

# Limits of population coding

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## Abstract

To understand whether the population response expresses information better than the aggregate of the individual responses, the sum of the individual contributions is frequently used as a baseline against which to assess the population's coding capabilities. Using information processing theory, we show that this baseline is illusory: the independent baseline case is theoretically impossible to apply consistently to any population. Instead, we use as a baseline the noncooperative population, in which each neuron processes a common input independently of the others. Using the information transfer ratio, the ratio of Kullback-Leibler distances evaluated at a population's input and output to measure a population's coding ability, we show that cooperative populations can perform either better or worse than this baseline. Furthermore, we show that population coding is effective only when each neuron poorly codes information when considered out of context of the population.

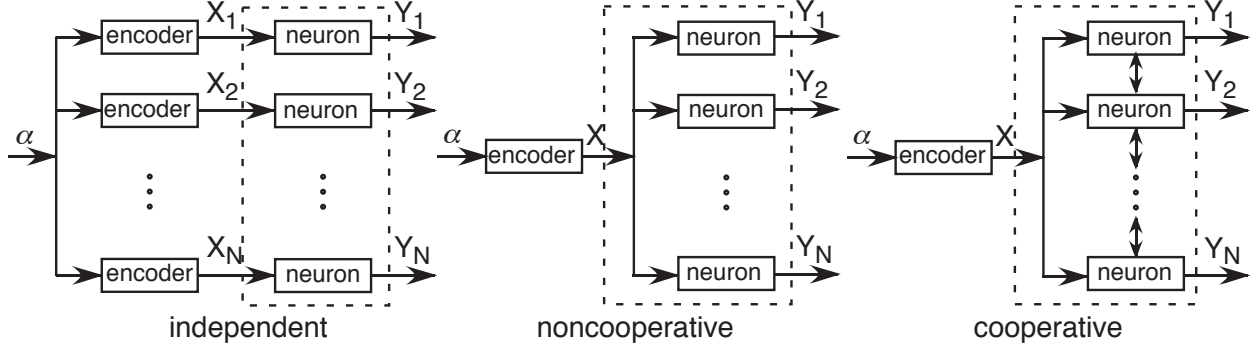
## 1 Introduction

Recordings have shown that population coding, which we define here as the cooperative encoding of information by a collection of neurons, does indeed occur [1, 5]. The measures used to assess population coding (entropy, mutual information, Kullback-Leibler distance) have the so-called *additive property*: if a population's components are statistically independent, the measure applied to the population as a whole will equal the sum of component values. Under the presumption that this sum defines a *baseline* against which to assess population coding, the notions of *synergy* and *redundancy* have arisen. If the population's measure exceeds the sum of measures taken from the component neurons, synergy occurs; if less, redundancy occurs. It is true that any discrepancy between the measured and baseline values indicates that the population outputs are statistically dependent on each other, presumably meaning that some kind of population coding is occurring. Because this analysis was not derived in the context of a theory of population coding, interpreting these measures has proven difficult. This paper elaborates a view of population coding presented at an earlier meeting [3] that frames how the Kullback-Leibler distance measure reflects population coding. This paper adds to that work by showing that

- the usual baseline for assessing population coding is misleading;
- population coding gain over that provided by stimulus-induced dependence can occur when either synergy or redundancy occurs; and
- population coding probably occurs only when the individual neurons do not code the stimulus well.

## 2 Results

In the theory of information processing, information theoretic distance measures, particularly the Kullback-Leibler distance, quantify how well stimuli are encoded regardless of the code employed [2]. Information-theoretic distances have the property that the distance between two responses, whether they be obtained from a single neuron or from a population, must exceed the distance between outputs of any neural system that processes them. Mathematically, if  $\mathbf{X}(\alpha)$  represents the input response that depends on the stimulus parameter vector  $\alpha$  and  $\mathbf{Y}(\alpha)$  denotes the output, information-theoretic distances  $d_{\mathbf{X}}(\alpha_0, \alpha_1)$  between responses



**Figure 1:** A neural population is a group of neurons that receive a common input  $\mathbf{X}$ . The input encodes the stimulus, which is expressed by the parameter vector  $\alpha$ . The simplest population, the independent one shown at the left, has statistically identical and independent inputs, which makes the outputs statistically independent. The noncooperative configuration has neurons with a common input but no other interactions, and thus reflects stimulus-induced dependencies. In the cooperative case shown on the right, the neurons interact and thus express stimulus- and connection-induced dependencies. For graphic simplicity, only nearest-neighbor interactions are shown; in general, any kind of interactions are allowed.

to the stimuli corresponding to  $\alpha_0$  and  $\alpha_1$  must exceed the distance  $d_{\mathbf{Y}}(\alpha_0, \alpha_1)$  between the corresponding outputs.

$$d_{\mathbf{Y}}(\alpha_0, \alpha_1) \leq d_{\mathbf{X}}(\alpha_0, \alpha_1) \quad \text{or} \quad \frac{d_{\mathbf{Y}}(\alpha_0, \alpha_1)}{d_{\mathbf{X}}(\alpha_0, \alpha_1)} \stackrel{\text{def}}{=} \gamma_{\mathbf{X}, \mathbf{Y}}(\alpha_0, \alpha_1) \leq 1 \quad (1)$$

Equality in (1) means that the output represents the stimulus parameter change with the same fidelity as the input even though the output code may differ from that of the input. For example, the input could arise from a single neuron that innervates a population or from a population innervating another population. In either case, a ratio of one means perfect transmission of information. The smaller the ratio, the less effective the system’s processing of the input. Thus, the *information transfer ratio*  $\gamma_{\mathbf{X}, \mathbf{Y}}(\alpha_0, \alpha_1)$  quantifies the ability of a population to represent the information expressed by the input. It is this quantity that we use to analyze population coding by studying how it depends on  $N$ , the number of neurons comprising the population.

Figure 1 shows the three population structures we study here. When each neuron’s input is statistically independent of the other neurons’ inputs and the neurons do not cooperate, we have the *independent* population. In an independent structure, the individual neuron responses are statistically independent of each other and, as we show later, this population exhibits *no* information processing beyond that of a single neuron. In a *noncooperative* population, the common innervation of population neurons means that each neuron’s response is statistically dependent on the others to some degree; we refer to this dependence as *stimulus-induced dependence*. In a *cooperative* population, the neurons interact with each other via collaterals and/or interneurons — cooperate — to create *connection-induced dependence* as well as stimulus-induced dependence. The individual neuron probability function  $p_{Y_n|X}(y_n|x)$  expresses the input-output relation for the  $n^{\text{th}}$  neuron.

The three population structures are mathematically specified by the different forms they yield for  $p_{\mathbf{Y}^{(N)}}(\mathbf{y}; \alpha)$  the joint probability function of the aggregate population output  $\mathbf{Y}^{(N)}$  of  $N$  neurons. For the independent structure, the stimulus drives a set of statistically independent inputs that serve a population of noncooperative neurons. The outputs are thus statistically independent, and the population’s probability function factors:  $p_{\mathbf{Y}^{(N)}}(\mathbf{y}; \alpha) = p_{Y_1}(y_1; \alpha) \cdot p_{Y_2}(y_2; \alpha) \cdots p_{Y_N}(y_N; \alpha)$ , which can be more succinctly expressed using the product notation  $p_{\mathbf{Y}^{(N)}}(\mathbf{y}; \alpha) = \prod_{n=1}^N p_{Y_n}(y_n; \alpha)$ . The noncooperative structure has the property that for each specific input, the population output has statistically independent components. “Specific input” here means a particular value for the neural input  $\mathbf{X}$ , a specific sequence of spike times for example, but not some particular stimulus. Mathematically, this property means that the outputs are

statistically independent for each specific input:  $p_{\mathbf{Y}^{(N)}|\mathbf{X}}(\mathbf{y}|\mathbf{x}) = \prod_{n=1}^N p_{Y_n|\mathbf{X}}(y_n|\mathbf{x})$ . The omission of  $\alpha$  from terms in the product is intentional; this notation expresses the assumption that each neuron has no knowledge of the stimulus attribute other than through its input  $\mathbf{X}$ . The  $n^{\text{th}}$  neuron's output probability function and the population's joint probability function are

$$p_{Y_n}(y_n; \alpha) = \int p_{Y_n|\mathbf{X}}(y_n|\mathbf{x}) p_{\mathbf{X}}(\mathbf{x}; \alpha) d\mathbf{x} \quad (2)$$

$$p_{\mathbf{Y}^{(N)}}(\mathbf{y}; \alpha) = \int \prod_{n=1}^N p_{Y_n|\mathbf{X}}(y_n|\mathbf{x}) p_{\mathbf{X}}(\mathbf{x}; \alpha) d\mathbf{x} \quad (3)$$

Because of the integral, the joint probability function does not factor and thus the outputs are not independent. In the *cooperative* case, the conditional probability function  $p_{\mathbf{Y}^{(N)}|\mathbf{X}}(\mathbf{y}|\mathbf{x})$  defines the population's input-output relation. What form it takes depends on the details of the cooperative structure.

The Kullback-Leibler distance between random vectors having statistically independent components equals the sum of the distances between each component [2]:  $\mathcal{D}_{\mathbf{Y}^{(N)}}(\alpha_1||\alpha_0) = \sum_{n=1}^N \mathcal{D}_{Y_n}(\alpha_1||\alpha_0)$ . For the independent population, such as shown in the left portion of figure 1, its outputs as well as its inputs are statistically independent of each other. Thus, the population's input and output distances are easily expressed in terms of the component distances.

$$\mathcal{D}_{\mathbf{X}}(\alpha_0||\alpha_1) = \sum_{n=1}^N \mathcal{D}_{X_n}(\alpha_0||\alpha_1) \quad \mathcal{D}_{\mathbf{Y}^{(N)}}(\alpha_0||\alpha_1) = \sum_{n=1}^N \mathcal{D}_{Y_n}(\alpha_0||\alpha_1)$$

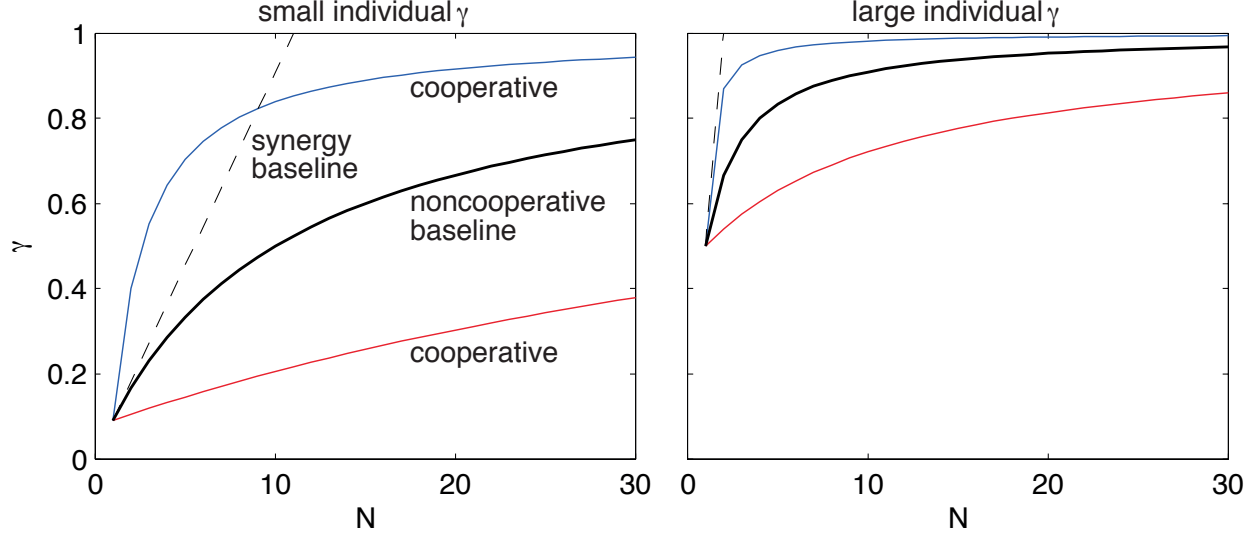
For the simple case in which the inputs have the same statistical properties and individual neurons have the same characteristics, the input and output distances are each proportional to population size. In this case, the information transfer ratio is a constant, equal to that of an individual neuron. For the more general (inhomogeneous) case, simple bounding arguments reveal that the overall information transfer ratio is bounded by the best and worst performing neurons.

$$\min_n \gamma_{X_n, Y_n}(\alpha_0, \alpha_1) \leq \gamma_{\mathbf{X}, \mathbf{Y}}(\alpha_0, \alpha_1) \leq \max_n \gamma_{X_n, Y_n}(\alpha_0, \alpha_1)$$

Thus, *from an information processing viewpoint, the independent population is ineffective*: one neuron could serve the purpose of many.

The community's definitions for synergy and redundancy are flawed in that they *only* consider how the output distance behaves. By using the independent population structure as the baseline, the output distance is proportional to the population size *only* because the input distance is also increasing. The number of inputs to a neural population is presumably fixed, which means that the input distance is constant. Even if synergy occurs, the output distance cannot continue to exceed the sum of component values. The reason for this is that the information transfer ratio cannot exceed one; if the input distance is fixed, the output distance cannot exceed this value no matter how large the population. Thus, a population may show synergy for a small population, but as more neurons enter the population (by including them from population recordings), it must eventually demonstrate redundancy because the information transfer ratio  $\gamma$  for *any* population structure cannot be proportional to  $N$ . Figure 2 illustrates the problem.

In contrast, *any* nontrivial noncooperative population (i.e., each neuron has a nonzero information transfer ratio) can ultimately represent its input information *perfectly* [6]. As population size  $N$  increases, the information transfer ratio monotonically increases ( $\gamma(N+1) > \gamma(N)$ ) whether the population is homogeneous or not. Furthermore, the information transfer ratio approaches one ( $\lim_{N \rightarrow \infty} \gamma(N) = 1$ ), regardless of each neuron's input code, of how each neuron processes its input, and of how each neuron encodes the processed input in its output. This result contrasts with the independent population's behavior, which shows



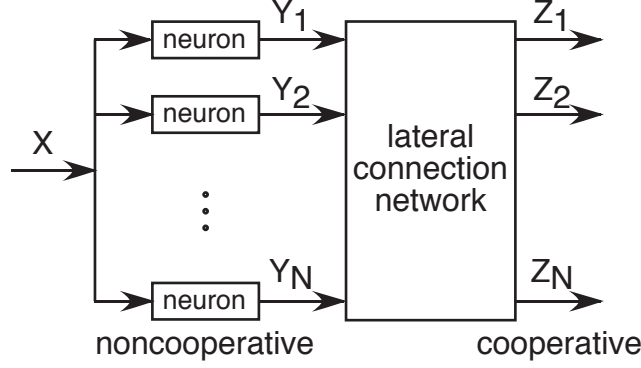
**Figure 2:** Each panel displays the information processing analysis for two populations having different individual processing characteristics. Each “neuron” simply adds Gaussian noise to its input that can be correlated to that added by other neurons. In the left panel, individual neurons process information poorly ( $\gamma(1) = 0.1$ ); in the right panel, individual neurons have much larger information transfer ratios ( $\gamma(1) = 0.5$ ). The dashed line shows the usual synergy baseline. The thicker solid line in each panel shows the noncooperative baseline. The curve having a larger information transfer ratio corresponds to the case where the additive noise is negatively correlated, and the smaller curve results when the noise is positively correlated.

no variation in the information transfer ratio. The way  $\gamma(N)$  increases with the population size for large populations depends on the way the *input* encodes the stimulus attribute. If the input uses a rate code (only the number of spikes occurring in a time interval encodes the stimulus), the information transfer ratio approaches one exponentially. If the input encodes the stimulus in continuous variables, such as spike timing or latency,  $\gamma(N)$  approaches one hyperbolically [6].

$$\gamma(N) \stackrel{N \rightarrow \infty}{\approx} \begin{cases} 1 - k_1 \exp\{-k_2 N\} & X \text{ is discrete-valued} \\ 1 - k/N & X \text{ is continuous-valued} \end{cases} \quad (4)$$

The constants  $k$ ,  $k_1$ , and  $k_2$  depend on the nature of both the input and each neuron’s coding scheme, but these asymptotic results apply *regardless* of the coding each neuron uses. In the continuous-valued case, examples indicate that the formula  $\gamma(N) \approx 1/(1 + k/N)$  more closely approximates the actual information transfer ratio than the asymptotic formula. Asymptotically, this approximation has the same form as the second part of (4). We use this empirical formula in figure 2 to show how the information transfer ratio for a noncooperative population increases with population size. Thus, stimulus-induced dependence among population components suffices to encode information expressed by the input.

In a cooperative population, the neural components interact with each other beyond just having a common input (figure 1). This population structure expresses connection-induced as well as stimulus-induced dependence. Note that having both stimulus-induced and connection-induced dependence does *not* necessarily mean that the statistical dependence is stronger. As shown in figure 3, we have found a lateral connection network that can cancel stimulus-induced dependence [4]. Because this network is mathematically invertible—the input can be found from the output, its information transfer ratio  $\gamma_{\mathbf{Y}, \mathbf{Z}}(\alpha_0, \alpha_1)$  equals 1. By the cascade property of the information transfer ratio [6], the overall information transfer ratio equals that of the noncooperative population. This example differs from the independent population in that it has the same information transfer ratio as the noncooperative population. Because the outputs are independent,



**Figure 3:** To make the outputs of a noncooperative population statistically independent of each other, a system can be defined in many cases that interacts the noncooperative population outputs  $Y_1, \dots, Y_N$  to produce statistically independent outputs  $Z_1, \dots, Z_N$ . The lateral connections make the resulting population having  $\mathbf{Z}^{(N)}$  cooperative.

the population information transfer ratio does equal the sum of the individual ratios; however, the information transfer ratio computed for each of the network's output  $\gamma_{\mathbf{X}, Z_n}(\alpha_0, \alpha_1)$  decreases with  $N$  because of the lateral connection network's properties. Overall, the information transfer ratio  $\gamma_{\mathbf{X}, \mathbf{Z}}(\alpha_0, \alpha_1)$  increases with population size in accord with the information transfer ratio of the noncooperative population.

Does a cooperative population's connection-induced dependence result in an information processing gain beyond that of the stimulus-induced dependence expressed by the noncooperative population? We have not yet been able to derive a general result of what the maximal information transfer ratio might be. Preliminary theoretical considerations indicate that the asymptotics of the noncooperative population (equation 4) apply as well to the information transfer ratio of the cooperative population. In one example—each neuron simply takes its input and adds noise correlated with the noise added by other neurons—we can explicitly calculate the information transfer ratio (figure 2). *Smaller* information transfer ratios result when the additive noise is positively correlated among neurons. From an information processing viewpoint, a cooperative structure yielding a smaller information transfer ratio than the noncooperative structure is pointless: if a noncooperative structure performs better than a cooperative one, why use the worse performing, more complex alternative? Consequently, consider only those cooperative structures that exhibit some processing gain over that of a noncooperative population, which occurs in this example when the noise is negatively correlated among neurons. The greatest increase occurs when individual neurons don't code well (i.e., the information transfer ratio for a single neuron is small which means each neuron in the population does not represent its input well when it is considered out of the population context). In these examples, one population crosses the synergy baseline and other doesn't. Thus, *synergy is not a necessary property for populations to exhibit greater information processing capability than a noncooperative population.*

### 3 Conclusions

These purely theoretical considerations indicate that analyzing population coding is more complicated than first thought. In the theory presented here, the nature of the population code is deliberately not specified, and these results apply regardless of the coding mechanism. Furthermore, the individual neurons need not employ the same code for these results to apply.

Information processing theory shows that cooperative populations, those demonstrating connection- as well as stimulus-induced dependence, can encode information better or worse than noncooperative (stimulus-induced dependence only) counterparts. When a population coding gain does occur, the increases in the information transfer ratio can be large, but only in cases where the individual neurons don't encode the information well. From this perspective, poor coding by single neurons means that population coding can be effective.

Unfortunately, analyzing population recordings in the light of this theory remains a complicated issue. Rarely can the input and the output to a population be recorded. In this theory, they need not be recorded simultaneously; even so, estimating information transfer ratios is daunting. What can be measured is the Kullback-Leibler distance for the population [2]. This theory predicts that as more of the actual population's neurons included in recordings, the Kullback-Leibler distance will increase monotonically, saturating at some value. We have shown that synergy is not a good indicator of information processing. Theoretically, population sizes that show synergy merely indicate that larger information transfer ratios can be obtained with even larger populations. In fact, synergy becoming anti-synergy as more neurons are included in the population might be a better indicator of the population's actual size and coding. However, even this guideline need not occur for all populations: the example in the right column of figure 2 never showed synergy but does express significant information processing capability.

## References

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