

Percept and the single neuron

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Work reported in this issue has derived the long-sought analytical link between neural readout weights and choice signals in the standard model of perceptual decision making. This fresh perspective opens the door to experimental assessments of percept formation from the activity of sensory neurons.

Decades of research have taught us that our mental lives are reflected in the activity of neurons. Yet when we perceive an uncertain stimulus—was that a friend hustling by on the other side of the street?—which neurons are really implicated in the formation of the mental percept? When deciding on whether to shout “hello” or not, do our brains exploit all the sensory information available at the neural level? A first answer to these questions was given about 15 years ago, with the surprising finding that the activity of single sensory neurons can show detectable traces of a visual percept¹. When a monkey has to make a decision based on weak or nonexistent visual information, small fluctuations of single-neuron activity in the visual cortex are slightly predictive of the animal’s final choice. However, this observation alone does not tell us whether such neurons actively participate in forming the animal’s percept or are simply influenced by it. In this issue of *Nature Neuroscience*, Haefner *et al.*² report significant conceptual progress in resolving this long-standing puzzle.

The authors studied the ‘standard model’ of percept formation in the context of a two-alternative forced-choice task (Fig. 1a): a subject is presented with a set of stimulus values s with little informative power, such as a noisy set of horizontally moving dots, and must decide whether $s > 0$ (overall motion toward the right) or $s < 0$ (overall motion toward the left). Neurons in visual cortex fire whenever the physical stimulus is close to their preferred stimulus. The relative strength of their firing can be interpreted as a vote for their preferred

stimulus. In the standard model, the animal’s percept P , meaning its internal estimation of the stimulus s , is formed by weighting the firing rates r_k with ‘readout’ weights β_k and summing them across the population. The readout weights capture the nature of percept formation in the task: if a neuron’s readout weight is zero, it does not contribute to the percept; if the weight is nonzero, it contributes, however weakly. Finally, the animal’s binary choice in each trial is computed by asking whether $P > 0$ or $P < 0$.

To determine each neuron’s contribution to the visual percept, we therefore need to figure out the readout weights. Even though we can only monitor the neural activity and the animal’s choice, this goal seems reachable: if a neuron’s readout weight is large, any trial-to-trial variability in its firing rate will influence the animal’s decision. This influence can be measured by the choice probability (CP), the probability of correctly predicting the animal’s choice in each trial based on the neuron’s activity (Fig. 1b). Unfortunately, however, a large CP value does not automatically imply a large readout weight. Imagine a neuron that receives synaptic inputs from a second neuron with a large readout weight (and thus a large CP value). Through this input, the first neuron’s activity will partly reflect that of the second, leading to a substantial CP value. For all we can tell, however, the first neuron’s readout weight may very well be zero.

More generally, researchers have noted that if the activity of pairs of neurons covaries from trial to trial—that is, if neural firing rates are correlated—then it is nontrivial to discern the link between CP values and readout weights. Although several previous studies have explored this link for a few specific scenarios using computer simulations, Haefner *et al.*² now provide the general solution, by deriving the link between CP and readout weights analytically. The authors’ main result

is the following: a neuron’s choice probability depends on the sum over all of its firing rate covariances with other neurons, C_{kj} , weighted by their respective readout weights, β_j :

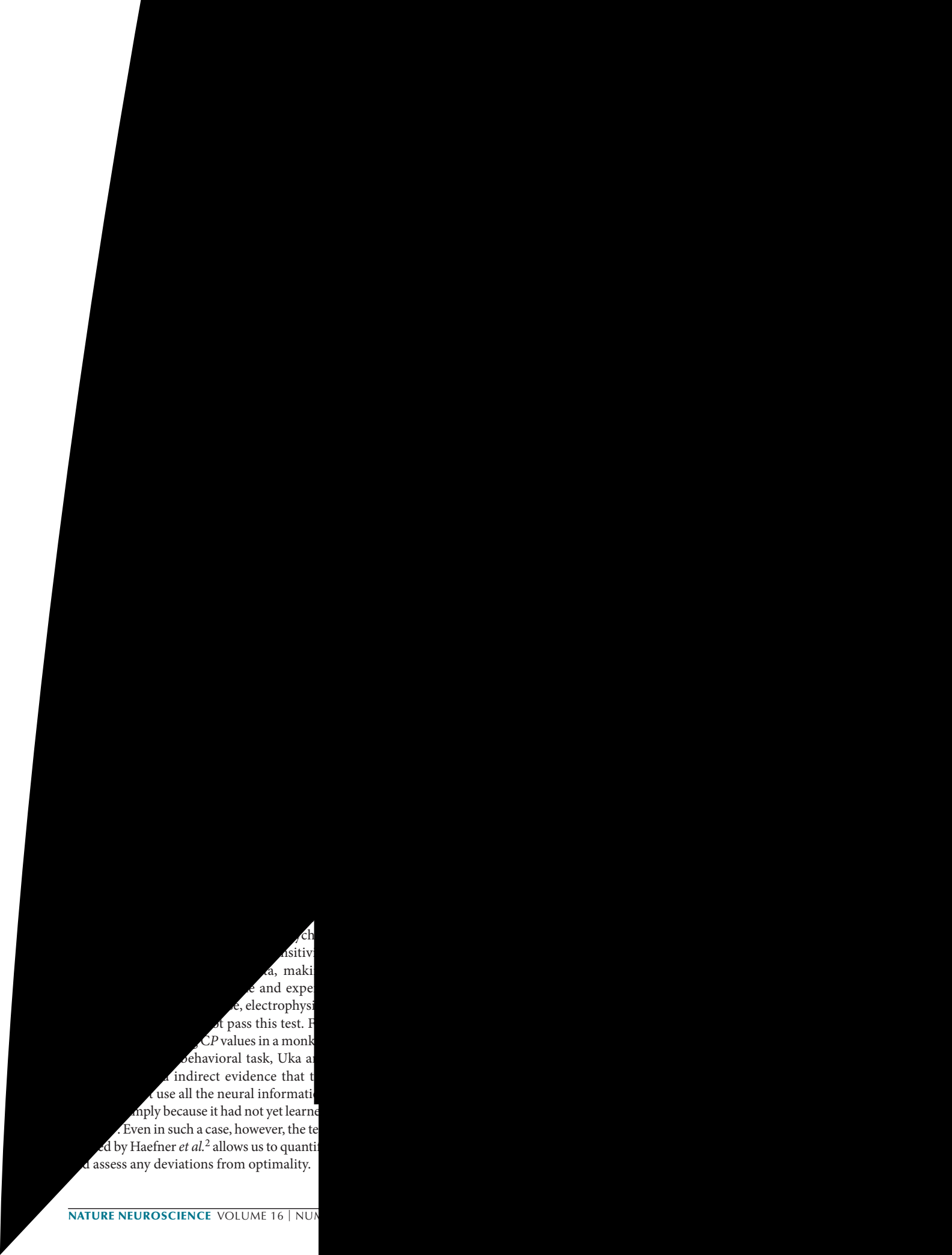
$$CP_k - \frac{1}{2} = \alpha \sum_{j=1}^n C_{kj} \beta_j \quad (1)$$

where α is a normalization factor. This formula (which is only approximate; the authors also supply an exact version) provides the long-sought relationship between choice probabilities and readout weights in the presence of noise correlations (Fig. 1c). It essentially relies on the matrix product $\mathbf{C}\boldsymbol{\beta}$, which is simply the trial-to-trial covariance between neural activities r_k and percept P in the standard model. Although it has been intuitively clear that CP measures something along these lines, Haefner *et al.*² now give mathematical grounding to this intuition.

Obtaining the readout weights β_k may seem straightforward now: we need to solve equation (1) by inverting the covariance matrix, \mathbf{C} . Unfortunately, that is impossible: because experimenters record from only selected ensembles of neurons for a finite number of trials, the covariance matrix cannot be fully determined. It is known only through samples of its elements C_{kj} , and with finite accuracy. How, then, are we to concretely exploit the beauty of the CP formula? Haefner *et al.*² provide two insights into this question.

The first insight—probably the more useful in practice—exploits the concept of optimality. Ideally, the organism should choose the readout weights $\boldsymbol{\beta}$ optimally, to maximize the vector of sensitivity, or signal-to-noise ratio (SNR), of percept P . This optimal choice, Fisher’s linear discriminant, is well known from the statistical literature and relies on the inverse of covariance matrix \mathbf{C} . As a result, when the optimal readout weight vector $\boldsymbol{\beta}^{(\text{opt})}$ is used, matrix \mathbf{C} is eliminated from equation (1). Better, the exact expressions of $\boldsymbol{\beta}^{(\text{opt})}$ and

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