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Emergence of functional modularity from phenotypic adaptation to independent constraints

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Introduction: So far the methods employed in determining functional modularity have primarily followed the same premise, namely that finding *structural modules* in a network would also identify the *functional modules*. Such *structural modularity* is indicated by the presence of densely connected groups of nodes with sparser connections between groups [1] and graph community detection algorithms have been used to identify such groups. *Functional modularity*, on the other hand, is indicated by the presence of modules that perform a specific function semi-autonomously in relation to other modules. [2]. While in some cases the structural modules of a network can be identified easily, and consequently the functional modules [3] inferred, there can be cases, as we show in this paper, where although there are no easily identifiable structural modules, the functional modules can be clearly delineated. The apparent absence of structural modularity, therefore may not preclude the presence of functional modules in the system. The factors leading to the origin of functional modularity in biological are far from being clearly understood. While it is rather plausible that on higher levels of biological organization functional modularity is innate, i.e, encoded in the genotype and therefore arising through evolutionary dynamics [4] , it is less clear that this is the only possible scenario. In particular, one can pose the question as to whether functional modularity can arise on much shorter time-scales than evolution, namely through phenotypic adaptation, or learning.

Results:

- We propose a method that identifies functional modules in a network without resorting to structural measures. This method is based on the notion of *differential robustness* and is one that is not based on graph community detection algorithms. The method comprises of elucidating the error in the output response of a network upon removal of one of its nodes, and thereby inferring the functional contribution of that node.

- We also investigate if there are any general principles governing the emergence of functionally specialized modules in learning systems. Using a neural network model, we present a *proof-of-principle* study to show that functional modules can indeed emerge through learning. Our fundamental premise is that biological networks are in constant interaction with the environment to which they adapt. In general, the environment is comprised of many processes or features, which include *statistically independent* ones. We show that adaptation to statistically independent features in the environment can lead to the formation of functional modules in a network, even if at the beginning of the process, the network has a completely

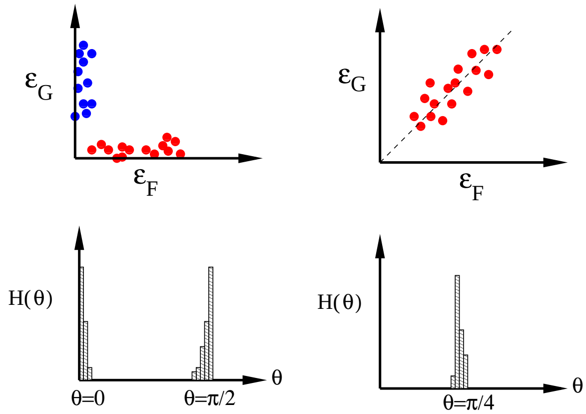

FIG. 1: The measurement of differential robustness in a network that performs two functions F and G. Top: (a) Perfectly modular systems: Each node when removed results in an error in only one of the two functions (b) Perfectly non-modular systems: Every node contributes significantly to the performance of both functions and therefore induces a non negligible error in both functions when removed. Bottom: The histogram $H(\theta)$ of polar angles θ associated with each point on the scatter. Points with polar angles $\theta = 0$ and $\theta = \pi/2$ correspond to nodes contributing only to one of the two functions.

homogeneous, non-modular structure. We demonstrate this in the context of a visual task, and also for the learning of arbitrary Boolean functions.

- We also identify other key factors that are required for the emergence of functional modularity, which include the size of the network, and the form of the update rules used for learning.

Discussion: We show that modularity on a single hierarchical level in a network of sufficiently many learning units can emerge through adaptation to statistically independent features in the environment, if the learning rule has certain key properties. We propose the method of differential robustness using which one can uncover functional modules, if they exist, despite the apparent absence of structural modules.

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