ADDING CONTINUOUS COMPONENTS TO L-SYSTEMS

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Summary

Constructions are shown for cellular developmental models with continuous parameters, such as concentration of nutrients or inhibitors, size and age of cells or compartments. It is proposed that we can make use of some of the L-system results for these continuous component models.

Introduction

Developmental descriptions with the help of L-systems are based on discrete symbols which stand for discrete states of cells. In accordance with our present-day understanding of cellular processes, the "state of a cell" at any time is assumed to consist of the "state of the genome" and of the "state of the cytoplasm" at that time. By the "state of the genome" we mean the configuration of active and inactive genes at that time. The genes being discrete entities which are either repressed or not at any one time, the combination of active genes forms a naturally discrete "genomic state". Nevertheless, if the number of genes n involved in developmental regulation were large, then the number of possible combinations of active ones, 2^n, could be unmanageable. This, however, does not seem to be the case in the developmental processes investigated so far, not more than a handful of genes being at most implicated in each case.

But the "cytoplasmic states" are an entirely different matter. The cytoplasm consists of thousands of different proteins, nucleic acids, metabolites, and other compounds, each at continuously varying concentrations. Most of these materials are necessary for the normal functioning of the cell and are not involved in developmental regulations. Again, the number of those compounds which are developmentally impor-

tant, such as growth hormones, inducers, cell division regulators and the like, is probably small. Nevertheless, their diffusion and reaction rates must be taken into account, as well as their concentrations, in order to compute their effect on various cells. Ever since the constructions of A.M. Turing's diffusion-reaction model for morphogenesis,[1] a considerable number of developmental models have been published with computer instructions and partly based on the production, diffusion, and decomposition of morphogenetically active compounds (morphogens)*. Among these we may mention the models of D. Cohen[2] for branching structures, of D.A. Ede and J.T. Law[3] for the early development of chick limbs, of C.P. Raven and J.J. Bezem[4] for the development of snail embryos, of A.H. Veen and A. Lindenmayer[5] for leaf position determination on shoot apices, and of Baker and Herman[6] for heterocyst initiation in blue-green algae. Only the last of these models has to do with simple (unbranched) filaments of cells, so we chose it as the first example to introduce our ideas. What we propose to show is how developmental models with both discrete genomic and continuous cytoplasmic states can be expressed as counterparts of L-systems, and that in fact these new systems represent a useful extension of the original concepts, with the hope that the results and insights gained on L-systems will carry over to them.

The correspondence between "dynamic" systems (described by differential equations) and discrete algorithmic systems, with reference to diffusion-reaction mechamisms, has recently been commented upon by H.M. Martinez and R.M. Baer[7]: "discreteness can

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* Since the references are mostly to biological papers, we deviate from the format of this volume and list the references at the end of the article.

also be dynamic. It can correspond to the steady states of a physical system maintained far from thermodynamic equilibrium (a dissipative structure). One is accordingly tempted to view this dynamic discreteness as the essential ingredient of any biological process at the cellular level having a programmed nature".

For a more detailed biological justification of L-systems see my review[8], and my chapter in the book of Herman and Rozenberg[9]. For formal definitions and results see Salomaa's chapter on Lindenmayer-systems[10], and the rest of the above mentioned book.

Heterocyst initiation in growing algal filaments of Anabaena

In order to account for the differentiation of heterocysts at more or less regular intervals (every 10 cells or so) in growing filaments of the blue-green alga Anabaena, Baker and Herman[6] made the following assumptions (which are widely accepted by biologists).

The heterocysts produce an inhibitor which diffuses along the filament, and into the surrounding medium as well. A cell in which the inhibitor concentration falls below a certain threshold value turns into a heterocyst, and starts producing the inhibitor. Cells which are inhibited from turning into a heterocyst (vegetative cells) can divide upon reaching a certain age.

Diffusion of the inhibitor is governed by the equation

$$\frac{\Delta c}{\Delta t} = k\,(\ell - c) + k\,(r - c) + k\,(e - c)$$

where c is the concentration of inhibitor in the cell under consideration, ℓ, r and e are concentrations of inhibitor in the left and right neighbour cells, and in the environment. From this equation we get

$$\Delta c = k.\Delta t.(\ell + r + e - 3c).$$

Assuming for the present that e = o, and choosing (footnote 1) $\frac{1}{4}$ as the value of $k.\Delta t$, we have then the formula

$$\Delta c = \frac{1}{4}(\ell + r - 3c)$$

which was used in the simulation of Baker and Herman[6]. The fact that e = o means that each cell of the filament continually looses inhibitor to the environment. This is why the inhibitor concentration does not keep increasing in the filament as would be expected since the heterocysts keep producing the inhibitor.

The simulation was carried out by the program CELIA which Baker and Herman[11] and Herman and Liu[12] constructed for generating cellular one-dimensional growing arrays. In the program the state of each cell consists of a certain number of attributes. The next state of the cell, or - if it divides - of its daughter cells, is determined by its present state, and possibly also by the states of its left and right neighbour cells. This means that each attribute has to be computed at each time step for each cell. The instructions used by Baker and Herman[6] in their first simulation in the paper can be given as follows (in a somewhat modified form):

Let w = (< -, x, ->, <a, y, u >, < -, z, - >) be a cell-triple. Then

(1) if y > t and u > 0 then w $\longrightarrow$ < a, f (x, y, z), (u - 1)>,

(2) if y $\leq$ t and u $\geq$ 0 then w $\longrightarrow$ < b, h, 0>,

(3) if y > t and u = 0 then w $\longrightarrow$ < a, f (x, y, z), $S^{10\%}_{6000}$ > < a, f (x, y, z), $S^{10\%}_{6000}$ >.

Finally, let

(4) < b, h, 0 > $\longrightarrow$ < b, h, 0 >.

The attributes of each cell are shown between sharp brackets. The first attribute

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Footnote 1. The diffusion rate constant k is taken here to be the same between cells along the filament, and between cells and the environment. This obviously is a gross simplification. The choice of the value $\frac{1}{4}$ for $k.\Delta t$ has the consequence that if the length of the time step Δt can be estimated from other data then k can also be estimated. Baker and Herman considered $\Delta t \cong 10$ sec. a valid estimate from life cycle data, which gives then $k = 0.025\ sec^{-1}$ as the estimate for the diffusion rate constant, a rather high rate.

of a cell has only two values, a or b, standing for vegetative cells and heterocysts, respectively. The second attribute is the concentration of the inhibitor, and the third attribute is the age of the cell. The first instruction states that the center cell in state < a, y, u >, with its left neighbour having an inhibitor concentration x, its right neighbour an inhibitor concentration z, if y is greater than threshold t and u > 0, must go into a cell in state < a, f (x, y, x), (u - 1) >. The function f in this case comes from diffusion considerations and is assumed to be

$$f(x, y, z) = y + \frac{1}{4}(x + z - 3y)$$

by using the formula derived previously. The age of the cell is computed by subtracting 1 from u at each step. Thus, as long as the inhibitor concentration remains in a cell above the threshold concentration t (chosen as t = 3 in this simulation), the cell remains in the vegetative state a, its inhibitor concentration changes according to the diffusion law, and its (reverse) age decreases by one.

The second instruction specifies that if $y \leq t$ and $u \geq 0$ then the center cell turns into a heterocyst (b), its inhibitor concentration goes to a constant value of h, and its age to 0. According to the fourth instruction, cells of this type remain from then on in the same state.

The third instruction specifies a division of the cell < a, y, u > into two new cells, each in the state <a, f (x, y, z), $S^{10\%}_{6000}$ >. The term $S^{10\%}_{6000}$ stands for a stochastically chosen value of age from an integer set with average 6000 and standard deviation of 10%. This transformation takes place if y > t and u = 0, in other words, when an inhibited vegetative cell reaches age 0.

The genomic states in this developmental system are clearly the states of the first attribute of each cell, a and b, standing for its vegetative and heterocyst condition. The switch from one genomic state to another (a → b), and the decision for a cell to divide (a → aa) or not to divide (a → a), are controlled by the two cytoplasmic attributes (inhibitor concentration and age) with respect to the two threshold values (3 and 0). Once a cell is in state b, it remains so (b → b).

The simulation of Baker and Herman was successful in generating acceptable heterocyst distributions along growing filaments. For practical reasons they allowed the

inhibitor concentration in any cell to assume integer values only, those between 0 and 999 (in the heterocysts the concentration was at the constant value h = 999). The use of integer values did present some difficulties when the inhibitor concentration in the environment had to be varied ($e > 0$). As we have seen, the instructions of this developmental system were, however, formulated with the help of the continuous function $f(x, y, z)$ and its computations could be carried out to any desired degree of accuracy.

The point we wish to make concerning this developmental system is that it could demonstrably be formulated in a manner analogous to an L-system with two-sided inputs (called a "2L-system" or "$< 1,1 >$L-system") in spite of having continuous and stochastic functions as components. Furthermore, the analogy of this model with L-systems goes much deeper than just a common form of expression. For all practical purposes the computation of the function $f(x, y, z)$ would be carried out only to some finite accuracy, which would mean that the concentration parameter would in fact be discretized (just as Baker and Herman have done it). Any discretized parameter within finite bounds could be regarded as a finite set of states. Thus, although we define the developmental system by a continuous function, we would in reality be working with a discrete state system, in other words, an L-system. The stochastic aspect of the above instructions could also, for most purposes, be replaced by non-deterministic ones.

Once we recognize that certain developmental systems with continuous and / or stochastic components are fundamentally related to certain types of L-systems, the results available for the latter become directly or at least by analogy applicable to the former.

Unfortunately the theory of L-systems with interactions is not sufficiently strong yet to provide many useable results concerning the behaviour or equivalence properties of such systems. The only theorems we might mention are those of Rozenberg[13] concerning the normal forms of L-systems with $\underline{k}$ left and $\underline{\ell}$ right neighbours with inputs. He showed that for any $\underline{k}$ and $\underline{\ell}$, the class of $< k,\ell >$ L-languages is identical with the class of $< k+\ell-1,1 >$ L-languages, or with the class of $< 1,k+\ell-1 >$ L-languages. Furthermore he proved the existence of a hierarchy of $< k,\ell >$ L-systems, in the

sense that for every k and ℓ one can find a language which cannot be generated by a $< k,\ell >$L-system, but can be generated by a $< k+1,\ell >$L-system. In a simulation, the sizes of k and ℓ correspond to the rates at which active substances can travel along a filament in one or another direction. Thus these results may have a bearing on the simulation parameters chosen in a particular biological model.

The results on growth functions of L systems with interactions [14, 15], may also be eventually useful in answering questions concerning growth rates of filaments when growth is regulated by a process involving interactions among the cells, such as (possibly oriented) diffusion of hormones.

As more properties of L systems with interactions become known, more insights will hopefully be gained of development governed by diffusion-reaction mechanisms, such as the one concerning heterocyst differentiation discussed here.

Branching growth of barley roots

The situation concerning useable L-system results is quite different when we consider developmental processes in which no interaction takes place among the units, as illustrated in the following.

We take as basis of this example the mathematical description by C. Hackett and D. A. Rose[16] of the development of the seminal root of barley. The essential features of their description are: each root member grows at its apex by a constant rate, and produces subapically branches at constant distances from each other. According to their observations: "The development of the root system of barley . . . proceeds in such a manner that relations between the total number, length, surface area and volume of root members remain approximately constant during the vegetative stage of growth. The existence of this property of root development implies that the plasticity of root form so evident to the eye is achieved within a framework of some remarkably constant principles."

In a simplified form, the description of Hackett and Rose consists of giving apical growth rates $v_0, v_1, v_2, \ldots$ and branching densities $q_0, q_1, q_2, \ldots$ for zero, first, second, etc., order branches. Growth rates v_i are given in terms of mm per day, and branching densities q_i are in terms of branches per mm. They derive approximations of the total numbers and total lengths of first, second and third order branches as functions of time, and attempt to show how these formulas can be fitted to observations by suitable choice of parameters (the v_i and q_i values).

Our purpose is to show that this developmental model can be expressed in a formalism analogous to OL-systems, and that, in spite of the continuous parameters employed, recurrence formulas can be found for the developmental sequence it generates (cf. **17**).

Let us assume the following interactionless production rules for all $i \geq 0$:

(1) if $x < \frac{1}{q_i}$ then $< a_i, x > \longrightarrow < a_i, x + v_i >$,

(2) if $x \geq \frac{1}{q_i}$ then $< a_i, x > \longrightarrow < b, \frac{1}{q_i} > \left[<a_{i+1}, 0> \right] <a_i, x + v_i - \frac{1}{q_i}>$,

(3) $< b, x > \longrightarrow < b, x >$ for all $x \geq 0$.

Each cell in this case represents a root segment, either an apical segment (above the highest branch), or an internodial segment (between two branches), or a basal segment (below the lowest branch and the branching point). The square brackets indicate branches, as in previous articles. The state of each segment consists of two attributes. The first attribute has the value $\underline{a_i}$ and $\underline{b}$, standing for apical segments and for internodial or basal segments, respectively. The second attribute indicates the length of the segment.

The first instruction determines that as long as the length of an apical segment on an $\underline{i}$th order branch is below the required distance between branches $\frac{1}{q_i}$, the segment should grow by an amount v_i.

The second instruction states that once an apical segment on an $\underline{i}$th branch exceeds the required distance $\frac{1}{q_i}$ it should produce a new branch of order $(i + 1)$ with zero length at a point $\frac{1}{q_i}$ distance above the last branch. An internodial segment is cut off this way in state $< b, \frac{1}{q_i} >$, and a new apical segment is formed which receives the left over length of the original segment (which has been extended by v_i).

The third instruction shows that internodial segments do not grow or branch any further.

For the sake of this simple example let us assume that for all $i \geq 0$, $v_i = v$ and $q_i = q$. Consequently we also have $a_i = a$. Let us designate $\frac{1}{q}$ as $\underline{r}$. The constants $\underline{v}$ and $\underline{r}$ may take any positive real value. The term $\lfloor x \rfloor$ designates the lower integer bound of x. The series of integers $k_1, k_2, k_3, \ldots, k_i, \ldots$ are defined as $\left\lfloor \frac{r}{v} \right\rfloor$, $\left\lfloor \frac{2r}{v} \right\rfloor$, $\left\lfloor \frac{3r}{v} \right\rfloor, \ldots, \left\lfloor \frac{ir}{v} \right\rfloor, \ldots$.

The following developmental sequence can then be obtained from the axiom $< a, 0>$.

$S_0 = < a,0 >$

$S_1 = < a,v >$

$S_2 = < a,2v >$

$\vdots$

$S_{k_1} = < a,k_1v >$

$S_{k_1+1} = < b,r > [< a,0 >] < a, (k_1+ 1) v - r >$

$S_{k_1+2} = < b,r > [S_{k_1-k_1+1}] < a, (k_1 + 2) v - r >$

$\vdots$

$S_{k_2} = < b,r > [S_{k_2-k_1-1}] <a, k_2v-r >$

$S_{k_2+1} = < b,r > [S_{k_2-k_1}] < b, r> [< a,0 >] < a, (k_2+ 1) v - 2r >$

$S_{k_2+2} = < b,r > [S_{k_2-k_1+1}] < b,r > [S_{k_2-k_2+1}] < a, (k_2+ 2) v - 2r >$

$\vdots$

$S_{k_3} = < b,r > [S_{k_3-k_1-1}] < b,r > [S_{k_3-k_2-1}] < a, k_3v - 2r >$

$S_{k_3+1} = < b,r > [S_{k_3-k_1}] < b,r > [S_{k_3-k_2}] < b,r > [< a,0 >] <a, (k_3 + 1) v - 3r>$

$S_{k_3+2} = < b,r > [S_{k_3-k_1+1}] < b,r > [S_{k_3-k_2+1}] < b,r > [S_{k_3-k_3+1}] <a,(k_3+ 2)v - 3r>$

$\vdots$

It is not difficult to see that the following formulas can be obtained, for all integers $\underline{i}$ and $\underline{m}$ such that $i \geq 1$ and $0 < m < (k_{i+1} - k_i)$.

$S_{k_i} = \overset{i-1}{\underset{j=1}{*}} (< b,r > [S_{k_i-k_{j-1}}]) < a, k_iv - (i - 1) r>$

$S_{k_i+m} = \overset{i}{\underset{j=1}{*}} (< b,r > [S_{k_i-k_{j-1}+m}]) < a, (k_i+ m)v - ir >$

The $*$ operator in these formulas indicates concatenation of strings.

The length x of the apical segment (the right-most segment in each string) is always such that $0 \leq x < r$. This we can prove by recognizing that

$$\left\lfloor \frac{ir}{v} \right\rfloor v < ir$$

for any r and v. Thus we also have

$$k_i v - (i - 1) r < r$$

and $$(k_i + m) v - ir < r$$

The above general formulas apply to strings produced at every step n such that $n > \left\lfloor \frac{r}{v} \right\rfloor$, but they are actually not recurrence formulas, because the difference-terms $(k_{i+1} - k_i)$ and the length-terms of the apical segments may keep changing in an irregular fashion as i increases without bound. However, since in all practical examples $\frac{r}{v}$ is a finite fraction, both the difference-terms and the apical length-terms must follow a cyclically repeating sequence. Thus, if for some r and v values the cycles of terms are determined, we can also obtain true recurrence formulas for these systems.

The availability of recurrence formulas for such continuous component systems is clearly of great advantage. Among others, formulas for total numbers and lengths of different orders of branches are then obtainable.

It is of some interest to ask in general what requirements must a developmental system with continuous components fulfill in order to yield recurrence formulas. One requirement is obviously that no interactions should take place among the units. Another one seems to be that the numerical values which appear in the formulas should remain between certain bounds.

Inflorescence development in Aster

Our third example of a developmental system with continuous components is that constructed by D. Frijters and A. Lindenmayer (in these Proceedings) for the growth and flowering of Aster novae-angliae. This developmental process combines certain aspects of both of our previous examples: branching filamentous growth (as in the root) as well as differentiating structures (like the heterocysts) are involved in it. A new aspect of this process is that an environmentally triggered major change occurs

in the course of development: a change from vegetative to flowering condition takes place when the lengths of days under which the plants are growing get shorter than a certain critical value. Asters are namely "short-day" plants, they are induced to flower only when day-length falls below about 10 hours, in late August at our latitude. This major change in developmental program is presented in the form of two tables of instructions, one for vegetative and one for floral development.

Four attributes are used for each segment of the plant. The first attribute (again the controlling genomic attribute) has three values in this case: 1 for apical segments or flowers, 3 for internodial segments, and 6 for lateral buds or for basal segments). The second attribute is a biological age parameter (called here "number of plastochrones", related to the plastochrone index of R.O. Erickson and F.J. Michelini [16]). The third attribute is segment length, just as in the case of root segments. The fourth attribute is "bulk", interpreted as "assimilate intake-capacity", and having a role similar to the inhibitor concentration in the blue-green algal model.

In addition to these four "local" or "cellular" attributes, two other attributes, A and K, are also computed for each segment. A is computed as the sum of the lengths of the segments from the nearest branching point to the internodial segment under consideration. K is a variable standing for an inhibition value controlled by the "bulk" value of the first internode on a branch. The value of K thus represents an inhibitory effect imposed on a whole branch depending on the position of the branch.

Sets of instructions are given for both vegetative and floral conditions. Some of the instructions take into account not only the attributes of the segment itself which is being computed, but also those of its nearest left neighbour segment. These two properties of the model, having two "tables" of instructions, and taking the

left neighbours into account, would make it a T 1L-system with continuous components, were it not for the fact that the variables A and K are not locally computed . This feature of the model is, however, not essential, A and K values could be carried along as two additional attributes for each segment. This would make the computation less efficient, however.

Assuming that we are dealing here with a continuous counterpart of a T 1L-system, we can make use of the recent results concerning those systems (cf. Lee and Rozenberg[19]).

L-systems with continuous components

We have discussed three examples of developmental descriptions with continuous parameters, the first one a counterpart of a non-deterministic 2L-system, the second one of a deterministic 0L-system, and the third one of a deterministic T1L-system (all of them were propagating systems, i.e., without cell death). We might ask what properties, in general, would be required, from a biological point of view, of L-systems with continuous components.

First, let us consider interactionless L-systems (0L-and T0L-systems) with continuous components. We could formulate deterministic production rules in the following completely general form:

$$\langle a_1, a_2, \ldots, a_n \rangle \rightarrow \langle f_1(a_1, \ldots, a_n), f_2(a_1, \ldots, a_n), \ldots, f_n(a_1, \ldots, a_n) \rangle,$$

if no division takes place, or

$$\langle a_1, a_2, \ldots, a_n \rangle \rightarrow \langle d_1(f_1(a_1, \ldots, a_n)), \ldots, d_n(f_n(a_1, \ldots, a_n)) \rangle \ldots \langle d_1(f_1(a_1, \ldots, a_n)), \ldots, d_n(f_n(a_1, \ldots, a_n)) \rangle \ldots \langle d_1(f_1(a_1, \ldots, a_n)), \ldots, d_n(f_n(a_1, \ldots, a_n)) \rangle,$$

(m-times)

if division takes place. We let here each cell have n attributes; we allow each attribute to influence the values of all the attributes at each computation step by specifying the functions $f_1, f_2, \ldots, f_n$,; and, finally, when a cell divides into m new cells, we introduce distribution functions $d_1, d_2, \ldots, d_n$ to distribute the new values of the attributes over the newly produced cells.

We are thus proposing here a next-state function $F = (f_1, f_2, \ldots, f_n)$ and a distribution function $D = (d_1, d_2, \ldots, d_n)$ such that for each i, $1 \leq i \leq n$, f_i is a

mapping from A^n into A, and d_i is a mapping from A into A^m, where A is the set of values over which the functions range. We have thus

$$F : A^n \times A^n \longrightarrow A^n$$

$$D : A^n \longrightarrow A^m \times A^n$$

The functions $f_1, \ldots, f_n$ may be of very simple form. For genomic attributes they usually consist of simple step-functions, such as represented in the root example by the first-attribute rules for all $i \geq 0$ that : if $x < \frac{1}{q_i}$ then $a_i \rightarrow a_i$,

if $x \geq \frac{1}{q_i}$ then $a_i \rightarrow b\ [a_{i+1}]a_i$.

Similar step-functions with externally determined (constant) thresholds are built into the other two examples discussed. One should in fact, require on biological grounds that in each L-system with continuous components there must be one genomic attribute, and the next-state function for this attribute must be a step-function with one or at most two previously specified thresholds (the thresholds may not be computed). The reason for this requirement is the well-known Jacob-Monod model for gene activation and repression. For the same reason, the genomic attribute should always be a discrete one.

The next-state functions for the other attributes may be freely chosen as long as their values remain non-negative and between finite bounds. In no biological situation would one expect to find a parameter which increases without bound or which becomes negative.

The distribution functions $d_1, \ldots, d_n$ are in most realistic systems rather simple. In our first example the distribution function is the identity function for both new cells as far as the second attribute is concerned (both new cells receive the same inhibitor concentration $f(x, y, z)$). In our second example the distribution function for the second attribute is such that the new length $x + v$ of an apical segment (where $x + v$ exceeds the threshold value) is divided into three portions of lengths r, 0, and $x + v - r$, respectively, which together add up to $x + v$, Distribution functions are mostly of one of the above two types, most biological parameters being such that either they appear at the same value in both daughter cells (concentration, temperature, etc.) or they are subdivided among the daughter cells (length, mass, etc.). Occasionally there is also need for an unequal and non-addi-

tive distribution function, such as the age assignment (the third attribute) in Baker and Herman's model.

The construction of non-deterministic L-systems with continuous components presents no particular problems. One simply has to specify the set of new cells or strings of cells from which one can choose the next-state of a cell. Similarly, continuous component table L-systems can be easily constructed, as shown by Frijters and Lindenmayer (in these Proceedings).

An additional remark: in a sense the principal effects exerted by next-state functions in interactionless L-systems are timing effects. Certain parameters increase or decrease to a point where they exceed a threshold value, when a new genomic state comes into operation, but no spatial effects can be exerted by them. The fact that OL-systems are composed of timing sequences and cycles was recognized and further elaborated by D. Wood [20].

In systems with interactions we have, in addition to timing sequences, the possibility of sending and extinguishing signals, and setting up oscillations (standing or propagating waves). In continuous component L-systems with interactions the next value of each attribute may, in general, be a function of not only all the attributes of the same cell but also of all the attributes of the neighbouring cells. As shown by the models of Baker and Herman and of Frijters and Lindenmayer, the next-state function of one attribute may depend only on the same attribute in neighbouring cells, or on several attributes. The genomic attribute is usually involved in the functions of all other attributes.

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