Antero-posterior segments are generally viewed as modules, but left and right halves of the segment could also be viewed as modules if we accept Palmer’s argument that there are two medio-lateral axes.

Patterns of asymmetry:

1. Grasshopper mandibles have been described as directionally asymmetric, not the rest of the head.
   1. H0: No difference in shape between mandibles, i.e. no directional asymmetry.
   2. H1: Left and right mandibles are systematically different and on the same side, i.e. directional asymmetry is present.
2. If b., asymmetric mechanical loads from mandibles may also cause directional asymmetry in other head structures.
   1. H0: No directional asymmetry in the head structures aside from mandibles.
   2. H1: Directional asymmetry “spills over” to other structures, even though they may have different segmental origins. Distance to mandibles (e.g. to their centroid) influences the amount of spill over asymmetry.

Link between modularity and asymmetry

1. In bilaterians, asymmetric structures must be separate modules from symmetric structures
   1. H0: The whole head does not have different modules.
   2. H1: Directionally asymmetric structure (mandibles) form (a) separate module(s) from symmetric structure (head capsule/sensory organs).
2. If b. is true, then:
   1. H0: Both mandibles form one integrated functional module.
   2. H1: To achieve differentiated left and right shapes, the developmental programs of the left and right medio-lateral axes are to some extent disconnected, producing a different module for each mandible.

Link between asymmetry and performance:

1. Directional asymmetry of mandibles is functionally necessary to achieve occlusion-cutting-crushing, it is under selection because it influences feeding performance.
   1. H0: No relation between bite force performance and directional asymmetry.
   2. H1: Quadratic relation, with an optimum level of DA allowing best performance.
   3. H2: Linear relationship, with individuals with larger DA being at a disadvantage compared to more symmetrical individuals.
2. Fluctuating asymmetry of mandibles / the whole head / only the head parts, reflects quality of individuals, and possibly fitness / performance.
   1. H0: No relationship between fluctuating asymmetry and bite force performance.
   2. H1: Negative linear relationship between bite force and fluctuating asymmetry.