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

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Box S1. How animals process information
Box S2. Testing processing bias
Box S3. Estimating processing efficiency in visual communication

Box S1. How animals process information

Information processing describes the mechanisms that produce a behavioral output from a stimulus input. For most behavioral outputs, animals do not simply reflexively respond to external events, or stimuli; rather, they build meaning by extracting and transforming information from these stimuli. Information processing requires three brain systems: perception, cognition and emotion (**Figure S1,** [1, 2]).

Perception is the foundational system of information processing and its function is to build an internal representation of the external world. This is achieved by first converting a stimulus into a neural code, and then by hierarchically extracting information from this code. The extracted information is increasingly complex (e.g., simple line segments in early visual stages and entire objects in higher stages) and global (e.g., neurons respond to stimuli spanning the whole visual field only in higher stages; [3]). Cognition is the brain system where highly integrated processes occur. It helps build a meaningful representation from perception by providing knowledge about the environment, which notably requires memory. Information processed by perception and then by cognition gives rise to a cognitive evaluation of a stimulus (along a continuum of negative to positive) that indicates the costs or benefits of the stimulus for the receiver.

The third brain system, emotion, also gives rise to an evaluation, consciously experienced or not, along a continuum of negative to positive, reflecting the receiver's interaction with the environment [4]. For example, fear of predators is a negative emotional evaluation that reflects a highly costly interaction. Like its cognitive counterpart, the emotional evaluation influences preference, and the behavior [5]. The emotional and cognitive evaluations have nevertheless distinct neurochemical bases, and most importantly they differ in the timing of their effects, the emotional evaluation developing earlier during information processing than the cognitive evaluation [6].

Emotions are determined by affects, which play an important role in informing the receiver about the rate of progress toward a goal, and reward it for successful progress [7]. The core rewarding affect is pleasure [8]. In addition to mediating the emotional evaluation, affects also have a meta-informative function: they evaluate progress in information processing [7] and thereby help regulate the process of information gathering. Depending on how pleasurable information processing is, the receiver will continue the same processing strategy, change its strategy, or stop processing information [7].

The cognitive and emotional evaluations, and a misattributed meta-informative evaluation (see Section 4) are judgments that influence preference at varying degrees depending on the behavioral task. For example, when facing a predator, the emotional evaluation can override other judgments to enforce a fast and adaptive response ("emotional behavior"; [4]). However, in most communication systems, including in animal courtship, the relative contribution of these different judgments is an unexplored research area.

The tri-partite model of information processing is a highly simplified description of how animal brains process information. Yet it has two main advantages that make it useful for evolutionary biology. First, it excludes brain processes that are still hotly debated among cognitive scientists, such as the relative importance of feedback interactions between cognition and perception [9]. Second, the model likely applies to most if not all brained animals. Even tiny brains such as those of insects are capable of complex cognitive operations (reviewed in [10]) and emotions. Compared to cognition, non-human emotions have been historically more controversial, but interest in their study has increased in recent years, with the development of experimental frameworks for their analysis [4, 11]. For example, using an experimental approach similar to those used in humans to study pessimism and optimism (an 'half-full vs. half-empty glass' approach), a recent study found that bees who experienced a punishing or a rewarding event were more likely to subsequently respond negatively or positively, respectively, to an ambiguous task [12]. As in humans, these animal emotions are modulated by affects [12], which also monitor the dynamics of information processing [13].
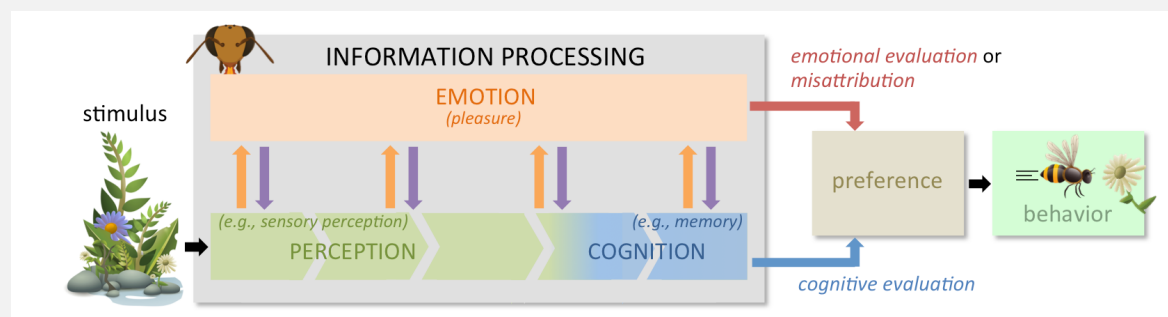

Figure S1. Information processing in animal brains. The information conveyed by a stimulus (e.g., a flower) is processed by perceptual and then cognitive neurons of the receiver (e.g., a bee), leading to a cognitive evaluation of the costs and benefits of the interaction outcome (e.g., quantity of nectar; blue arrow). Along the processing pathway, pleasure is triggered when processing is effective or efficient (e.g., conspicuous flower; orange arrows). This pleasure could contribute to a fast emotional evaluation of the costs and benefits of interacting with the signaler or of the direct energetic benefits of processing an efficient stimulus (red arrow). Alternatively or in addition, pleasure can result from evaluating progress in information processing and thereby help regulate the process of information gathering [7](violet arrows). Because the receiver is not aware that pleasure is triggered by efficient processing, by default s/he misattributes it to the stimulus, which may bias preference toward this stimulus (red arrow).

Box S2. 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 [14]). 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., [15]). 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 S3).

Box S3. 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 [16], 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 [17]. 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; [18]) for the former, and the 1/f spectral slope [19, 20] or fractal dimension D [21, 22] 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 [23], or by training a set of basis functions (each one modeling one neuron) to encode images of visual stimuli as sparsely as possible [24]. Then, efficiency is modeled by estimating the sparseness of the neuronal responses to a stimulus image [25-28]. Here, sparseness is measured as the proportion of neurons activated (i.e., with a non-zero response), or the kurtosis of the response distribution [27]. 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 [29]. 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 [30]. 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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