Position Read from Concentration Is Equally Fine Everywhere with Proportional Error, Coarser Far Away with Count Error

— An exponential gradient with decay length **0.2** is laid across a tissue of length **1**, and cells read their position from the number they receive — the separator is whether the error is set as a fraction of concentration or by the number of molecules — [Paper 799]

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September 2026

— *From thinking to syncing.* —

Abstract

Can a cell read its own position from the concentration of the molecules forming a gradient?Two ways of setting the error are applied to the same exponential gradient, and where and by what the position error is set is counted with the first-order formula, numerical integration and random numbers.No new theorem or law is claimed. First, with the error set as a fraction of concentration, the position error does not depend on place——0.020000 by the first-order formula, 0.020260 by numerical integration, and three positions agreeing at 0.020393111 with the same random numbers (Section 2). **Second, and this is the core. With the error set by the number of molecules, reading grows exponentially coarser away from the source——0.002568 at position 0.1, 0.018975 at 0.9, a ratio of $e^2 = 7.389056$** (Section 3). **Third, the first-order formula, numerical integration and random numbers agree within the width of fluctuation——at position 0.9, 0.019196 by integration and 0.019203 by random numbers; the sum of squared deviations over five positions is 12.979778** (Section 3). **Fourth, a gradient sent from one side cannot be read finely to the far end——positions can be read to within one cell only up to 0.921034, and the error at the end is 0.024365** (Section 4). **Fifth, sending gradients from both sides greatly reduces the molecules needed——the worst error falls by a factor of 4.936090, and the molecules needed per source to read the whole tissue to within one cell drop from 14841.315910 to 609.124698, a factor of 24.364988** (Section 4). **Sixth, the separator is whether the error is set as a fraction of concentration or by the number of molecules——"a concentration gradient determines position" does not fix where and how finely it does so until one says which way the error is set** (Section 5). **Keywords**: positional information, concentration gradient, morphogen, counting fluctuation, exponential gradient, decay length.

Scope of this paper (scope note): **No new theorem or law is claimed——the idea of positional information (Wolpert 1969), that the precision of reading position from a concentration gradient is limited by the number of molecules (Gregor et al. 2007), and that in an exponential gradient a fractional concentration error becomes a position error proportional to the decay length are all known.Embryos are not treated——actual molecules, receptors, read-out mechanisms, and what precision any embryo achieves are not the subject.The model is dimensionless——tissue length 1, decay length 0.2, 10000 source molecules and a cell width of 0.02 are values for comparison.Only two ways of setting the error are examined——a uniform fractional concentration error, and the counting fluctuation of molecules (mean equal to variance, approximated by a normal distribution). Receptor binding and averaging over time are left out.The gradient is a steady exponential——its formation and the growth of the tissue are left out.The two gradients from both sides are independent and combined with inverse-variance weights.Relation to earlier papers**: **Paper 648 showed that the same stripes are cut by a clock and a front in somites and by diffusion in Turing patterns, and its scope note stated "which one works in real embryos is not discussed"——there, what sets the stripe width was laid out. Here, before the stripes, it is counted how finely a single gradient can determine position. Not discussing embryos follows the same line.Paper 191 showed that diffusion, which should smooth, makes the pattern, with the barrier set by the ratio of two diffusion speeds——there diffusion made the pattern. Here the gradient diffusion makes is seen from the fineness of reading it.**What is added is **applying two ways of setting the error to the same gradient and showing that in one the error is independent of place while in the other it spreads by e^2, confirming the first-order formula by numerical integration and random numbers, deriving by closed form and bisection the position 0.921034 readable to within one cell from one side, and that the molecules needed fall by a factor of 24.364988 with two sides**, and **placing the separator on whether the error is set as a fraction of concentration or by the number of molecules**.

1. Notation and the Question

Setting: **a source sits at the end $x = 0$ of a tissue of length $L = 1$, and the mean number of the molecules forming the gradient (the morphogen) falls exponentially. A cell reads its own position from the number k it receives.**

$$\bar{k}(x) = N_0\, e^{-x/\lambda}, \qquad \hat{x} = \lambda \ln \frac{N_0}{k}$$

Take $N_0 = 10000$ source molecules, decay length $\lambda = 0.2$ and cell width $w = 0.02$. The position error takes two forms depending on how the error in the number is set.

$$\sigma_k = \varepsilon\, \bar{k} \;\Rightarrow\; \sigma_x \approx \lambda \varepsilon, \qquad\qquad \sigma_k = \sqrt{\bar{k}} \;\Rightarrow\; \sigma_x \approx \frac{\lambda}{\sqrt{N_0\, e^{-x/\lambda}}}$$

Question: **where, and by what, is the fineness of reading position from concentration set?**

2. Setting the Error as a Fraction of Concentration

Computation 2.1: **with a fractional concentration error $\varepsilon = 0.10$, the position error was derived by the first-order formula, numerical integration, and 20000 random draws (the same draws at three positions).**

method	position error
first-order formula $\lambda\varepsilon$	0.020000
numerical integration	0.020260
random, position 0.1	0.020393111
random, position 0.5	0.020393111
random, position 0.9	0.020393111

> **Observation 2.2**
>
> **with the error set as a fraction of concentration, the position error does not depend on place.The estimate becomes $x - \lambda \ln(1 + \varepsilon g)$, and x drops out of the error, so with the same random numbers three positions agree to every digit. The gap between the first-order 0.020000 and the integrated 0.020260 is the curvature of the logarithm——an exponential gradient maps a fractional error to the same position error everywhere.**

3. Setting the Error by the Number of Molecules

Computation 3.1: **with the counting fluctuation of molecules (mean equal to variance), the position error at five positions was derived by the first-order formula, numerical integration, and 20000 random draws. The last column is the gap between random draws and integration divided by the standard error.**

position	mean molecules	first order	integration	random	gap
0.1	6065.306597	0.002568	0.002569	0.002601	+2.562
0.3	2231.301601	0.004234	0.004236	0.004185	−2.440
0.5	820.849986	0.006981	0.006991	0.007011	+0.574
0.7	301.973834	0.011509	0.011557	0.011578	+0.359
0.9	111.089965	0.018975	0.019196	0.019203	+0.069

Observation 3.2

this is the core: with the error set by the number of molecules, reading grows exponentially coarser away from the source.Against 0.002568 at position 0.1, position 0.9 gives 0.018975, a ratio of $e^{0.8/(2\lambda)} = e^{2} = 7.389056$——farther places receive fewer molecules, so the fractional fluctuation is larger and the same gradient determines position there only coarsely.

Observation 3.3

the first-order formula, numerical integration and random numbers agree within the width of fluctuation.The sum of squared gaps over five positions is 12.979778, inside the 0.1 percent point 20.515 for five degrees of freedom. The first-order formula comes out smaller than the integral at farther positions (0.018975 against 0.019196 at 0.9)——where numbers are small, the first-order formula slightly flatters the fineness.

4. From One Side, from Both Sides

Computation 4.1: for a gradient sent from one side, the range over which the position error stays within one cell width w was derived by closed form and by counting on a 10^{-4} grid. The worst error with the same gradient sent from both sides was also derived.

$$x^{*} = \lambda \ln \frac{N_0 \, w^2}{\lambda^2}$$

quantity	value
end readable within one cell, x^* (end counted on the grid)	**0.921034** (0.9210)
worst error from one side (position **1**)	**0.024365**
worst error from both sides (position **0.5**)	**0.004936**
ratio $\sqrt{2}e^{L/(4\lambda)}$	**4.936090**

Computation 4.2: **the source molecules needed to read the whole tissue to within one cell were derived by closed form and by bisection (the two agreed to within a relative 10^{-15}).**

$$N_1 = \frac{\lambda^2}{w^2}\, e^{L/\lambda}, \qquad N_2 = \frac{\lambda^2}{2\,w^2}\, e^{L/(2\lambda)}, \qquad \frac{N_1}{N_2} = 2\, e^{L/(2\lambda)}$$

quantity	value
from one side, N_1	**14841.315910**
from both sides, per source, N_2	**609.124698**
ratio N_1/N_2	**24.364988**
sum of both sources (fraction of one side)	**1218.249396** (0.082085)

> **Observation 4.3**
>
> **sending gradients from both sides greatly reduces the molecules needed.From one side, positions beyond 0.921034 cannot be read to within one cell and the error at the end is 0.024365, but from both sides the worst error is 0.004936 at the middle, and the molecules needed fall by a factor of 24.364988 per source, the two together being 0.082085 of one side——a place far from one source is near the other.**

5. The Separator

Observation 5.1

the separator is whether the error is set as a fraction of concentration or by the number of molecules.Set as a fraction, the position error is 0.020000 everywhere (0.020260 by integration); set by number, it spreads 7.389056 times between positions 0.1 and 0.9, and from one side positions beyond 0.921034 cannot be read finely——"a concentration gradient determines position" does not fix where and how finely until one says which way the error is set.

Observation 5.2

beside Papers 648 and 191.Paper 648 laid out whether stripe width is set by a clock and a front or by diffusion, and Paper 191 showed that diffusion makes patterns——here, before that, the fineness with which one gradient determines position was counted from the numbers the reader receives.

Observation 5.3

what is not said.Molecules in real embryos, receptor binding, averaging over time, formation of the gradient and growth of the tissue are not treated——what is shown is that the way the error is set can make the fineness of position independent of place or exponentially coarser.

6. Roll Call and Closing

1. **first-order value set as a fraction, 0.020000** (Observation 2.2): **independent of place.**
2. **numerical integration, 0.020260** (Computation 2.1): **the curvature of the logarithm.**
3. **set by number, 0.002568 at position 0.1** (Computation 3.1): **near the source.**
4. **set by number, 0.018975 at position 0.9** (Computation 3.1): **far from the source.**
5. **ratio 7.389056** (Observation 3.2): **the core; e^2.**
6. **sum of squared gaps 12.979778** (Observation 3.3): **agreement within fluctuation.**
7. **end readable from one side, 0.921034** (Computation 4.1): **short of the end.**
8. **worst-error ratio 4.936090** (Computation 4.1): **from both sides.**

9. **ratio of molecules needed, 24.364988** (Computation 4.2): **per source.**
10. **fraction or number** (Observation 5.1): **the separator; Papers 648, 191.**

Closing: **How finely position is read from concentration is the same everywhere if the error is set as a fraction of concentration, and coarser farther from the source if it is set by the number of molecules.With an exponential gradient of decay length 0.2 across a tissue of length 1, a uniform 10 percent concentration error gives a position error of 0.020000 everywhere by the first-order formula (0.020260 by integration), and with the same random numbers three positions agree to every digit——an exponential gradient maps a fractional error independently of place.With the counting fluctuation of 10000 source molecules, the error spreads $e^2 = 7.389056$ times between 0.002568 at position 0.1 and 0.018975 at 0.9, positions beyond 0.921034 cannot be read to within one cell from one side, and sending from both sides cuts the molecules needed per source by a factor of 24.364988——because farther places receive fewer molecules.The separator is whether the error is set as a fraction of concentration or by the number of molecules.Placed among the earlier papers——Paper 648 laid out what sets stripe width, and Paper 191 showed that diffusion makes patterns. This comes before them, counting how finely one gradient determines position.To be honest——the model is dimensionless, and neither real embryos, receptors, nor averaging over time are treated.**

References

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