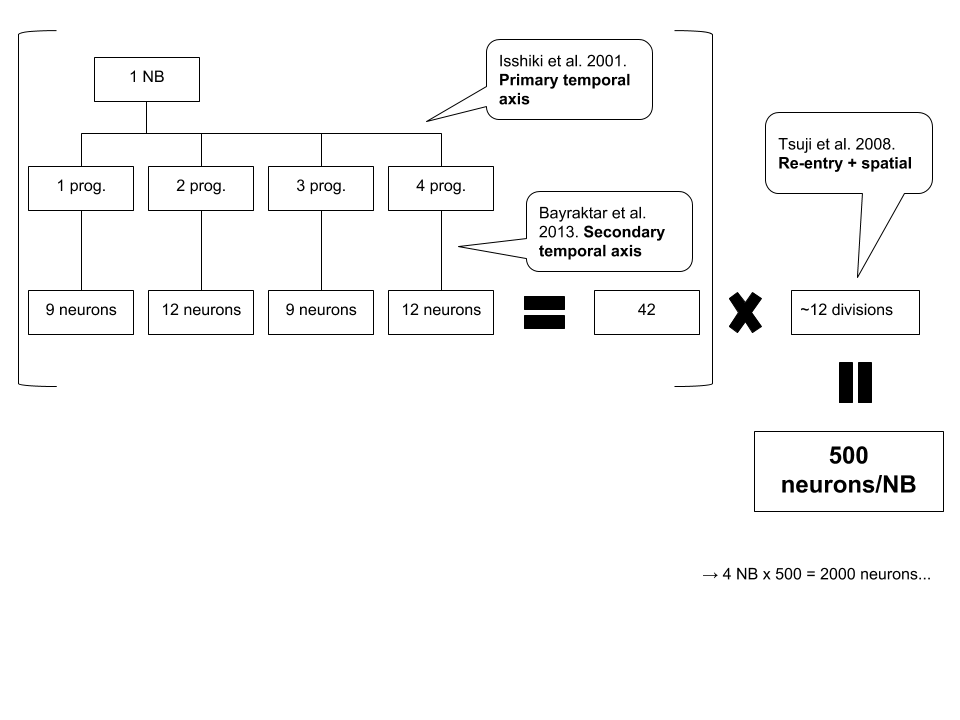
How does the drosophila mushroom body, a structure composed of ~2000 cells (and implicated in such diverse functions as sensory processing, sociability and motor output) arise from merely 4 neuroblasts? Possible solution in Fig 1.

**Timing, timing, timing…**: Advances in chemical stains which incorporate into DNA during S-phase allowed the identification of precise proliferation patterns using 3H-thymidine ([White and Kankel 1978](#_ENREF_7)) and BrdU ([Ito and Hotta 1992](#_ENREF_3)). A seminal study used mosaic analysis with a repressible cell marker (MARCM) and found sequential birth of three distinct types of mushroom body neurons from a single neuroblast (γ, αβ, α’β’) ([Lee, Lee et al. 1999](#_ENREF_4)). The pioneer αβ cell type was identified in a follow up MARCM study ([Zhu, Chiang et al. 2003](#_ENREF_8)).

So how does this timing come about? An amazing finding was that neuroblasts sequentially express a series of four transcription factors along a **primary time axis** via asymmetric cell division: Hunchback (Hb) 🡪 Seven-up (Svp) 🡪 Krüppel (Kr) 🡪 Pdm1/Pdm2 (Pdm) 🡪 Castor (Cas) ([Isshiki, Pearson et al. 2001](#_ENREF_2)). Another amazing finding was that a **secondary time axis** exists in which Dichaete 🡪 Grainyhead 🡪 Eyeless transcription factors are serially expressed to produce additional neural subtype diversity ([Bayraktar and Doe 2013](#_ENREF_1)). Reactivation of neuroblast divisions following quiescence ([Tsuji, Hasegawa et al. 2008](#_ENREF_6)). Restricted TF expression is due to cross-repressive interactions ([Li, Chen et al. 2013](#_ENREF_5)). Therefore dual temporal transcription factor sequences control the temporal change of NBs and fate of their progeny.

**Location, location, location…**: Aside from binary fate decisions of cell division that result from temporal patterning on a dual axis, spatial proximity to each other have a role. For example, Tsuji et al. used tandem eagle-Gal4;UAS-GFP crosses and BrdU labeling to identify NB3-3 progenitors (Fig 3 of Tsuji). They found that antp and adb-a, Hox genes, can spatially regulate NB quiescence ([Tsuji, Hasegawa et al. 2008](#_ENREF_6)).

Figure 1 – Back of the napkin algebra

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