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Concepts, goals and the control of survival-related behaviors

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Scientists have long studied the actions that impact basic survival in various domains of life, such as defense, foraging, reproduction, thermoregulation, and so on, as to reveal the nature of emotion. Each domain is characterized by a repertoire of distinct actions, and each action is presumed to be caused by a dedicated neural circuit, called a *survival circuit*. Survival circuits are said to be triggered by sensory events in the world, producing a range of actions from obligatory, stereotypic reflexes to more flexible, deliberate responses. In this paper, we consider recent evidence from behavioral ecology that even so-called 'reflexes' are better understood as purposeful, flexible actions that unfold across a range of temporal trajectories. Reflexes are highly context-dependent and tailored to the requirements of the situation. We then consider the neuroscience of motor control, which suggests that motor actions are *assembled* by neural populations, not *triggered* by simple circuits. Finally, we consider the value of these suggestions for understanding both species-general and species-specific contributions to emotion.

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What knowledge informs us about the nature of human emotion? The motivational states and functional organization of behaviors closely linked to survival across species would seem to be a natural entry point to this complex question. Accordingly, some scientists propose that emotions evolved long ago to ensure survival during defense, foraging, reproduction, thermoregulation, and fluid intake, such that humans and many non-human animals should share the neural circuits for emotion (or at least some types of emotion [1]). In this view, emotions are assumed to be species-general — fundamentally conserved states that cause species-specific actions. For example, rats are assumed to be fearful when they protect themselves from a predator and flies are assumed to be angry when they attack each other. An emotion state is thought to trigger one of several distinct actions, and each action is thought to be executed by a dedicated neuronal apparatus. Discovering the brain basis of emotions, in this view, de facto means carefully mapping the circuitry that controls survival-related behaviors. Consider the domain of defense (i.e. fear), for example, when an animal must protect itself or its offspring from a potential threat. Various taxonomies of defensive behaviors (i.e. fear) have been proposed, organized by type of threat [2], proximity of the threat [3], or proposed computations [4]. These taxonomies differ in various ways, but share a common assumption: that a mammalian brain contains some number of innate, dedicated circuits — fear circuits — each of which triggers a fixed reaction pattern such as freezing, flight or defensive aggression when activated by the sensory features of a threat, such as a predator. From this perspective, fear is a specific adaptation associated with a specific state caused by specific neural circuitry.

An alternative account proposes that the circuitry for emotional instances is assembled by a brain as needed via the interplay of evolved mechanisms, some that are species-general and others that are species-specific. The circuitry that controls survival-related actions — *survival circuits* — is not assumed to be the circuitry for emotion, and therefore is only one ingredient in making human emotions. As a consequence, understanding the brain basis of emotion requires more than just the careful mapping of the circuitry that supports survival-related action: it also requires understanding the neurobiology of how these actions and their sensory consequences are made meaningful as emotions in the brain (e.g. [5–10]). Taxonomies make an appearance in some versions of this approach as well. One influential taxonomy, for example, assumes that defensive behaviors can be organized along a continuum of flexibility and control, anchored at one end by defensive reflexes, which are said to be executed in an obligatory, rapid manner, with little variation from instance to instance, and at the other end by flexible, goal-directed actions that result from forecasting future outcomes, with fixed action patterns and defense habits falling somewhere in between [11]. In this view, animals (including humans) deal with threats flexibly because they have a repertoire of behavioral options to choose from, each with its own specific circuitry. From this perspective, the specific circuit that produces each defensive behavior is thought to be a necessary but not sufficient ingredient for human fear.

In this paper, we suggest several friendly amendments to this survival-circuits perspective. First, we consider recent evidence from behavioral ecology and related fields that even 'reflexes' are purposeful, flexible responses that are context-dependent and take shape within various time frames. In contrast to other approaches that take an ethological approach [70], our approach is more holistic (i.e. less atomistic) because it draws insights from a broader range of species. Second, we suggest a revision to the view that survival behaviors are triggered by dedicated neural circuits by bringing those behaviors into alignment with current research on the neural basis of purposeful motor control, which suggests that motor actions are assembled by neural populations that are flexibly constructed in a context-sensitive way. We end the paper by considering whether our suggestions offer new opportunities to study both the species-general and species-specific contributions to instances of emotion. For practical reasons of word count, we focus our discussion on defensive behaviors.

What is a reflex?

In behavioral ecology, behavioral choices (including those that allow an animal to avoid or escape a predator) are regarded as *economic choices* about energetics and other biological resources (e.g. [12]). From our point of view as an apex predator, cushioned by culture, this might seem a trivial observation. But for most animals in the wild, such as a sparrow or mouse, the calculations that balance fleeing, fighting, feeding, copulation, and caregiving penetrate every moment of life. Incorrect calculations are consequential, and can mean the difference between life and death for an individual animal, and can even risk the survival of a species. (Incorrect calculations are consequential for humans, as well, and likely contribute to the growing incidence of metabolic-related illnesses such as diabetes, heart-disease, depression, and Alzheimer's disease, but this discussion is beyond the scope of our paper).

All potential actions have an energy cost, and an animal's brain weighs these against potential rewards and revenues in the service of balancing its global energy budget. Economic choices about actions, therefore, are necessarily influenced by a number of situation-specific considerations about an animal's physical state and the state of the surrounding environment. A partial list of these situated influences includes the animal's immediate and long-term goals, the animal's current physiological condition (e.g. parasite load, pregnancy, etc.), predator type, alarm calls from conspecifics, social group size, and the environmental context such as ambient temperature, habitat density, their ability to influence the risk of being preyed upon, and even landscape features such as the amount of grass on the ground (e.g. [13–17]). These factors not only influence *which* defensive action is executed, as suggested by some taxonomies of defensive behaviors (e.g. [2–4,11]), but also *how* any given action is implemented. When defensive actions are considered in their broader ethological contexts, it becomes clear that the nature of the animal's current state and its developmental and evolutionary history provide a context for any response.

Recent research from evolutionary robotics reinforces these observations. This research, which uses 'genetic' algorithms to select successful survival strategies in virtual, real, and hybrid environments, has revealed novel insights about the ways in which co-evolving predators and prey interact with one another, and with environmental variations to shape defensive behaviors (e.g. [18,19]). In this approach, behavior is understood as *emerging* from a nonlinear, dynamical process that involves the agent's body, its control system (i.e. its brain, including past experiences of interactions with particular predators in specific environments), and the conditions of the immediate environment [20]. The contributions from different influences must be studied holistically because they cannot be separated in a reductionist way, implying that defensive actions do not deterministically issue from simple neural circuits: even complete knowledge of the individual elements governing the interactions provides little insight into the behavior emerging from their interactions.

With these observations in mind, it becomes clear that the degree of flexibility and context-dependence in naturally occurring defensive actions is vastly underestimated by current laboratory research on survival circuits (for a notable and important exception, see [21,22]). Defensive behaviors arising from threat in typical laboratory settings arise in contexts that have intentionally removed the variation that is inherently present in normal ecological contexts. A rodent who is isolated in a featureless box is without the myriad of defensive choices that animals normally seek out in the wild. This context is not only spatially impoverished but is also temporally artificial: the animal is removed from its normal social setting (so conspecifics cannot signal the presence of a predator) and is exposed to threats such as loud noises or shocks that offer no obvious contingent response (the way a real predator might). This typical laboratory experiment is also biologically impoverished: an animal's current physical state and the integration of other energetic concerns (such as normal 'foraging') are rarely considered. The consequence of stripping away this multidimensional context is that defensive behaviors — even those that are now called 'reflexes' — will be more immediate and stereotyped than those that are studied within their natural ecological contexts. This makes organizing a taxonomy much easier, because researchers are better able to categorize behaviors as all or none. These artificially constrained, laboratory-evoked responses are then mapped on to neural circuits without opportunity to observe the graded, contingent and goal-directed nature of natural avoidance and escape behaviors, features which make the term 'reflex' all but useless.

To illustrate, consider the defensive responses of perhaps the simplest extant vertebrate nervous system: the larval zebrafish. These creatures are approximately 5 mm long, virtually experience-free, and are heavily preyed upon. When faced with a predator, a freely-swimming larval zebrafish is capable of producing a suite of overlaid escape behaviors, modulating its response according to predator nearness inferred from several sensory sources with different temporal dynamics, the quickest being changes in the electrosensory environment and longer processing times for the amount and rate of visual field occlusion [23,24]. Zebrafish, like most fish, have 'Mauthner neurons' in a premotor system within their brainstem, which integrates multiple sources of sensory information to produce an extremely rapid escape flip opposite the direction of occlusion (called a C-bend escape maneuver). In response to looming stimuli, zebrafish can execute a C-bend flip in under 24 msec. This behavior would quickly become ineffective if it was the only escape behavior available to the larval zebrafish. Predators thrive on the predictability of their prey; they learn to anticipate their prey's responses, either during lived experience or via natural selection [25–27]. As a consequence, if the fish has a leisurely additional 50 msec to organize itself, its Mauthner neuron will be progressively eliminated from the computation, producing escape behaviors that are more spatially random. At longer durations (up to 200 msec), places to hide and other environmental affordances can be integrated into the decision, with the locus of computation now extended throughout the brain. The escape behavior of the larval zebrafish illustrates that even 'reflexes' in the most minimal vertebrate brains vary in their movements and temporal dynamics and at times their neural mechanisms extend through the entire brain. When behaviors are studied in their ecological context, words like 'reflexive', 'considered' and so forth are, at best, of little mechanistic help, and are, at worst, confusing with their unfounded connotations of innateness, source of volition and conscious control.

The important insight here is that defensive behaviors — whether they are executed within milliseconds or minutes of a threat — are, fundamentally, purposeful motor actions. Duration should not be confused with control (Malcolm MacIver, personal communication). The current scientific consensus about the neural control of purposeful motor behavior is increasingly at odds with the idea of fixed action (or reaction) survival circuits. We turn to this topic next.

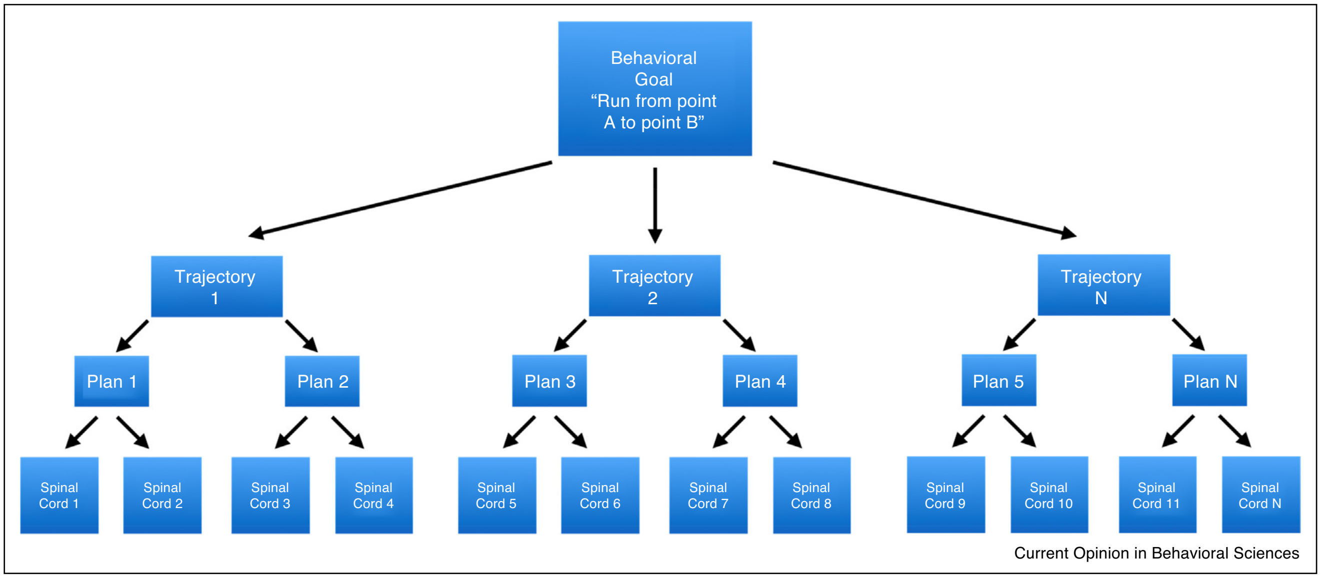
Assemblies of neural populations, not pre-set motor programs in simple circuits

A detailed discussion of the neuroscience of motor control is beyond the scope of this article, but a general sketch will serve our purpose. Motor movements are assembled compositionally from a large number of neural elements to create a much larger variety of actions [28,29]. That is, actions are constructed, they are not simply triggered by fixed, preprogrammed circuits. Similarly complex combinatorial systems in biology include language, genes, the retina, and the autonomic nervous system.

The distributed nature of motor control is apparent both in its command structure and in the complexity of its real-world execution. A single behavior, like running, requires a configuration of muscle contractions within the limbs and trunk that is specific to the physical conditions of the immediate environment. Is the running surface smooth or bumpy? Uphill, downhill or level? Hard or soft and pliable? Must obstacles be avoided or met? How fatigued or energized are the animal's muscles? How much salt and water are available in the animal's body? An animal's nervous system has to deal with these varying physical features when preparing the specifics of the muscle, joint and tendon movements that constitute the motor action. The sensory features of the environment are also integrated as part of the neural representation of motor actions [30] in a way that takes into account the current sensory state of the animal's body (e.g. [31,32]), because these, too, are in the service of motor control. In addition, the mechanical implications of executing a specific set of movements are not always perfectly predictable in a novel environment, making stored patterns of neuromuscular activity arising from fixed neural circuits ill-suited to the task of motor control. Instead, movements are assembled by selection from various levels of a representation hierarchy that spans cortex to spinal cord. An intention to run is represented in pre-motor cortices. The initiation of forward motion is influenced by midbrain computations, with basal ganglia input. The alternating limb movements of running engages spinal cord modules, further implemented by the joint-angle arrays and the 'muscle synergies' of cross-body co-activations of spinal and brainstem origin. Together, this hierarchy assembles motor movements in a generative way that is more flexible and functional than what could be accomplished with pre-set motor programs for specific muscle contractions and joint movements alone (see Figure 1).

In a given instance, then, a single motor action arises from the assembly of *widely distributed populations* of neurons embedded in synchronized activity [33], stretching from

Figure 1



A schematic depicting a motor hierarchy. The goal 'to run from point A to point B' can be accomplished via movement along multiple trajectories. Any given trajectory can be implemented by various plans involving different combinations of hip, knee and ankle joint movements. And any joint movement can be achieved with a variety of muscle movement combinations because there are many muscle fibers around each joint. Therefore, as a motor control signal is assembled, each level of motor control can decompress into multiple lower-level neural patterns. This means that any given defensive behavior has the potential to become specified in more than one higher dimensional pattern; that is, an action goal, as a compressed, multimodal summary, supervenes on, or can be entailed by, more than one lower level pattern of motor signals. In this way, a behavioral goal is transformed into a particular set of motor commands that reaches the bottom of the motor hierarchy, which is occupied by the spinal cord pattern generators and simple motor circuits (modules for specific patterns of muscle fiber activity and joint movements).

association cortices (important for action planning and sensory sampling) and primary motor cortex (important for execution of motor actions) all the way down to the motor neurons in the ventral horn of the spinal cord that contain the modules which impose a specific pattern of muscle fiber activity and joint angles.

Goals and concepts

Neurons in premotor association areas, which are positioned at the highest level of the motor hierarchy, integrate multiple sources of sensory, motor and visceromotor information to represent an *action goal* [30]: they represent an intention to execute an action in specific physical surroundings. Premotor cortices, for example, are heteromodal association cortices that represent information from more than one modality. These multimodal summaries are referred to as *abstractions*. As information is learned, neural activity propagates (in layers 2 and 3 of the cortical sheet) along a lamination gradient in the cerebral cortex from primary sensory cortices containing smaller neurons with fewer connections to cortices containing progressively larger neurons with more connections, representing shared information with progressively more efficient neural summaries [34]. The largest neurons, found in association cortices in the front of the brain, including some premotor cortices, integrate across sensory modalities by summarizing their shared information (i.e. the statistical relationships in their patterns of activity) [35], effectively achieving dimensionality reduction. This functional integration suggests the hypothesis that an action goal is represented as a distributed, embodied *action concept* [6,7] — an integrated summary of multimodal information about motor actions in a particular sensory context (where the context includes the state of the world *and* the body). Premotor cortices can be thought of as representing the more abstract features of these concepts (rather than the entire concept). Action concepts not only give rise to motor movements but they also allow animals to anticipate and understand the actions of others [36].

Degeneracy and the integration of distributed action components

An action goal 'to run from point A to point B in a particular context and at a particular speed' is a general plan that must be translated, via progressively more detailed instructions, into a set of specific muscle fiber contractions and joint movements. Neural signals that begin as the most abstract features of an action concept (in premotor cortices) must be decompressed to recruit neural populations in primary motor cortex and sensory cortices [37], as well as cascade through the midbrain, brainstem and spinal cord modules that combine to specify the initiation, termination and dynamic forces that drive body movements (Figure 1 is a highly schematized depiction of the neural hierarchy that controls purposeful motor behavior). The hierarchical architecture of the motor system allows information to be translated in a one-to-many pattern, termed *motor equivalence*: one action goal can be implemented by more than one plan of muscle contraction and joint movement, each with some prior probability of being functional in a given situation or context (e.g. [38]). In biology, motor equivalence is described as 'degeneracy': the ability of structurally different elements to perform the same function [39], which has been well-documented in the brain (e.g. [40–42]). Systems with degeneracy efficiently carry more information (i.e. are high in complexity), are information-gaining (i.e. are generative), and are robust to damage [43]. Degeneracy in the motor control hierarchy allows for greater movement flexibility than would be possible with fixed action circuits, thereby allowing motor actions to remain functional in novel circumstances. Flexibility and robustness derive not only from *which* action is executed (as suggested by [2–4,11]), but also *how* any given action is implemented in a specific pattern of muscle contractions and joint angles.

The importance of prediction

Action concepts are not just degenerate in their execution of motor control, but they implement this control by *prediction*. Evidence from motor neuroscience suggests that the motor system runs a *forward model*, which represents the causal relationships between potential future actions and their sensory consequences [44,45]. The model represents initial conditions (in both the body and in the environment) and constructs a situated action concept — the motor system's best guess as to which actions will be most functional in a given context and how those actions can be most efficiently implemented in that context. The 'best guess' is rooted in similarity — the brain 'remembers' neural patterns from prior experiences that are similar to present conditions, which then predict the future state of the system to guide behavior. These neural signals are effectively inferences that predict forward in time and space to anticipate how the motor system's state will change as a function of the motor command, as well as anticipate the expected sensory consequences of those motor movements (based on similar experiences in the past). Action concepts, therefore, can be thought of as the neural signals that decompress as they cascade from association cortices to the spinal cord circuits and pattern generators to predictively control the body as well as to neurally infer the resulting perceptions and sensations. This is how brains are thought to represent the causal relationship between actions and their sensory consequences [46]. In effect, prediction signals are candidates for categorizing incoming sensory inputs to make them meaningful; the associated motor movements can be thought of as part of the ensemble of information that makes sensations meaningful [6,7].

Research on forward motor models belongs to a larger, mathematically-formalized, neuroscience-inspired account of how brains work, referred to as predictive coding or active inference (e.g. [7,47–49,69]). It has been hypothesized, based on both anatomical [35] and functional evidence [6,47,50; for additional references see 65], that active inference offers a unified computational account of how a brain functions as an internal model of its body in the world. Active inference, within this internal (forward) model, is thought to equip a brain to anticipate the needs of the body and attempt to meet those needs before they arise [52], referred to as allostasis [51], thereby allowing efficient control of purposeful motor actions in the service of a balanced energy budget.

If prediction signals are the brain's hypotheses for future states, then incoming sensory inputs are the data used to test those hypotheses. A brain monitors errors in exteroceptive sensory domains and in interoceptive sensory domains (interoceptive prediction errors are called reward prediction errors and are thought to be associated with the midbrain dopamine system, as discussed in [53]). Discrepancies between actual and predicted sensory inputs are essential for motor control because they allow a brain to fine tune motor actions to avoid future mistakes. In effect, by encoding prediction errors, the brain updates its (forward) internal model to improve future predictions. In addition, smooth motor movements require the correction of any movement errors as they arise. A brain can process prediction error via a variety of pathways, but one important pathway for error correction involves the cerebellum. Sensory prediction errors that correct motor movements are acquired and processed too slowly to allow for fine-grained motor control, however. To compensate for these delays, the cerebellum estimates the sensory state of the world [45] and the body [31], in effect allowing it to estimate the upcoming sensory prediction errors that are necessary to correct its forward model. This is called an *observer model* [44]. Many motor movements only unfold after prediction error is sufficiently minimized, and the resulting representations serve as inferences about what caused the sensory events and associated actions in the first place [46]. In some cases, such as when immediate action is required (recall the C-bend flip of the zebrafish larvae), prediction error is a luxury that an animal cannot afford, and motor movements will be executed without correction.

Insights for the neural control of survival-related behaviors

What can we learn about the neural control of survival-related behaviors from our brief peek at the behavioral ecology literature, combined with our sketch of the neural hierarchy that controls purposeful motor actions? For a start, we might question whether any defensive behavior is ever encoded in a pre-programmed, specific neural circuit. If defensive actions and other survival-related behaviors are like other purposeful motor actions, then they are much more context-dependent and flexible than is observed in current laboratory paradigms, even when behaviors occur mere milliseconds after the appearance of a threat. This flexibility *not only* arises from having a repertoire of actions (as suggested by the existing taxonomies), but *also* because survival-related actions are governed by an animal's internal model. This is likely true not only for some types of defensive behaviors (as suggested by [2–4,11]), but for all defensive behaviors. Research showing that motor actions are largely assembled in a flexible neural hierarchy, rather than triggered by pre-set motor programs in simple circuits, suggests that even the 'reflexes' that are present in spinal cord circuits and pattern generators are flexibly modulated in a context-dependent way, and evidence supports this hypothesis [54].

Moreover, if defensive actions and other survival-related behaviors are like other purposeful motor actions, then any given action has more than one neural assembly that supports it. Motor movements appear to be assembled from an action concept by degenerate, distributed neural populations that can implement the same action via variable low-level muscle, joint and tendon patterns. This degenerate architecture will involve much more than neurons in the amygdala, the basal ganglia, the hypothalamus and the periaqueductal gray: if survival-related behaviors are like other purposeful behaviors, then they are controlled by a flexible hierarchy involving neurons that span many brain areas, including the cortex and the cerebellum. This suggests a many (neural assemblies)-to-one (action) relationship, rather than the one-to-one relationships that populate existing taxonomies. And, indeed, a growing number of scientific studies lend some support to each of these hypotheses (e.g. in the domain of protecting against a threat [55–64]; also see findings from the behavioral ecology literature discussed above). The most basic reflexes, such as startle responses, may not be entirely influenced by centrally-generated intentions to move (i.e. action goals), but neither are they completely free from the influences of those intentions. Sensory events in the world (i.e. stimuli) do not determine a specific motor response; they set the occasion for it [30].

The nature of emotion

Our discussion thus far leads us to suggest that the current menu of 'survival circuits' are only a small part of a much richer, more flexible, context-sensitive complex system for assembling and controlling survival-related behaviors. This discussion suggests a role for concepts and goals in the construction of those behaviors. And the degree of complexity and abstraction in the concepts and goals constructed by a brain reveals important insights about the nature of emotion and its possible variation in humans and non-human animals. For example, the hierarchy in Figure 1 can be further abstracted to include a functional multimodal concept (e.g. to protect against a predator), which itself contains various action concepts (behavioral intentions to run, to attack, to freeze, to faint, to signal conspecifics) that are similar to one another for the purposes of meeting that function in a specific context. Each action concept supervenes on a broad array of implementation plans, which in turn can be realized by multiple combinations of muscle movements, and so on, as suggested by Figure 1. This is a central idea motivating the theory of constructed emotion (e.g. [6,7]). It is hypothesized that emotional events are assembled when the brain constructs emotion concepts, on the fly, as part of its forward internal model. An emotion concept includes a behavioral intention — a descending cascade of potential visceromotor and motor patterns, sometimes (but not always) resulting in a survival behavior. An emotion concept also includes the corresponding prediction signals that simulate the expected sensory consequences of the expected motor movements (called an efference copy or corollary discharge). It is further hypothesized that some of these expected sensory consequences eventually become the basis of perception and experience [6,7,47,65]. In humans, an experience of emotion is not always reportable: consciousness is distinct from awareness, so that emotions can be experienced without awareness.

From this perspective, what distinguishes humans and non-human animals is not the computational principles that govern neural representations, but the content that those computations give rise to. The computational role of many major brain parts remains stable across the vertebrate lineage. All brains, when functioning in a predictive mode, can be described as automatically and effortlessly forming ad hoc concepts to categorize anticipated sensory inputs and guide action. What may differ among species is the type of concepts that a brain is capable of constructing because of general brain-scaling functions [66] and the information available in an animal's niche (discussed in [6]). For example, the human brain has expanded association cortices in the frontal lobes, parietal cortex and inferotemporal cortex when compared to other primates, including other great apes [67,68]. This expansion potentially allows for increased information compression and dimensionality reduction, suggesting the possibility that human brains are capable of multimodal summaries (i.e. concepts) characterized by greater abstraction. This hypothesis in no way diminishes the importance of survival-related behaviors in human emotion, nor invalidates the importance of studying survival-related behaviors in animal models for the purposes of understanding part of the biology of human emotion and its disorders. This hypothesis does suggest, however, that solving the puzzle of human emotion may require creating a science of 'emotion ecology' involving both species-general and species-specific processes, such that understanding the brain-basis of emotion and its disorders requires more than just mapping the circuitry for survival-related circuits.

Conflict of interest statement

Nothing declared.

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