FIRST SHOW "INPUT OUTPUT" SLIDES FROM DAY 1 AGAIN

- RC Circuit → Differential Equation
- Differential Equation → solution
  - Euler method: simulation
  - Exact solution
- Solution → INPUT-OUTPUT PROPERTIES

Response Kernel $K(t)$

Principle of superposition.

Impulse response & system characterization

- ABBOTT + DAYAN CH. 5.1 – 5.7
- GABBIANI + COX CH. 2 – 3

Equiv. circuit

model of single neuron dynamics

· GABBIANI + COX FIG. 2.2

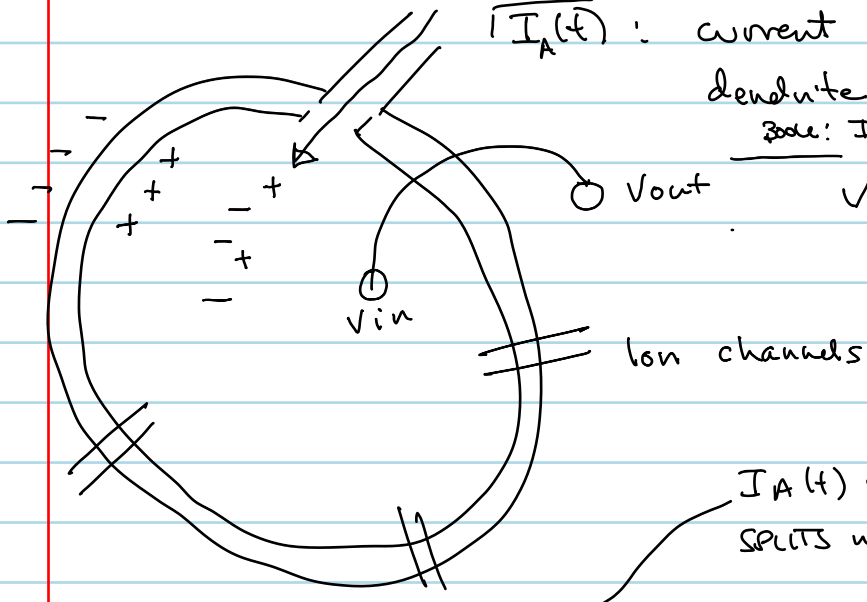
INPUT

$I_A(t)$: current (net + charge), from dendrite (OR experimenter) e.g.

Book: $I_{stim}(t)$

$V = V_{in} - V_{out}$, voltage

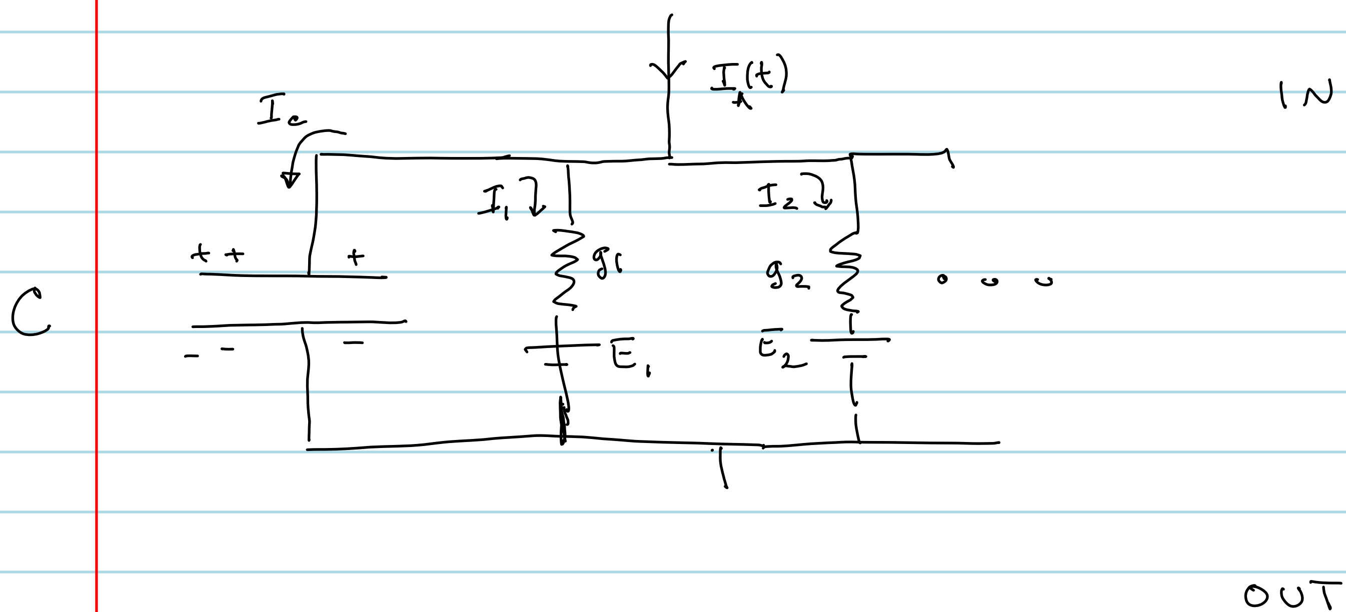
(1)



$I_A(t)$ must go somewhere!

SPLITS into $\underbrace{I_c}_{\text{capacitive current}} + \underbrace{I_1 + I_2}_{\text{ion channel currents}} + \dots$

(2)



CAPACITOR: $Q = CV$ Q: Charge on "top" wall / plate

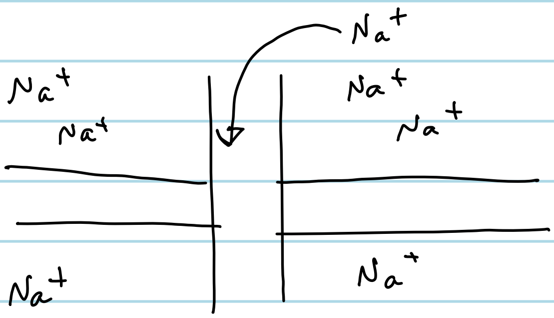
C: capacitance

$\frac{dQ}{dt} = I_C$ Current: Change in charge / unit time

$$\Rightarrow I_C = \frac{d}{dt}(CV) = C\frac{dV}{dt} \quad (5.2, A+D)$$

OHM'S LAW

② Ion channel: $I_1 = g_1(V - E_1)$.   See Abb-Dayan Fig 5.1



- passes specific type or types of ions only, eg Na^+
- conductance $g \approx \frac{1}{R}$

"how open it is"

- Two "forces" drive current:
  - (1) Diffusion: is there more Na^+ inside or outside
  - (2) Voltage V, which pushes on charges

E_1 is "reversal" potential where these balance.

- Repeat for other channels. Pass different ions $\longrightarrow$ different E_k

- $I_A(t) = I_c(t) + \sum_k I_k(t)$

$$I_A(t) = C\frac{dV}{dt} + \sum_k g_k(V - E_k) \quad \ldots \text{so} \ldots$$

(1)
$$C\frac{dV}{dt} = I_A(t) + \sum_k g_k(E_k - V)$$

GABBIANI + COX (2.10)

A+Dayan (5.6)

- Passive Membrane / "RC Circuit" form of (1).

Combine all currents k that have g_k conductances that are approximately constant over time →

"net" current

$$C\frac{dV}{dt} = I_A(t) + g_L\,(E_L - V) \quad \ldots$$

AND ignore other "spike generating," etc currents.

(Formally, redefine $V \to V - E_L$)

- For convenience, set $E_L = 0$.

⟶ RC Circuit eq^{ns} below

$$C\frac{dV}{dt} = I_A(t) - gV = I_A(t) - \frac{1}{R}V$$

$$\frac{dV}{dt} = \frac{-1}{RC}V + \frac{I_A(t)}{C}$$

- Differential equations + linear systems.

$$\frac{dy}{dt} = f(y, t)$$ [...rule / rate of change...]

$$\frac{y(t+\Delta t) - y(t)}{\Delta t} = f(y, t)$$

$$y(t+\Delta t) = y(t) + f(y, t) \cdot \Delta t \quad ; \; y(0) = y_0 .$$

Euler method! Works for ANY $f(\,)$.
$\Rightarrow$ (often only option...)

- Example:

$$\frac{dV}{dt} = V \quad ; \quad V(0) = V_0 = 1.$$

Solution: $V(t) = V_0 e^{t}$ (check).

Euler-illustrateV.m

(use $\Delta t = 0.1$, 0.001 + zoom)

Accuracy?

→ Challenge: Use T-series to show this...

Each timestep, make local error $= k \cdot \Delta t^2$

Global error: $\underbrace{\frac{T_{max}}{\Delta t}}_{\#\ \text{timesteps}} \cdot k\,\Delta t^2 = k_2 \cdot \Delta t$

"1st order accurate method"

(R-K methods - like ode45 - get $k\,\Delta t^4$ - explain why important)

Write on Board. Students work on own.
Intermittently have students "give" code / tell what to write..

- LAB WORKSHOP EXERCISES:

(1) Let Tmax = 10, find Δt that gives Global error of

10% of True Solution
1%
0.1%.

What do you notice about how Δt varies to achieve this?

Use code Euler-illustrate-V.m, provided.

(2) Modify your code to solve:

$$\frac{dV}{dt} = \sin(t) \quad ; \quad V(0) = 0$$

Compare numerical and exact answers.

SAVE CODE w/ new name!

(3) Modify your code to solve RC circuit equation:

$$\frac{dV}{dt} = \frac{-V}{RC} + \frac{I_A(t)}{C} \quad , \quad V(0) = 0$$

where $I_A(t) = \sin(t)$.

[Save code as euler_illustrateRC.m]

[show key euler step on board]

(OPTIONAL BONUS ...)

(4) Modify again, to solve case where $I_A(t)$ is itself the solution of a differential equation:

$$\frac{dI_A}{dt} = -I_A + \sin(t) \quad ; \quad I_A(0) = 0$$

$$\frac{dV}{dt} = \frac{-V}{RC} + I_A(t) \quad ; \quad V(0) = 0$$

BONUS: Compare with analytical solution.

GAB. + COX SEC 3.1:

- Back to our circuit ... solve for $V(t)$ ... ANALYTICALLY, for RC circuit example.

Goal: Insight into neural response!

Int. factor ... rewrite

$$e^{t/RC}\frac{dV}{dt} = e^{t/RC}\left(-\frac{V}{RC}\right) + e^{t/RC}\frac{I_A(t)}{C}$$

$$\frac{d}{dt}\left[V e^{t/RC}\right] = e^{t/RC}\frac{I_A(t)}{C} \quad ; \int_0^t \text{ both sides}$$

$$V(t)e^{t/RC} - V(0) = \int_0^t e^{s/RC}\frac{I_A(s)}{C}\,ds$$

$$V(t) = V_0 e^{-t/RC} + \int_0^t \frac{e^{-(t-s)/RC}}{C} I_A(s)\,ds$$

$$= V_0 e^{-t/RC} + \int_0^t K(t-s)\, I_A(s)\,ds \; ; \quad \text{let } t' = t-s$$

$$= V_0 e^{-t/RC} + \int_0^t K(t')\, I_A(t-t')\,dt'$$

Kernel: weight on inputs t' in past

$$K(t') = \frac{e^{-t'/RC}}{C}$$

$[= K * I_A [t]]$

- RC Circuit obeys SUPERPOSITION* ...
  * (if $V_0 = 0$ or t is large)

THAT IS ... input $I_A(t) = I_1(t) \longrightarrow V_1(t)$

$I_2(t) \longrightarrow V_2(t)$

Then ... input $I_A = I_1(t) + I_2(t) \longrightarrow V_1(t) + V_2(t)$.

- CHECK: plug into exact solution

- Euler_RC.m for... $I_A(t) = 1$ or $1 + I$ ... shows neur. doing 1+1 = 2
  - or $= \sin(t)$
  - or $= 1 + \sin(t)$ [cut/paste sol^ns in MATLAB]

Demo: euler_illustrateRC_two_inputs.m

- Generalize... if $I_A(t) = \sum_k c_k I_k(t)$ and each $I_k(t)$

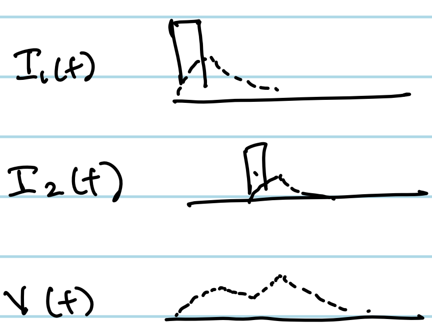
  gives response $V_k(t)$, then

  $I_A(t)$ gives $V(t) = \sum_k c_k V_k(t)$.

— . —

- CONSEQUENCES
  - (1) Predict response to complex stim. from simpler components
  - (2) SUMMATION:

    Brief inputs at different times INTERACT...



[← ! Simulate this in MATLAB!]

euler_illustrateRC_two_inputs.m

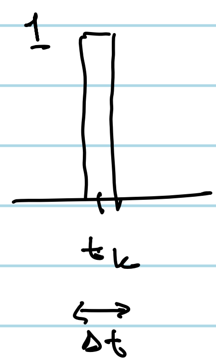
(LAB ASSIGNMENT)

(Cooperate → push over spike threshold OR exc./inh. impulses CANCEL.)

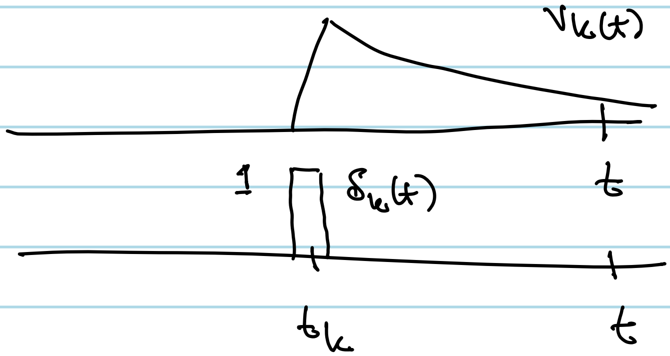
[Skip to (4), come back if time.]

(3) This IMPULSE response provides complete description of response to ANY input.

$$I_A(t) = \sum_k c_k \, \delta_k(t) \quad ; \quad \delta_k(t) =$$



$$v(t) = \sum_k C_k \, v_k(t)$$

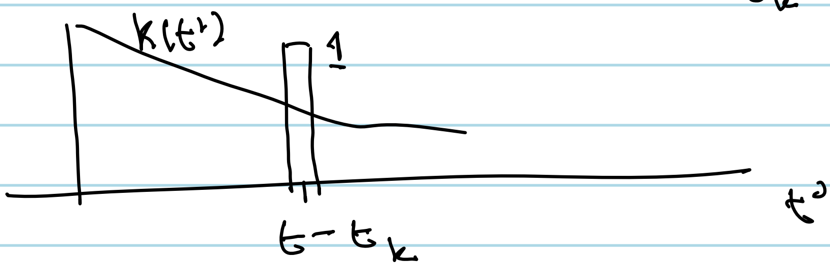


"Sum of Δt-impulses"

Relate to solution:

$$v_k(t) = \int_0^t K(t')\, \delta_k(t-t')\, dt'$$

[Think: pulse when argument $= t_k \rightarrow t - t' = t_k$
$t' = t - t_k$
or: $t - t_k$ "into past"]



$$\approx \Delta t \cdot K(t - t_k)$$

$\rightarrow$ Impulse response related to kernel K ...
but Δt in way!

- Get rid of pesky Δt: apply $\frac{1}{\Delta t} \delta_k(t')$

$$\rightarrow \quad v_k(t) \approx K(t - t_k)$$

- What Δt should we use?

Small $\Delta t \rightarrow$ More accurate!

Definition: δ-function "at t_k": $\delta(t' - t_k)$, is

$\frac{1}{\Delta t} \delta_k(t')$ in limit of small Δt.

Definition: **Impulse response:** Impulse(t)

impulse at time $t' = 0$.

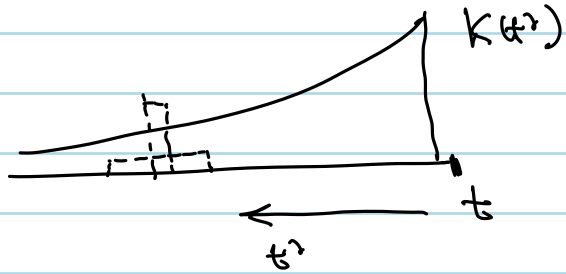
$V(t)$ in response to $\delta(t - 0)$

Fact: Impulse(t) = K(t).

- **Consequence:** We can discover our system response Kernel FROM the impulse response — they are the same.

4) The filter K(·) illustrates which components of the signal affect response V(t)... + which are ignored.

[Eg.



wide + short vs. tall + skinny inputs give same responses...

→ Kernel NOT invertible!

... ! Add some more ...

... pos/neg cancellation example.

Hey! This is like the spike-triggered average and the optimal linear filter!

(2.7 Abbott - Dayan):

$$L(t) = \int_0^\infty d\tau\, D(\tau)\, s(t-\tau) \sim \sum_\tau D(\tau)\, s(t-\tau)$$

$D(\tau) \leftrightarrow K(\tau)$ $\quad$ $s(t-\tau) \leftrightarrow I_A(t-\tau)$ $\quad$ "D DOT S"

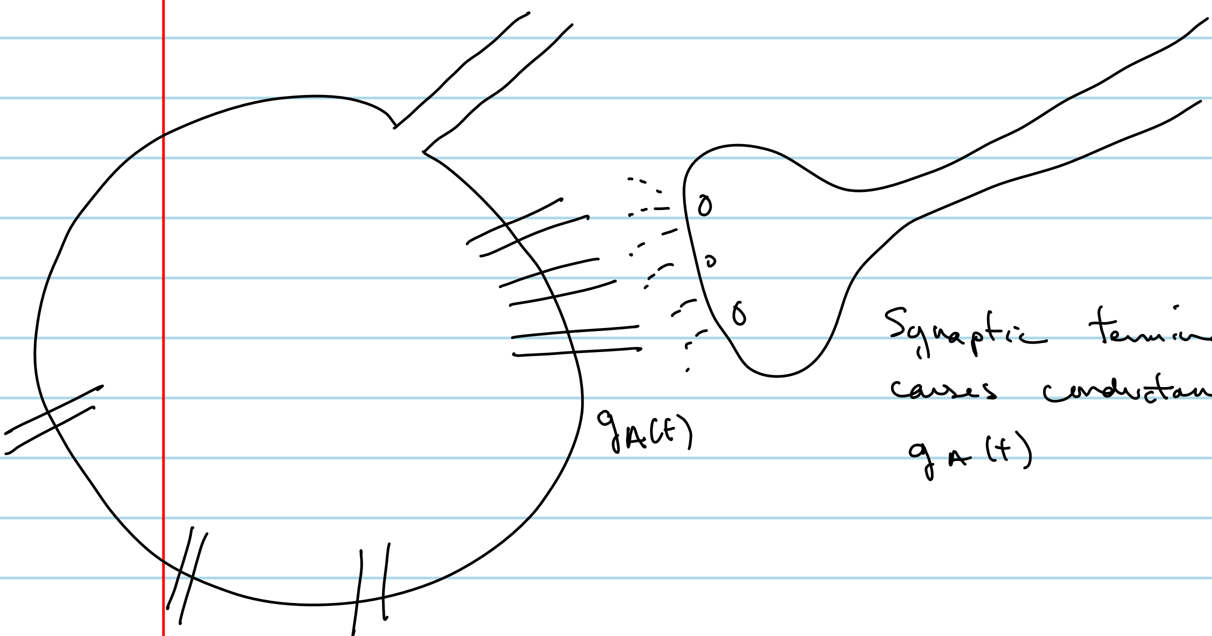
Stamp filter D onto stimulus S

- If firing rate ~ V, then this gives firing rate in time.
- Connects BIOPHYSICS to COMPUTATION! Membrane biology shapes K(t') and hence extracted stim. features.

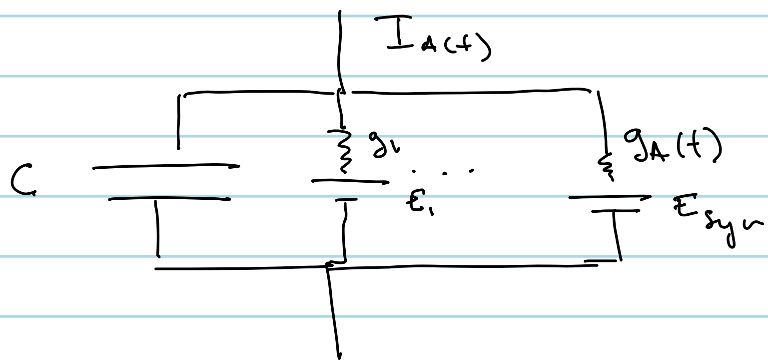
Synaptic, or conductance-based, inputs.

GAB. + COX SEC 2.5

ABB+ DAYAN 5.7.



Synaptic terminal ... causes conductance "input" $g_A(t)$



Simplest case for notation:

"RC circuit," $g_1 = \frac{1}{R}$, $E_1 = 0$

$$C \frac{dV}{dt} = -\frac{V}{R} + g_A(t) \left[E_{syn} - V \right]$$

GABB. + COX (2.12)

Rewrite as

$$\frac{dV}{dt} = \frac{-V}{\tau} + g(t) \left[E - V \right]$$

Euler_IllustrateRC_conduct.m

Conductance - Based Inputs:

Reversal potential

$$\frac{dV}{dt} = -\frac{V}{\tau} + g(t)\,(E - V) \qquad ; \times \exp\left(\int_0^t \frac{1}{\tau} + g(t')\,dt'\right)$$

$$\rightsquigarrow \frac{d}{dt}\exp(\sim) = g(t)\,E \cdot \exp(\sim)$$

$$V(t)\exp(\sim) - V(0) = E\int_0^t g(t') \cdot \exp\int_0^{t'} \left(\frac{1}{\tau} + g(s)\right)ds \; dt'$$

ASIDE: $\int_0^{t'} - \int_0^t$

(*)

JUST WRITE THIS!

$$V(t) = V_0 \exp - \int_0^t \left(\frac{1}{\tau} + g(s)\,ds\right) + E\int_0^t dt'\, g(t') \cdot \exp - \int_{t'}^t \left(\frac{1}{\tau} + g(s)\right)ds$$

let $P(t) = \exp - \int_0^t \left(\frac{1}{\tau} + g(s)\,ds\right)$

ASIDE

CHECK

Write sol^n in easiest form: from (*)

$$V(t) = V_0 P(t) + P(t) \cdot E \int_0^t g(t') \overset{\exp +}{\int_0^{t'}} \left(\frac{1}{\tau} + g(s)\right)ds \cdot dt'$$

$$V' = V_0 P(t)\left(-\frac{1}{\tau} - g(t)\right) + \left(-\frac{1}{\tau} - g(t)\right)P(t) \cdot E \int_0^t g(t') \overset{\exp +}{\int_0^{t'}} \left(\frac{1}{\tau} + g(s)\right)ds \cdot dt'$$

$$+ \underbrace{P(t) \cdot E \cdot g(t) \overset{\exp +}{\int_0^t} \left(\frac{1}{\tau} + g(s)\right)ds}_{= E \cdot g(t)}$$

$$\rightarrow V' = V\left(-\frac{1}{\tau} - g(t)\right) + E \cdot g(t) \qquad \checkmark$$

Calculus aside:

$$\frac{d}{dt}\int_0^t f(t', t)\, dt' = \frac{1}{\delta t}\left[\int_0^{t+\delta t} f(t', t+\delta t)\, dt' - \int_0^t f(t', t)\, dt'\right]$$

$$\simeq \frac{1}{\delta t}\left[\int_0^{t+\delta t}\left[f(t', t) + \frac{\partial f}{\partial t}\cdot \delta t\right] dt' - \int_0^t f\right]$$

$$\simeq \int_0^t f(t', t)\, dt' + \int_0^t dt' \, \frac{\partial f}{\partial t}(t', t)$$

So...

$$\frac{d}{dt}\left[\int_0^t dt'\, f(t') \cdot \int_{t'}^t g(s)\, ds\right]$$

$$= \quad f(t)\int_{t'}^t g(s)\, ds + \int_0^t dt'\, f(t') \cdot g(t) \quad ✓$$

• Don't worry about specific form. PART. Say

input $g_A(t) = g_1(t) \longrightarrow V_1(t)$

$g_2(t) \longrightarrow V_2(t)$

THEN . . .

input $g_A(t) = g_1(t) + g_2(t)$ does NOT give $V_1(t) + V_2(t)$ . . .

- Interaction among inputs
- Basic nonlinear computation. ie, one input "blocks" next, in demo.

DEMO:

euler_illustrateRC_two_inputs_conductance.m

why?

$\rightarrow$ Nonlinear entrance of $g(t)$.

ie... take $g(t) = g_1(t) + g_2(t)$

$$\exp(g(t)) \neq \exp(g_1(t)) + \exp(g_2(t))$$

$$= \exp(g_1(t)) \cdot \exp(g_2(t))$$