

MINDS AND BODIES IN ANIMAL EVOLUTION

MICHAEL TRESTMAN

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ABSTRACT

Animal minds and animal bodies evolved together. When did consciousness emerge and what animals have it? Consciousness has a distinct structure: a predictive, temporalized stream of intentional content. I argue that this structure also solves the biocomputational problem of controlling a complex, active animal body in space. This problem has been solved three times in animal evolution: in vertebrates, in arthropods, and in cephalopod mollusks. This supports the hypothesis that consciousness itself arose near the root of each of these lineages.

I INTRO

Consciousness is a notoriously elusive notion, in part because it points to a cluster of related phenomena (see Van Gulick, 2014 for a broad overview. See Godfrey-Smith, 2015, and Trestman and Allen, 2015 for discussions of this issue in the context of the evolution and phylogenetic distribution of consciousness). My target notion is subjective experience—having any experience at all. This is sometimes called the ‘phenomenal’ or ‘phenomenological’ notion of consciousness. When I am aware of anything at all, I have an experience, and I am the subject of that experience. That experience is what it is like to be me in that given situation, the ‘experiential quality’ of my existence in that moment. If there is something it is like to be a given creature, that creature is conscious. Which animals are conscious in the sense of experiencing their presence in the world? How can we tell? The strategy I employ here is to use insight from phenomenological analysis of consciousness to generate differentiating empirical predictions about the behavior of animals that have consciousness and

those that don't. This 'Structural-Functional' approach (Trestman and Allen 2015, part 5) relies heavily on the assumption that the intentional structure of consciousness as revealed through phenomenological analysis of consciousness can be mapped meaningfully to the computational structure of cognition, as considered from the perspective of the behavioral sciences such as behavioral psychology, ecological psychology, ethology, and functional neuroscience (Varela 1996). This assumption is rooted in the naturalistic stance that consciousness is an aspect of our biology, that it is grounded in the interaction of our body with our environment. We are (more or less) our bodies; the experiential dimension of consciousness (subjective experience) just is what it is like to be a certain kind of body. Cognition, intentionality, and information-processing are abstractions for describing the processes that mediate sensation and behavior. We use this level of abstraction to understand our own experience as we make sense out of the world, extracting meaning from what we see and hear, and how it provokes us to feel and respond. We also use it to understand how others do the same. Because it is an abstraction, it inevitably loses detail and directness—an abstraction never fully captures what it is an abstraction of, and in that sense we can never fully know the experience of any other sentient being (human or otherwise). Nonetheless, this abstraction layer allows for meaningful contact between the 'first-person' perspective of phenomenology and the 'third-person' perspective of the behavioral and brain sciences, allowing us to ground our reasoning about others' experiences in empirical evidence. I present here a model of the cognitive structure of consciousness that was developed to answer the question:

(Q1) What is the cognitive sub-structure of consciousness that makes possible its temporal dimension?

I believe it also answers a very different question:

(Q2) What is the core information processing structure required for an adaptive control-system for complex active animal bodies?

That the model answers both Q1 and Q2 suggests that the cognitive structure described by the model—consciousness—was a key evolutionary novelty that contributed to the diversification of animals with complex active bodies. This implies that the emergence of consciousness has a detectable signature in evolution: adaptive radiation driven by diversification of complex active bodies.

II THE STRUCTURE OF CONSCIOUSNESS

As a conscious subject, one is immersed in a changing flow of sensation, perception, thought and feeling. Normally, one's attention is occupied not by low-level sensations (pixels, color patches, edges, tones, pressure or stretch on the skin) but objects, things in the

world like trees and dogs and humans and cups of coffee, and the features and conditions of these that are most salient to one's preferences and intentions. Typical experience situates us in a world with a coherent spatial structure—objects are located out there, and we are aware of their relation to our body (itself a kind of special object with a spatial structure) and in particular to the cyclopean hole in the center of our face that we experience as the locus of our visual perspective (Merker 2013). We perceive a scene of worldly objects through a changing array of sensations. How does this interpretation work? How does worldly, situated experience emerge from sensory flux? Intentionality—'aboutness' in the sense that a perception or thought is about an object—implies experiencing a sensory image as an appearance of an object that transcends—exists apart from—the appearance (Husserl, 1963; Zahavi 1999). If you see a cup sitting on a table, you implicitly understand that the cup can appear differently. Its appearance will change slightly in one way if you move your head to the left, in another if you move your head to the right. If you reach out and touch it, the cup will feel a certain way in your hand. These are all appearances of the same cup, the object, which therefore transcends the constantly changing ways in which it appears. Intentionality implies identity in multiplicity—high-level patterns persist as sensations change. Perception is fundamentally dynamic, temporal. Understanding the scene before you is a matter of understanding what is happening. If a ball is in the middle of a table, you cannot tell from a snapshot whether it is sitting still or rolling, but perceiving a ball roll is different than perceiving a ball sitting still. Perceiving an object involves an awareness of its trajectory—where it has been and where it is going, how it has appeared and how it will appear. One's sense of what is happening, of one's situation in the world, is extended in time. James (1890) observed that the sense of the present has an extension of about 3 to 10 seconds. Within this range we are aware of the fine-grained temporal structure of events—properties like duration and rhythm. Longer into the past than that, we can remember or figure out how things were in terms of their temporal properties, but our judgments over these extended time-scales have the character of inference rather than perception, relying on background information about events with known durations or labeled time coordinates (dates and times). A wide variety of subsequent research has confirmed that the time-scale of about 3 seconds seems to have a special status as a 'window of temporal integration' for perception, judgment and action (Poppel, 2009; Wackerman 2007). We experience a rich sensory array that persists for a few seconds, allowing us to notice details and recognize objects; afterwards, what we remember is very selective and depends heavily on what we were paying attention to and how we interpreted the scene (Block, 2011; Pinto et al., 2013). Consciousness has a tripartite structure: our impression of the sensory present is accompanied by a retention of the previous impression, as well as an open-ended anticipation or protention of upcoming impressions, to use Husserl's terminology (Husserl, 1963; Zahavi 1999). Further, this retention- impression-protention (R-I-P) structure, is iterated: the retention associated with the current impression itself has

an R-I-P structure. What we retain from the previous moment of awareness isn't just the sensory impression, but that moment's full sense of past-present-future. This is implied by the experience of surprise, an awareness of mismatch between prior expectations and actuality (Trestman 2014). The iterated R-I-P structure (ItRIP), is essential for capturing the structural property of 'flow' exhibited by consciousness. Our sense of time is not a static linear series, but a series with an internal motion defined in relation to a perspective—the now—which we, as subject, occupy. Future events approach and past events recede. Crucially, a given event (e.g. a book falling to the floor, taking a sip of wine) maintains an identity as it traverses the different 'zones' of future, present, and past: The sound-of-the-book-hitting-the-floor that I hear now is then, a moment later, the very same sound-of-the-book-hitting-the-floor that I am aware of as having just occurred. The sip I anticipate is the same sip I take, and the same sip I then remember—even if my expectations were slightly off, they were slightly-off-expectations of that sip, how it would appear to my senses in the moment. The structure of iterated retention allows moments of experienced time to emerge as invariants across the series of retained moments. The point in time that I first anticipate, then experienced as now, and then experience as past, is the same point in time. This cross-time identity of moments supports identity of events over time, since events are happenings that are temporally bound. In turn, this supports objects as things that can persist across time—I can understand that the cup that I saw sitting on the table a moment before is the same cup that I'm now holding. Our experience of time is not only extended across time—'temporally thick', it is also extended across alternate possibilities—it is 'modally broad'. We experience time as having a branching structure in the future direction—hence the name BItRIP (Branched, Iterative Retention-Impression-Protention) for the full model (Trestman 2014). This is fundamental to our experience of agency in its most basic form: body ownership. I experience my body as the medium of my actions, and the medium of my perceptions. What I do, I do with my body; What I perceive, I perceive through my body. This is what distinguishes my body from other objects; my hand is an object that I can see, but I can also feel with it, and do with it (Husserl, 1963; Carman, 1999). My body is under my control in a direct, immediate way that nothing else is. But to experience control of my body is to experience a plurality of future possibilities—to protend multiple branching sequences. Ultimately your divided intent resolves or collapses—I can do [x, y, z] becomes I do x. We retain a sense of what we could have done, choices we made and did not make slipping into the past. This implies that the branched structure of protention is retained within R-I-P elements in the retentional sequence. Bodily agency is a ubiquitous feature of conscious experience, especially when we consider its role in perception of objects and the spatial structure of the environment (Trestman 2014). Space is experienced in relation to the body's axes of orientation and capacities for action. Ego-centric spatial positions are invariants relative to the body's dynamics (Mossio and Taraborelli 2008; Merker 2005, 2013), so positions in space relative

to the body must be defined in terms of positions in time. To experience a stable, spatially coherent world depends on an animal's ability to predict and compensate for sensory change due to saccades, postural shifts, and any other bodily actions that influence the optic array exposed to the eye (Merker 2013). The branching nature of our experience of time is also fundamental to another core feature of consciousness—ffective valence. There are a variety of theories of hedonic experience, but a broadly shared theme is that it involves both anticipation and comparison—specifically, comparison of alternate ways one's situation could change (see Aydede 2013 for a review of theories of pain). Roughly, experiencing something as aversive is wanting it to cease/not happen, and experiencing something as pleasurable or desirable is wanting it to continue/happen. Human judgments of temporal properties such as order and simultaneity have a limit at short time- scales. Fusion intervals for stimuli are generally on the order of about 30-40ms, suggesting a cyclical process of general perceptual integration operates on this timescale (Poppel 2009; Wackerman 2007). This timescale corresponds approximately to the $\sim 40\text{hz}$ oscillations of thalamocortical reentrant neural activity by which low-level perceptual features are bound into higher-level object-oriented perceptual contents (Baldauf and Desimone 2014), and which has been advanced as the neural correlate of consciousness in vertebrates (Tononi and Edelman 1998; Crick and Koch 1990, 2003; Singer and Gray 1995). If, as I have argued, consciousness is constituted by an iterated sequence of sensory impressions, retentions and protentions, the 30-40ms timescale suggests the rate of iteration. If 3 seconds represents a typical window of the experienced present, and this experienced present is constituted by an iterated series of R-I-P elements retained at a rate of $\sim 1/30$ ms, then the experienced present is typically composed of on the order of 100 R-I-P iterations.

III THE COGNITIVE PREREQUISITES TO CONTROLLING A BODY

A complex active body (CAB) is one equipped for perceptually guided, powered motion: swimming, crawling, climbing, leaping, flying, burrowing; and object manipulation (grabbing, carrying, turning, crushing, tearing, separating, etc.). Such a body has the following attributes (Trestman 2013):

- many degrees of freedom of controlled motion;
- senses that can quickly gather distal information (vision, hearing);
- anatomical capability for active, distal-sense-guided mobility (fins, legs, jet propulsion, etc.);
- anatomical capability for active object manipulation (e.g., chelipeds, hands, tentacles, sensitive mouth-parts).

Millions of living animal species display an astonishing diversity of CABs, but they exist in only three out of roughly 35 animal phyla: arthropods (e.g. insects, spiders, crustaceans), chordates (e.g. humans, salmon, pterodactyls), and mollusks, within the cephalopod lineage (squids, octopus, cuttlefish). Other lineages include animals that are diverse in many ways, including size and shape, metabolic and ecological specializations such as symbioses and parasitisms, chemical, visual, or mechanical defenses and signaling systems, complex multi-stage life-cycles, and elaborate modes of reproductive. But brains, sensory organs, skeletomusculature and behavioral repertoires remained relatively simple outside of these three taxa. In the evolution of each lineage, the appearance of CABs precipitated prolific radiation—if a lineage can produce one kind of CAB, it can produce others. Morphological diversification corresponded to behavioral and ecological diversification, with animals in these lineages rapidly exploring the space of possibilities for crucial types of behavior, including foraging, anti-predator defence, and selecting and/or constructing favorable habitats. This macroevolutionary pattern strongly suggests that complex active bodies evolve only together with an adaptable cognitive tool-kit for controlling those bodies (Trestman 2013). It also points to a general and open-ended developmental tool-kit for producing complex active bodies and the brains that control them, rather than a brittle or 'one off' solution. There are no animals with CABs surrounded phylogenetically by animals without CABs. I use the term Basic Cognitive Embodiment (BCE) to refer to the suite of cognitive phenotypes required for control of a CAB (Trestman 2013). These are capacities without which CABs could not evolve, since the reliable development of ecologically valid repertoires of coherent goal-direct behavior with a CAB would be all but impossible. Not every item on the lists below is strictly necessary, some are more complex than others and build on the more fundamental. Cognitive embodiment comes in a spectrum of complexity as well as a wild diversity of forms. BCE has three main categories or dimensions: spatiality, object-orientation, and action-orientation.

Spatiality

Adaptive control of a CAB requires animals to flexibly track and coordinate behavior to the following sorts of spatial invariants in the body-environment system.

- *Orientation* of an animal's body toward external targets is fundamental to much of behavior. For animals with CABs, orientation is a complex problem requiring coherent activity throughout the body that is specific to the target orientation (Merker 2005, 2103). Orientation is relative to an animal's bodily structure, and capacities for action. A single body may have many different ways to orient itself toward a target, such as orienting whole body posture, head, eyes, ears. Actions often need to be readied by orienting special parts of the body to grab, reach, or otherwise move toward a target. Many animals with CABs can orient simultaneously to multiple targets in different

respects, for example turning the head to track a suspected threat while readying the body to dash back toward the safety of a burrow. Maintaining orientation to a target that is out of direct perceptual contact through a series of bodily movements requires path integration.

- Many targets of interest in an animal’s environment move, as does the animal itself, so rather than a static relative position, orientation will often be toward the trajectory of a target.
- *Distances and Sizes* must be judged in a myriad of ways. Usually what is relevant to an animal is not size or distance in objective terms, but in terms of invariants that relate the animal’s body and behavior to an object. For example, animals must often judge if they can grab something, if they can fit through an opening, or how quickly they can reach a spot. One example of a generally useful invariant is Tau of a gap—the size of a gap divided by its current rate of closure. This invariant affords powerful control heuristics for guiding behavior: if the animal decelerates its approach such that tau is maintained at exactly $1/2$, the motion will stop just as the gap closes; keeping tau lower stops the motion before the gap closes; the higher tau is (above $1/2$), the more energetic the collision will be. David Lee and colleagues have demonstrated apparent use of tau to control behavior in a number of vertebrates. Examples include: humans performing familiar behaviors such as parking a car or catching a ball as well as unfamiliar experimental tasks; bats landing on a perch using echolocation; pigeons landing on a perch using visual control; hummingbirds inserting their bill into a feeder; gannets closing their wings as they dive into water (reviewed in Lee 2004, 2009). In principle Tau-based heuristics apply not only to the spatial gap between an animal and a target toward which it is moving, but also to any gap between a target state and its current state along a continuous dimension.
- *Objects* will be discussed below, but much of what defines an object is spatial binding—an object is a cluster of features that travels together through space.
- *Places* are occupiable region of space with certain predictable properties, and can be considered a sort of object. Places differ in food availability, safety, and many other important respects. Making best use of a CAB implies evaluating places in terms of these qualities and moving the body so as to spend the most time in the most advantageous places. Creating a burrow or nest, foraging out into the environment, and then returning is a common behavioral pattern across many arthropods, vertebrates and cephalopods, but no other animals (as far as I know), but requires the ability to find the location again.
- *Paths* are ways of moving through an environment from one location to another target location, through intermediate, less intrinsically desirable locations. Animals with

BCE use a variety of tactics to track paths, such as computing path integrations, recognizing landmarks, and scaffolding the environment with trail-markers.

- *Detours* are novel, indirect, multi-part paths to a target in situations where a direct or familiar path is unavailable. Detour use has been demonstrated in a wide variety of vertebrates and in spiders (Reviewed in Jackson and Cross 2011). Experiments have failed to document detouring in cephalopods although this is likely due to experimental limitations, as wild cephalopods probably use detours in their natural behavior (Alves et al., 2007).

Object-Orientation

The environment contains repeatable, predictable chunks—objects—that can be good (food, friendly conspecifics, mates, safe places), or bad (predators, environmental hazards, social conflicts) for an animal. These features are structural invariants of the environment—they are there regardless of how or whether they are detected, and they are there regardless of what the animal is doing. Objects as such have distinctive spatial properties invariants. They:

- have a single location at a time. Location changes smoothly (no teleportation);
- have persistent state;
- have dispositions (they will change or respond depending on what happens), including affordances—potentials for the animal to interact with the object;
- can have spatial parts with distinct properties and affordances. These:
 - usually move together through space; they predict each other’s location;
 - often have predictable spatial relations (e.g. the shell has food inside it).
- fit into categories—clusters of strongly associated properties, features and affordances.

A search image is set of perceptual features an animal uses to detect a specific type of target object (or unique target object) in its environment (Tinbergen 1960; Ishii and Shimada 2010; Jackson and Cross 2011). Possessing or using a search image makes an animal more likely to detect the target object and less likely to detect others, particularly in a noisy or hostile environment where objects are disguised or hidden. Search images have been described in many vertebrates, and more recently in some invertebrate species, including parasitoid wasps (Ishii and Shimada 2010) and jumping spiders (Jackson and Cross 2011). For most animals with CABs, many salient objects in the environment are other animals, affording predator/prey interactions, sexuality, resource competition, cooperative sociality, communication, social learning, etc. Animals with CABs, and therefore BCE, have distinctive invariants that can be tracked for effective interaction:

- orientation
- gaze
- heading
- action trajectories
- states of awareness (e.g. has this predator noticed you?)
- action capacities and dispositions to respond to environmental conditions, and the perceiving animal’s own behavior (including communication).
- goals as dynamic invariants toward which the animal’s behavior is directed (Trestman 2010, 2012).

Action-orientation

Nearly everything that an animal needs to know must be in relation to its own body’s requirements and capacities for action. To behave in a coherent, goal-directed way, an animal must compose complex actions from simpler units of behavior (Trestman 2010, 2012). At every level of this compositional hierarchy, there exist structural invariants in the environment and sensorimotor-dynamic invariants in the interaction between the animal’s body and the environment. These invariants must be discovered and continuously calibrated as body and environment change. From an associative learning perspective, the problem is to select the correct behavior for the right situation. Complex behaviors must be formed through chaining and shaping (Skinner, 1981). From an ecological perspective, an animal’s core cognitive/perceptual problem is to track invariants that allow for recognition and exploitation of affordances—opportunities for interaction (Gibson, 1979). Affordances are relational—they are about the coupled dynamics of animal and environment, about what possibilities are offered by a situation given the body’s capacities. In addition to the associative clusters that correspond to objects, the most important associations to be built are between affordances and behaviors that exploit them. Simple associative learning—classical conditioning and operant conditioning for atomic behaviors—is ubiquitous among even the simplest animals, and appears to be wide-spread in single-celled organisms, including bacteria. More complex kinds of learning, those that build associations between objects and actions in the senses I’ve developed here are found only in arthropods, vertebrates, and cephalopods. Social learning processes such as local enhancement, stimulus enhancement, vicarious conditioning, emulation, imitation have differing cognitive prerequisites related to the elements of BCE described here. Other than the simplest, local enhancement, these forms of learning are found only in the three taxa with BCE. For the most part, they have only been demonstrated in vertebrates and bees (Avargues-Weber et al., 2014), but research on complex and social learning has been sadly lacking in invertebrates (but see Perry, et al., 2016; Hollis and

Guillette, 2015).

IV BITRIP AS SCAFFOLDING FOR BASIC COGNITIVE EMBODIMENT

Consciousness is a stream of sensory and motor information, consumed by the process of extracting intentional objects (objects, properties, events, space and the body) in order to guide action with motivationally valenced anticipations of consequences. This shares the structure of the information- processing problem facing a brain in a complex, active body: extracting spatial, object-oriented and action-oriented invariants from a stream of sensorimotor data. Just as the **BitRIP** structure described above is required to explain the phenomenology of experience, it is also required to account for the extraction of invariants crucial for perception and behavior. As conscious animals, sensory impressions inform our understanding of the world around us, and our understanding of the world lets us predict our incoming sensory impressions. This ability to predict allows us to move our bodies to effectively gather information and reduce the uncertainty in our understanding of our world. We iteratively refine our understanding of the world by gathering information, making predictions, moving our bodies, and comparing our previous expectations to new sensations. Subjective experience is the highest level integration of this flow from gathered information into expectation and intention to act. The things that we perceive in the world—affordances, people, places, features, properties, etc., are invariants that emerge in this flow. The ability to predict the next few seconds based on the last few seconds is essential to experience, perceptual control of behavior, and also the learning that makes complex cognition, perception, and action possible. This is especially clear in Rescorla-Wagner learning, wherein degree of learning depends on degree of surprise, and in operant conditioning with negative reinforcement, wherein the absence of an inhibiting stimulus reinforces a behavior. The same sequence of environmental conditions can serve as a reward or a punishment, depending on the salient alternative possibility. Affective valence is at the core of our experience, and it is also a crucial driver of adaptive behavior (Ginsburg and Jablonka 2007, 2015). It binds our past, through learning, to our present actions, which shape the future. It drives our attention, our motivation, and our learning, determines what we value, seek and avoid. Consciousness, the predictive extraction of intentional content from a temporalized stream of perception- and action-data, provides the cognitive structure crucial for control of a **CAB**. Therefore, it is a good bet that consciousness emerged in evolution together with complex active bodies; the cognitive structures essential to consciousness are crucial prerequisites to having a **CAB** as well. Consciousness and **CABs** may also have been lost together in evolution, for example in taxa with parasitic lifestyles and extreme reduction in size and bodily complexity (e.g. some mites). The strength of my argument relies on the strength of association between the

cognitive and bodily traits I've identified. How well do the cluster of cognitive and bodily traits hold together in evolution within the three taxa I've identified? Are there peaks of bodily or cognitive complexity of the relevant sort in other taxa? These are open questions. My argument also relies on the analysis of what cognitive structure is essential to consciousness. There is more work to be done on all fronts, but I hope to have outlined a promising approach to the phylogenetic question of consciousness.

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