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## SUMMARY

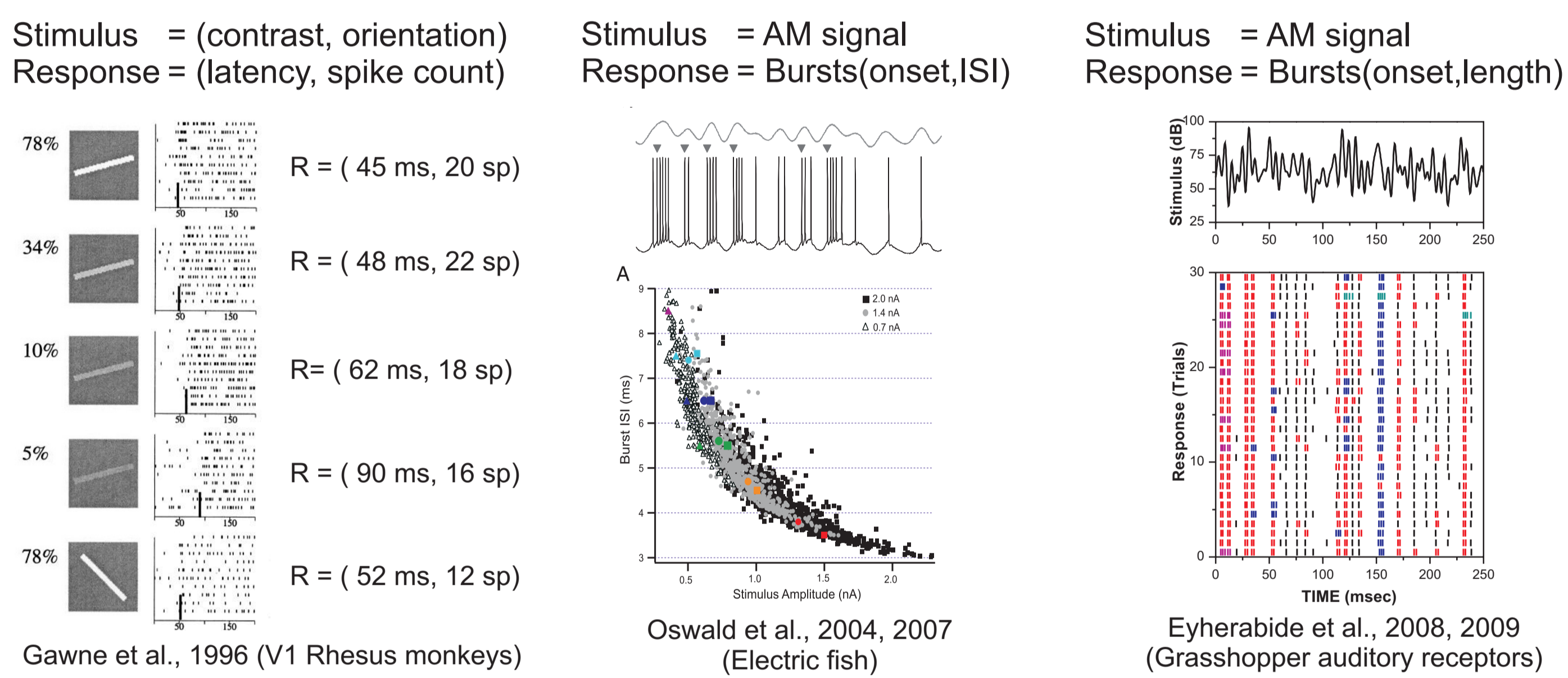
Sensory stimuli are usually composed of different features (the **what**) appearing at irregular times (the **when**). Intuitively, the **what** and the **when** are assumed to be encoded in the identity and timing of the elicited patterns, respectively. However, this intuitive view may be inaccurate, as for example, in latency codes. In addition, the **what** and the **when** might also be correlated in the stimulus, i.e. they might not be independent aspects.

In this study, we establish the relation between the **what** and the **when** in the stimulus with the information conveyed by the timing (**time information**) and the categories (**category information**) of spike patterns. A formal framework is developed to assess the conditions under which the information about the **what** and the **when** coincide with the **time and category information**, as well as the departures from this ideal case. Finally, we study the capabilities of different neural codes to represent the **what** and the **when** in the neural response.

## 1-PATTERN-BASED CODES

The neural response can be described in different ways (see left) such as a sequence of spikes or a set of parameters (aspects). Indeed, the set of parameters is a reduced representation of the neural response.

In general, different aspects of the neural response are associated with different aspects in the stimulus. For example, Gawne et al. (1996) have associated the latency and spike count of the response with the contrast and orientation of bars, respectively.



In realistic conditions, different sensory stimuli (features) arrive at random times. Previous work has shown that, in the neural response, stimuli may be encoded as a sequence of spike patterns (Oswald et al., 2004, 2007; Eyherabide et al., 2008, 2009). Intuitively, different sets of patterns (categories) are associated with **what** stimulus feature happened, while their time positions are related with **when** the stimulus features occurred.

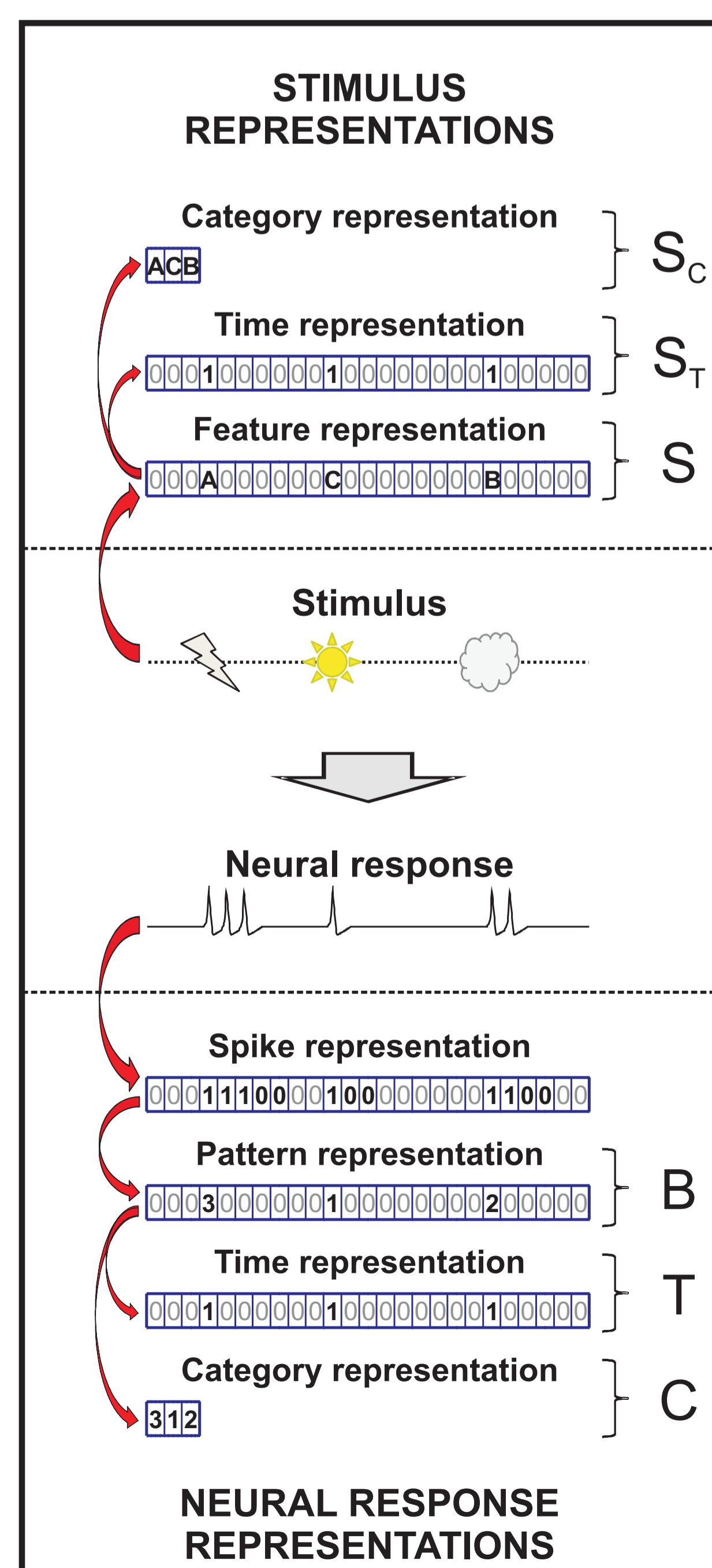
## 2-TEMPORAL AND CATEGORICAL ASPECTS

In this analysis, the stimulus is a sequence of features (**middle**). Each feature elicits a spike pattern in the response.

The stimulus may be represented as a sequence of symbols (**S**), each one representing a different feature category (top). The **what** (**S<sub>c</sub>**) is represented by preserving the symbols while discarding their timing. Conversely, the **when** (**S<sub>t</sub>**) is symbolised by preserving their timing while discarding the differences among symbols.

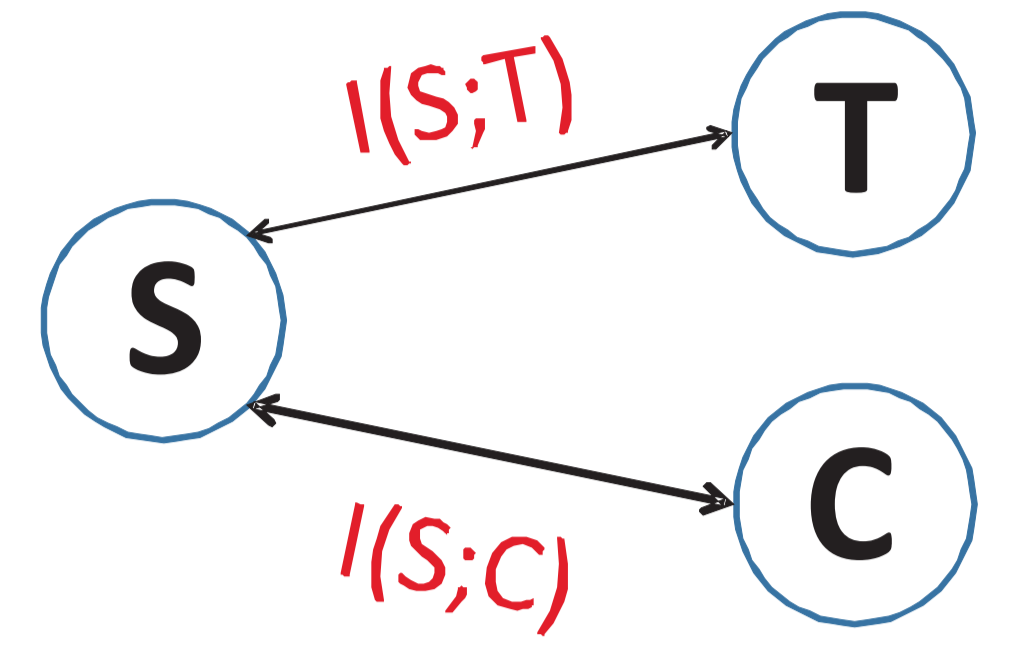
In the same way, similar patterns can be grouped into categories, so that the neural response is represented as a sequence of pattern categories (**B**). In this representation, the timing and categories of patterns are preserved (bottom). The timing of patterns is represented by ignoring differences among categories (**T**), whereas their categories are represented by ignoring their detailed timing (**C**).

These formal representation of the stimulus and the neural response allow us to analyse the correspondence between the timing and categories of spike patterns and stimulus features.



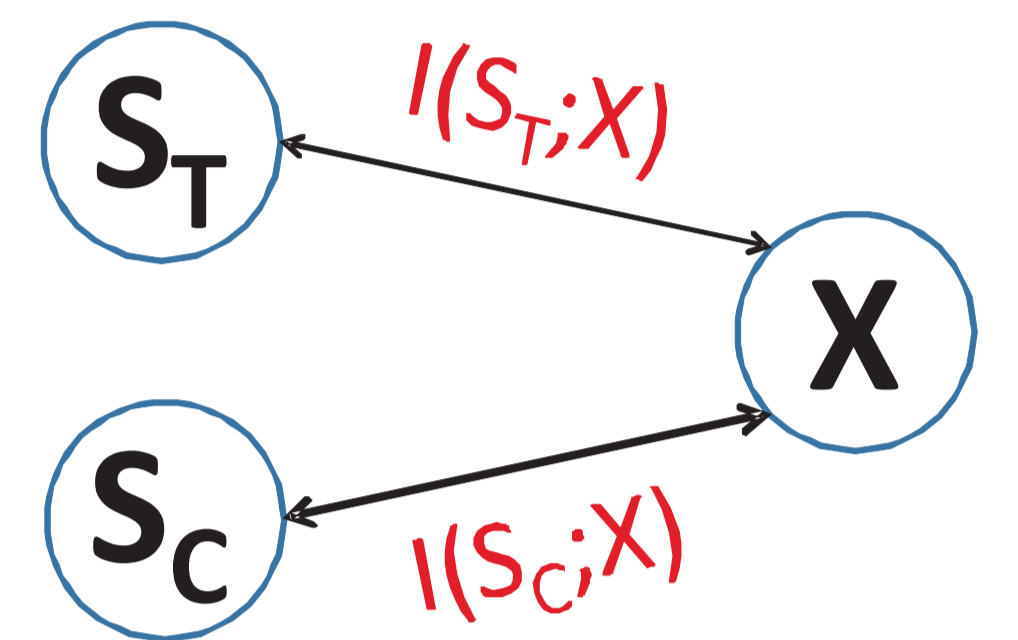
## 3-TIME AND CATEGORY INFORMATION

Different aspects of the neural response may convey information about the stimulus. Here, we define the **time information** as the information  $I(S;T)$  conveyed by the timing of patterns **T**. In the same way, the **category information** is the information  $I(S;C)$  provided by the categories of patterns **C**.



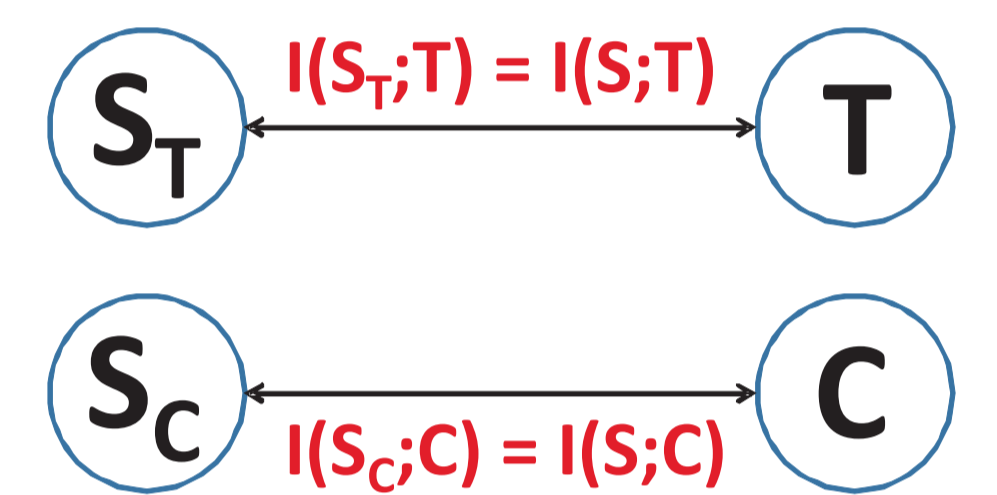
## 4-INFORMATION ABOUT WHAT AND WHEN

Any aspect **X** of the neural response may convey information about the timing of features (**S<sub>t</sub>**), as well as their identities (**S<sub>c</sub>**). The information  $I(S_t;X)$  represents the information conveyed about the **what** in the stimulus, whereas the information  $I(S_c;X)$ , the one conveyed about the **when**.



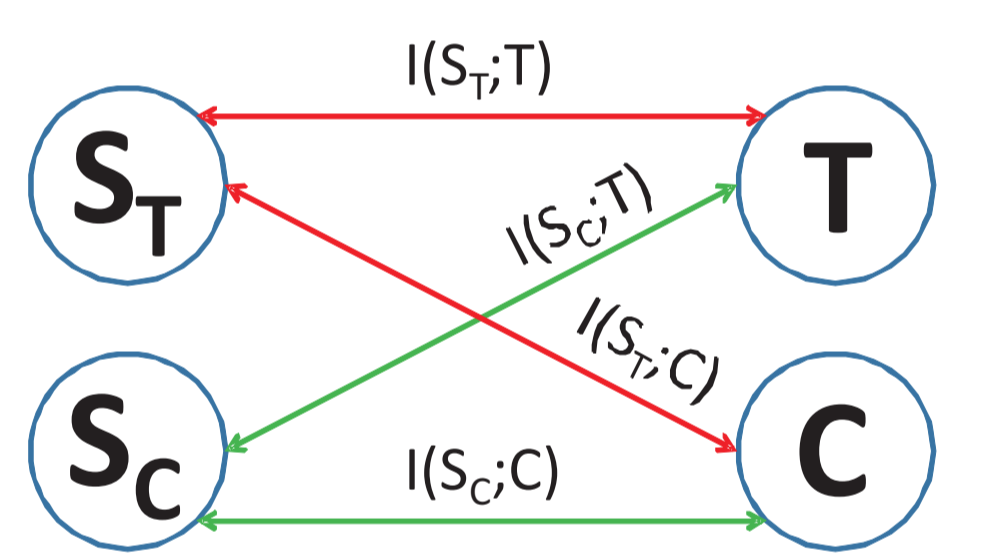
## 5-INTUITIVE ROLE OF PATTERNS

Intuitively, the pattern categories encode **what** stimulus features happened, whereas their timing encodes **when** the features occurred. We formally express this by defining an ideal feature extractor as shown in the left figure. In this system, any information on the **what** (the **when**) conveyed in the timing (categories) of patterns is completely redundant with the information conveyed about the **when** (the **what**).



## 6-THE GENERAL CASE

In general, the timing of patterns **T** may convey information on the **what** ( $I(S_t;T)$ ) and the **when** ( $I(S_c;T)$ ), which might be synergistic or redundant. For the pattern categories **C**, analogous considerations hold. Thus, the **what** and the **when**, as well as the information provided about them, might not be separable concepts.



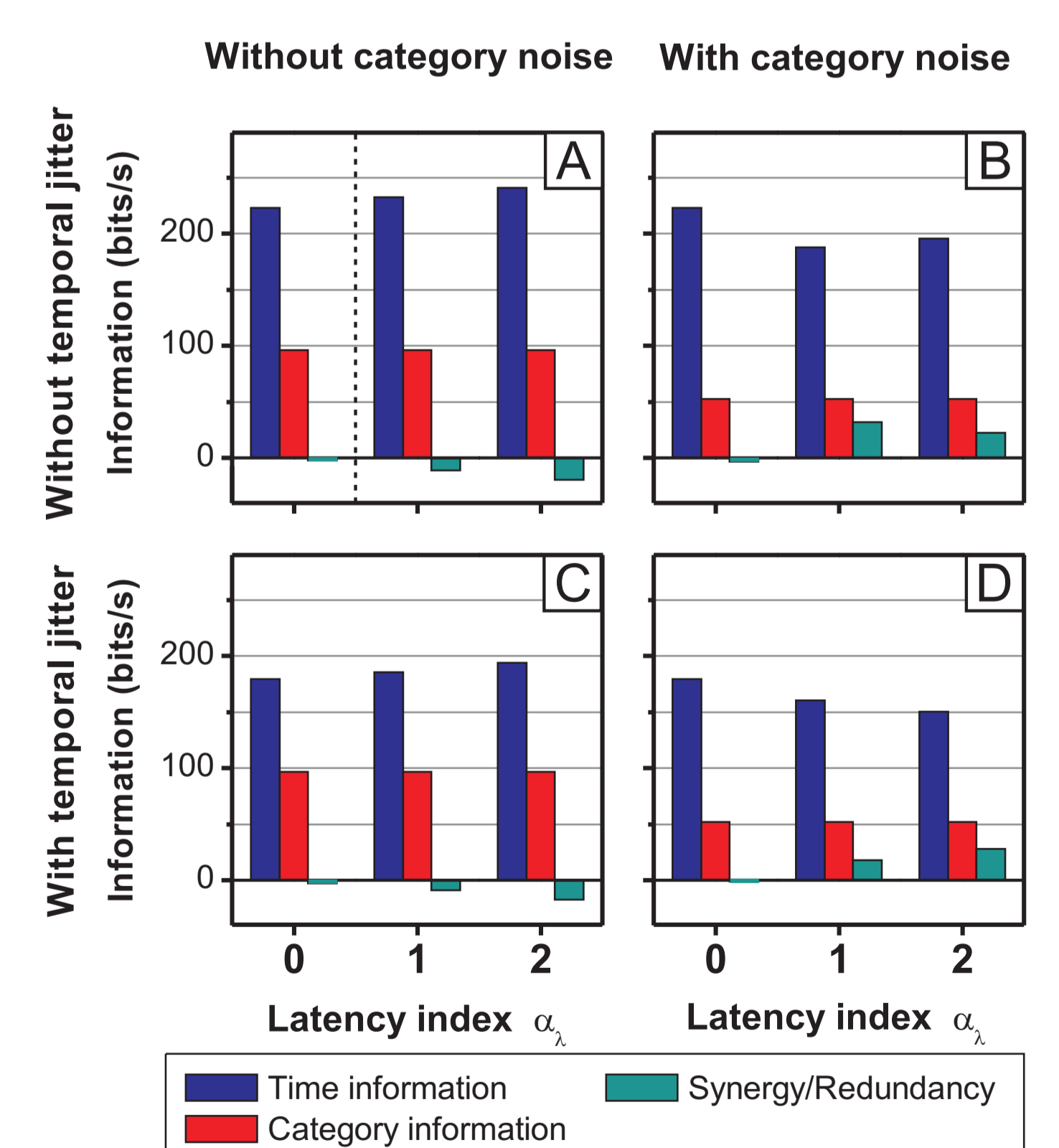
In this general picture, one can also assess whether all the information about the **when** (**what**) is contained in the timing (categories) of patterns **T** (**C**), i.e. whether  $I(S_t;B) = I(S_t;T)$  (whether  $I(S_c;B) = I(S_c;C)$ ).

## 7-EXAMPLES

The figure shows a system that encodes four stimulus features with different patterns, which may have different latencies. For the case with no latency, the system is an ideal feature extractor, and for the noiseless case, the time and category information coincides with the time and category entropy in the stimulus. Adding noise diminishes the transmitted information, such that temporal (category) noise reduces the time (category) information.

On the other hand, a latency code where the latency depends on the pattern category is not an ideal feature extractor. In panel A, it is shown that time information is not upper bounded by the time entropy of the stimulus.

Indeed, in this case, due to the fact that latencies connect the timing and the category of patterns, time and category information are related, and the nature of the noise shapes the synergistic or redundant aspect of the link between them.



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