# A New Form of Separability for the Study of Information Integration in the Brain

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## Abstract

In the neurosciences separability is commonly studied in the context of mean tuning curves. A mean tuning curve is called separable if it can be expressed as the product of terms selectively influenced by different stimulus dimensions. There is another notion of separability commonly used in psychophysics and mathematical psychology but seldom used in the neurosciences. This new notion addresses separability of entire response histograms, not just average values. We introduce such notion and show that it is unrelated to mean tune curve separability. We present preliminary results of an experiment illustrating how this new notion of separability may be used to analyze information processing in the brain.

## 1 Information Integration

The problem of separability/inseparability of different stimulus dimensions has received a great deal of attention in the cognitive and neuroscience communities. Separability is an important property that guides hypotheses about underlying information processing mechanisms. In neuroscience separability is commonly studied in the context of mean tuning curves. Here a tuning curve is a function $f$ that describes how the average firing rate of a neuron changes as a two or more stimulus dimensions are varied, i.e. $f(X_1, X_2) = E(R|X1, X2)$, where $E$ stands for expected value, $R$ for the neural response and $X_1, X_2$ are stimulus dimensions. A tuning curve is called (multiplicatively) separable if it can be decomposed as the product of two different factors each selectively influenced by a single stimulus dimension, i.e., $f(X_1, X_2) = f_1(X_1)f_2(X_2)$. For example, it has been shown that for many V1 neurons, temporal and spatial frequency have separable effects on the mean tuning curve (Hamilton, Albrecht, & Geisler, 1989) a property known as spatio-temporal separability.

There is a different notion of separability well known in psychophysics and mathematical psychology but seldom used in the neurosciences. Psychophysical experiments of information integration in humans show a consistent pattern of results: Ratios of response probabilities factorize into components selectively influenced by a single information source. This pattern has been called the *Morton-Massaro Law* (Movellan & McClelland, 2001). In the experiments in question, subjects are presented with inputs which are combinations of several treatment variables (e.g., combinations of stimuli and backgrounds) and are asked to report on some property of these inputs by choosing among a set of response alternatives. For simplicity consider the case in which there are only two treatment factors, $X_1, X_2$. According to the Morton-Massaro law, response probability ratios factorize into components, each selectively affected by only one of the information sources:

$$\frac{P(R = k \mid X_1, X_2)}{P(R = l \mid X_1, X_2)} = \left( \frac{\eta_{X_1}(X_1, k)}{\eta_1(X_1, l)} \right) \left( \frac{\eta_{X_2}(X_2, k)}{\eta_2(X_2, l)} \right), \tag{1}$$

where the $\eta_1$ are selectively influenced by factor $X_1$ and the $\eta_2$ terms are selectively influenced by factor $X_2$.

Morton (1969) showed that this particular form of separability could be found in a number of experiments examining the effects of context and stimulus information on word identification. Massaro and colleagues have shown that it holds in a remarkable range of experiments in domains such as word and letter perception, object identification, depth perception, audio-visual speech recognition, memory retrieval and recognition of emotions—See Chapter 6 of (Massaro, 1989) for a review.

Note that while the standard notion of separability used in the neurosciences applies to average responses, the Morton-Massaro law applies to entire response histograms. In this paper we investigate the relationship between the Morton-Massaro law and the classic notion of separability of tuning curves used in the neuroscience. We illustrate with an example that that these two notions are unrelated . We then present preliminary results on how the Morton-Massaro law could be used to analyze information integration at the level of single neurons in the visual system.

## 2 Optimality conditions

Movellan and McClelland (2001) explored the conditions under which the Morton-Massaro law is an optimal way of combining information from different stimulus dimensions. They showed that the law is optimal provided one is willing to assume a particular structure of the environment. This assumption, which is loosely known in the pattern recognition literature as *class conditional independence*[1], has been shown to work surprisingly well in a very wide variety of pattern recognition problems (Domingos & Pazzani, 1997). It is thus reasonable to infer that when the Morton-Massaro law, the assumption of conditional independence provides a useful approximation to the structure of the environment. Figure 1 illustrates the concept of class conditional independence. The figure shows the distribution of two stimulus dimensions given three different categories. Each point in the figure is an combination of two stimulus dimensions. The symbols (circles, squares, or crosses) indicate which category each point comes from. Note how the two stimulus categories are roughly independent within perceptual categories (class conditional independence) even though they are non-independent when collapsed across categories.

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[1] More precisely we assume that likelihood ratios factorize, a weaker assumption than class conditional independence.

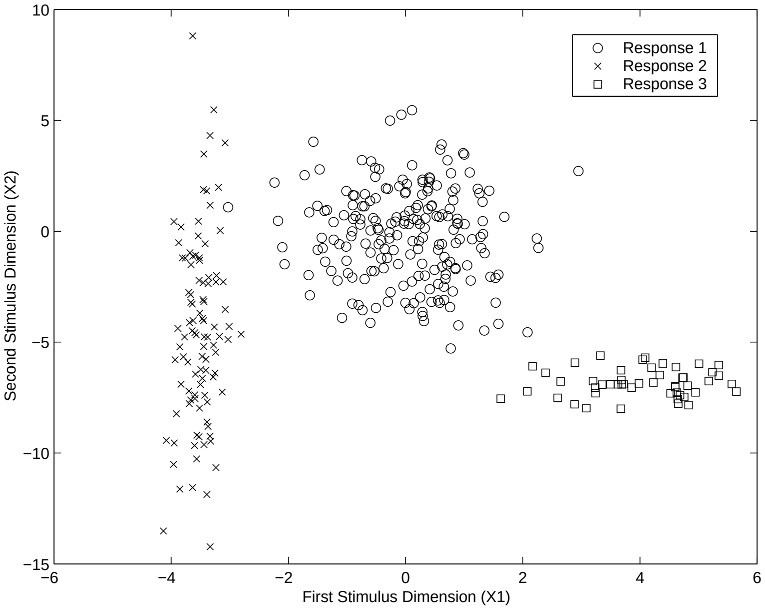

Figure 1: An illustration of the difference between conditional and unconditional independence. Each point represents is a combination of two different stimulus dimensions. There are three different perceptual categories, represented as circles, squares or crosses. The two stimulus dimensions are class conditional independent, even though they are not independent when collapsed across categories.

## 3 Relation to Mean Tune Curve Separability

The classic notion of mean tune curve separability is unrelated to the notion of separability in the Morton-Massaro law. This can be easily illustrated via examples in which one notion of separability holds while the other does not hold. The top row of Figure 2 shows a hypothetical neuron which exhibits the Morton-Massaro law but has non-separable mean tuning curves. For simplicity we divide the neuron's response into three categories: low response, medium response and high response. The ellipses on the Top-Left graph represent the conditional distribution of two stimulus dimensions $X_1$ and $X_2$ given the three different response categories. For example, when the neuron exhibits a moderate response rate then $X_1$ tends to be around 0 and $X_2$ tends to be around 1. When the neural response is low, then just about all possible combinations of $X_1$ and $X_2$ are equally likely. The Top-Right graph shows how the mean tuning curve for $X_1$ changes as a function of $X_2$. For example, the figure shows that when $X_1 = 0$ and $X_2 = -1$ then the average neural response tends to be small. Note how the tuning curve when $X_2 = 1$ is not a scaled version of the curve when $X_2 = -1$ and thus the mean tuning curve does not factorize.

The bottom row of Figure 2 shows a hypothetical neuron which does not exhibit the Morton-Massaro law but has separable mean tuning curves. The Bottom-Left graph shows that when the neuron exhibits a moderate response rate, $X_1$ and $X_2$ are negatively correlated while when the neuron exhibits a high response rate they are positively correlated. This condition is known to violate the Morton-Massaro law. The right side of the figure shows how the mean tuning curve for $X_1$ changes as a function of $X_2$. Since the curves are a scaled version of each other, separability holds.

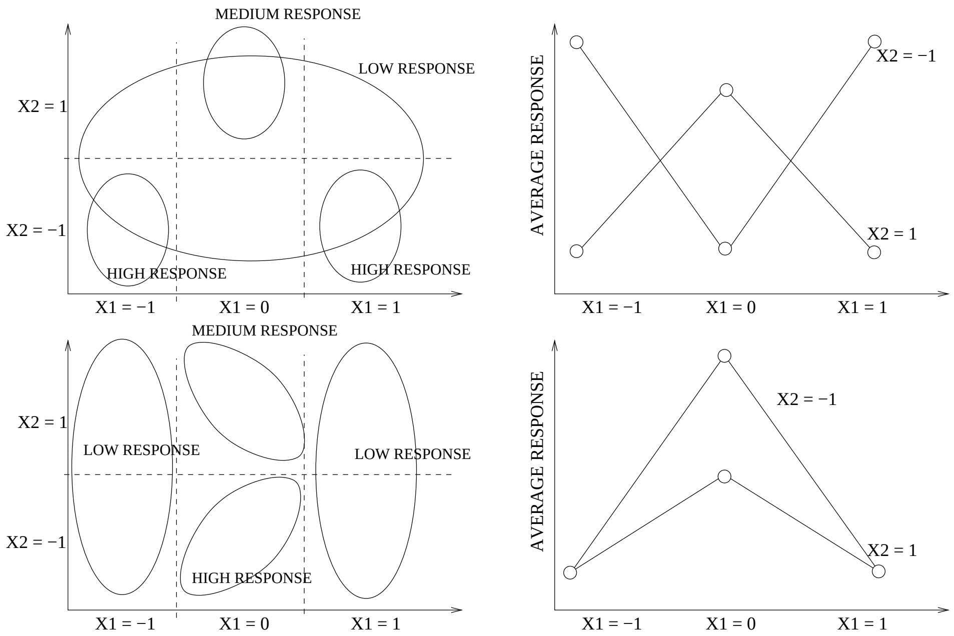

Figure 2: The top row shows an example of a hypothetical neuron with non-separable mean tuning curves and that exhibits the Morton-Massaro law. The bottom row shows an example of a hypothetical neuron with separable mean tuning curves and that does not exhibit the Morton-Massaro law. See the text for an explanation of the Figure.

## 4 Relation to neural circuitry

Movellan and McClelland (2001) showed that in neural network models with feedback connections there is an architectural constrain, which they named "channel separability" which is sufficient for the Morton-Massaro law to hold. Channel separability is defined as follows: First we identify the neurons which have a direct influence on the observed responses (e.g., the set of neurons which affect an electrode). For a given set of response units, the channel for source $X_i$ is defined as the set of units modulated by $X_i$ provided the response specification units are excised from the rest of the network (i.e., conductances to and from the response unit are set to zero). Two channels are called separable if they have no units in common. Channel separability implies that the influences of an information source upon the channel of another information source should be mediated via the response specification units (see Figure 3).

While the models used in Movellan and McClelland (2001) are a gross simplification of actual neural circuits, the analysis suggest that the Morton-Massaro law may be a useful paradigm for the study of information integration in the brain. In particular the analysis suggests that channel separability may be an architectural constraint used by the brain to enforce the assumption of conditional independence while maintaining the advantages of feedback circuitry.

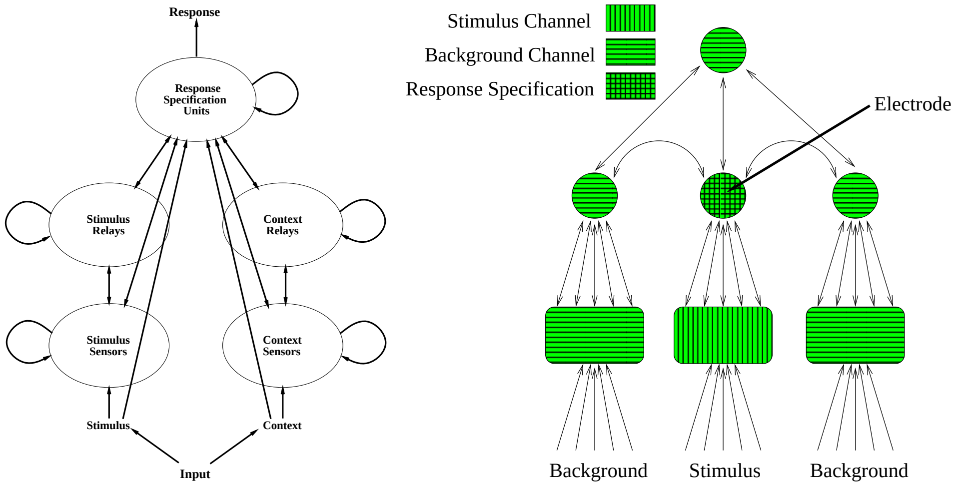

Figure 3: Left: A network with separable context and stimulus processing channels. The stimulus sensor and stimulus relay units make up the stimulus channel units, and the context sensor and context channel units make up the context channel units. Right: The arrows connecting the stimulus to the unit in the center represent the classical receptive field of that unit. External inputs affecting the classical receptive field are called "stimuli" and all the other inputs are called "background". The center unit determines the responses under consideration (e.g., spiking rates of that neuron). In this preparation the stimulus and background channels are separable.

The right side of Figure 3 shows an example of a brain structure with separable channels. In this case the response specification unit is the neuron whose response histogram is being recorded. Note that when the response specification neuron is excised from the rest of the network, the set of units influenced by the stimulus and the set of units influenced by the background are disjoint, i.e., the stimulus and context channels are separable. This particular structure is used in contemporary interpretations of how the context affects the response of neurons to stimuli within their classical receptive fields Thus, the prediction is made that non-classical receptive field effects may adhere to the Morton–Massaro law, i.e., the spike rate histograms should factorize into terms selectively controlled by the stimulus and the background. We performed a pilot experiment to explore this prediction. Our main goal was to explore the possibilities of the Morton-Massaro law as a new paradigm to study information integration in neural systems.

## 5 Experiment

**Methods:** Extracellular recordings were collected in primary visual cortex (V1) of two macaque monkeys. The monkeys were awake and fixated a small spot on the screen. Receptive field locations were at 2-6 degrees of visual angle from the fixation spot, in the lower hemisphere of the visual field. Once a neuron was isolated, its receptive field properties (location, size, orientation selectivity etc.) were determined using flashed and moving bars of different size, orientation, and color. Stimuli were squares of color, diameter twice as large as the receptive field. They were presented for 500 ms, while the monkey was fixating. Data were collected for a total of 77 neurons.

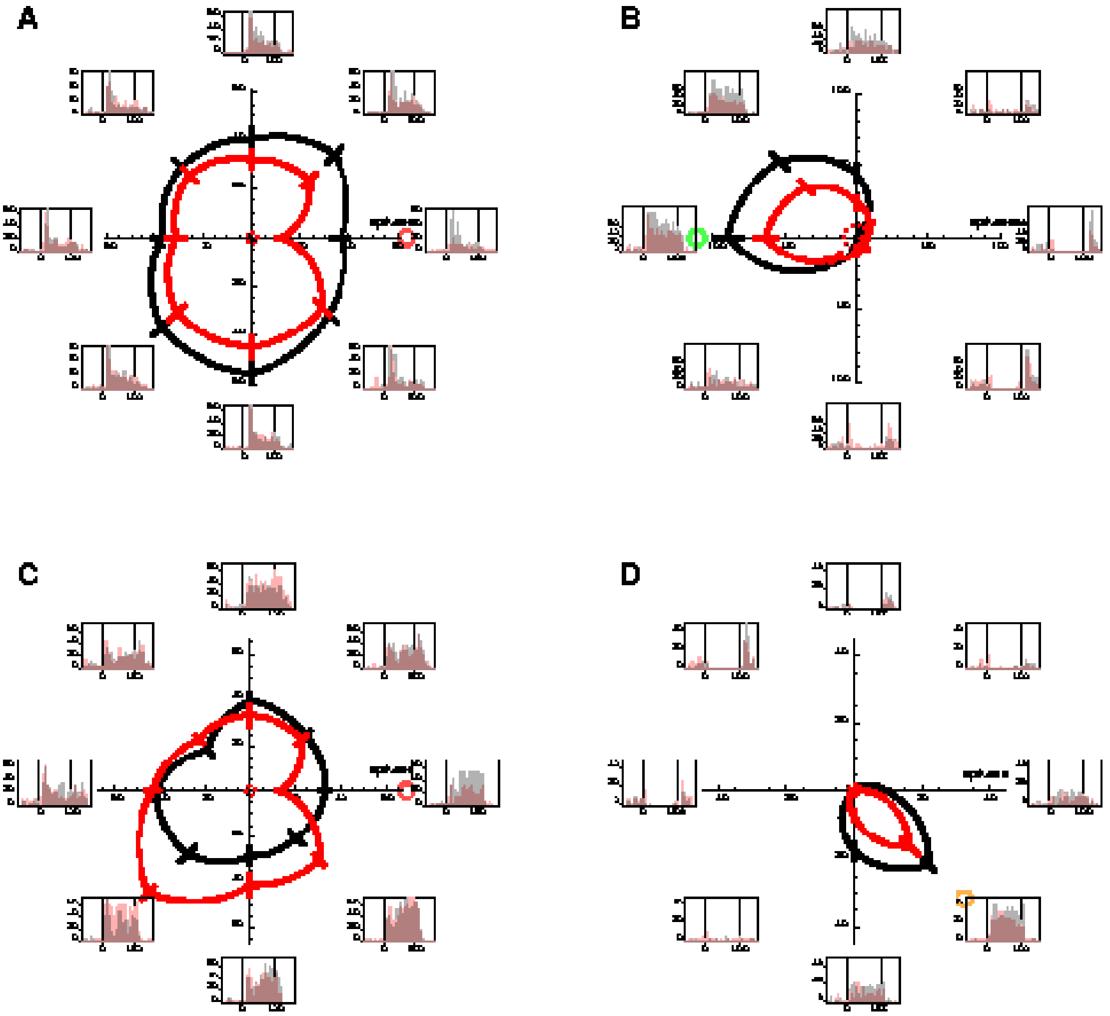

Figure 4: Effect of the stimulus and background on the chromatic mean tuning curves of 4 neurons. The thick red and black lines show mean responses in the isoluminant plane (x axis: L-M cone variation; y axis: S cone variation) for the two background conditions. Black: gray background; Red: colored background; the color of the background is indicated by a small circle in each plot showing its direction in color space. The 8 boxes around each tuning curve shows the response histograms of the neuron for colors on the region in color space occupied by that box.

**Stimuli:** Stimuli were color squares, twice as large as the receptive field, presented at the receptive field location for 500 ms. The animal adapted to a homogeneous gray background (luminance 48 cd/m$^2$). Stimulus colors were defined in a color space similar to those introduced by MacLeod and Boynton (MacLeod & Boynton, 1979) and Derrington Derrington, Krauskopf, and Lennie (1984), with coordinate axes corresponding to (L-M), S, and (L+M+S) variation, measured relative to the values at the origin. Stimulus colors were chosen from a set of 15 predefined colors. One of these colors was the color of the gray background. The other colors had a fixed color contrast (0.15) with respect to the background (distance from origin of color space) but corresponded to modulation in different directions in color space. Eight of the colors were isoluminant with the background, two were purely achromatic, and four were pure L- and M-cone stimuli (increments and decrements), respectively. In one condition, the stimuli were presented on the gray background. In a second condition, the color of the background changed during stimulus presentation (i.e., for 500 ms) to a different color. This color was isoluminant with the gray background, was in the direction of a stimulus color to which the cell showed a response, but was of lower contrast (0.1) than the stimulus colors. Thus, the stimuli were presented in two different contexts: Either on the gray background, or on a colored background. All stimulus conditions (stimulus and background colors) were presented in random order.

The response of a cell to a stimulus was measured by the distribution of the number of spikes fired in a 100 ms time window starting 50 ms after stimulus onset. We chose this limited time window because color tuning was usually more pronounced in the first response phase as compared to later periods of the response. The data were organized into histograms with 10 bins each: 0 spikes, $\cdots$, 8 spikes, and 9 or more spikes. On average there were 20 trials per histogram.

Figure 4 shows four examples for background color affecting chromatic tuning. The small colored circles in each subplot denote the color direction of the background that was chosen for each of the four experiments. While the effects can vary for different cells, in each case there is a response reduction for stimuli in the direction of the colored background.

## 6 Analysis

There were 15 stimulus conditions, 2 background conditions, and 10 response alternatives, one per bin in the spike histogram. In this case, the Morton-Massaro model requires $(10-1)(15+2-1) = 144$ parameters. For each neuron there is a total of 30 histograms, each with (10-1) independent probability estimates, thus there is a total of 270 independent probability estimates per neuron. It would not be surprising for a model with this many parameters to fit the data well. Indeed the median correlation between obtained and predicted histograms was above 0.99. Instead we tested the Morton-Massaro law on a generalization task. For each neuron, one of the 30 experimental conditions was left out and the 144 parameters of the Morton-Massaro law were trained on the 29 experimental conditions left. After training, the Morton-Massaro law produced a prediction for the histogram left out and the prediction was compared to the actually obtained histogram. This process was repeated 30 times per neuron, each time leaving a different condition out. It is crucial to notice that when tested on generalization tasks models with a large number of parameters are actually at a disadvantage. Simple models with a small number of parameters tend to generalize better than more complex models.

For each neuron we computed the correlation coefficient in the generalization task between the predicted and obtained histograms. The median correlation was 0.617

(best= 0.95, worst =0.11). To get a sense of the expected goodness of fit in neurons for which the Morton-Massaro law holds, we performed the following analysis. For each neuron we computed the histograms predicted by the Morton-Massaro law. We then sampled from these histograms as many times as there were samples from the original neurons. This procedure gave us data from simulated neurons which, were it not for the effects of random sampling, would perfectly follow the Morton-Massaro law. We then fitted the Morton-Massaro law to the simulated data following the same procedure as with the empirical data. In this case the median correlation was 0.7037 (best= 0.94, worst = 0.11). Thus, the Morton-Massaro law provided a goodness of fit close to the upper limit achievable, given the effects of random sampling.

## 7 Discussion

The goal of this paper was to introduce a new notion of separability seldom used in the neuroscience community. The work presented here is exploratory and clearly more data is needed to fully evaluate it. However it is already clear that the Morton-Massaro law may provide a promising new framework to analyze information integration in the brain. The preliminary results of our experiment are consistent with the idea that the effects of stimulus and background on response histograms of simple neurons in V1 are separable in the Morton-Massaro sense. This suggests that structural organizations in terms of classical receptive fields modulated by the background via lateral connections may be nature's way of implementing the Morton-Massaro law.

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