SUPPLEMENTARY INFORMATION

Processing Bias: Extending Sensory Drive to Include Efficacy and Efficiency in Information Processing

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Box S1. Testing processing bias

Testing processing bias will require disentangling the different types of judgments influencing preference (i.e., processing, emotional, and cognitive evaluations). This can be challenging with natural communication signals where pre-existing bias and emotional or cognitive evaluations may coevolve and ultimately align to jointly reinforce preference (see main text). Yet, carefully designed behavioral experiments could reveal the effect of processing bias on preference. For example, a first approach could measure how preference changes when manipulating the efficacy and efficiency of information processing while keeping emotional or cognitive evaluations constant, or manipulating these judgments from positive to negative. Finding that preference for a stimulus remains unchanged or increases while increasing its efficacy (e.g., color contrasts), while simultaneously increasing its negative emotional value, would reveal an influence of processing bias in preference (see also [1]). A related approach could analyze the difficulty of reversing a preference (e.g., the number of trials necessary to achieve reversion) by manipulating emotional and cognitive evaluations at different levels of efficacy and efficiency; reversal should be more difficult for highly effective or efficient stimuli.

Manipulating emotional and cognitive evaluations requires associative learning, for example with classical conditioning, e.g., training an animal with a shock or other aversive stimulus to increase negative emotional evaluation. Manipulating processing efficacy is usually achieved in psychology using subliminal priming (e.g., [2]). Subliminal priming reveals processing bias because the duration of exposure is too short to allow other judgments to take place. An alternative to manipulating efficacy is to exploit naturally occurring signal variation. This approach is even better suited for efficiency. Efficiency is difficult to manipulate in a controlled setup, but variation can be quantified in natural signals (see Box S2).

Box S2. Estimating processing efficiency in visual communication

Efficiency characterizes information processing at low metabolic cost. Empirically estimating efficiency thus requires measuring the energetic cost of processing and comparing it between alternative processing strategies [3], or to the same strategy applied to structurally different but functionally similar stimuli (e.g., the sexual signals of different males in a population). In lab studies with primates and rodents, the standard approach is to analyze functional connectivity using brain imaging, which estimates whether the distance travelled by information throughout different brain areas is minimized [4]. The study of brain functional connectivity is limited to model species, however, and thus most studies in evolutionary biology would rely on more indirect methods.

Efficiency can be estimated indirectly with statistics that describe spatial redundancy in stimuli. The most well-studied and commonly used statistics are spatial auto-correlation and scale invariance, which can be estimated using Principal Component Analysis (PCA; [5]) for the former, and the 1/f spectral slope [6, 7] or fractal dimension D [8, 9] for the latter. These statistics indicate the efficiency of information processing because animal perceptual systems have evolved to reduce spatial redundancies occurring in natural environments. Thus the most efficiently processed stimuli have spatial statistics matching most closely those of natural environments.

Processing efficiency also can be estimated using models of perception and cognition. Neurons selective to locally oriented line segments (as found, for example, in the primary visual cortex of mammals or in the tecto-isthmic area in fishes) can be computationally modeled using simple Gabor filters [10], or by training a set of basis functions (each one modeling one neuron) to encode images of visual stimuli as sparsely as possible [11]. Then, efficiency is modeled by estimating the sparseness of the neuronal responses to a stimulus image [12-15]. Here, sparseness is measured as the proportion of neurons activated (i.e., with a non-zero response), or the kurtosis of the response distribution [14]. One limitation to this approach, however, is that efficiency is estimated at one level of neural processing only.

Convolutional Neural Networks (ConvNets) –the tool of choice for deep learning and artificial intelligence– are a promising approach for estimating efficiency throughout the processing pathway. Although the primary goal of ConvNets is not to reproduce the mechanisms behind animal perception and cognition, the different layers of a ConvNet have been found to accurately model multiple levels of neuronal processing [16]. ConvNets could thus be used to compare efficiency across early perceptual and higher cognitive processing by calculating the sparseness of neuronal activation at each layer of the network. Finally, computer scientists have recently used information theory to study the efficacy of information transmission across ConvNets [17]. By simultaneously estimating the efficacy and efficiency of processing a given stimulus, future research should be able to address how these two components interact to influence preference and the evolution of signal designs.

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