complex physicochemical predicate) F'; and by the time he had uttered F the wretched thing would probably have grown, multiplied and died! So 'gastrula' itself would in all likelihood be retained as a convenient definitional abbreviation for the complex predicate F; and the actual science of embryology would carry on as if nothing, philosophically or methodologically, had altered it. There are many more examples of problematic terms, drawn from the lexicon of embryology that I roughly categorised above, that would similarly resist definitional reduction save at the unbearable cost of hopeless complication, even should agreement on details ever be attainable. But why is it that we are not capable of such circumlocutory precision, and prodigious logical manipulation, so that scientific practice can be made consonant with reductionist conviction? Or, better, why is it that we do science with a language and with concepts that, in deference to such reductionist convictions, would have to be dispensed with in favour of highly complex definitions in reducing terms, only to be resuscitated as convenient abbreviations for them? For a philosopher to suggest to

evolutionary biologists the following answer to such a question is to carry coals to Newcastle. But suggest it I shall: I think we have been naturally selected to carve up reality in various ways: to see interactions in terms of the organismic and the functional. So we are to a large extent handicapped in our deeper theoretical endeavours by the very cognitive heritage that has enabled us to survive. The same view, which I shared with a biologist, was expressed elsewhere as follows (Tennant & von Schilcher, 1984):

As long as it is the brains of human organisms that do science, there will be a special place in science for the organismic and the human: and this is in spite of the long drawn out cosmological fact that the physical brought forth the human and the social. Because ours is a world of purpose quite by chance, our only chance is to see purpose.

Not all is lost, however, on the logical front. In a technical sequel to this paper (Tennant, in press (b)) I shall examine various counter-arguments that have been given to the application of Beth's theorem in the manner I have been concerned here to describe. I shall argue that these counter-arguments do *not* succeed in preventing the slide, greased by Beth, from determinationism to reductionism. But I shall *also* argue that there *are* definitive objections which *do* halt that slide. So the determinationist need not be in the position of refusing to agree with the thesis of reductionism merely on *practical* grounds. His refusal could be based also on the absence of any cogent *logical* grounds.

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