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Canalization and Developmental Stability of the Rodent Skull

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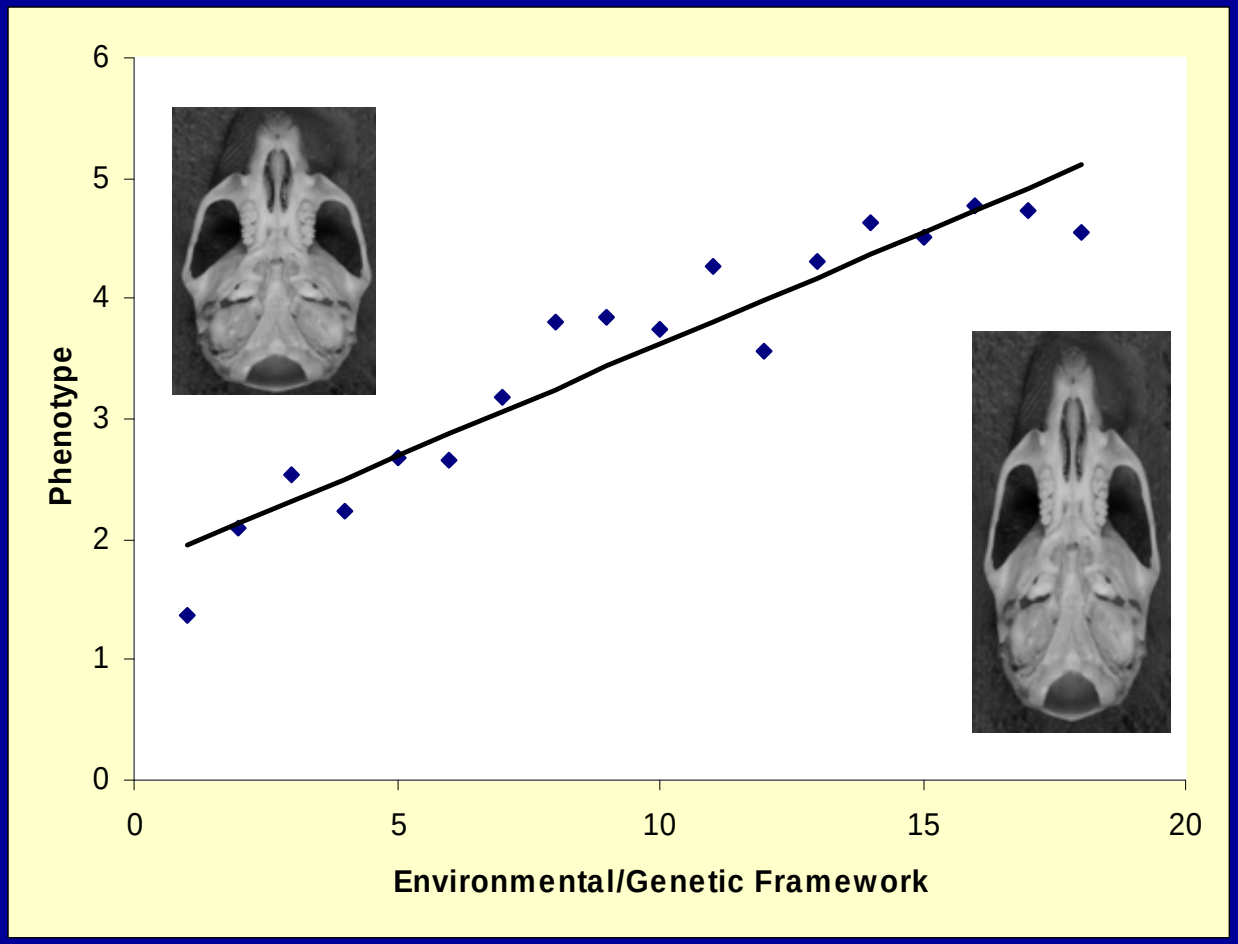
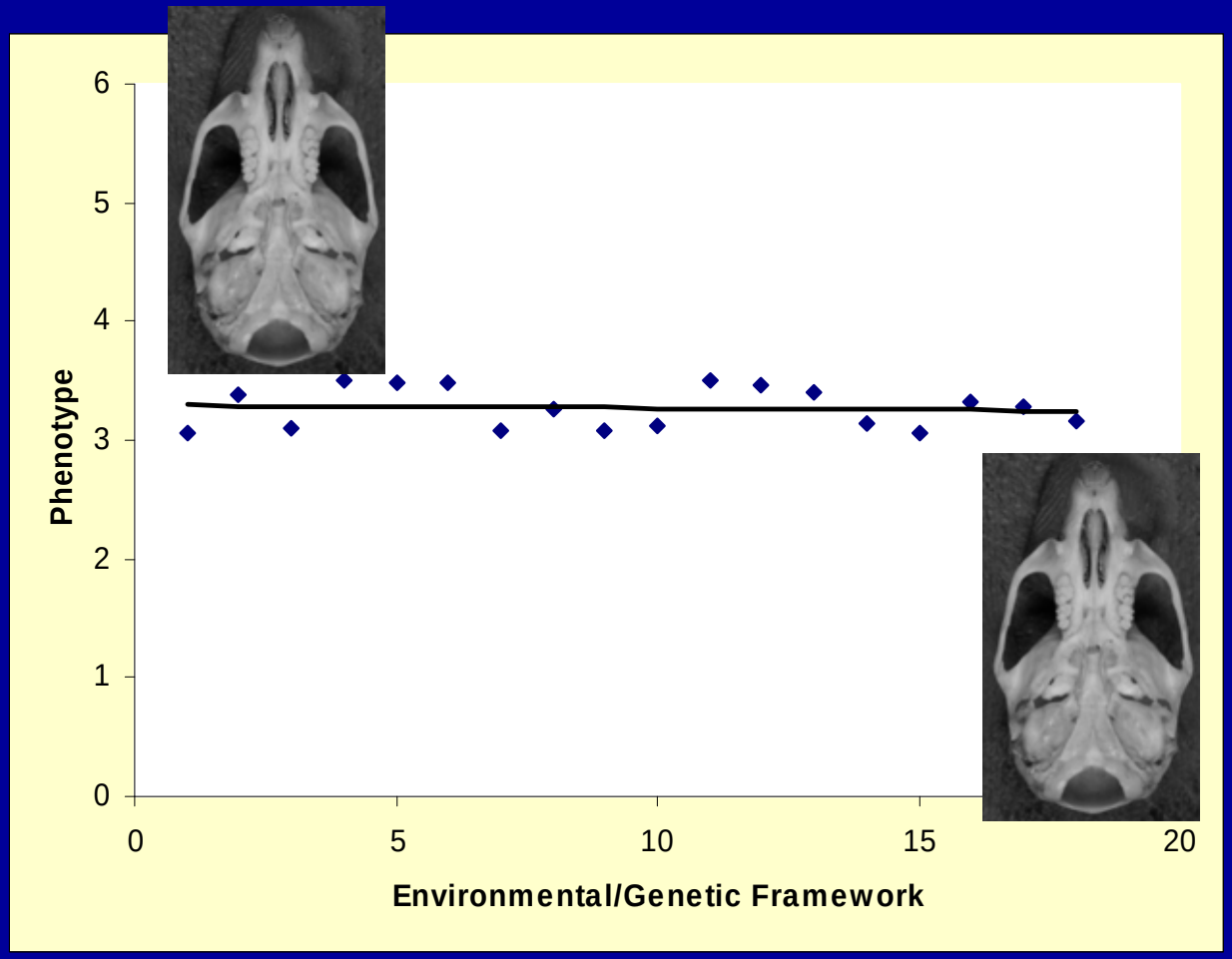
Canalization vs. Developmental Stabilization

- Canalization buffers individuals against genetic and environmental sources of variation, thereby reducing variation around the normal morphology. It is commonly measured by variance.

Canalization reduces / limits variation



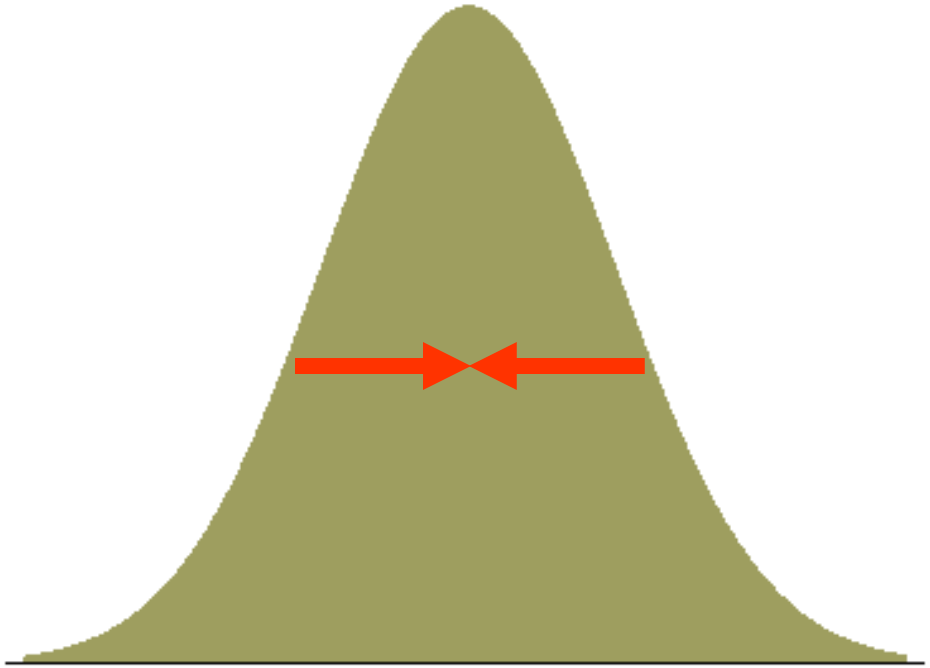
Canalization reduces/limits variation

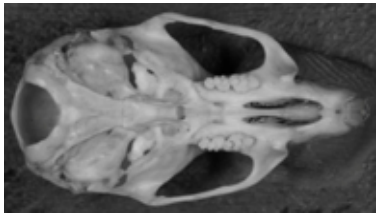


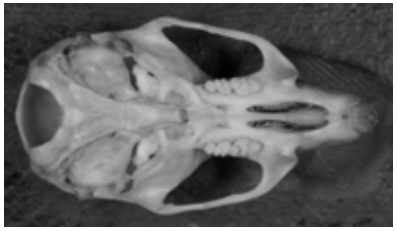
Canalization vs. Developmental Stabilization

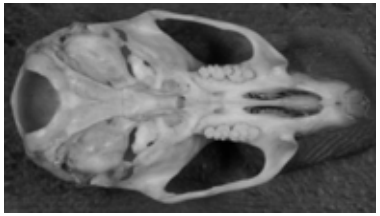
- Developmental stabilization reduces developmental “noise,” the random errors of development. It is commonly measured by fluctuating asymmetry.

Developmental stabilization reduces/limits random "noise"









Canalization vs. Developmental Stabilization: Common Mechanisms?

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- Because canalization and developmental stabilization are thought to buffer against different kinds of perturbations, the possibility that they use common mechanism has important evolutionary implications.

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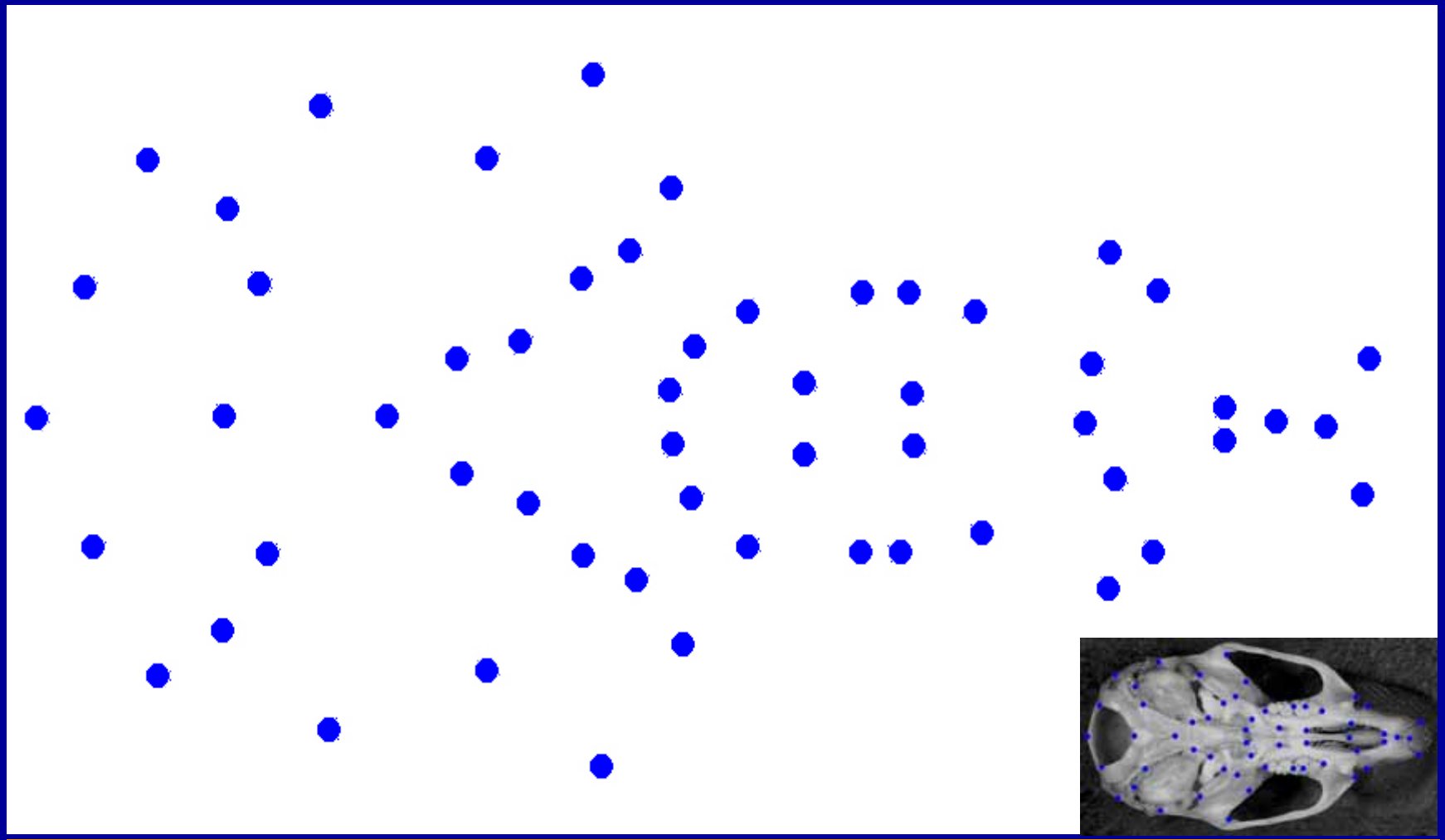
- By taking an ontogenetic approach, we can ask whether canalization and fluctuating asymmetry coincide temporally
- Previous analyses on rodent skulls have shown that variance decreases early in postnatal growth and remains nearly constant thereafter
- Our question: Does developmental instability, as measured by fluctuating asymmetry, also follow this temporal pattern?

Mus musculus domesticus

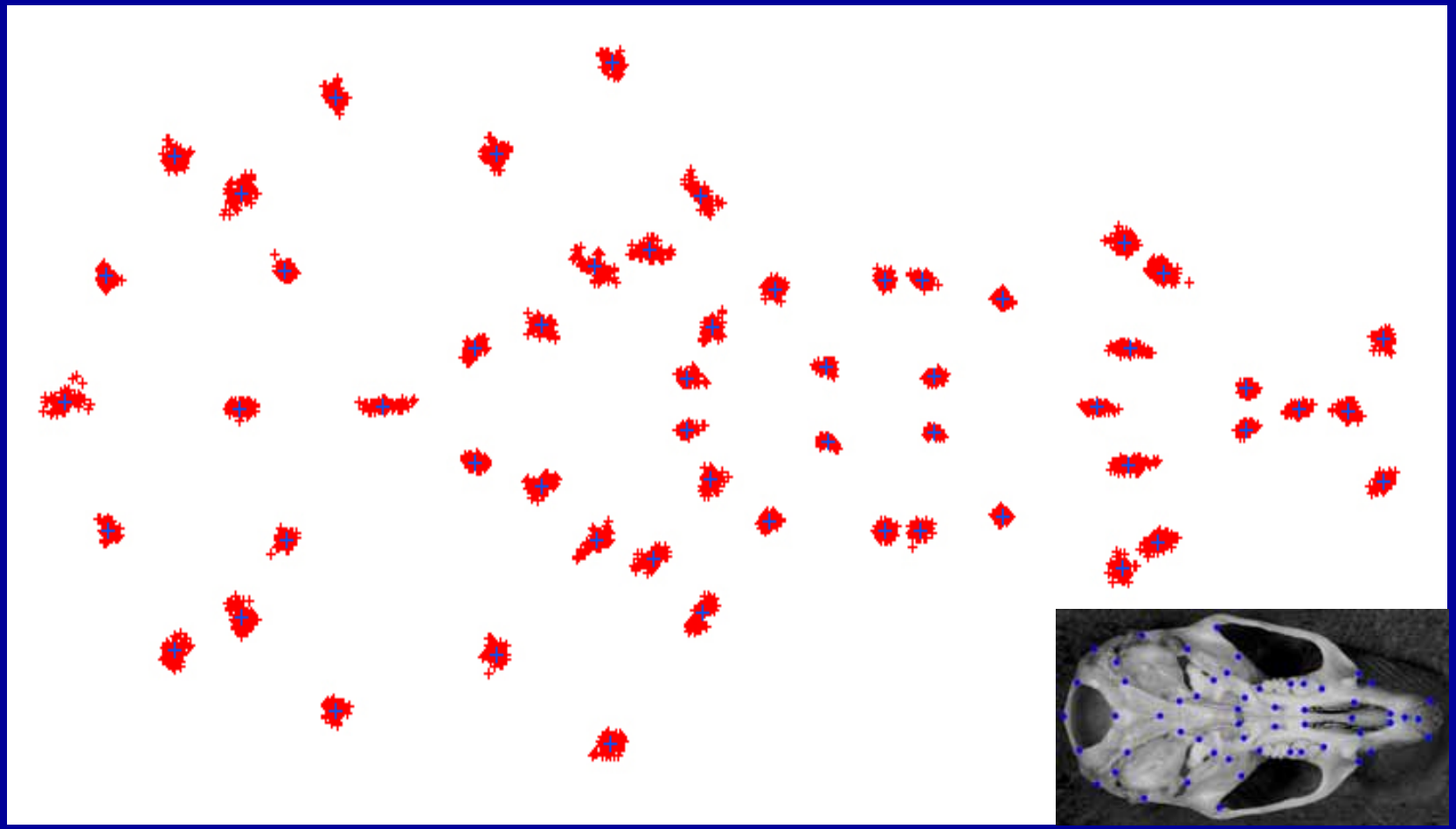
Samples

- Lab reared randombred mice
- Specimens of the following ages (days postnatal):
  - 10 (*N* = 22),
  - 15 (*N*=19),
  - 20 (*N*=15),
  - 25 (*N*=15),
  - 30 (*N*=13),
  - 40 (*N*=25),
  - 50 (*N*=28),
  - 60 and 70 (*N*=10)
- 25 paired, 6 unpaired landmarks from ventral view

All analyses are based on landmark-based geometric morphometrics methods



Variance of shape: a measure of the scatter around optimally superimposed landmarks



Components of the variance of shape (of bilaterally symmetric structures)

Total Shape Variance =

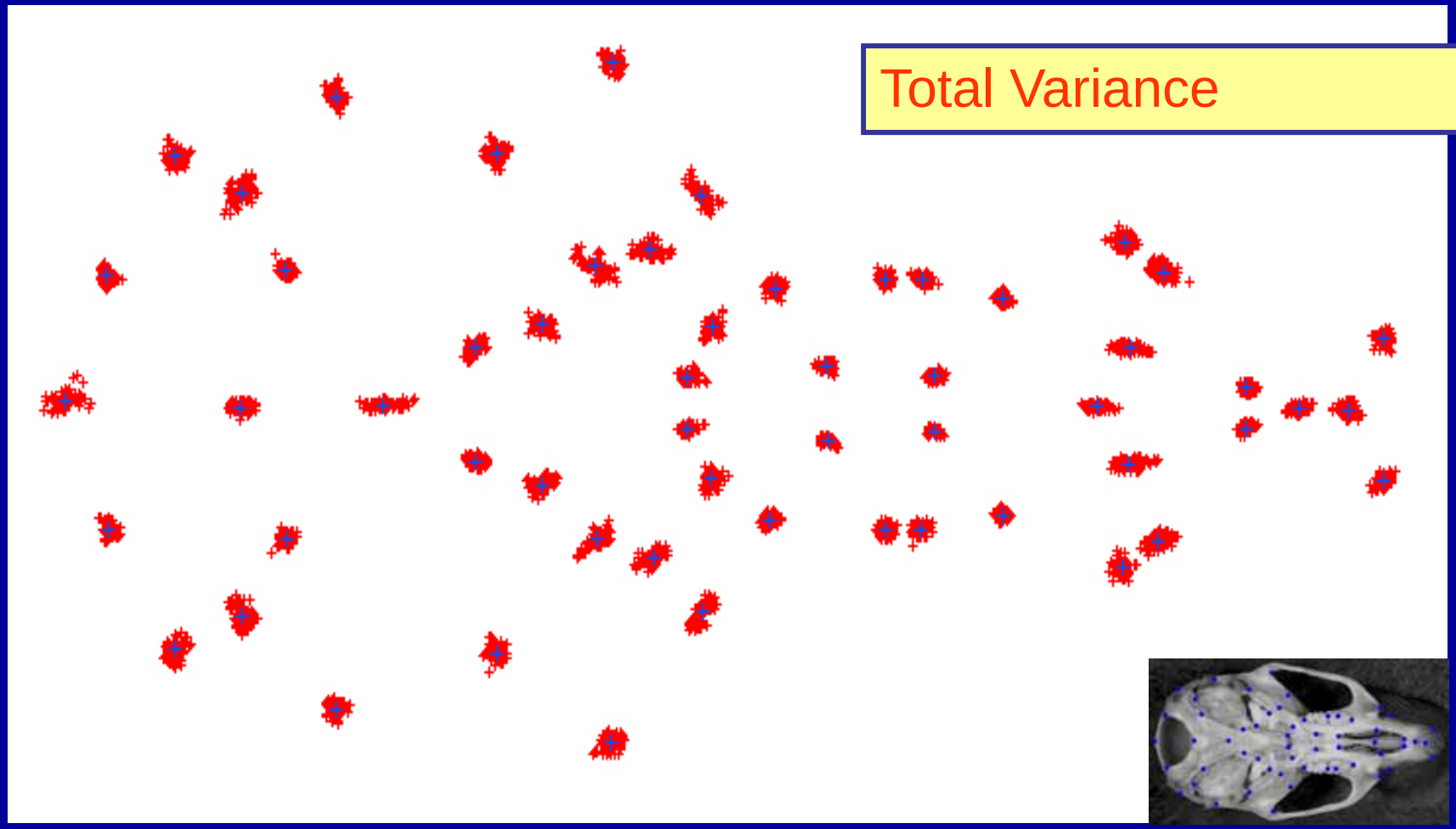
Symmetric Variance (SV) +

Directional Asymmetry (DA) +

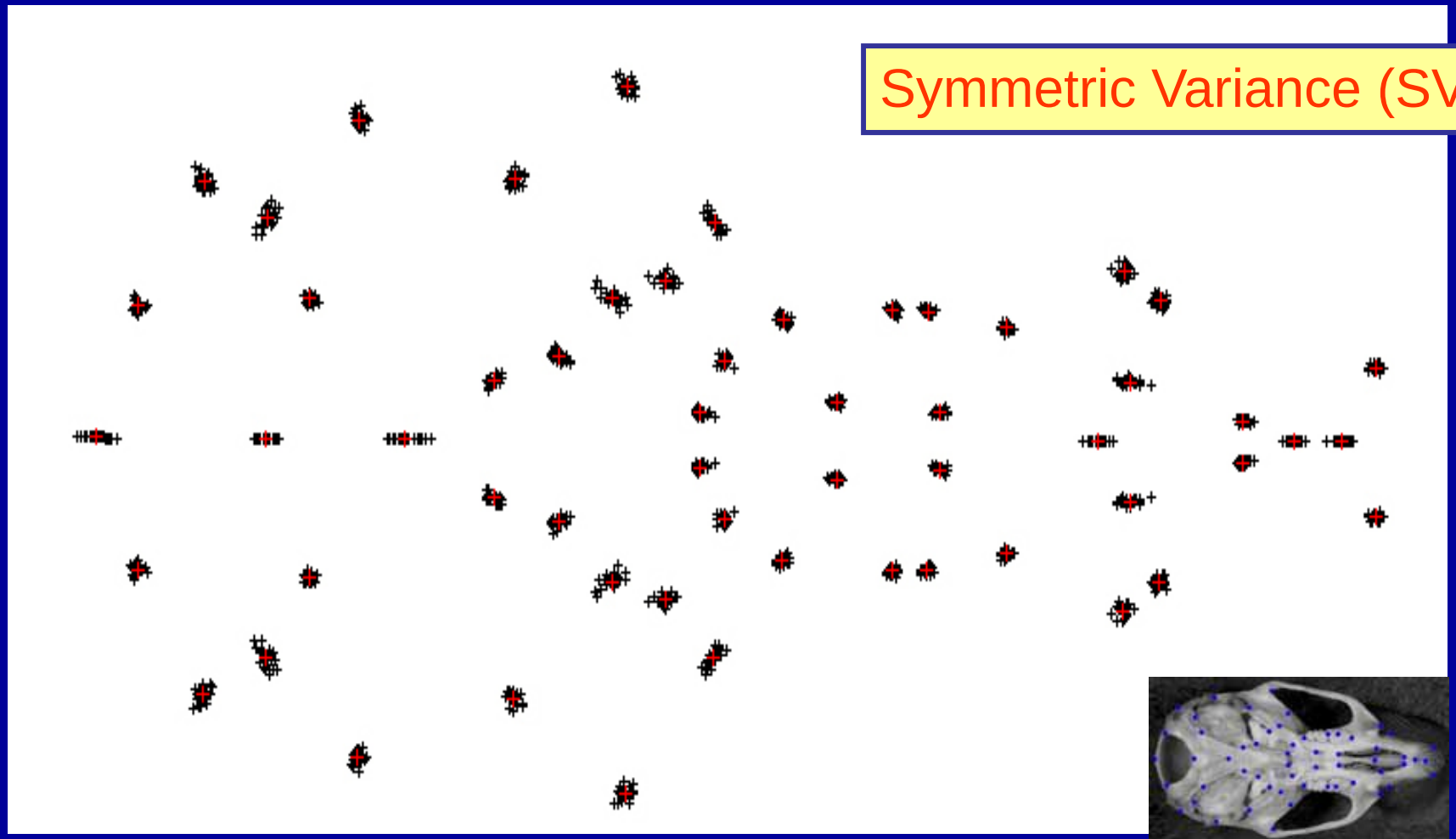
Fluctuating Asymmetry (FA) +

Measurement Error

Components of the variance



Components of the variance



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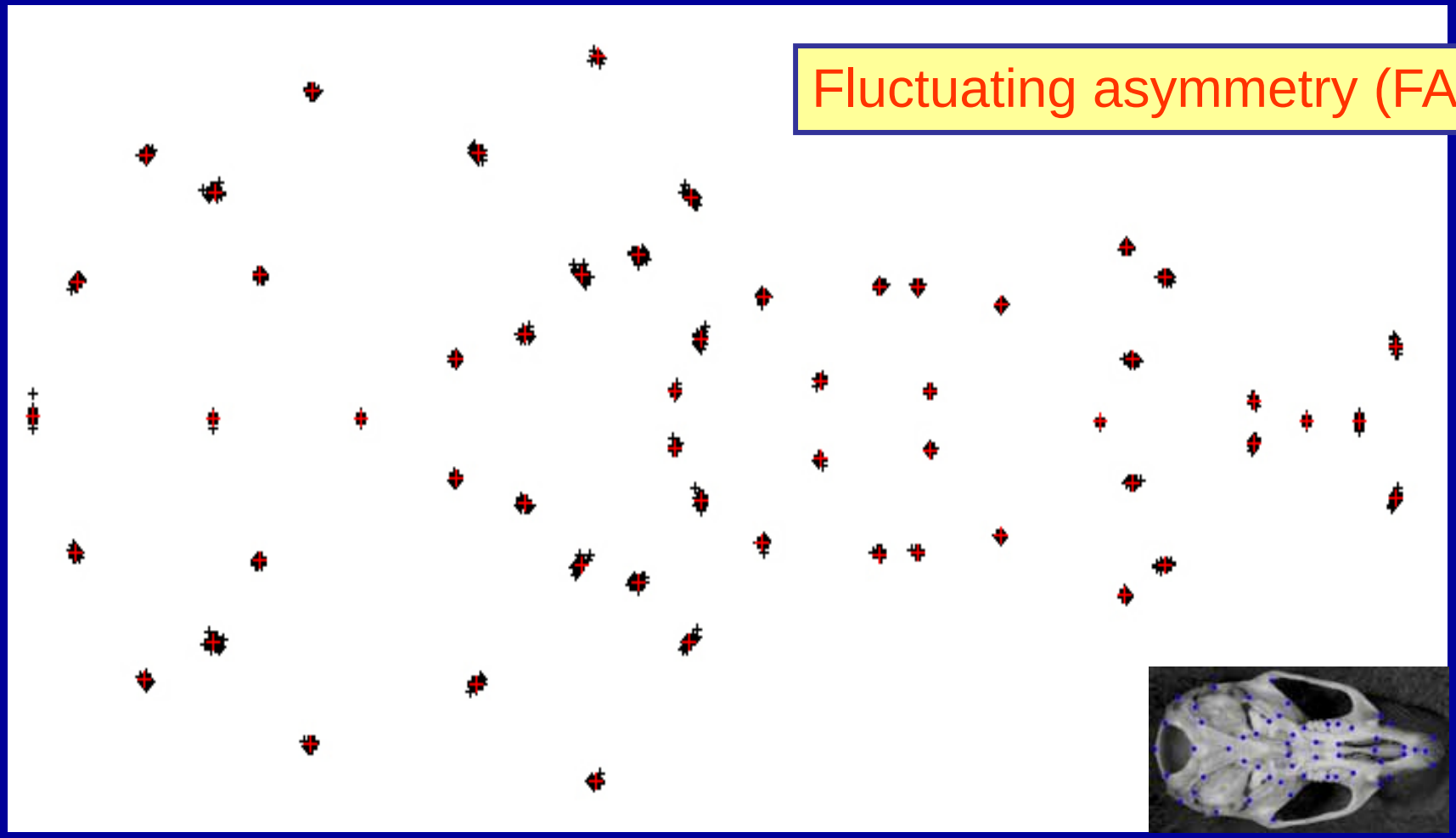

Statistical analyses

- Two-way mixed model ANOVA
- Multivariate extension: MANOVA
  - Same hypotheses, more powerful tests
- Permutation tests

Statistical results

- Significant symmetric variance (SV) in all ages: individuals vary more than do sides of the same individuals

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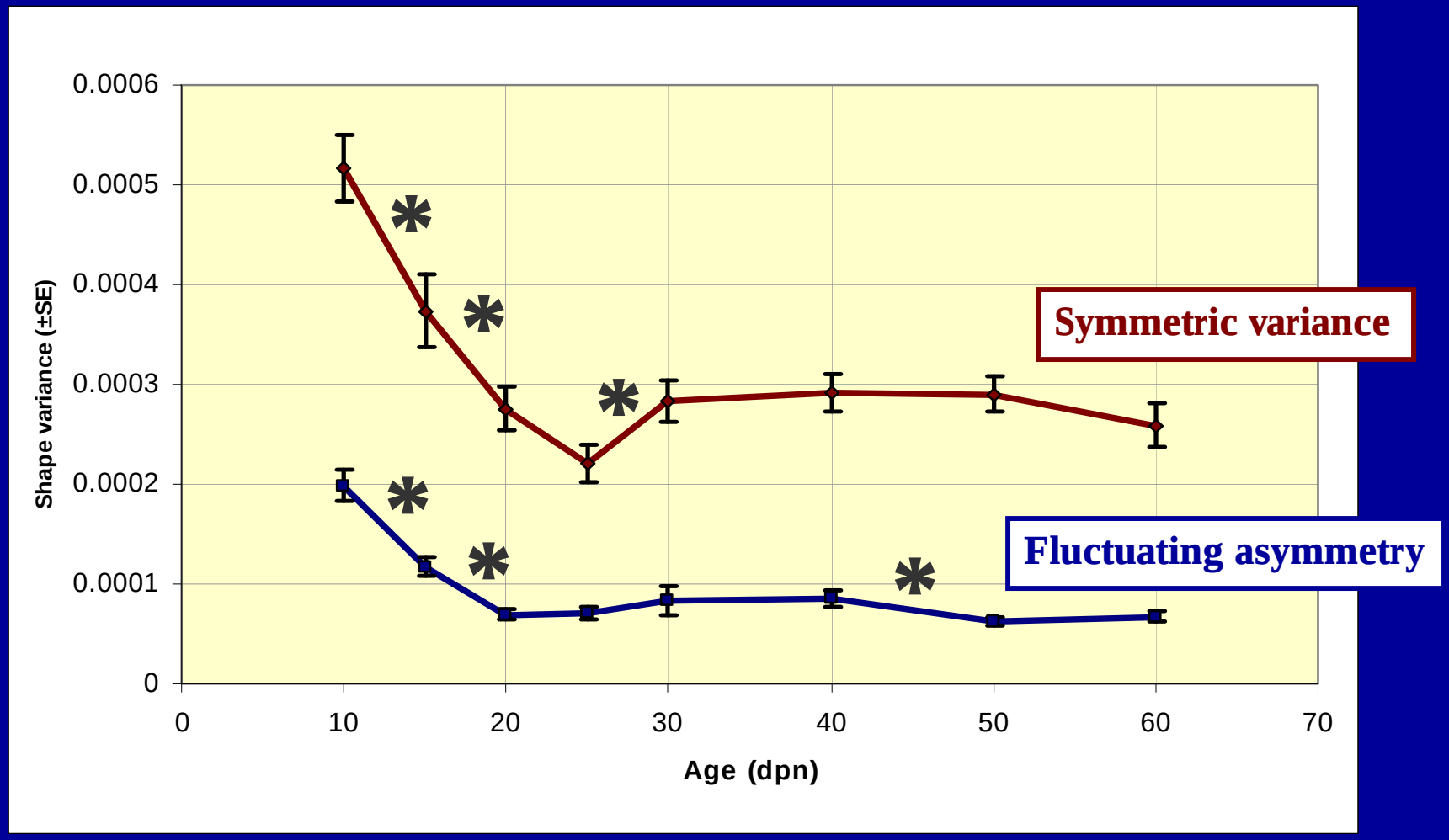
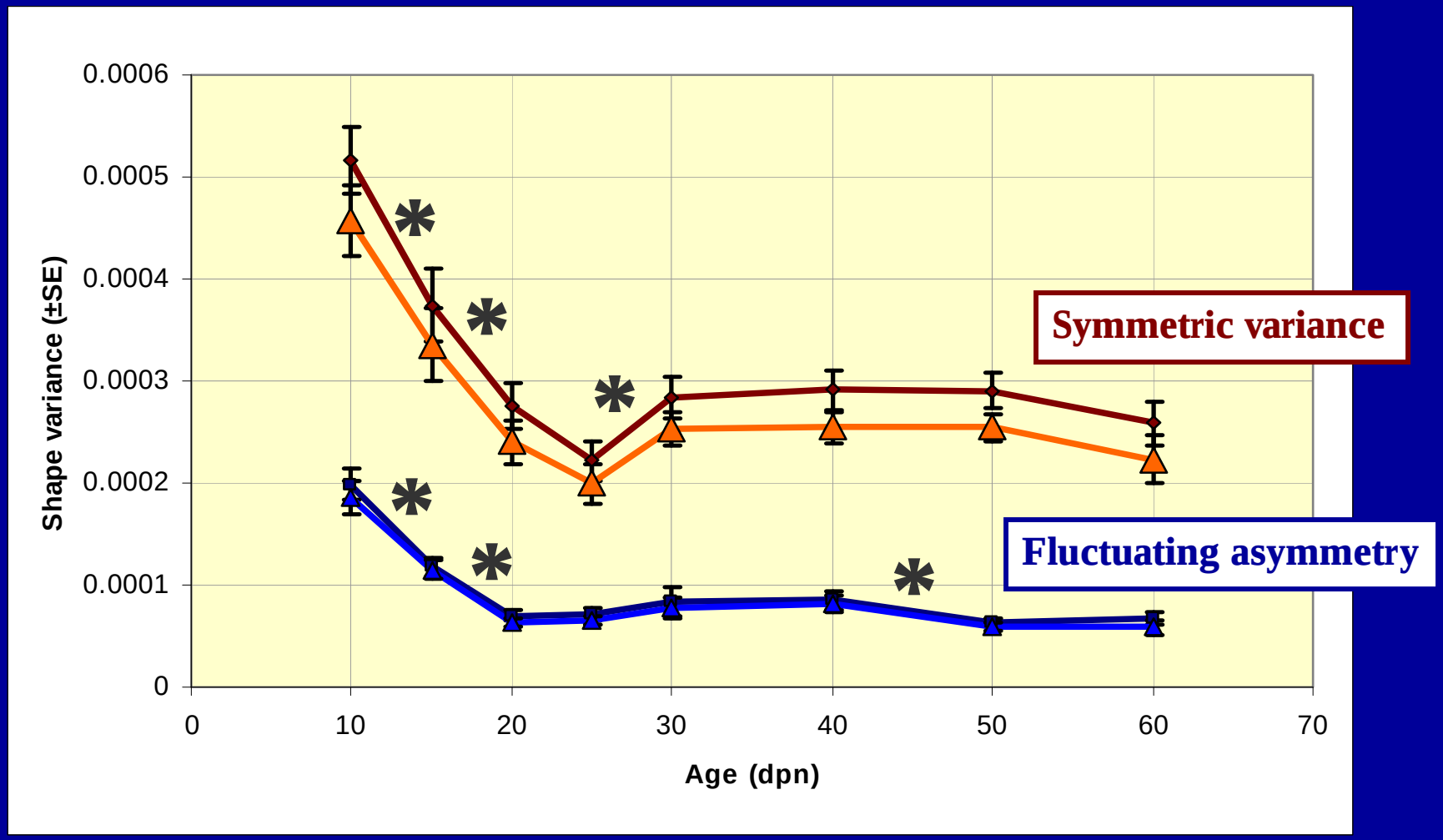
- Significant symmetric variance (SV) in all ages: individuals vary more than do sides of the same individuals
- Significant fluctuating asymmetry (FA) in all ages: differences between sides of single individuals are higher than measurement error
- Non-significant directional asymmetry (DA): weak or no bias in asymmetry

Ontogeny of variance (full landmark set)



Variance in shape is not a function of variance in size



Spatial organization of the variance

- Is there a common spatial pattern to variance and FA?

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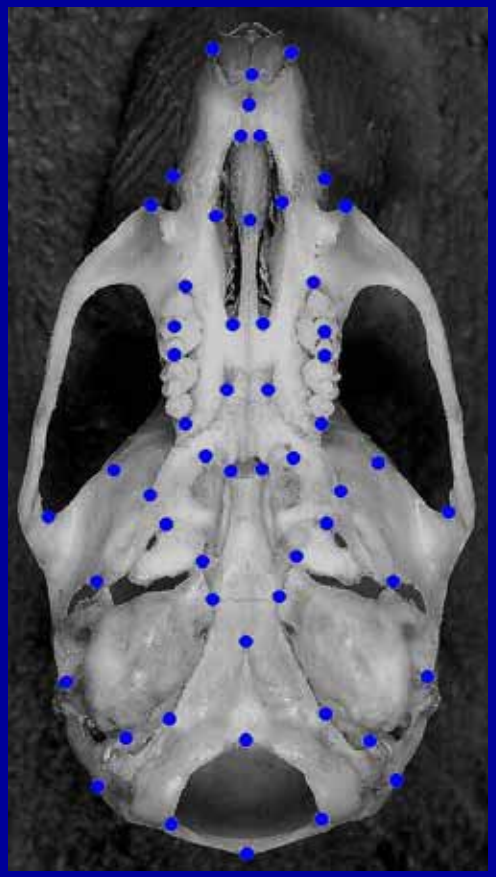
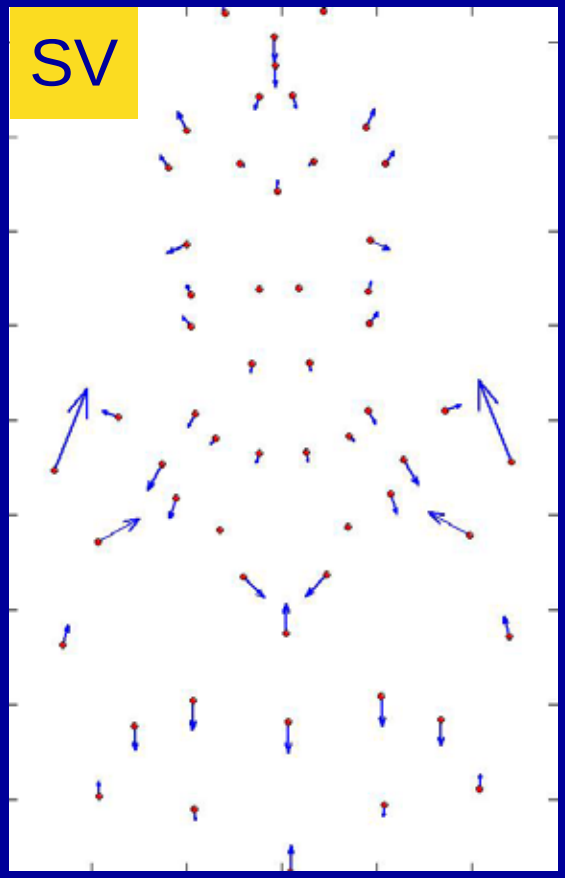
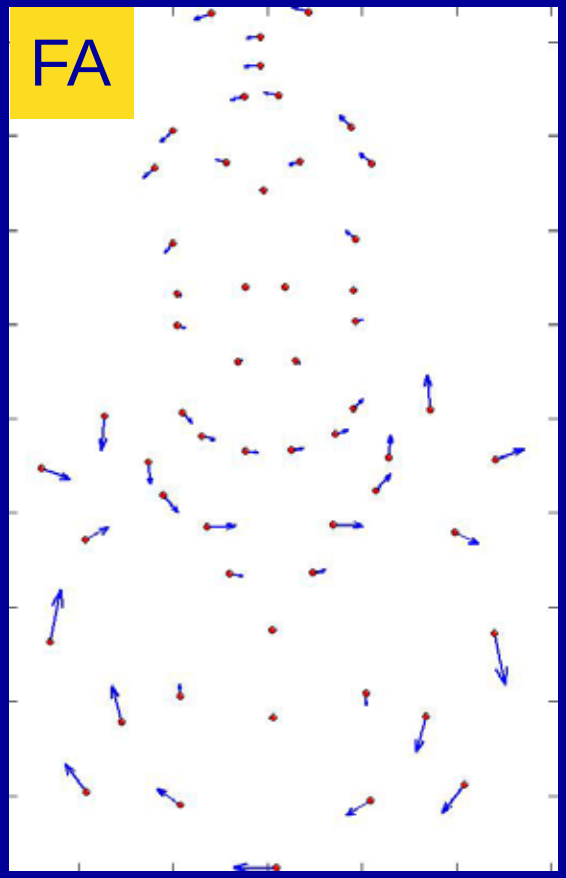
- Is there a common spatial pattern to variance and FA?
- Comparative approaches :
  - Visual inspection of principal component plots
  - Subspace comparisons
  - Matrix correlations
  - Partial Least Squares

Comparison of Principal Components: 10 dpn

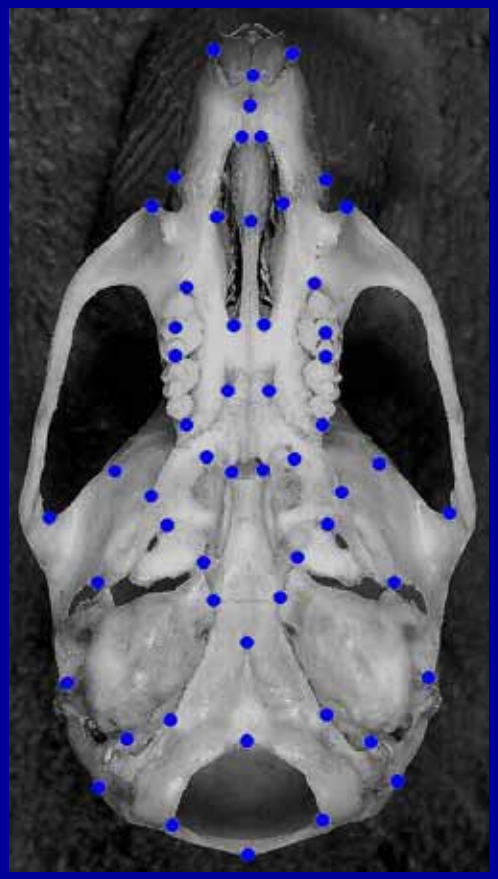


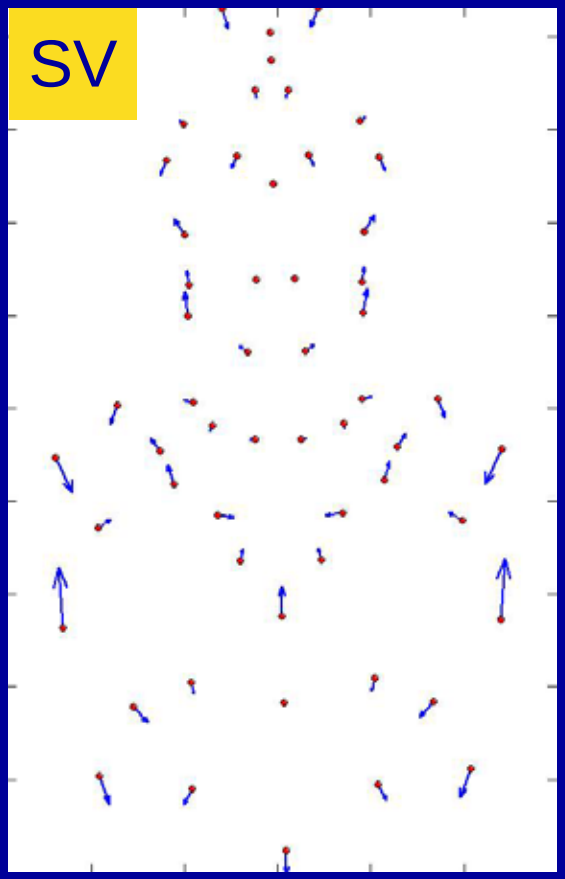


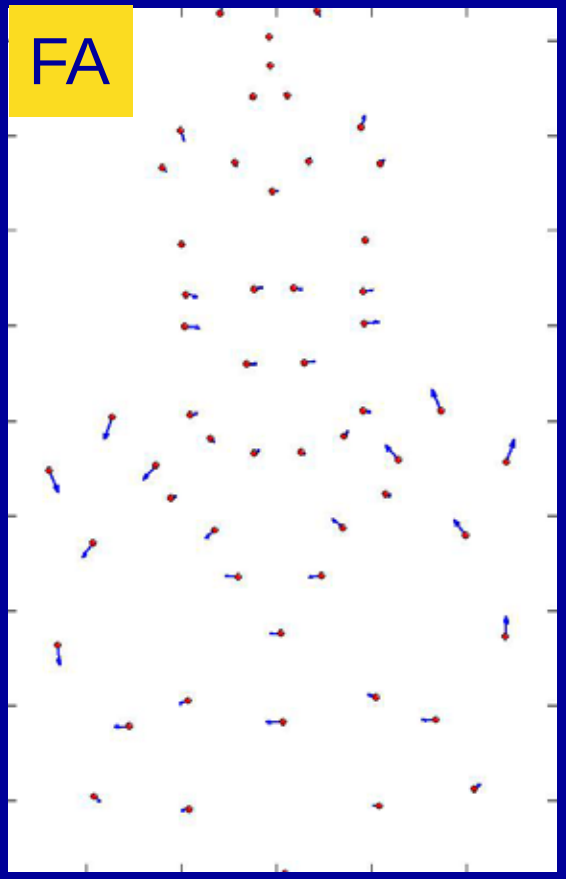


PC1: 22.32% 29.60%

Comparison of Principal Components: 10 dpn

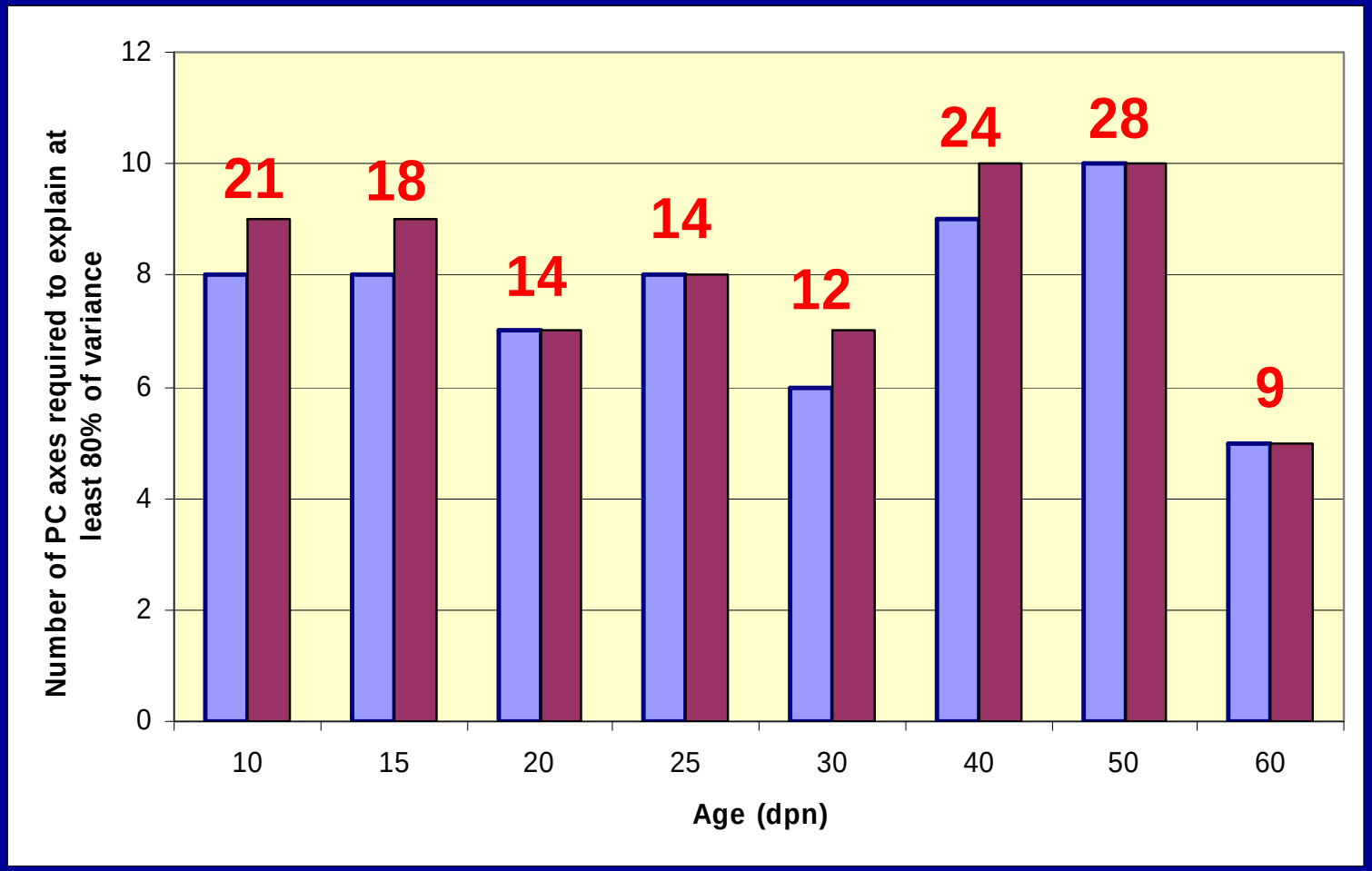






PC2: 12.82% 12.06%

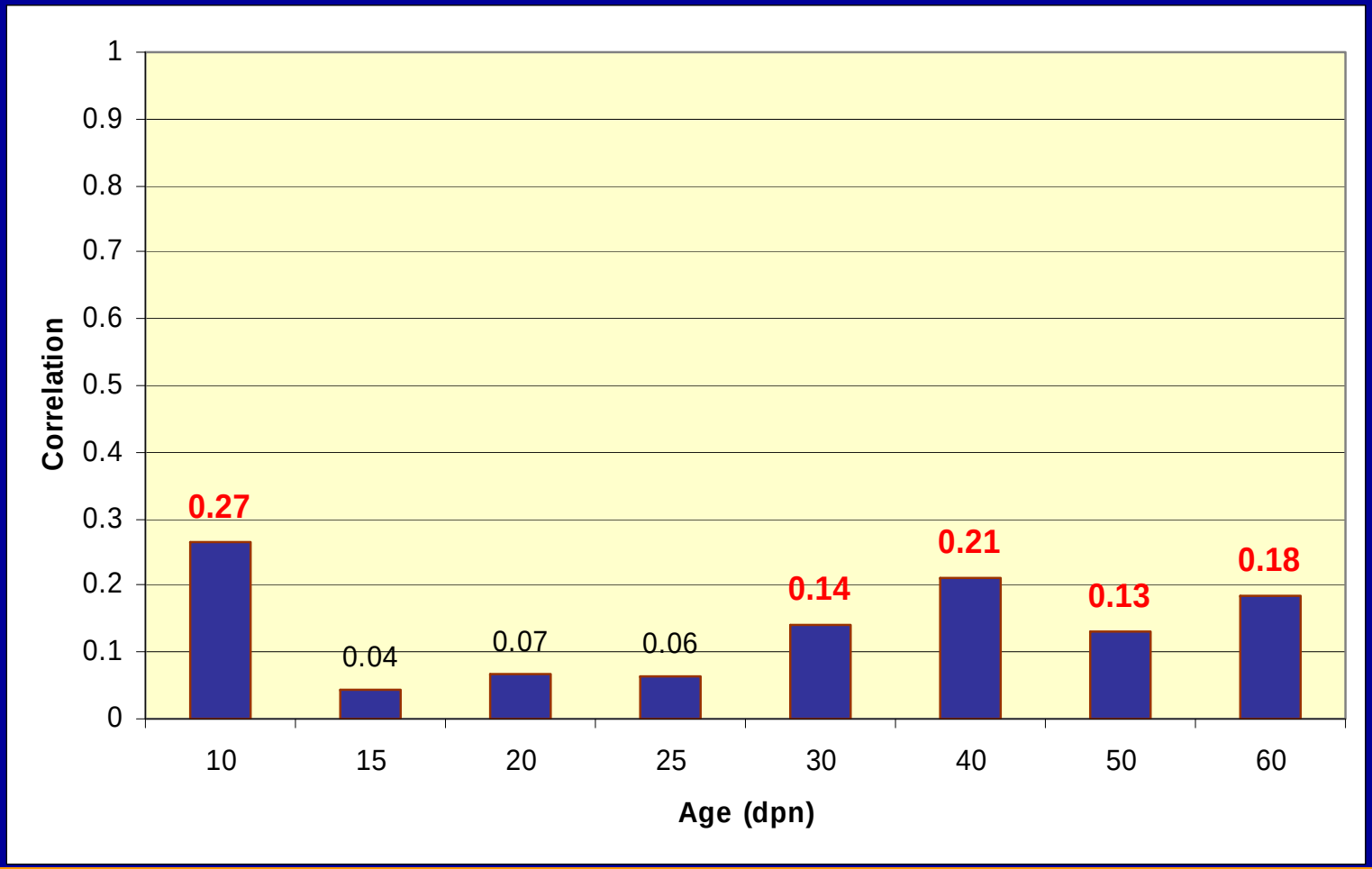
Symmetric Variation and FA are highly diffuse (high dimensionality)



Angles between subspaces measure the difference between subspaces of SV and FA

- Angles between SV and FA are significantly higher than expected by chance in all samples
  - Symmetric variation and fluctuating asymmetry do not share a common subspace

Matrix correlations are correlations across individual entries of covariance matrices



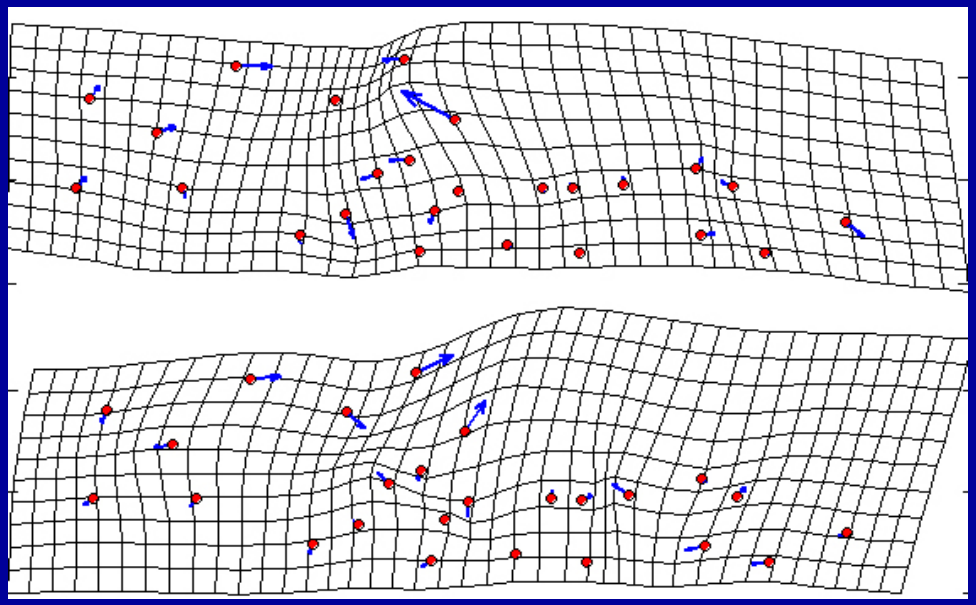
Common factors shared by SV and FA

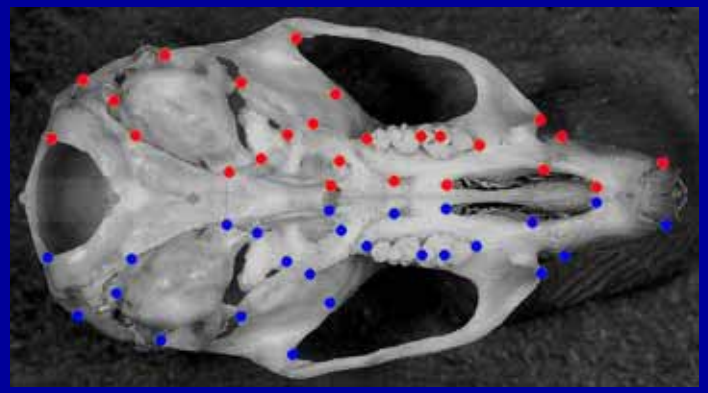
- Even though SV and FA differ in spatial structure, they may share common factors

Common factors shared by SV and FA

- Partial Least Squares: given two sets of variables, PLS discovers linear combinations maximizing their covariance
  - These combinations might not be spatially congruent but could still indicate a correlation between SV and FA

Partial Least Squares





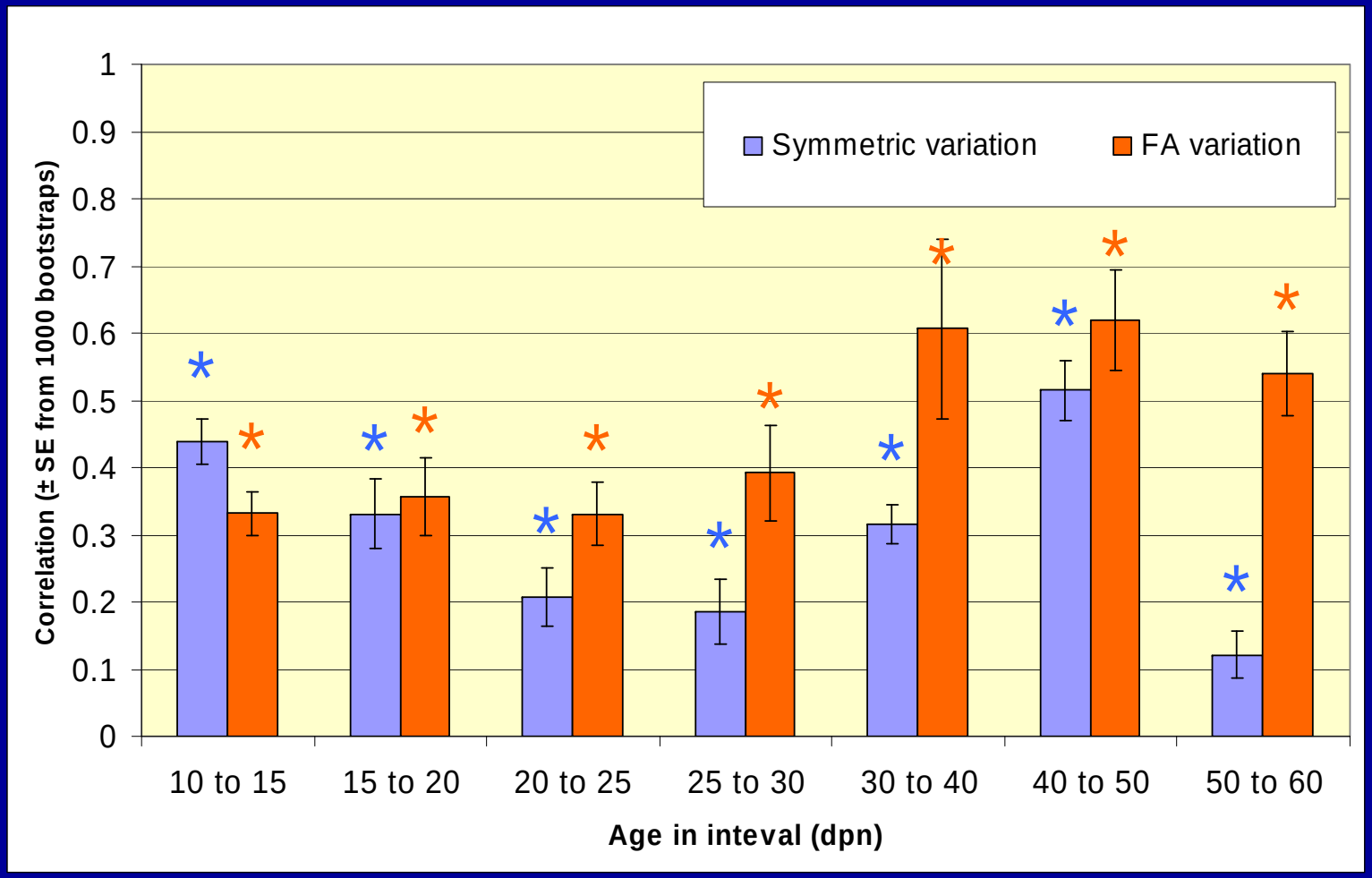
First PLS vector (10 dpn):

- Correlation between vectors: 0.77
- % Explained covariance: 35.6% (**no more than expected by chance**)
- Consistent with expectations of random variation

Temporal organization of the variance

- Is the spatial structure of FA dynamic or constant from age to age?

Age to age correlations of SV and FA



*Significantly higher than a the correlation of two random matrices, from 1000 random permutations ($p < 0.01$)

Summary of results

- Both SV and FA decrease significantly between 10 and 20 days postnatal
- There is little evidence of any spatial congruence between symmetric variance and FA
- There is little evidence of common factors affecting symmetric variance and FA
- The spatial structure of FA changes from age to age, although it remains diffuse throughout ontogeny

Conclusions

- If SV and FA are regulated by a common mechanism, then it produces no spatial signal shared by both forms of variance, nor correlations between them
- The similarity in time over which both decrease does suggest that there might be a common developmental basis for canalization and developmental stabilization, but one that is not spatially predictable

Two possible explanations:

1. Early in postnatal growth, skeletal growth is prone to developmental accidents because musculoskeletal interactions are poorly coordinated. As their coordination increases, muscle loading and unloading also becomes more organized, which normalizes bone shape. These processes are local, so may not occur in the same place on both sides.

Two possible explanations:

2. The processes generating variance may be independent of those removing it. Both symmetric and asymmetric variance may be buffered by the same processes, but they differ in spatial patterning due to differences in processes generating them.

Acknowledgements

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- We thank Ted Garland, Jr. for providing the ontogenetic series of mice.