**The Biology of Memory**

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Introduction

This year, the general theme of our Enaction Summer School is « Memory ». In this talk, I want to address this question from the point of view of biology. Maybe some of you would thereby expect me to talk about neural networks and connectionism; but although this is undeniably an important field for cognitive science, I have nothing particular to say about it. In a somewhat similar vein I could have talked about the Immune System, where "cognitive" metaphors are interesting, and on which I did some work with Francisco Varela (Stewart 1994). However, I prefer to talk about two questions, both of which are in my view absolutely fundamental but which are very inadequately addressed by contemporary biology. My hope is that I will thereby spark an ambition in some of the young scientists here at this meeting to address these questions. The first of these questions concerns unicellular organisms; the second concerns multi-cellular organisms.

I. The origin of genetic systems.

The paradigm of enaction in cognitive science is rooted in the theory of autopoïesis as a definition of "life". The prototypical example of an autopoïetic system is a unicellular organism such as a bacterium. A minimal example is the "tessellation automaton" (Varela 1979). This simple automaton is already sufficient to illustrate the principle of a circular organization, in which all the components are produced by other components in the system, so that collectively the whole system produces itself. Thus, the *metabolism* produces B-components that are necessary to repair the membrane; and the *membrane* is necessary to catalyse the metabolism and to maintain a high concentration of the B-components.

This minimal model does however have some limitations – even if it is enriched by the addition of a "cognitive" interaction with its environment by way of a sensory-motor cycle (Bourgine & Stewart 2004). Firstly, such entities are strictly individual – there is no significant sense in which a collection of them could form a *population.* Secondly – more seriously, and more related to our theme – they have no *memory.* These entities are so simple that, given a suitable supply of matter and energy (the A-molecules in the environment), one can imagine them arising through spontaneous generation as dissipative structures. This is of course an advantage if

we are trying to imagine scenarios for the origin of life; but the downside of this is that if such an entity collapses (if its membrane collapses due to stochastic fluctuations), it disappears *without leaving any trace.* In this respect, such entities are like natural dissipative structures such as cyclones: they can arise for millennia (as long as suitable boundary conditions continue to exist), but each of them eventually peters out and there is no possibility of significant *evolution.* There is no possibility of *cumulative learning* by a population over the generations.

It is of course a major attraction of the theory of autopoïesis that if offers a welcome breath of fresh air, away from the stifling dogma of gene-centred molecular biology. I will not repeat here the critique of this dogma, which treats "genes" as though they were autonomous entities which moreover direct the production of the whole organism (see Stewart 2004 for an extensive discussion). It is enough here to recall that there are few biological molecules as inert as DNA, which put in solution in a test-tube does nothing at all; genes do *not* produce themselves, nor do they "reproduce themselves" (placed in the context of a suitable organism, they can *be copied* but that is something else again). But at the same time, it is important not to throw out the baby with the bathwater. Maturana and Varela (1992) speak persuasively of "natural drift"; but when all is said and done, Darwinian natural selection *does* remain a major biological process. There is an undeniable sense of "progress" in the succession of life-forms from the very first ones, simple enough to have arisen by spontaneous generation, to prokaryotic bacteria, to eukaryotic cells, to multi-cellular organisms, to vertebrates with central nervous systems, to our hominid ancestors. This progression is incomprehensible without the creative potential of natural selection; and this requires what I will call a "genetic system".

In what follows, I will draw heavily (but not uncritically) on a beautiful little book by Cairns-Smith (1985). By a "genetic system", I mean a structure with the following abstract properties :

i) it contains information (! – this may surprise those of you who are familiar with my critique of the computational paradigm in cognitive science – but I will come back to this point);

ii) it can be copied;

iii) it is susceptible of variation (this necessary for it to contain information), such that the variant forms can be copied more or less faithfully (a certain rate of error, or mutation – neither too high nor too low – is

necessary), so that there is a phenomenon of inheritance (of the variation).

Cairns-Smith argues – rightly, I think – that

*iv)* *if* there is such a structure, and

*v)* *if* the variations cause differential reproduction of the organisms that carry such structures (i.e. variation in Darwinian fitness), and

*vi)* *if* there is potential overproduction, so that not all organisms will be able to survive to produce offspring themselves,

*vii)* *then* these entities will get better at reproducing their kind.

He writes: "There can be no accumulation of appropriate accidents, no kind of progress, without the means to remember". So here we are, squarely in our theme of memory.

In case you are nervous that I am abandoning and/or betraying all critique of gene-centred biology and the dogma of genetic determinism, let me specify that I am using the term "information" in the strict sense of Shannon, fully respecting the limitations that go with it. A "genetic structure", in this sense, is *strictly differential:* all other things being sufficiently equal, a *difference* in a genetic structure causes a *difference* in the phenotype of the organism that bears it. Thus, genetic information is constitutively blind to everything that is *invariant* in an organism (including, first and foremost, its autopoïesis) – point that I have made at laborious length in Stewart (2004).

Thus, I am arguing for something of a "middle way", which might have pleased Francisco Varela. Contrary to Cairns-Smith, I am most emphatically *not* considering that genetic information is a "set of instructions about how the rest of the organism, its phenotype, is to be made and maintained". But on the other hand, I am *not* considering that genetic information is therefore inexistent or impossible. If the famous *ceteris paribus* clause *is* satisfied – if "all other things *are* sufficiently equal" (and they can be) – then genetic differences can encode differences in phenotypes; and as I have argued, this can give rise to memory… and creative progress in the course of phylogeny.

So we come now to the question: how could a genetic system, thus defined, come into existence? In order to answer this question, the first method to be tried is that of working backwards from the present situation. There are two variants to this method: characterizing the last common ancestor of all contemporary forms; and simplifying, taking away elements from a contemporary organism (e.g. a bacterium)

to try and get to a "minimal form". These two variants have in common the result that they run headlong into an impasse. The "last common ancestor" (more or less akin to contemporary archeo-bacteria) is still *far* too complicated to have arisen by spontaneous generation. The same goes for all attempts at a "minimal" bacterium: the circularity between genes (necessary to produce proteins) and proteins (necessary to replicate and to decode nucleic acids) seems insurmountable.

Cairns-Smith provides a solution to this conundrum, using the metaphor of an arch. In a finished arch, each stone holds in place the others: take away any one stone, and the whole arch collapses. So, how can an arch ever be built piecemeal, stone by stone? The answer is: by using scaffolding. First, one simply makes a pile of stones. Then, the stones that will form the future arch can be placed one by one on top of the scaffolding, and if necessary fixed to each other. Then, when the future arch is already in place, one can take away the scaffolding – which can perfectly well disappear without leaving a trace. Running this scenario backwards, we see that the solution to the impasse of an "irreducible minimal form" is to *add* elements of the scaffolding, so as to get to a point where the entire scaffolding can hold the "circular" superstructure; at which point, the elements of this superstructure *can* be removed without causing total collapse.

So much for the metaphor. How can we apply it to the question at hand, i.e. the origin of a genetic system? Cairns-Smith argues for a "primitive" genetic system, sufficiently simple and "low-tech" that it *could* arise by spontaneous generation; yet nevertheless satisfying all the properties i) – vi) above so that it could evolve, gradually, by way of natural selection. He considers that this is a plausible route for organisms with a gradually complexifying biochemistry, progressively incorporating carbon-based molecules such as sugars, amino acids, nucleotides…. proteins, nucleic acids; until the point comes when the present RNA/DNA system could be built on top of this scaffolding. It is at this point that the present biochemical substrate for the "genetic system" could *take over* from the primitive system; and the latter could quietly disappear, without leaving a trace. This, in a nutshell, is the scheme that Cairns-Smith calls the "Genetic Takeover"; personally, I think that it is brilliant, original, and far more plausible than any other scenarios elaborated so far by mainstream molecular biologists.

If we accept, even provisionally, this abstract scheme of a "genetic takeover", a major question is the identification of this hypothetical "primitive genetic system". The task is difficult, of course, because by hypothesis it has disappeared without

(necessarily) leaving any traces at all. Cairns-Smith argues, attractively if not entirely convincingly, for *clay crystals* that, in his view, constituted "naked genes" which gradually acquired an "indirect phenotype" composed of carbon-based biochemical cycles. Personally, I would prefer to envisage a dual origin for the bacterial "last common ancestors", composed of two aspects A) and B).

A) A purely dynamic dissipative structure, a sort of "chemical whirlpool" – but which is already (practically?!) autopoïetic, without having a genetic system. A key question here is the nature of the energy source for the dissipative structures. (Virtually) all present-day organisms rely directly or indirectly on sunlight, and the photosynthesis of organic molecules with the corollary of creating an atmosphere with free oxygen. However, as Reichholf (1993) has argued convincingly, photosynthesis is almost certainly a later development: not only is it energetically so powerful and potentially destructive that it is difficult to keep under control, but it requires already protein synthesis – which can only come *after* the "genetic takeover". The original system was much more likely based on the far gentler oxydo-reduction potentials of iron ($Fe^{+++}$ - $Fe^{++}$) and/or sulphur. A variant possibility, which is currently generating some interest, is that the initial proto-biological dissipative structures fed on the energy from undersea geo-thermal vents.

B) A primitive "genetic system", simple enough to arise independently by spontaneous generation, but already complex enough to put in place the basic potentialities i)-vi). Crystals are indeed an attractive possibility here – but clays are not the only candidates. The essential requirements for such a primitive system are that it should be capable of variation; with suitably faithful copies of the variant forms; and, last but not least, a potential for coupling with a type-A system so as to set up the scheme of genetic variation in the phenotypes of autopoïetic organisms.

My proposals here are obviously sketchy in the extreme; but the stakes are high, because in my view the possibility of significant phylogenesis does absolutely require some form of trans-generational memory; and this can only be provided by something like what I have called a "genetic system". This is the point at which I will leave this first question – saying "over to you!"

## II. The organization of ontogeny.

### *II.1. The nature of the problem*

About 600 MY ago[1], there occurred what is arguably the most momentous event in the whole of biological evolution after the origin of life itself; this event is known as the "Cambrian explosion" (Gould 1989). Up until that time, all living organisms were unicellular and microscopic – bacteria, amoebae and the like. Then, within a mere geological instant[2], a whole range of macroscopic multi-cellular animals made their appearance[3]. Beyond the drama of the historical event – the Cambrian explosion itself – the very existence of multi-cellular animals raises the question of ontogeny, i.e. the process leading from a fertilized egg-cell to an adult multi-cellular organism. I want to focus here on the question of the mechanisms underlying the process of ontogeny; because even before we go into it properly, it is immediately evident that the fantastic *regularity* of this process, awe-inspiring in its complexity, must one way or another involve something like a "memory of the species".

At a purely empirical level, the process of ontogeny has been very well described, in particular from a morphological point of view. More recently, the observations of the classical anatomists have been usefully supplemented by non-invasive techniques of visualisation. These images serve to underline the apparent fragility of the developing embryo (for example, I have caught myself wondering anxiously, "will those tiny buds at the ends of the arms *really* turn into properly-formed hands and fingers?!"). And this in turn emphasizes the impressive *robustness* of the process: serious congenital malformations are astonishingly rare[4]. This

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[1] MY = a million years. This is the "natural" time-scale for biological evolution.

[2] The process must have taken taken the order of one or several MY (see above); but in terms of fossils, the space of time was so short that it there is no trace in the geological record of intermediate stages: in one strata of rocks there is nothing (i.e. only microscopic protozoa); in the next, the whole range of the Cambrian fauna.

[3] All present-day animals belong to one of seven major Orders, each characterized by a specific *Bauplan* or bodily architecture (with either radial or bi-lateral symmetry). These Orders are: Sponges, Corals (including jellyfish…), Annelids (worms, leeches…), Molluscs (shellfish, snails, squids…), Echinoderms (starfish, sea urchins), Arthropods (crustaceans, insects, spiders…), and Chordates (notably vertebrates). One might have thought that sponges and jellyfish are "primitive", and vertebrates (including ourselves) are "advanced"; but the fact is that these seven orders *all* appeared at the time of the Cambrian explosion. Not only that, but there were also an equal number of other *Bauplans*, some of which appear to us touchingly bizarre, which then disappeared without leaving any evolutionary descendants. It is to be noted that no new *Bauplans* have been invented since that time. This striking configuration – all the creativity in terms of the *Bauplans* of multi-cellular animals being crammed into a tiny period, with nothing either before or since – clearly calls for explanation; this is one of the questions which we may take up in the discussion.

[4] The rate of « failures » is probably somewhat higher than it appears, because fairly recent research indicates that a substantial number of miscarriages, particularly very early in

combination of complexity and fragility on one hand, and robust reliability and regularity on the other, makes ontogeny arguably one of the most fascinating of all biological phenomena. It is also, to date at least, one of the least well understood.

What we do know, in very general terms, is that this regularity is not a merely static phenomenon; it arises, robustly, from principles of dynamic self-organization. A particularly striking example is that of identical twins : if a developing embryo is separated in two, the result is not one left-half and one right-half individual, but two complete, perfectly-formed individuals; and this is the case even if the separation is made astonishingly late in embryogenesis. Starting in the 1920's, Spemann and others, initiated a programme of experimental embryology, investigating the consequences of perturbing the process in various ways. Starting in the 1940's, Waddington put forward the concepts of "epigenetic landscape" and "chreode" (i.e. an attractor extended over the time of a developmental process), and this represents a step towards a possible mathematical formulation (e.g. employing the "catastrophe theory" of Thom) in order to characterize the general nature of the process. And I may also mention the work of Medawar (1957) who provides the outline of an explanation for the phenomenon of senescence, which is indeed specific to multi-cellular organisms[5]. But what I want to emphasize here is that none of this work, valuable though it is in setting the problem, constitutes a proper scientific *explanation* of the regularity of ontogeny. What are the *mechanisms?* How does it come about that the process is so regular? We do not know. And it is this absence of a proper scientific explanation that lends its superficial appeal to the disastrous notion of a "genetic programme": *descriptively,* ontogeny does indeed unfold *as though* it were "programmed"[6].

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gestation, serve to eliminate defective embryos. But quite apart from the fact that this sort of spontaneous abortion is itself a form of adaptation, the overall rate of success, well over 95%, remains remarkably high.

[5] If we consider that doubling in volume and dividing in two is not « dying » (and this seems to me correct!), then it follows that all unicellular organisms are (potentially) immortal: all those that are alive today are as old as the origin of life! By contrast, it is a feature of ontogeny is that it after maturation to an adult, it continues through senescence to death at the term of a limited life-span characteristic of the species - if not before by accident, and here lies the rub. Medawar argues that "senescence" only occurs in animals kept in protected captivity, but practically never in the wild. In his view, nothing is less natural than so-called "natural death from old age"; and indeed it is *because* of this that the process of senescence exists, rather than being eliminated by natural selection.

[6] I will not, here, go into a full-scale critique of the notion of "genetic programme", for which I refer to Oyama (1985) and Stewart (2004). In a nutshell, the problem with the notion of a "programme" is the same as that of the "dormitive principle" invoked by the doctors in Molière's play to "explain" (!) why opium makes you sleep: the fault is to take the *result* of a process, to give it a pretentious high-sounding name, and then to talk as though this name

### *II.2. Form and Matter*

Let us go straight to the heart of the matter: if the processes of ontogeny have so far resisted scientific explanation, it is for a deep reason. Oyama (1985) has pointed out that this reason resides in a deep prejudice, which colours the whole of Western thought since Plato and Aristotle, concerning the relation between *Form* and *Matter.* This prejudice consists of considering that matter, left to itself, is essentially inert or at best chaotic. It then follows that any material process which is "organized" must have been literally "in-formed" from a source essentially *exterior* to the process itself. In the case of a living organism, and in particular a developing embryo, there are two potential reservoirs of external information: one is the environment (which is manifestly external to the organism); the other is genetic information[7]. Oyama explains that this is why the hoary "nature versus nurture", alias "innate versus acquired" debate is so persistent.

All this changes, however, if we recognize that material processes are not necessarily inert or chaotic; on the contrary, under certain conditions, they can display remarkable properties of *self-organization.* And this can represent a complete turn-around in our attempts to understand the organisation of ontogeny. The insight is not particularly new: D'Arcy Thompson (1917) already remarked that morphogenesis in living organisms is necessarily based on the same physical principles as morphogenesis in natural non-living systems. D'Arcy Thompson was particularly impressed by landscapes and coastlines; another suggestive example, even closer to biology, is provided by the shape of a small jellyfish (Figure X, on the left). (JS: Figure missing, sorry!). It might seem, at the sight of it, that a considerable amount of "genetic information" would be required to "in-form" such a complex shape. But now look at the right of the Figure, which shows a form remarkably similar to the jellyfish. The point is that this form was not produced by a living organism at all – but simply by a drop of paraffin oil falling into water. Suddenly, the need for "genetic information" seems less compelling. This is exactly the sort of approach we need; but we do have to push it further to account for the *regularities* of ontogeny.

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were the explanation. In addition, if one examines the matter properly, even if there were a "programme" there is no good reason to suppose that it is "genetic" (other than the dogmatic pretension of Molecular Biology to explain everything). But the spectre of a "genetic programme" will only be laid to rest if we manage to do our job, and come up with a proper explanation of the regularities of ontogeny.

[7] Of course, the genes are *physically* situated in chromosomes in the nucleus at the heart of each cell; but epistemologically, genes are indeed exterior to phenotypic somatic processes; See Stewart (2004) for a detailed analysis.

***II.3. Snowflakes***

In order to understand how a morphogenetic regularity can exist without the need for "information" or a "programme", it will be useful to start with an example which is clearly inorganic. Snowflakes, observed under the microscope, have quite remarkable structures (see Figure Y – missing again, JS). Every single snowflake has six arms, each of which has a structure which is so intricate that there have clearly never been two snowflakes which were exactly the same – in all the trillions of snowflakes that have ever fallen. And yet, *within* any given snowflake, each of the arms is quite remarkably similar to the five others. How is such a thing possible? How can each arm "know" what form the others are adopting, in order to conform to the pattern? The temptation is almost as great as in the case of biological ontogeny, to suppose that there must a "programme" somewhere, external to the arms themselves, which is "in-forming" them as to the morphology they should adopt. But the advantage of the case of the snowflake, simple though it be, is that in this case we know full well that there is no such "programme", neither in the environment nor lodged at the heart of the snowflake.

It seems that the explanation of this phenomenon is the following (Begley & Carey 1983). The process of ice crystallisation, passing directly from the gaseous phase to the solid phase, is close to the critical point where the three phases (solid, liquid, gas) meet; because of this, the crystallisation is extremely sensitive to the precise combination of three physical variables, temperature, pressure and humidity. If the six arms are practically identical, it is because they share the same history of fluctuations in their common local microclimate. The unique nature of this history is multiplied by the fact that there is a fourth factor which is determining for the morphology of the growing arm: this is the pre-existing shape of the arm at that precise moment. This fourth factor is also identical, from moment to moment, for each of the six arms; but progressively different from one snowflake to another (this is reminiscent of the phenomenon of deterministic chaos). In other words, the astonishing similarity of the six arms turns out to be nothing other than a strict application of a basic scientific principle: the same causes produce the same effects.

This analysis leads us to two important conclusions. First, if there is anything like a "programme", it is not localized anywhere; rather, it is *distributed* over all the elements that enter into interaction in the course of the process. Secondly, the putative "programme" does not even pre-exist; the "in-formation", if one insists on keeping this concept, is created step by step, in real time, by the very process which

"expresses" it. In fact, to sum up, a proper explanation in terms of physical processes renders the notion of "programme" superfluous: a "programme" that is not localized anywhere, and which does not even pre-exist with respect to the processes it is supposed to be directing, is hardly worth calling a "programme" at all. The leading idea we can draw from this example is that it may well be the same in the case of biological ontogeny: if the process is so regular, it is because its organization is based on regularities which are reliably produced by the developmental process itself[8]. We shall now attempt to apply this insight to an understanding of the very first steps in embryogenesis.

***II.4. Early embryogenesis***

The very first steps in embryogenesis, which are common to a large number of multi-cellular animals (notably vertebrates and echinoderms, but not insects and of course not plants), are shown schematically in Figure Z. (missing again JS). We shall see that a fairly simple analysis of these steps shows that it is indeed a "historical" process, which regularly creates for itself the conditions for its further unfolding.

Thus, the very first series of cell divisions of the fertilized egg-cell give rise to a *morula*, a mass of relatively undifferentiated cells which overall has a spherical shape (Figure Zb). Why is the morula a sphere – rather than being a 2-dimensional sheet, or a 1-dimensional string, or simply a collection of cells dispersed in the liquid environment? Well, essentially for the reason that an oil droplet suspended in water is also roughly spherical: the free energy of contacts between the cells (or the oil molecules) is less than the free energy of contacts with the aqueous environment; and thus the overall shape which minimizes the global free energy is that which minimizes the surface/volume ratio in a 3-dimensional space; and this shape is … a sphere. This mechanism is not written in any genes, and so the shape which results from it does not need to be either. Besides, the interactions between the cells with each other and with the aqueous environment which lead to the actual accomplishment of this shape, although they are perfectly predictable and reliable, are produced by the embryological process itself and thus do not pre-exist.

This "historical" nature of the embryological process is only strengthened during the following steps. *Because* of the spherical form of the morula, certain cells

[8] In order to avoid misunderstanding, I recall here that I am considering the *invariant* aspects of the process, the *regularities* of ontogeny. As soon as we seek to explain *differences* (cf section I), genetic information becomes relevant again. For example, if we seek to explain why the offspring of pigs are *not* like the offspring of cats, genetic differences are undeniably important.

will inevitably be placed at the surface, in contact with the aqueous environment, whereas other cells will be placed inside and surrounded by other cells. This difference will arise on the sole condition that the morula is (approximately) spherical; from the point of view of the organization of ontogeny, it can therefore be used as a perfectly reliable signal to trigger an appropriate differentiation between the two types of cells. In the event, the interior cells react by secreting a fluid. This *explains* how the embryo comes to have the form of a *blastula,* a hollow sphere filled with liquid surrounded by an epithelial membrane (Figure Zc).

Resulting from the previous stage, the blastula in turn provides the pre-condition for the next stage. The form of the "hollow sphere" allows for a special sort of movement called "gastrulation": a group of cells initially situated on the surface of the blastula plunge into the centre of the hollow sphere to give rise to the characteristic form of the *gastrula.* As shown in Figure Zd, these cells form the *endoderm,* which will later give rise to the gut; the cells which remain on the surface form the *ectoderm,* which will give rise to the skin and also to the nervous tissue; and the cells situated in between will form the *mesoderm*, which will be at the origin of the skeleton, the muscles and the blood. The essential task of embryology as a science is to determine how the signals which give rise to this cellular differentiation into three types – endoderm, mesoderm and ectoderm – arise from their respective position in the developing embryo. In one sense, the relational topology between endoderm, mesoderm and ectoderm is totally contingent; but in another sense, we can understand that it is actually inevitable (and therefore reliable and regular) precisely *because* it arises from the embryological process itself. In other words, the fact that the essential "information" for organizing the process does not pre-exist, but is constituted step by step during the unfolding of the process itself, is the key which enables us to understand scientifically the robust regularity of ontogeny.

To be fair, none of this means that it would be sufficient to create a cluster of cells whose nuclei had been destroyed by a laser, in order to obtain an embryo. The distinctive properties of a cell surface are largely determined by the proteins which are inserted in the cell membrane; and without genes, the cell could not make proteins. Moreover, in differentiated cells, the genes which are "expressed" (and consequently which proteins are made) are different; and the expression of genes is controlled by "transcription factors" which are themselves proteins made with the help of other genes. For a complete understanding of ontogeny, all these details will have to be worked out. Nevertheless, *in the last resort* the regulation of gene

expression *must* be determined by physico-chemical signals generated by the developmental process itself; it is this, and only this, which can confer a reliable, dynamic regularity to the process as a whole.

***II.5. Beyond outside versus inside***

The possibilities for the sort of self-organization that we have envisaged in the previous section, far from declining, will actually be multiplied and enriched as the embryo develops and becomes ever more complex. In this section I want to make the point that in the constitution of these relational regularities, there is no essential distinction between those which are "internal" to the organism, and those which arise from its "external" relations with its ecological niche. (Actually, this was already true of the formation of the spherical morula). In addition, Jacob (1981) has most usefully noted, biological organization is very typically "tinkering" which opportunistically takes advantage of contingent relations… on the sole condition that these can be made contextually reliable. I will now illustrate both of these features by another example, taken from a much later stage in ontogeny.

This example, taken from Oyama (1985), concerns the organisation of a critical moment in the ontogeny of a particular species of fruit-fly: the hatching of the young adult which must come out of the cocoon. Because of the climate where this particular species lives, the problem is very delicate. In this geographical location, the nights are very cold, so that if the young fly hatches during the night it will die of cold. On the other hand, the days are extremely hot and dry, so that if the fly hatches during the day, it will be "fried" before its wings and body have time to harden by contact with the air. In order to survive, the fly must hatch at a rather precise time in early morning, when it has begun to be a bit warmer, but before the violent dry heat of full day. One might have thought that there would be a fairly simple and direct solution to the problem: just use a thermo-receptor to wait for the moment when the temperature has risen. But it so happens that this organisation would not be viable. The hatching process requires a certain time to be accomplished, after it has been triggered; and so if the process were initiated by a detectable increase in temperature, it would be too late – by the time that the young fly would actually have gotten out of the cocoon, it would already be so hot and dry that the fly would be well and truly fried.

What is the solution to this problem? Well, it so happens that in this particular location, the sky begins to lighten about one hour *before* the heat increases. Thus, if the hatching process is triggered by *photo*-receptors, the fly will come out of the

cocoon at the ideal moment. And this is just how this particular species organizes this critical phase of its ontogeny. But this seemingly idiosyncratic and rather far-fetched example illustrates how *contingent* this organization is. Light, as such, has no intrinsic importance for the fruit-fly. The proof of this is that if this species were transported to another region where these contingent relations between light, heat and humidity no longer held, this mode of organization would no longer be viable. Nevertheless, *in context,* it is remarkably reliable and robust.

This example illustrates how the very unfolding of ontogeny can itself create organization opportunities that can be seized upon. It is the fruit-fly itself, in the logic of the organization of its ontogeny, which creates the possibility that the light of early dawn can be taken as a sign announcing that the heat will soon increase. Without the fruit-fly, the environment "in itself" is nothing, or at least nothing of all that. Conversely, the organization that ensures the regularity of development cannot be confined within the organism: the fruit-fly relies on certain relations (the time-lag between light and heat) that are contingent but nevertheless locally sufficiently reliable that the organization of ontogeny can be built on them.

Conclusions.

I want to conclude by two rather cursory remarks, leaving the rest for our general discussion.

The first remark concerns the relation between phylogeny and ontogeny; which amounts also to the relation between part I and part II of this talk. The point I want to make is that a genetic system can only encode for phenotypic variation that can actually arise, given the sort of organism we are dealing with. To take an absurdly surrealist example[9], there is just no way that *any* genetic information could encode for a sort of cow that would indulge in jumping over the moon – because that is a phenotype that does not and cannot exist. To put it crudely, there is just not much that unicellular organisms can actually *do,* other than swim around and feed and metabolize. Of course, in one sense that is already an enormous amount; and we have seen that the enrichment of a metabolic system can allow for the invention of the nucleic acid – protein system, and the "genetic takeover"; which is itself surely a

[9] Inspired by the traditional English Nursery Rhyme:
*Hey diddle diddle, the cat and the fiddle,*
*the cow jumped over the moon.*
*The little dog laughed to see such fun,*
*And the dish ran away with the spoon.*

pre-condition for multi-cellular life. But in another sense, the range of possible unicellular life-forms is extremely limited – at least compared with the vast range of possibilities that are opened up by multi-cellular life forms. The point here is that ontogeny is such a rich and complex process, that it can give rise to vast variation in phenotypes. And this *creates* the possibility for genetic systems to encode for a far greater range of phenotypic variations. The genomes of multi-cellular organisms do tend to be larger than those of unicellular organisms: but between a eukaryotic yeast, and a simple jellyfish, the difference is not so enormous.

The second and more important point that I want to make, is to return to our central question of "memory". But this is where I am going to sit back and turn the question over to you. Arguably (and I *do* argue!) everything I have said, in both parts I and II, *does* relate to memory. But even if you were to accept everything I have said (and I sincerely hope you will not!), this raises far more questions than it answers. And maybe the central question is: what, after all, *is* this phenomenon that we are tempted to call "memory"? Is it a real phenomenon – or may it not, after due examination, fade away in the same way that the notion of an ontogenetical "programme" does?

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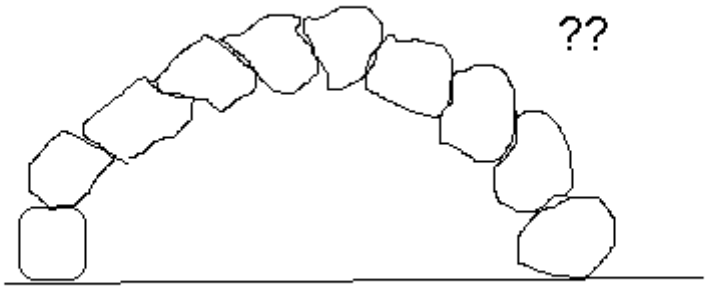


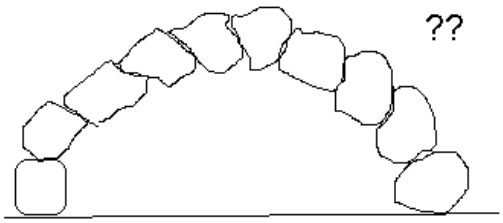


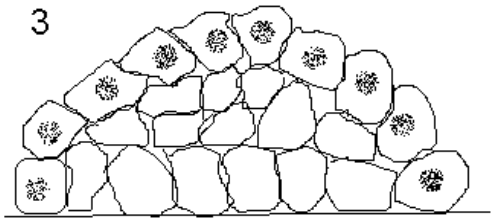


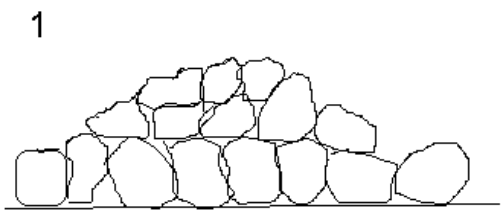


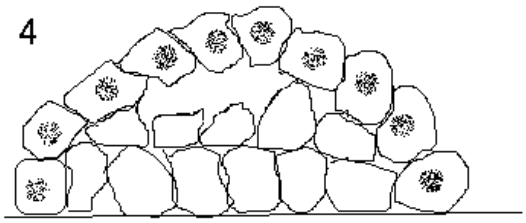


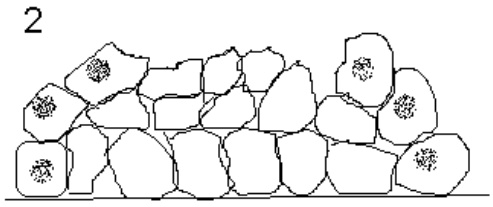


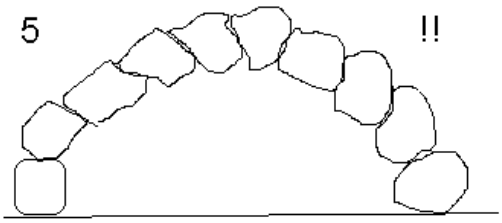

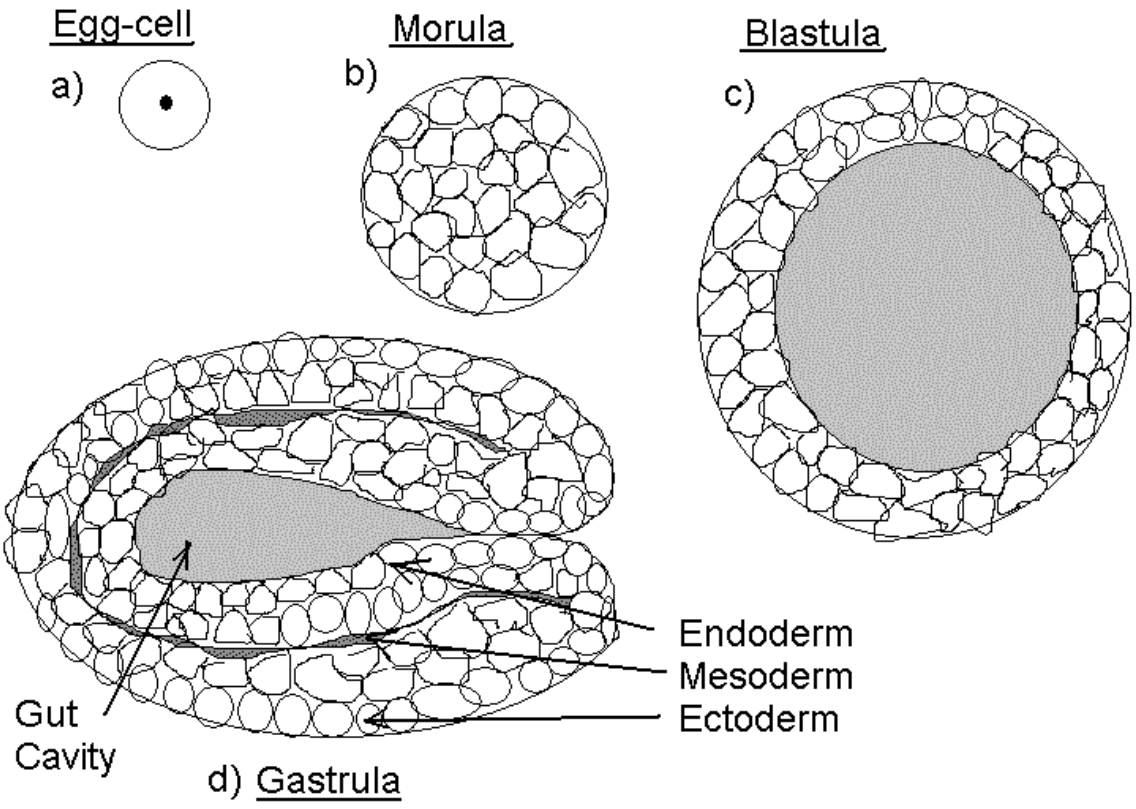
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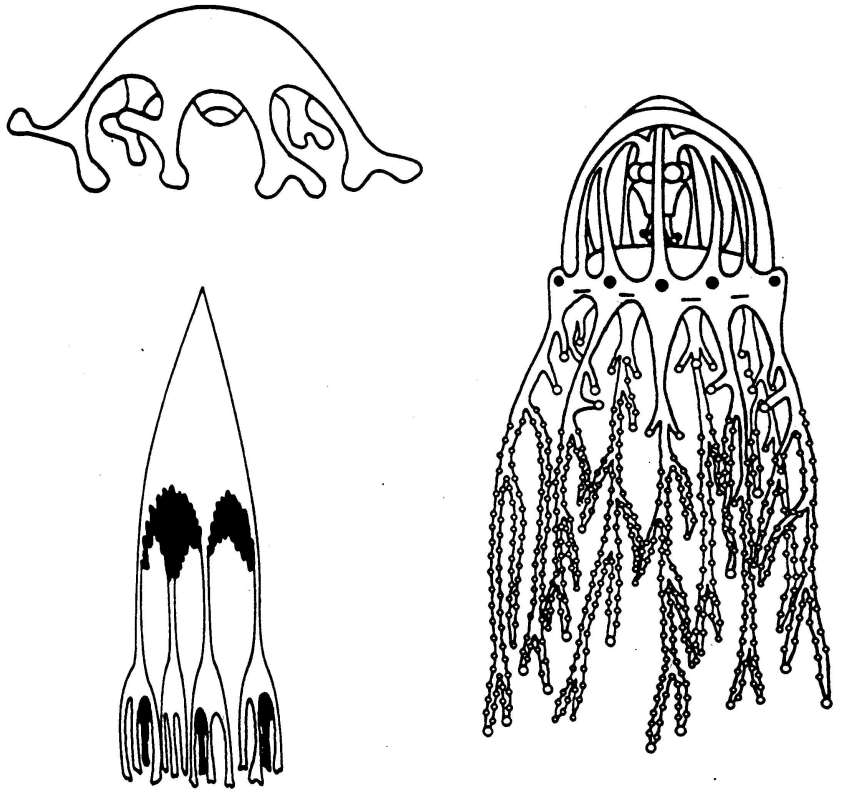
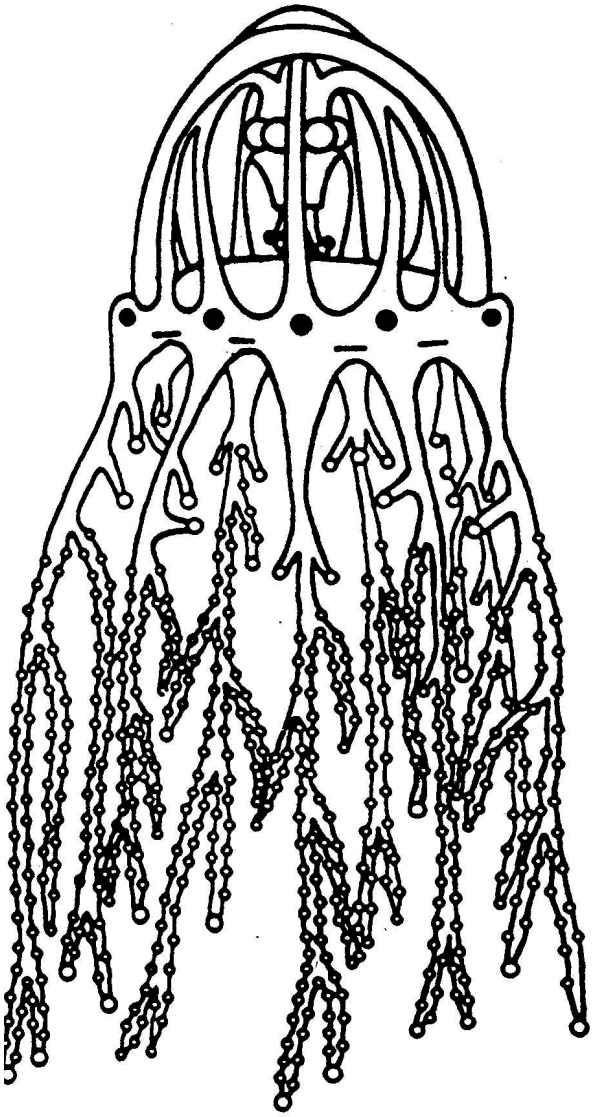
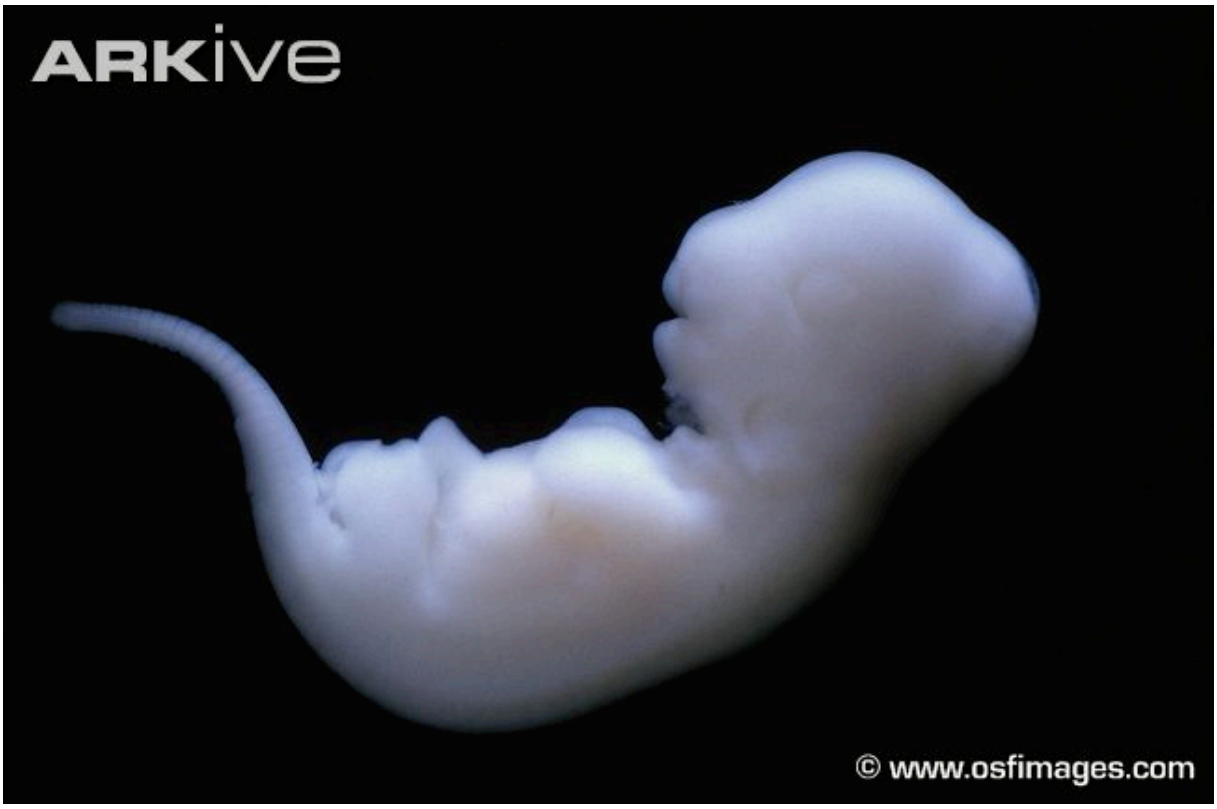
Gut
Cavity
d) Gastrula



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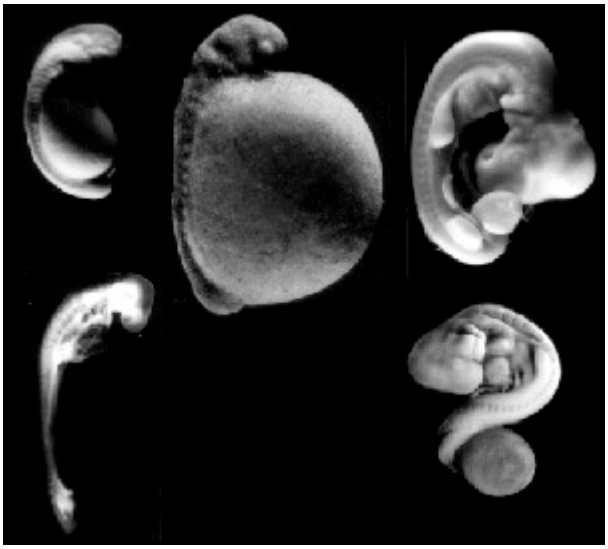

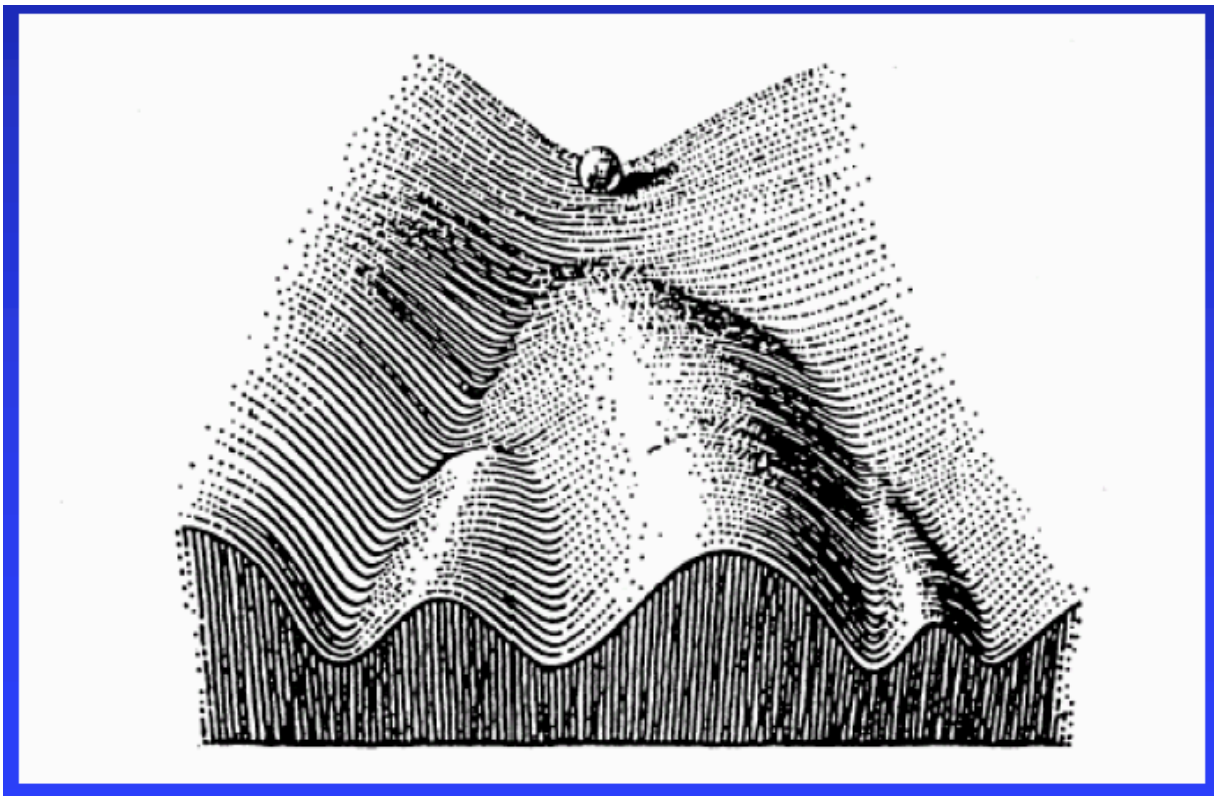

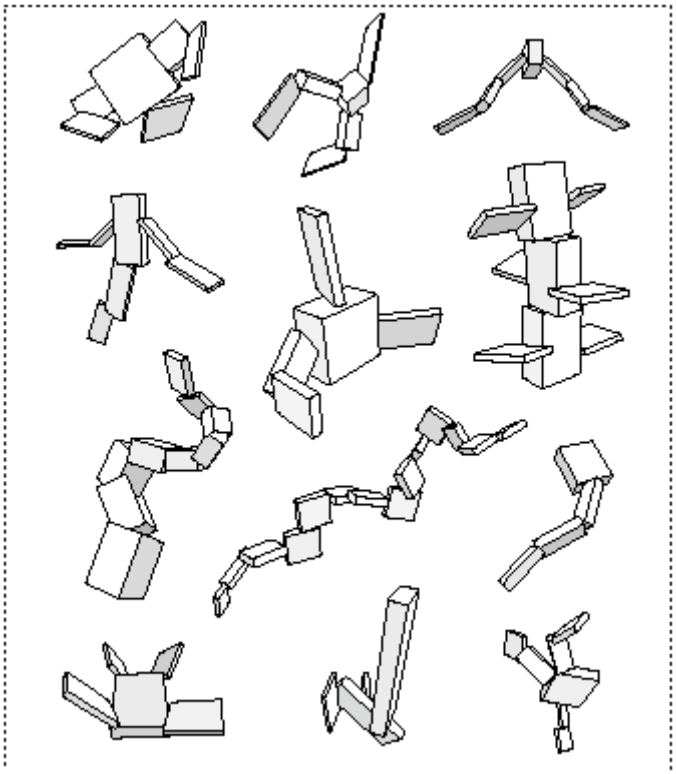

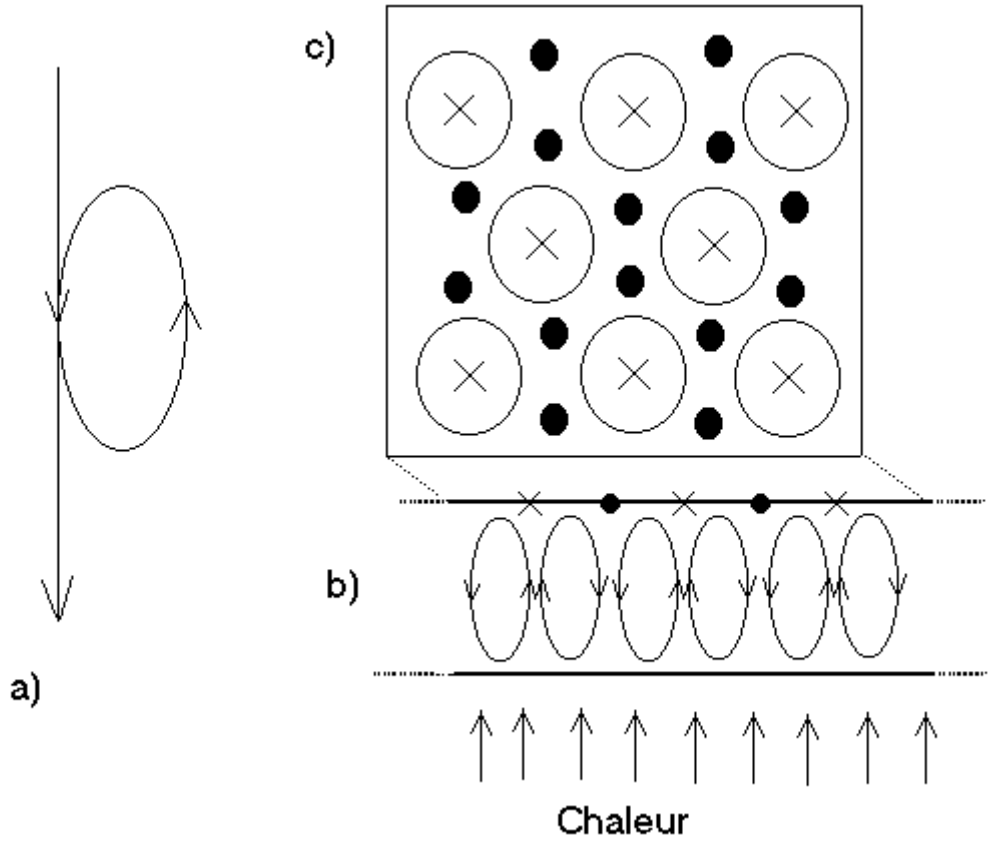
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