Current Biology

CellPress

Review

# An Algorithmic Approach to Natural Behavior

Andrew M. Hein[1,2,3,*], Douglas L. Altshuler[4], David E. Cade[2,5], James C. Liao[6], Benjamin T. Martin[1,2,7], and Graham K. Taylor[8]

[1]Southwest Fisheries Science Center, National Oceanic and Atmospheric Administration, Santa Cruz, CA 95060, USA
[2]Institute of Marine Sciences, University of California, Santa Cruz, CA 95060, USA
[3]Department of Ecology and Evolutionary Biology, University of California, Santa Cruz, CA 95060, USA
[4]Department of Zoology, University of British Columbia, Vancouver, BC V6T1Z4, Canada
[5]Hopkins Marine Station, Department of Biology, Stanford University, Pacific Grove, CA 93950, USA
[6]The Whitney Laboratory for Marine Bioscience, Department of Biology, University of Florida, 9505 Ocean Shore Blvd., St. Augustine, FL 32080, USA
[7]Institute for Biodiversity and Ecosystem Dynamics, University of Amsterdam, Amsterdam, The Netherlands
[8]Department of Zoology, University of Oxford, 11a Mansfield Road, Oxford OX1 3SZ, UK
*Correspondence: ahein@ucsc.edu
https://doi.org/10.1016/j.cub.2020.04.018

Uncovering the mechanisms and implications of natural behavior is a goal that unites many fields of biology. Yet, the diversity, flexibility, and multi-scale nature of these behaviors often make understanding elusive. Here, we review studies of animal pursuit and evasion — two special classes of behavior where theory-driven experiments and new modeling techniques are beginning to uncover the general control principles underlying natural behavior. A key finding of these studies is that intricate sequences of pursuit and evasion behavior can often be constructed through simple, repeatable rules that link sensory input to motor output: we refer to these rules as *behavioral algorithms*. Identifying and mathematically characterizing these algorithms has led to important insights, including the discovery of guidance rules that attacking predators use to intercept mobile prey, and coordinated neural and biomechanical mechanisms that animals use to avoid impending collisions. Here, we argue that algorithms provide a good starting point for studies of natural behavior more generally. Rather than beginning at the neural or ecological levels of organization, we advocate starting in the middle, where the algorithms that link sensory input to behavioral output can provide a solid foundation from which to explore both the implementation and the ecological outcomes of behavior. We review insights that have been gained through such an algorithmic approach to pursuit and evasion behaviors. From these, we synthesize theoretical principles and lay out key modeling tools needed to apply an algorithmic approach to the study of other complex natural behaviors.

## Introduction

Natural behaviors often seem unapproachably complex. Even routine behavioral sequences — for example, the maneuvers of a dragonfly as it takes flight, pursues and captures a passing fly, then returns to its perch [1] — involve rich streams of incoming sensory data and intricate cascades of responses that appear delicately tuned to the situation at hand. Among the many challenges involved in decoding such behavior is the difficulty of understanding how processes at different levels of brain organization interact to transform dynamic, high-dimensional sensory data into maneuvers that are both flexible and precise. While this complexity can be daunting, some of the most exciting and most pressing problems in biology and medicine demand that we better grasp the mechanisms and function of natural behavior [2].

Natural behaviors are difficult to study, in part, because generating effective behavior in a dynamic world is inherently a multi-scale problem [3]. An animal's actions result from sensory stimulation, neural processing, and muscle contractions. Yet, these processes occur on timescales far shorter than those of the most conspicuous behavioral goals: for example, capturing a passing prey or evading an attacking predator. The problem of understanding how animals generate effective natural behavior thus requires that we link the neural and biomechanical mechanisms that control an animal's elementary behavioral actions to fitness-relevant goals that are achieved over much longer timescales. We are unlikely to fully solve this problem by reducing natural behaviors to more tractable behavioral tasks [4,5]. Rather, if we are to shed light on the mysteries of how extended, flexible sequences of natural behavior are generated, and how such behaviors operate and evolve, we need methods that can reveal how subcomponents of behavior are integrated to form a functional whole.

In this review, we explore insights gained through studies of animal pursuit and evasion: two ubiquitous behaviors that are beginning to serve as models of natural behavior [6,7]. A key finding of these studies is that flexible, responsive sequences of pursuit and evasion behavior appear to be constructed through relatively simple behavioral rules that transform sensory input to motor output. We refer to these rules as *behavioral algorithms* [3,8]. More specifically, we define a behavioral algorithm as a repeatable, quantitative mapping from sensory input to motor output. Examples include guidance algorithms that relate the relative motion of visual targets to steering during pursuit maneuvers [6,9–11] and obstacle avoidance [12,13], collision-detection algorithms that translate tactile, visual, or acoustic stimuli into

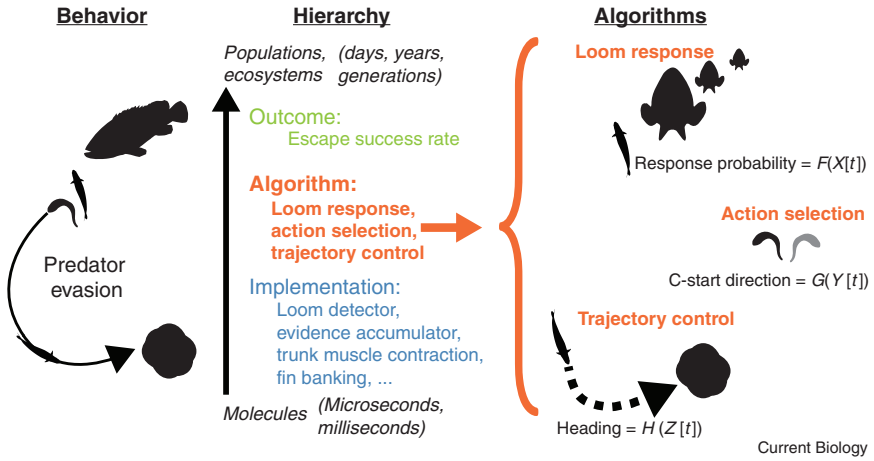



**Figure 1. A hierarchical view of pursuit and evasion behavior.**
Pursuit, evasion, and other natural behaviors involve processes that span levels of organization and occur on many different timescales. At a coarse level, the Outcome (for example, escape or capture) depends on how the behavior is executed. This execution depends on the behavioral Algorithms used to construct a behavioral sequence from incoming sensory input. Algorithms are executed through neural and biomechanical processes at the Implementation level. For example, one algorithm (described by the function $F(X[t])$) may describe how looming visual input, $X[t]$, determines whether an escape maneuver is initiated (for example, the acceleratory 'C-start' response of fish). Another algorithm ($G(Y[t])$) may determine the initial direction of the escape maneuver as a function of the stimulus sequence received prior to initiation. A third ($H(Z[t])$) may describe how incoming sensory data drives trajectory control during movement toward a safe shelter [38].

escape responses [14–18], optomotor algorithms that translate wide-field visual motion into turning behavior [19,20], and plume tracking algorithms that translate measurements of wind direction and odor detections into flight patterns [21,22].

An intriguing characteristic of many behavioral algorithms is that they can be described with high fidelity by simple, low-dimensional mathematical models. Researchers have exploited this agreement between behavioral data and tractable models to better grasp the logic of natural behavior. By identifying behavioral algorithms and building mathematical models to describe them — for example, using control equations [6,23] or stochastic processes [24] — studies have proceeded to explore the mechanisms behind pursuit and evasion behaviors, using algorithmic models to find clues about which elements of the nervous system might implement a given behavior [11,15,18,25]. Another branch of research is using algorithms to move in the opposite direction — toward the ecological and evolutionary implications of natural behavior — using algorithmic models to guide ecological analyses and computational modeling [23,26–29].

In the following sections, we review insights that have come from applying this *algorithmic approach* to the study of pursuit and evasion behavior. We synthesize theoretical principles, experimental findings, and modeling tools that have been central to the success of this approach. Finally, we discuss emerging methods that could help researchers apply algorithmic models both more systematically and more broadly to probe the mechanisms and implications of natural behavior.

## Pursuit and Evasion as Models of Natural Behavior

Whether feeding, fighting, fleeing, or mating, animals have been chasing one another since at least the Cambrian. Pursuit and evasion behaviors are often extraordinarily conspicuous and clearly goal-driven [6,7], but these behaviors also involve some of the best understood of all neurons and neural circuits: from elementary motion detectors and optic-flow sensitive interneurons [30], to Mauthner cells and squid giant axons [31]. Importantly, the ultimate outcomes of pursuit and evasion influence fitness in very direct ways; these behaviors are ecologically and evolutionarily relevant, and at the same time well-defined and tractable enough to study with the high degree of precision offered by modern neuroscience and biomechanics. All these attributes make the pursuit–evasion problem a strong model through which to study natural behavior.

Like many natural behaviors, pursuit and evasion involve processes that occur at different levels of organization, on different timescales, and at different degrees of removal from ultimate fitness consequences. To organize these scales, a hierarchical view of these behaviors is particularly useful (Figure 1) [5,8,32]. The coarsest level of the hierarchy, the *Outcome*, describes whether a particular pursuit or evasion behavior is successful or not. Ecologists have long studied interactions between predators and prey by focusing on this level alone. One could ask, for example, how the speed of flowing water influences the ability of a fish to capture prey suspended in the water column [33], or how mortality of songbirds from attacking predators depends on the level of acoustic noise in urban environments [34]. Studying behavior at this level alone, however, limits one to a descriptive understanding of behavioral outcomes. Patterns can be described but rarely predicted in any precise way. To move beyond this, the *Outcome* must be connected to the manner in which the behavior is executed (Figure 1). The behavior is composed of a collection of behavioral *Algorithms* as well as the rules that govern transitions between these algorithms. Algorithms are executed through a physical *Implementation* involving the animal's sensory organs, musculoskeletal system, and nervous system (Figure 1).

While the definition of an algorithm used here is more restricted than that used in past work (for example [8,35,36]), the hierarchical view of natural behavior shown in Figure 1 has much in common with schema developed in the past to help organize questions about behavior, most notably Marr's levels of analysis [8], Tinbergen's four questions [32], and recent elaborations of these frameworks [5,36]. The essential point of such hierarchical schemes is to emphasize that behavior seldom involves processes occurring on a single timescale or at a single level of organization. Rather, natural behavior almost always involves coordination between actions and goals that span a range of scales.

## The Importance of Algorithms

In the hierarchy shown in Figure 1, *Algorithms* occupy a special position: they are poised between the neural and biomechanical implementation and the ecological outcome of behavior. Algorithms thus provide the connection between success or failure of a particular behavior, and the physical attributes of the animal — the structure of sensory receptors, the geometry of limbs and fins, the organization of circuits in the brain — that evolve through natural selection. From the perspective of a researcher, algorithms are also useful because they connect actions and goals that occur on different timescales. For example, the guidance algorithms that predators employ during pursuit maneuvers involve turning to stabilize the visual location or line-of-sight angle of a moving target [6,9–11], but this near-term goal of stabilizing apparent target motion ultimately allows the animal to achieve a longer-term goal that is more directly related to fitness: intercepting the target. By building mathematical models of algorithms and analyzing them, the relationship between these goals often becomes clear [12,37,38].

In Box 1, we describe a general approach for identifying, modeling, and comparing candidate algorithms. This algorithmic approach to behavior is based on a hypothesis, which states, first, that there exist low-dimensional features of sensory inputs that produce consistent, repeatable motor outputs, and second,

**Box 1. Identifying and modeling behavioral algorithms.**

The process of identifying, comparing, and testing candidate algorithms can be broken down into a sequence of four steps.

**Step (1): identify the problem.** Identify a fitness-relevant objective the animal is attempting to satisfy. In the case of pursuit and evasion behaviors, objectives are often clear, which is one benefit of using these behaviors as models. For other types of natural behavior, determining the objective may start with a review of the ecology of the animal, or new studies that characterize when and how the behavior is used in nature. Once an objective is identified, one can lay out the initial conditions of the problem as well as the conditions for success or failure. For example, in the case of a predatory hawk or falcon pursuing prey (Box figure) [6,28] the initial conditions are the bird's position and velocity as well as the initial position and velocity of its prey. To succeed, the predator must capture its prey before the prey escapes to a refuge.

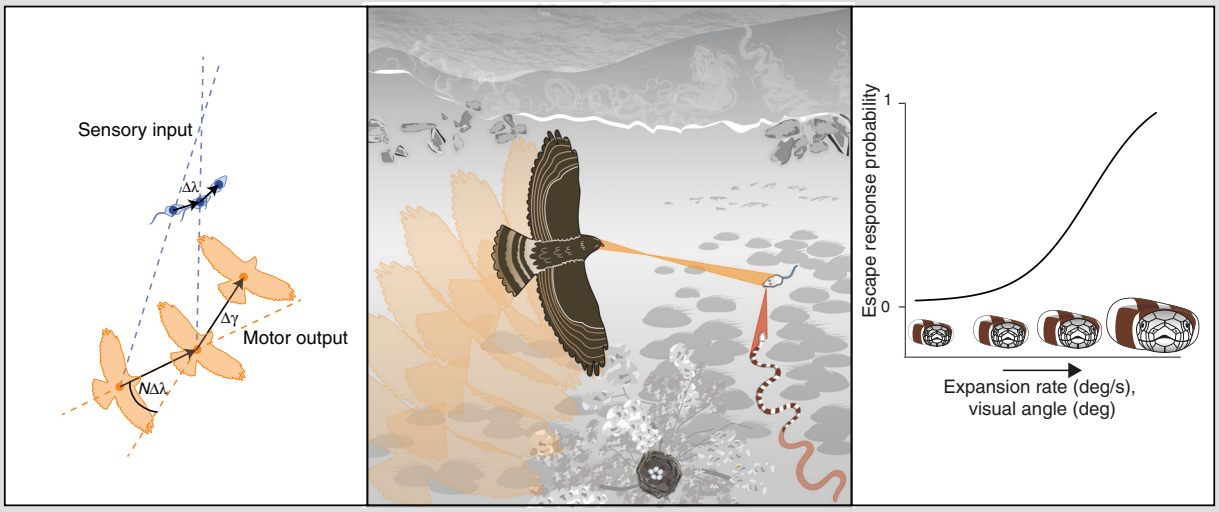
**Step (2): identify the constraints.** In complex behavioral tasks, a given objective can often be achieved in many different ways [39]. Which of the many possible solutions ends up being implemented often depends on constraints. Two crucial constraints are what the animal can measure — constraints on the 'inputs' that inform a behavioral decision — and how the animal can respond to measurements — constraints on motor capabilities or behavioral 'outputs'. Relevant constraints on sensory inputs include things like the accuracy with which measurements can be made by each sensory modality, and processing delays that occur when integrating signals from each modality [23, 94]. On the output side, constraints may include things like the maximum angular acceleration an animal can achieve, or the biomechanical delays associated with responding to different kinds of motor commands [104]. For example, during high-speed attacks by diving falcons [26], limits on visual precision, response delay, wing loading, and roll acceleration are key constraints.

**Step (3): identify candidate algorithms and build mathematical models to describe them.** The next step is to identify candidate algorithms that satisfy the objective and obey the constraints. In some cases, it may be possible to deduce candidate algorithms just by writing down the key parameters of the problem as Yuan [43] did when deriving strategies for intercepting a moving target. In other cases, the connection between the ultimate objective and near-term goals may be less clear. In such cases, careful measurements of the behavior may be the best way to proceed (for example [11–13]). The candidate algorithm (the input-to-output mapping) should then be described using a mathematical relationship between sensory input and motor output, for example in the form of a differential, difference, or state equation, or a stochastic process. The steering of hawks and falcons during pursuit maneuvers is consistent with a proportional navigation guidance algorithm (Box figure) [6,28]) that links changes in the angle of the animal's velocity vector, $\gamma$, to changes in perceived line-of-sight angle to a target, $\lambda$, according to the relationship: $(d\gamma/dt) = N(d\lambda/dt)$. The navigation constant, $N$, determines how strongly the animal changes its direction of motion in response to a change in the line-of-sight angle.

**Step (4): compare and test algorithms.** Before using the algorithm to explore implementation or outcomes, it is important to determine whether the input-to-output mapping embodied in a particular algorithm is sufficient to accurately describe behavior. In many cases, more than one algorithm could potentially solve the problem. Step 4 therefore involves designing experiments that test predictions of candidate algorithms. Returning to the example of a predatory bird pursuing fleeing prey suppose the bird must chase its prey through clutter. The pursuer has at least two goals: capture the prey and avoid injury. The second goal requires not colliding with the surrounding clutter. Studies of vision-guided obstacle avoidance have identified two primary algorithms animals use to avoid obstacles. The first, found in honeybees [105] and parakeets [106], is to balance the velocity of optic flow on the left and right sides of the body. The second, found in hummingbirds [13], is to balance the rate of image expansion on the two sides. An experiment to distinguish the two algorithms would be to fly trained hawks through a passage with static and moving patterns while tracking how the animal moves in response [13]. Mathematical models of the two competing algorithms can be used to make quantitative predictions, and the predictions can be compared to data. Often, none of the originally proposed algorithms will adequately predict the animal's behavior. In such cases, algorithm development (step 3) and algorithm testing (step 4) really represent a cycle, where the researcher hypothesizes algorithms, tests them with experiments, quantifies discrepancies that lead to new hypothesized algorithms, and so on [6,28].

*(Continued on next page)*

**Box 1. *Continued***




Behavioral algorithms guide interactions among organisms. Left panel: a hawk measuring the line-of-sight angle to a mouse, and turning to counteract changes in that angle using a proportional navigation guidance algorithm [28]. Right panel: an approaching snake from the perspective of the mouse. The visual angle — the angular region of the mouse's visual field taken up by the snake — and its expansion rate encode information about the predator's approach [14], and the probability that the mouse will initiate a high-speed escape maneuver depends on this angle, its expansion rate, and other parameters of the visual scene [107].

that these input-to-output mappings can be well approximated by simple mathematical relationships. Why such low-dimensional mappings should exist when the apparent degrees of freedom of biological systems are so numerous is a deep question [39,40], and one that we expect will attract considerable attention in the coming years. At present, however, the algorithmic hypothesis is largely motivated by empirical findings: although patterns of behavioral output can be intricate and highly dynamic [41,42], these patterns can often be predicted with surprising accuracy by simple mathematical models [12,37,38]. For example (Box 1), during pursuit maneuvers, hawks and falcons follow trajectories that are often tortuous and seemingly idiosyncratic, but the relationships between incoming visual input and turning behavior can be explained by variants of a simple guidance algorithm known as proportional navigation [6,26,28].

In the cases where algorithms have been used most effectively, the key to identifying the algorithm has been to determine *which* low-dimensional outputs are essential, and *which* inputs are predictive of those outputs (Box 1). Perhaps surprisingly, successful efforts to identify the relevant inputs, outputs, and the mapping between them have often been guided, at least initially, by theory (for example [14,43]) rather than by data.

## Algorithm to Implementation

Identifying and modeling behavioral algorithms can be extremely useful when studying how the nervous system generates behavior. Knowledge of algorithms can drastically narrow the range of possible measurements the animal could be using to guide its actions. This knowledge can also provide clues about how sensory measurements are stored, compressed, and transduced. An instructive case comes from the study of how animals detect and respond to impending collisions. The ability to anticipate a collision is, of course, crucial both for predators and prey [24,44]. The groundwork for the modern understanding of how animals detect impending collisions was largely laid by two psychologists, Gibson [45] and Lee [14], in work that was primarily theoretical in nature. This work emphasized that apparent expansion or 'looming' of a visual object could indicate when the object was on a collision course with the viewer, and in some cases, even encode the time to collision [14]. Predictions of this early theory were borne out in psychophysical experiments in which subjects were presented with expanding visual objects ([44] and references therein).

Motivated by these results, researchers began to search for neurons in the visual system that respond selectively to looming stimuli, and found them in the descending contralateral movement detector (DCMD) and lobula giant movement detector (LGMD) of locusts [15,46], and in specialized neurons within the nucleus rotundus of pigeons [16]. Research into the mechanistic underpinnings of collision detection continues to bear fruit. For example, the circuit-level mechanisms that allow animals to measure looming visual objects are now becoming clearer, at least in genetically tractable model organisms [24,47]. At the same time, we are learning more about how animals produce flexible responses to looming objects with different properties [18,24,48] and in different natural contexts [38].

The lesson from studies of collision detection is that a few key visual features of an approaching object — the object's apparent size and expansion rate — are sufficient to indicate an imminent collision, and to convey information about the time course of that collision [14]. Neurons in the visual system measure and encode

these variables [15,49]. Moreover, the mapping from visual input to behavioral response — in the form of initiation of rapid escape maneuvers — is low-dimensional, and the form of this mapping appears to be shared across distantly related species [37]. A mechanistic understanding of collision detection has also led to new questions about how animals control other elements of evasion behavior, including action selection early in an escape maneuver [18,48], and trajectory control during egress [38].

Thus, insights derived from collision avoidance algorithms have continued to open doors to the understanding of how animals generate complex behaviors to avoid being captured. Although these algorithms appear simple, escape behaviors are not rigid. Recent analyses have shown how gain control, multimodal sensory integration, and internal state dependencies — for example, dependence on hunger state [50] — modulate the basic rules of escape behavior [7]. These studies are particularly exciting because they have the potential to uncover the neural mechanisms behind patterns of behavior such as hunger-dependent risk-taking [51] that have long been observed in wild animals.

When generating pursuit and evasion maneuvers, animals must respond to incoming sensory cues in ways that are very rapid but also very precise [26]. Achieving speed and precision is difficult, in part, because there is a vast stream of sensory data entering the brain, only some of which is relevant to a given behavioral task. Moreover, different tasks may require using the same sensory data in different ways, creating conflicts that must be resolved quickly. As an example of this, many visual animals exhibit a behavioral reaction known as an optomotor response, during which the animal responds to perceived whole field visual motion on the retina by turning in a way that counteracts that motion [52]. This response stabilizes the animal's orientation relative to external landmarks.

After the discovery of this algorithm, researchers realized that the optomotor response could be problematic for maneuvering animals because it would counteract volitional turns. This problem could be solved if an 'efference copy' of the motor command related to turning were sent to the visual system to suppress the optomotor response during volitional turns [19,20]. A compelling example of such efference copy modulation was found in flies, which make rapid changes in walking or flying trajectory to evade threat stimuli [53]. These changes in trajectory involve a change in both body yaw and roll. In the roll direction, the optomotor response is beneficial because it allows the fly to keep its head aligned with the horizontal plane. In the yaw direction, however, an optomotor correction would cause a fly to turn back in the direction from which it began the turn. Turning flies appear to maintain optomotor responses to roll but suppress them to yaw. These behavioral observations led to the discovery of neural mechanisms that differentially suppress the optomotor response along different body axes: Kim *et al.* [54] experimentally demonstrated suppression of optic flow signals in fly lobula plate tangential cells that encode optic flow in the yaw direction. This work illustrates how identifying a behavioral algorithm and evaluating its consequences in different contexts can help reveal how the brain resolves conflicts to produce flexible responses that are suited to the challenges animals face when producing natural behavior.

## Algorithm to Outcome

Behavioral algorithms have been central in theory-guided investigations of the neural and biomechanical mechanisms behind pursuit and evasion maneuvers, but they have also helped reveal how long sequences of pursuit and evasion behavior are constructed, and how the outcome of such behaviors depend on features of the environment. One area where algorithmic models have been particularly important is in the study of how predators guide motion when chasing prey. As in the case of collision avoidance behavior, theoretical studies were behind many early insights about the relevant sensory features for pursuit behaviors. Theoretical treatment of pursuit algorithms was motivated by military applications, where the United States' Navy sought to develop self-guided missiles to intercept fighter planes [55]. One of the earliest algorithms proposed to guide such missiles was referred to as a 'pure pursuit' strategy because, at each point in time, the purser attempts to move toward the current location of the target by guiding its steering to null the difference between its velocity vector and the vector pointing to its target. This algorithm was simple to implement, but mathematical analysis revealed that, to intercept targets, it would often require angular accelerations that far exceeded performance capabilities of existing missiles [43,55].

This problem could be overcome, however, if rather than steering toward the current location of the target, the pursuer instead attempted to intercept the target at a predicted location some time in the future. While such a strategy would appear to require forecasting the future location of a target, Yuan [43] and others showed that this strategy could be effectively implemented using a simple reactive feedback control rule now referred to as 'proportional navigation', where the pursuer turns at a rate proportional to the rate of change in the line-of-sight angle to the target (Box 1). The strength of this algorithm is that by reacting to a readily measurable feature of relative target motion, the algorithm effectively predicts the future location of the target and executes a least-distance trajectory to intercept it, so long as the target velocity remains stable and target maneuvering is minimal.

Proportional navigation, pure pursuit, and related interception algorithms have provided starting points for identifying the sensory-motor transformations animals use to intercept their prey. For example, a surge of recent studies show that many predator species use proportional navigation, deviated pursuit, or similar reactive guidance laws for prey interception (for example [6,23,28,56,57]). Other studies use these algorithms as null models from which to build more complex descriptions of guidance behavior [11,58]. Studies of pursuit illustrate the importance of using models of candidate algorithms as quantitative hypotheses of how organisms transform sensory inputs into behavior. Without considering the theory behind pursuit algorithms [55], it is not at all clear why predators as diverse as flies [58], falcons [6] and beetles [56] should employ similar strategies when chasing down their prey. In the absence of algorithmic models and the theoretical principles derived from them, our understanding of animal interception behavior would look very different.

Interception algorithms have also been used to understand variation in behavior and to anticipate how behavioral outcome will vary with features of the environment. For example, when

targeting small perches, Egyptian fruit bats steer in a way that is consistent with a proportional-derivative guidance rule: the bat turns at a rate that is governed by both the deviation angle — the angle between the bat's velocity vector and its line-of-sight to target — and the rate of change in that angle [23]. Two key parameters govern the animal's ability to steer to target using this algorithm: the precision of measurements of the line-of-sight angle, and the delay associated with making and reacting to these measurements.

The bat visual system and biosonar system operate with different levels of precision and are associated with different delays; vision is more precise than biosonar, and the delays associated with visual responses are shorter. This leads to the prediction that the bat can apply higher steering forces when flying in the light, where vision can be used to measure angles, than when flying in the dark, where the animal must rely on sonar alone. These predictions were confirmed [23], revealing that the flight paths these animals use to approach targets may be fundamentally constrained by noise and delays in their sensory systems. The key point is that knowledge of the algorithm — in this case inferred through a combination of existing control theoretic results and patterns in data — can lead to precise, testable predictions about how performance should change in different sensory landscapes.

## Interactions between Pursuers and Evaders: Games between Algorithms

Among the most challenging aspects of pursuit and evasion, and of many other natural behaviors, is the fact these behaviors are employed during interactions with other organisms; in nature, pursuers and evaders interact with one another in a feedback loop, with pursuer and evader each adjusting its behavior to account for the actions of its adversary. In the past, most studies of pursuit and evasion have avoided the difficulties of pursuer–evader feedbacks by ignoring or experimentally eliminating responsive control of either the pursuer or evader. For instance, studies of evasion behavior often assume pursuers use simple, open-loop attack maneuvers [59], whereas the studies of these same attack maneuvers show that predators often use some form of feedback control to pursue prey [6,56,57]. Likewise, much of the theory used to study interception strategies are based on 'non-maneuvering' targets [55] rather than being based on targets that are, themselves, actively seeking to evade their pursuer.

Reconciling these inconsistencies, either through theory or experiments, requires that we more carefully consider how animals interact with one another. Again, building models of algorithms that guide pursuit and evasion maneuvers could help lead to a solution. Armed with candidate algorithms (Box 1), game theory [60] could offer a particularly potent tool for studying the dynamic interactions among organisms that react to one another. The goal of game theoretic analyses as they have been applied to pursuit and evasion behavior is typically to identify the best possible algorithm or set of algorithms *both* the pursuer and evader could use to combat one another [61,62], or to determine the performance properties of a given algorithm when it plays against a broad class of opposing algorithms [63]. Game theory adds an element that is missing from more traditional analyses: it explicitly considers the fact that the value of a particular behavior depends on the behaviors it is playing against. Concepts like 'evolutionary arms races' [64] and 'optimal' ecological strategies [61] hinge on this feedback between behaviors of interacting animals, which is why game theory has much potential to add rigor to these oft-cited biological concepts.

Game theoretic analyses of guidance algorithms help illustrate the kind of insights to be gained by applying game theory to study pursuit and evasion more broadly. Using the theory of differential games, Ho *et al.* [63] showed that proportional navigation is an optimal strategy for intercepting moving targets, assuming a set of conditions on pursuer and target motion are met. The performance of this algorithm as well as the simplicity of the computations it involves may help explain why it appears to have evolved across diverse animal lineages with vastly different brains [28,65].

But the optimality of proportional navigation requires strong assumptions. Among these are the requirements that the target's velocity is stable and maneuvering is minimal, and that there are no appreciable time delays between sensory input and responses of the pursuer. When a pursuer steers using proportional navigation with delays, steering can become unstable and the pursuer can lose control completely [66]. Animals appear to execute proportional navigation despite having sensory-motor delays of tens or even hundreds of milliseconds, raising the question of how they can implement this algorithm without losing control. The risk of losing control is greatest if the pursuer attempts to apply large correcting forces in response to perceived changes in line-of-sight angle [66,67], which may help explain both why animals tend to use turning gains lower than the theoretically-predicted optimal gains in delay-free systems [6,28], and why animals appear to adjust the steering forces they apply as a function of the delay associated with the sensory modality they are using (for example, biosonar *versus* vision [23]).

Future game theoretic analyses could address the question of how prey maneuvering [68] affects the success of proportional navigation and other pursuit algorithms. Certain types of target maneuver can destroy the optimality of proportional navigation and reduce the probability that the pursuer will intercept the target at all [69]. This raises questions about whether prey might evolve evasion behaviors that are particularly good at combating proportional navigation. A combination of differential games and stochastic control could be used to understand how evader behavior can disrupt pursuit algorithms (for example [70]), and to more rigorously address longstanding questions about whether producing random or 'protean' maneuvers when fleeing from predators [59,68] can be optimal.

Another emerging method for studying interactions between pursuers and evaders uses computational models of pursuit and evasion behavior built around data from pursuer–evader interactions in the field [26]. For example, Cade *et al.* [71] combined empirically measured attack maneuvers of humpback whales with experimental studies of the escape algorithms of their anchovy prey to understand how whales are able to capture thousands of anchovies in a single lunge [72], despite their limited maneuverability. By fitting an algorithmic model to anchovy escape responses, the authors of this study found that fish escape maneuvers are triggered by the strong visual stimulus produced when an approaching humpback opens its mouth to begin engulfment, revealing why humpbacks delay mouth

opening when attacking anchovy schools, but not when attacking slower, less responsive prey.

Wilson *et al.* [64] applied a similar approach motivated by the classic 'turning gambit' theory of Howland [73] to understand the biomechanics and behavior of interactions between lions and zebras, and cheetahs and impalas. They used a computational model of the terminal phase of predator–prey chases to reveal how both predator and prey could maximize success (capturing and avoiding capture, respectively), and to show that predators must come close to their absolute performance limits to reliably capture prey.

As we continue to advance our understanding of natural behavior, it will be crucial to consider the fact that many of the behaviors an animal executes are really responses to other

**Box 2. Coarse-graining and refinement of behavioral algorithms.**

Model coarse-graining and refinement are used to understand how processes at one scale emerge from, or influence processes at, another scale [80,108]. Both procedures begin with a mathematical model of a phenomenon of interest at a single scale, for example, a mathematical model of the behavioral algorithm that predicts whether an animal will exhibit a high-performance escape maneuver as a function of the sequence of visual stimuli it has experienced (Box figure) [18,24,48]). Refinement of this model might involve expressing model parameters as functions of a finer-scale process: for example, a more detailed model of the retina, or a model of the activity of neurons involved in the Mauthner cell circuit and related circuits [48]. Coarse-graining of the algorithmic model could involve averaging over possible sequences of sensory stimuli or conditions an animal might experience to calculate expected long-run performance (Box figure).

***Refinement.*** In a recent biological example of refinement, Bahl and Engert [78] developed a model to study how larval zebra fish discriminate the direction of whole-field visual motion from a field of projected dots that move with high or low coherence. The behavioral algorithm describing how sensory input drives an animal's turning behavior was well-described by a leaky integrator model of the form:

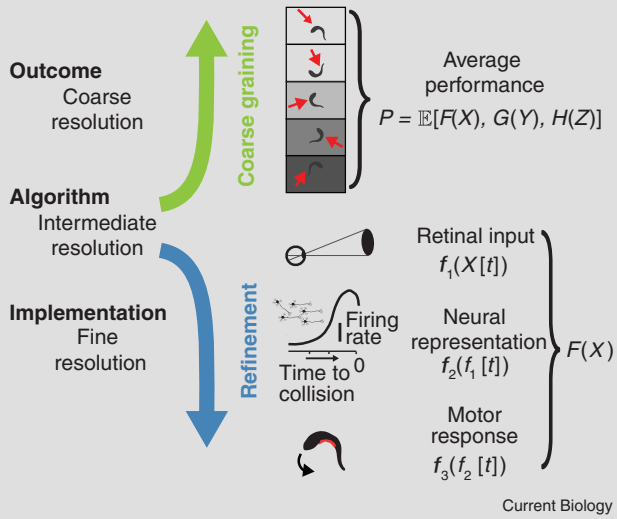
$$\tau \frac{dD(t)}{dt} = c(t) - D(t) + N(0, \sigma),$$

where $D(t)$ is a latent *decision variable* (the animal makes a decision to turn left or right when this variable crosses a positive or negative threshold, respectively), $c(t)$ is the coherence of the visual motion presented to the animal (a measure of the salience of the direction of dot motion), $\tau$ is the timescale of sensory integration, and $N$ is Gaussian noise with zero mean and standard deviation, $\sigma$. This algorithmic model states that the animal integrates past visual stimuli it has seen through a noisy integration process, with memory timescale $\tau$, and uses this information to decide when to turn. Fitting this model to behavioral data revealed that the memory timescale is on the order of seconds, far longer than the millisecond timescale most relevant to individual neurons [78]. To explain this long timescale, the authors used measurements from neural populations in the zebra fish hindbrain to motivate a network model of activity within populations of neurons that encode evidence for left *versus* right visual motion, and the corresponding evidence thresholds. This fine-scale model reproduced neural firing patterns, and was consistent with predictions of the algorithmic leaky integrator model, suggesting that the memory timescale is a property of neural populations rather than individual neurons. A final step in refining this model would be to mathematically derive the form and structure of the algorithmic model from the network model of neural activity so that quantitative properties at the algorithmic level could be predicted in terms of the properties of interlinked neural populations.

***Coarse-graining.*** Coarse-graining is used to move from more detailed to less detailed descriptions of a system by taking averages over some of the state variables [80,108]. Applying this method to behavior could involve starting with models of behavioral algorithms and successively averaging over details to retain only a few statistics of the typical dynamics (Box figure; for example [109]). Particularly instructive examples of coarse-graining are given by Flierl *et al.* [110] in the context of collective behavior, and Meshulam *et al.* [81] in the context of neural ensembles. Importantly, by averaging over dynamics that occur at short temporal and spatial scales, one sacrifices detailed predictions that can be made with a fine-grained model in exchange for a tractable description of the outcome and implications of behavior over longer timescales. In a recent example of this, Gil and Hein [27] studied the escape and foraging behavior of coral reef fish feeding in dangerous habitats in a coral reef. Fish make decisions to cease feeding and to flee based on visual cues about predatory threats and on visual cues produced by the actions and locations of neighboring fish. Although escape decisions depend on detailed sequences of sensory stimuli [38] (Figure 1), the average behavior of fish over minutes to hours can be captured by a stochastic process model that incorporates the way fish respond to a typical sequence of sensory stimuli. This coarse-grained model of behavior accurately predicted the long-run outcome of the many escape and feeding decisions animals make over the course of a day [27]. Importantly, because fine- and coarse-grained models describe the same processes, each model can be used to make predictions about the other [110]. This mathematical connection between coarse and fine scales allows for interesting scientific exercises that are impossible without it. For example, one can ask the question: "what would happen to long-run performance if behavior were performed differently?" In some cases, average performance might be unchanged, whereas in others, seemingly small changes in behavior — for example, changes in the way individual fish react to sensory stimuli produced by their neighbors — can have tremendous effects on performance [27]. Such counterfactual analyses have much to teach us about why behaviors operate as they do [32].

*(Continued on next page)*

**Box 2. *Continued***




Studies can *refine* understanding of behavior by investigating how the algorithm, $F(X)$, is implemented by the sensory system, brain, and musculoskeletal system. If $F(X)$, has been experimentally verified, plausible models of implementation should reproduce predictions of $F(X)$. To move in the opposite direction, the outcome of a particular set of algorithms can be rigorously studied by *coarse-graining*. This can be done by averaging over the range of sensory input and conditions the animal experiences (for example, different attack directions, light *versus* dark) and quantifying the outcomes achieved using algorithms $F$, $G$, and $H$.

animals that are, themselves, behaving. Game theory and computational models are likely to become increasingly important tools for studying the feedbacks that occur when algorithms play against one another.

## Using Algorithms to Bridge Levels of Organization and Analysis

A major advantage of building mathematical models of behavioral algorithms is that defining behavior mathematically raises the possibility of using mathematical analysis to connect processes that occur at different scales (Figure 1): at least in principle, algorithmic models can be derived from mechanisms at lower levels of organization, and used to derive models of phenomena at higher levels of organization. Of course, linking processes at different levels of organization is a stated goal of almost all integrative biological sciences. But, achieving this integration in practice can be exceedingly hard [74]. Indeed, moving rigorously from algorithm to implementation, or from algorithm to outcome (Figure 1) has been perhaps the most difficult step in past studies of pursuit and evasion. The most intuitive way to connect finer and coarser scales is to use construction: take all the details one knows about a system at the finest scale, and continue to include new details that appear when moving to higher levels of organization [75]. The problem with this strategy is that models become intractable almost immediately if all details are retained. If details are to be discarded, the question of which to discard must often be answered without knowing which are important for producing phenomena at higher levels of organization.

Several recent studies of pursuit and evasion have followed a different route. Researchers have bridged levels of organization using multi-scale models that add complexity judiciously, often capturing details at finer scales using statistical or phenomenological models that accurately represent known patterns (for example [23,24,26,47]). The hierarchy shown in Figure 1 helps to explain why such a modeling strategy can work: details that are crucial for understanding processes at one level of analysis or organization collapse into relatively few key state variables that matter at the next level. For example, at the implementation level, detecting a predator and initiating a turning maneuver may require several classes of motion detectors in the retina, a tight connection between retinal input and control of body bending and limb rotations, and a host of other coordinated mechanisms [18,47,76].

Yet in moving to the algorithmic level, such details are not necessary to understand that an animal nonlinearly integrates the size and expansion rate of a looming object to decide whether to flee [15,38]. Likewise, the algorithm the animal uses to select the initial direction of egress [77] and the algorithm used to convert visual input about the environment into an evasion trajectory [38] (Figure 1) collapse to a single number — the escape success rate — when one calculates how a given escape behavior affects the animal's ecological performance. The fact that details at one level collapse into a small set of core variables at the next is what makes it possible to move from one level of the hierarchy to another in a tractable way.

This philosophy of multi-scale modeling has much in common with formal techniques of *coarse-graining* and *refinement* used in mathematical physics (Box 2). The goal of both coarse-graining and refinement is to identify mathematical relationships between processes that operate at different scales. Doing this allows one to make detailed predictions about how processes at a finer scale (for example, the activity of populations of neurons) result

in properties at some coarser scale of description (for example, memory of past sensory stimulation [78]) and *vice versa*.

In perhaps the most famous application of such methods, Einstein used coarse-graining to show how the forces on a small object suspended in water depend on innumerable collisions with invisible molecules of water [79]. Not only did Einstein's mathematical formulation lead to incontrovertible evidence for the existence of atoms (a fact that was still not fully accepted at the time), it revealed a deep connection between an object's friction constant and its diffusion coefficient, two widely-studied properties of solid objects in fluids [80]. By explaining both friction and diffusion in terms of the micro-scale properties of molecular collisions, Einstein's analysis showed that a broad range of empirical phenomena emerged from the same micro-scale process. These discoveries enabled a tremendous leap in the theoretical physics of fluids, but also in the formal mathematical analysis of multi-scale phenomena [80].

As in physics, using coarse-graining and refinement to move from one level of description of behavior to another hinges on having well-defined mathematical models. In Box 2, we discuss *coarse-graining* and *refinement* and how they could provide a formal set of tools for bridging scales in the study of natural behavior. Similar approaches from statistical physics have been proposed and are currently being used to understand relationships between the properties of individual neurons and activity states of large neural sub-populations [81], traveling waves, and whole-brain states [82].

As Einstein's analysis showed, one benefit of having models that link processes across levels of organization is that such models can sometimes unify phenomena that initially appear unrelated. A biological example of this comes from studies of the neural basis of decision-making in multi-choice tasks, where an animal is tasked with choosing between alternative options and the temporal dynamics and outcome of the choice are recorded. One class of models used to analyze such behavioral choices, known as recurrent network models [83], describes firing patterns of populations of interconnected neurons as decisions are being made. By relating the activity state of neural populations to the outcome of a behavioral choice, these models relate neural and behavioral levels of organization to one another; model predictions can be tested using both measurements of neural activity and measurements of the timing and nature of behavioral choices. Recurrent network models have helped to explain several widely observed patterns in behavioral data, including how evidence for one choice versus another is weighted over time [84], speed-accuracy tradeoffs [85], and deviations from rational choice behavior [83]. These phenomena emerge from a combination of neural inhibition among populations of neurons and the manner in which population activity is read out and propagated through the decision circuit.

Multi-scale models that quantitatively link behavioral outcomes to the activity of neural populations have not yet been applied widely in the study of pursuit and evasion. However, neuroethological evidence suggests that such models could be extremely valuable. For example, Evans *et al.* [24] recently identified an algorithmic model that accurately described escape decisions of mice. The authors also showed that distinct neural populations in the mouse midbrain appear to encode decisions about whether to mount an escape response, and the vigor with which to flee. This study provided clues about how information relevant to escape decisions is encoded at the neural level. A future modeling step could be to develop a fully multi-scale neural-algorithmic model that derives properties of the decision-making algorithm from dynamics of neural ensembles.

In addition to providing a strong, quantitative connection between behavioral decisions and neural dynamics, refinement and coarse-graining may also allow us to use insights about behavioral algorithms to gain traction on biological processes that play out over much longer timescales. For instance, the rate of interactions between predators and prey is a fundamental rate parameter that governs dynamics of predator and prey populations. But *predicting* this rate is notoriously difficult. By incorporating realistic constraints gleaned from mechanistic studies of animal search behavior, it was recently shown that these interaction rates can be derived from behavioral models, in a way that relates them to animal sensory capabilities and decision-making [29,86]. Deriving ecological rates from mechanistic, data-driven models of behavior represents a fundamentally new way of building models of ecological populations and communities [87]. In the future, such analyses could provide a conduit through which findings in biomechanics and neuroscience could inform ecological and evolutionary analyses.

## Open Questions about Pursuit and Evasion Algorithms

The preceding sections might give the impression that many of the algorithms involved in pursuit and evasion have already been identified. In truth, the discovery of one algorithm for pursuit or evasion has often suggested the existence of others that have yet to be discovered. For example, we are beginning to understand the algorithms that govern the initiation of escape responses [7,37] and the initial choice of escape direction [77,88], but to evade a determined predator, an animal must have some way of guiding its trajectory beyond this initial maneuver. The algorithms involved in these later stages of evasion are not well understood. One intriguing idea is that simple, yet still undiscovered feedback control algorithms may guide evasion trajectories. Because a fleeing animal must not only maneuver out of the path of its attacker, but must also move in a way that allows it to reach shelter, such an algorithm must be able to balance multiple, potentially competing objectives.

An emerging hypothesis is that animals solve such multi-objective control problems by dynamically weighting the priority given to individual objectives. At one extreme, an animal may simply turn multi-objective control to a single-objective control by focusing only on the most immediate task [12] or that which can be achieved with the least disruption to some longer-term goal [89]. An alternative is to represent objectives in some form of common currency and to choose between them using heuristics [90] or time-varying weights [38]. The extent to which algorithms for evasion trajectory control resemble these alternatives and how such algorithms are implemented in the brain remain to be discovered.

Implicit in many algorithmic models of prey pursuit and collision avoidance is the assumption that an animal can isolate sensory stimuli from a particular target (for example, in the form of a change in the line-of-sight angle to a particular target) or a particular object that may be an approaching attacker (for example, in

the form of object size and expansion rate [15]). Yet in many natural settings, noise, clutter, and the presence of multiple prey or predators means that isolating stimuli from a specific source is not trivial. A key step forward in our understanding of pursuit and evasion algorithms will, therefore, be to understand how processes such as sensory filtration and selective attention might allow the animal to isolate an individual prey or predator. Neural mechanisms for filtration and selective attention have been identified (for example, [91,92]), but it is not known how error and noise introduced through these mechanisms affect pursuit and evasion behavior.

Most of the trajectory control algorithms discussed in this review have been modeled using simple, reactive feedback control that assumes steering behaviors are driven by continuous reactions to dynamic streams of incoming stimuli. However, growing evidence suggests that forecasting and motor planning are also critical in at least some pursuit and evasion behaviors (for example [11,93,94]). For example, Borghuis and Leonardo [94] found evidence that salamanders direct tongue strikes at the future location of moving prey rather than the prey's current location. By using a linear extrapolation of the prey's motion, the salamander is able to effectively forecast prey location, allowing it to strike fast-moving prey despite significant sensory-motor delays. This type of simple forecasting may prove common during the terminal phases of predator–prey interactions, where interactions take place at or below the timescale of typical sensory-motor delays. Known mechanisms for predictive coding (for example [95]) could facilitate such short-term forecasting.

A more challenging issue is determining whether feedback control, forecasting or state-estimation, and feed-forward planning are combined during pursuit and evasion behaviors [11]. The human motor control literature has grappled with related issues for many years and could provide a template for how research in this area could progress [96,97]. For example, the Optimal Feedback Control paradigm (OFC) [39,98], which has been central to the theory of human motor control, may also prove useful as a mathematical formalism for studying how animals combine planning, forecasting, and feedback control. In the past, OFC has primarily been used to understand how humans compensate for sensory-motor noise and external perturbations during simple motor control tasks, but future extensions of this framework could be used to better understand how animals might integrate feedforward and feedback mechanisms to achieve the more dynamic goals they face when interacting with predators and prey.

The issues raised in this section represent just a small sample of the open questions about pursuit and evasion algorithms. While resolutions to these questions would help us better understand pursuit and evasion specifically, they are also deeply relevant to challenges faced during many other natural behaviors. Thus, we expect that studies of pursuit and evasion algorithms will continue to deliver lessons about the general principles that structure natural behaviors.

## Conclusions

Using pursuit and evasion as models, we have shown how an algorithmic approach to the study of natural behavior can shed light on how animals produce flexible, goal-driven behavior in nature. This approach addresses the challenge of integrating processes that occur at different levels of organization, on different timescales, and at different distances from ecological and evolutionary implications (Figure 1; Box 1; Box 2). Rather than beginning at the bottom or the top of the organizational hierarchy, we advocate starting in the middle, where study of the behavioral algorithms that link sensory input to behavioral output can provide a solid theoretical and empirical foundation from which to explore both the implementation and the outcome of behavior. As should be evident from the examples discussed, this approach has already led to important insights. But there is an opportunity and perhaps even a pressing need to apply it more broadly, particularly in light of the revolution in methods for automated collection of behavioral data occurring in computational ethology [41,42,99,100].

There is understandable excitement around new tools for automatically measuring and classifying animal behavior. Yet, whether these methods fulfill their promise of revolutionizing the study of behavior [99,101,102] will depend on whether the massive data streams produced by new computational methods reveal new principles of animal behavior [103]. It is crucial that we remember the importance of theory in general, and algorithms in particular, when attempting to interpret the behavioral patterns these new methods can quantify. An algorithmic approach could provide a way to harness these new tools and use them to develop truly integrative, data-driven theories of behavior.

Gaining a full understanding of the complex, multi-scale processes involved in natural behavior is likely to require that we bridge levels of analysis and levels of organization [5]. If the goal of studying pursuit, evasion, or any other complex behavior is to understand how the brain generates sequences of goal-directed movements, how behavioral strategies play against one another, or how evolution feeds back on the structures that implement neural computations related to behavior, then we must link the implementation, algorithms, and outcome of behavior. Achieving these goals will require an invigorated focus on behavioral algorithms. We believe that the widespread adoption of an algorithmic approach to natural behavior is poised to change the way we study and understand animal behavior.

## ACKNOWLEDGEMENTS

We thank S. Heredia for assistance with figures and illustrations, and M. Gil and A. Fahimipour for critical readings of early drafts. This work was initiated as part of a workshop hosted by the Kavli Institute of Theoretical Physics at the University of California Santa Barbara and the authors acknowledge the institute's support. This research was supported in part by the National Science Foundation under Grant No. NSF PHY-1748958, NIH Grant No. R25GM067110, and the Gordon and Betty Moore Foundation Grant No. 2919.01. A.M.H., B.T.M., and J.C.L. were supported by NSF IOS grant no. 1855956. A.M.H. acknowledges the NOAA High Performance Computing and Communications Program, and Simons Foundation Grant 395890. This project has received funding from the European Research Council (ERC) under the European Union's Horizon 2020 research and innovation programme (grant agreement No. 682501).

## REFERENCES

1. Olberg, R.M. (2012). Visual control of prey-capture flight in dragonflies. Curr. Opin. Neurobiol. *22*, 267–271.

2. Bargmann, C., Newsome, W., Anderson, A., Brown, E., Deisseroth, K., Donoghue, J., MacLeish, P., Marder, E., Normann, R., and Sanes, J. (2014). BRAIN 2025: a scientific vision. In Brain Research through Advancing Innovative Neurotechnologies (BRAIN) Working Group Report to the Advisory Committee to the Director, NIH (2014).

3. Carandini, M. (2012). From circuits to behavior: a bridge too far? Nat. Neurosci. *15*, 507–509.

4. Jonas, E., and Kording, K.P. (2017). Could a neuroscientist understand a microprocessor? PLoS Comput. Biol. *13*, e1005268.

5. Krakauer, J.W., Ghazanfar, A.A., Gomez-Marin, A., MacIver, M.A., and Poeppel, D. (2017). Neuroscience needs behavior: correcting a reductionist bias. Neuron *93*, 480–490.

6. Brighton, C.H., Thomas, A.L.R., and Taylor, G.K. (2017). Terminal attack trajectories of peregrine falcons are described by the proportional navigation guidance law of missiles. Proc. Natl. Acad. Sci. USA *114*, 13495–13500.

7. Evans, D.A., Stempel, V., Vale, R., and Branco, T. (2019). Cognitive control of escape behaviour. Trends Cogn. Sci. *23*, 334–348.

8. Marr, D. (1982). Vision: A Computational Approach (MIT Press).

9. Reichardt, W., and Poggio, T. (1976). Visual control of orientation behaviour in the fly. Part I. A quantitative analysis. Q. Rev. Biophys. *9*, 311–375.

10. Land, M.F., and Collett, T.S. (1974). Chasing behaviour of houseflies (*Fannia canicularis*). J. Comp. Physiol. *89*, 331–357.

11. Mischiati, M., Lin, H., Herold, P., Imler, E., Olberg, R., and Leonardo, A. (2015). Internal models direct dragonfly interception steering. Nature *517*, 333–338.

12. Lin, H., Ros, I.G., and Biewener, A.A. (2014). Through the eyes of a bird: modeling visually guided obstacle flight. J. R. Soc. Interface *11*, 20140239.

13. Dakin, R., Fellows, T.K., and Altshuler, D.L. (2016). Visual guidance of forward flight in hummingbirds reveals control based on image features instead of pattern velocity. Proc. Natl. Acad. Sci. USA *113*, 8849–8854.

14. Lee, D. (1976). A theory of visual control of braking based on information about time-to-collision. Perception *5*, 437–459.

15. Hatsopoulos, N., Gabbiani, F., and Laurent, G. (1995). Elementary computation of object approach by a wide-field visual neuron. Science *270*, 1000–1003.

16. Wang, Y., and Frost, B.J. (1992). Time to collision is signalled by neurons in the nucleus rotundus of pigeons. Nature *356*, 236.

17. Haehnel-Taguchi, M., Akanyeti, O., and Liao, J.C. (2014). Afferent and motoneuron activity in response to single neuromast stimulation in the posterior lateral line of larval zebrafish. J. Neurophysiol. *112*, 1329–1339.

18. von Reyn, C.R., Nern, A., Williamson, W.R., Breads, P., Wu, M., Namiki, S., and Card, G.M. (2017). Feature integration drives probabilistic behavior in the Drosophila escape response. Neuron *94*, 1190–1204.

19. von Holst, E., and Mittelstaedt, H. (1950). Das Reafferenzprinzip. Naturwissenschaften *37*, 464–476.

20. Chan, W.P., Prete, F., and Dickinson, M.H. (1998). Visual input to the efferent control system of a fly's gyroscope. Science *280*, 289–292.

21. van Breugel, F., and Dickinson, M.H. (2014). Plume-tracking behavior of flying Drosophila emerges from a set of distinct sensory-motor reflexes. Curr. Biol. *24*, 274–286.

22. Balkovsky, E., and Shraiman, B.I. (2002). Olfactory search at high Reynolds number. Proc. Natl. Acad. Sci. USA *99*, 12589–12593.

23. Bar, N.S., Skogestad, S., Marçal, J.M., Ulanovsky, N., and Yovel, Y. (2015). A sensory-motor control model of animal flight explains why bats fly differently in light versus dark. PLoS Biol. *13*, e1002046.

24. Evans, D.A., Stempel, A.V., Vale, R., Ruehle, S., Lefler, Y., and Branco, T. (2018). A synaptic threshold mechanism for computing escape decisions. Nature *558*, 590–594.

25. Gonzalez-Bellido, P.T., Peng, H., Yang, J., Georgopoulos, A.P., and Olberg, R.M. (2013). Eight pairs of descending visual neurons in the dragonfly give wing motor centers accurate population vector of prey direction. Proc. Natl. Acad. Sci. USA *110*, 696–701.

26. Mills, R., Hildenbrandt, H., Taylor, G.K., and Hemelrijk, C.K. (2018). Physics-based simulations of aerial attacks by peregrine falcons reveal that stooping at high speed maximizes catch success against agile prey. PLoS Comput. Biol. *14*, e1006044.

27. Gil, M.A., and Hein, A.M. (2017). Social interactions among grazing reef fish drive material flux in a coral reef ecosystem. Proc. Natl. Acad. Sci. USA *114*, 4703–4708.

28. Brighton, C.H., and Taylor, G.K. (2019). Hawks steer attacks using a guidance system tuned for close pursuit of erratically manoeuvring targets. Nat. Commun. *10*, 2462.

29. Hein, A.M., and Martin, B.T. (2019). Information limitation and the dynamics of coupled ecological systems. Nat. Ecol. Evol. *4*, 82–90.

30. Hassenstein, B., and Reichardt, W. (1953). Der schluss von reiz-reaktions-funktionen auf system-strukturen. Z. Naturforsch. *8*, 518–524.

31. Hodgkin, A.L., and Huxley, A.F. (1952). The components of membrane conductance in the giant axon of *Loligo*. J. Physiol. *116*, 473–496.

32. Tinbergen, N. (1955). The Study of Instinct (Clarendon Press).

33. Piccolo, J.J., Hughes, N.F., and Bryant, M.D. (2008). Water velocity influences prey detection and capture by drift-feeding juvenile coho salmon (*Oncorhynchus kisutch*) and steelhead (*Oncorhynchus mykiss irideus*). Can. J. Fish. Aquat. Sci. *65*, 266–275.

34. Francis, C.D., Ortega, C.P., and Cruz, A. (2014). Noise pollution changes avian communities and species interactions. Curr. Biol. *19*, 1415–1419.

35. Hein, A.M., Carrara, F., Brumley, D.R., Stocker, R., and Levin, S.A. (2016). Natural search algorithms as a bridge between organisms, evolution, and ecology. Proc. Natl. Acad. Sci. USA *113*, 9413–9420.

36. Fairhall, A. (2014). The receptive field is dead. Long live the receptive field? Curr. Opin. Neurobiol. *25*, ix–xii.

37. Peek, M.Y., and Card, G.M. (2016). Comparative approaches to escape. Curr. Opin. Neurobiol. *41*, 167–173.

38. Hein, A.M., Gil, M.A., Twomey, C.R., Couzin, I.D., and Levin, S.A. (2018). Conserved behavioral circuits govern high-speed decision-making in wild fish shoals. Proc. Natl. Acad. Sci. USA *115*, 12224–12228.

39. Todorov, E., and Jordan, M.I. (2002). Optimal feedback control as a theory of motor coordination. Nat. Neurosci. *5*, 1226–1235.

40. Kao, T.-C., and Hennequin, G. (2019). Neuroscience out of control: control-theoretic perspectives on neural circuit dynamics. Curr. Opin. Neurobiol. *58*, 122–129.

41. Berman, G.J., Choi, D.M., Bialek, W., and Shaevitz, J.W. (2014). Mapping the stereotyped behaviour of freely moving fruit flies. J. R. Soc. Interface *11*, 20140672.

42. Marques, J.C., Lackner, S., Félix, R., and Orger, M.B. (2018). Structure of the zebrafish locomotor repertoire revealed with unsupervised behavioral clustering. Curr. Biol. *28*, 181–195.

43. Yuan, L.C. (1943). Homing and Navigational Courses of Automatic Target Seeking Devices (RCA Laboratories Princeton N.J.).

44. Fotowat, H., and Gabbiani, F. (2011). Collision detection as a model for sensory-motor integration. Annu. Rev. Neurosci. *34*, 1–19.

45. Gibson, J.J. (1958). Visually controlled locomotion and visual orientation in animals. Br. J. Psychol. *49*, 182–194.

46. Rind, F.C., and Simmons, P.J. (1992). Orthopteran DCMD neuron: a reevaluation of responses to moving objects. I. Selective responses to approaching objects. J. Neurophysiol. *68*, 1654–1666.

47. Klapoetke, N.C., Nern, A., Peek, M.Y., Rogers, E.M., Breads, P., Rubin, G.M., Reiser, M.B., and Card, G.M. (2017). Ultra-selective looming detection from radial motion opponency. Nature *551*, 237–241.

48. Bhattacharyya, K., McLean, D.L., and MacIver, M.A. (2017). Visual threat assessment and reticulospinal encoding of calibrated responses in larval zebrafish. Curr. Biol. *27*, 2751–2762.

49. Sun, H., and Frost, B.J. (1998). Computation of different optical variables of looming objects in pigeon nucleus rotundus neurons. Nat. Neurosci. *1*, 296–303.

50. Barker, A.J., and Baier, H. (2015). Sensorimotor decision making in the zebrafish tectum. Curr. Biol. *25*, 2804–2814.

51. Krebs, J.R. (1980). Optimal foraging, predation risk and territory defense. Ardea *55*, 83–91.

52. Cronin, T.W., Johnsen, S., Marshall, N.J., and Warrant, E.J. (2014). Visual Ecology (Princeton University Press).

53. Muijres, F.T., Elzinga, M.J., Melis, J.M., and Dickinson, M.H. (2014). Flies evade looming targets by executing rapid visually directed banked turns. Science *344*, 172–177.

54. Kim, A.J., Fitzgerald, J.K., and Maimon, G. (2015). Cellular evidence for efference copy in *Drosophila* visuomotor processing. Nat. Neurosci. *18*, 1247.

55. Nahin, J. (2007). Chases and Escapes (Princeton University Press).

56. Haselsteiner, A.F., Gilbert, C., and Wang, Z.J. (2014). Tiger beetles pursue prey using a proportional control law with a delay of one half-stride. J. R. Soc. Interface *11*, 20140216.

57. McHenry, M.J., Johansen, J.L., Soto, A.P., Free, B.A., Paley, D.A., and Liao, J.C. (2019). The pursuit strategy of predatory bluefish (*Pomatomus saltatrix)*. Proc. Biol. Sci. *286*, 20182934.

58. Wardill, T.J., Fabian, S.T., Pettigrew, A.C., Stavenga, D.G., Nordström, K., and Gonzalez-Bellido, P.T. (2017). A novel interception strategy in a miniature robber fly with extreme visual acuity. Curr. Biol. *27*, 854–859.

59. Domenici, P., Blagburn, J.M., and Bacon, J.P. (2011). Animal escapology I: theoretical issues and emerging trends in escape trajectories. J. Exp. Biol. *214*, 2463–2473.

60. Isaacs, R. (1965). Differential Games: A Mathematical Theory with Applications to Warfare and Pursuit, Control and Optimization (Wiley).

61. Alpern, S., Fokkink, R., Timmer, M., and Casas, J. (2011). Ambush frequency should increase over time during optimal predator search for prey. J. R. Soc. Interface *8*, 1665–1672.

62. Scott, W.L., and Leonard, N.E. (2018). Optimal evasive strategies for multiple interacting agents with motion constraints. Automatica *94*, 26–34.

63. Ho, Y., Bryson, A., and Baron, S. (1965). Differential games and optimal pursuit-evasion strategies. IEEE Trans. Automat. Control *10*, 385–389.

64. Wilson, A.M., Hubel, T.Y., Wilshin, S.D., Lowe, J.C., Lorenc, M., Dewhirst, O.P., Bartlam-Brooks, H.L.A., Diack, R., Bennitt, E., Golabek, K.A., *et al*. (2018). Biomechanics of predator–prey arms race in lion, zebra, cheetah and impala. Nature *554*, 183–188.

65. Fabian, S.T., Sumner, M.E., Wardill, T.J., Rossoni, S., and Gonzalez-Bellido, P.T. (2018). Interception by two predatory fly species is explained by a proportional navigation feedback controller. J. R. Soc. Interface *15*, 20180466.

66. Dhananjay, N., Lum, K.Y., and Xu, J.X. (2012). Proportional navigation with delayed line-of-sight rate. IEEE Trans. Control Syst. Technol. *21*, 247–253.

67. Strydom, R., Singh, S.P., and Srinivasan, M.V. (2015). Biologically inspired interception: a comparison of pursuit and constant bearing strategies in the presence of sensorimotor delay. 2015 IEEE Int. Conf. Robot. Biomim. *2015*, 2442–2448.

68. Moore, T.Y., Cooper, K.L., Biewener, A.A., and Vasudevan, R. (2017). Unpredictability of escape trajectory explains predator evasion ability and microhabitat preference of desert rodents. Nat. Commun. *8*, 1–9.

69. Zarchan, P. (1995). Proportional navigation and weaving targets. J. Guid. Control Dyn. *18*, 969–974.

70. Gutman, S. (1979). On optimal guidance for homing missiles. J. Guid. Control *2*, 296–300.

71. Cade, D.E., Carey, N., Domenici, P., Potvin, J., and Goldbogen, J.A. (2020). Predator-informed looming stimulus experiments reveal how large filter feeding whales capture highly maneuverable forage fish. Proc. Natl. Acad. Sci. USA *117*, 472–478.

72. Cade, D.E., Friedlaender, A.S., Calambokidis, J., and Goldbogen, J.A. (2016). Kinematic diversity in rorqual whale feeding mechanisms. Curr. Biol. *26*, 2617–2624.

73. Howland, H.C. (1974). Optimal strategies for predator avoidance: the relative importance of speed and manoeuvrability. J. Theor. Biol. *47*, 333–350.

74. Laughlin, R.B., Pines, D., Schmalian, J., Stojković, B.P., and Wolynes, P. (2000). The middle way. Proc. Natl. Acad. Sci. USA *97*, 32–37.

75. Anderson, P.W. (1972). More is different. Science *177*, 393–396.

76. Domenici, P. (2001). The scaling of locomotor performance in predator–prey encounters: from fish to killer whales. Comp. Biochem. Physiol. A *131*, 169–182.

77. Dunn, T.W., Gebhardt, C., Naumann, E.A., Riegler, C., Ahrens, M.B., Engert, F., and Del Bene, F. (2016). Neural circuits underlying visually evoked escapes in larval zebrafish. Neuron *89*, 613–628.

78. Bahl, A., and Engert, F. (2019). Neural circuits for evidence accumulation and decision making in larval zebrafish. Nat. Neurosci. *23*, 94–102.

79. Einstein, A. (1956). English transl. Investigations on the Theory of Brownian Movement (New York: Dover Publications), pp. 549–567.

80. Castiglione, P., Falcioni, M., Lesne, A., and Vulpiani, A. (2008). Chaos and Coarse Graining in Statistical Mechanics (Cambridge: Cambridge University Press).

81. Meshulam, L., Gauthier, J.L., Brody, C.D., Tank, D.W., and Bialek, W. (2019). Coarse graining, fixed points, and scaling in a large population of neurons. Phys. Rev. Lett. *123*, 178103.

82. Goldman, J.S., Tort-Colet, N., Di Volo, M., Susin, E., Bouté, J., Dali, M., Carlu, M., Nghiem, T.A., Górski, T., and Destexhe, A. (2019). Bridging single neuron dynamics to global brain states. Front. Syst. Neurosci. *13*, 75.

83. Wang, X.-J. (2012). Neural dynamics and circuit mechanisms of decision-making. Curr. Opin. Neurobiol. *22*, 1039–1046.

84. Wong, K.F., Huk, A.C., Shadlen, M.N., and Wang, X.-J. (2007). Neural circuit dynamics underlying accumulation of time-varying evidence during perceptual decision-making. Front. Comput. Neurosci. *1*, 1–6.

85. Furman, M., and Wang, X.-J. (2008). Similarity effect and optimal control of multiple-choice decision making. Neuron *60*, 1153–1168.

86. Borchering, R.K., Bellan, S.E., Flynn, J.M., Pulliam, J.R.C., and McKinley, S.A. (2017). Resource-driven encounters among consumers and implications for the spread of infectious disease. J. R. Soc. Interface *14*, 20170555.

87. O'Dwyer, J.P. (2019). Beyond an ecological ideal gas law. Nat. Ecol. Evol. *4*, 14–15.

88. Domenici, P., Blagburn, J.M., and Bacon, J.P. (2011). Animal escapology II: escape trajectory case studies. J. Exp. Biol. *214*, 2474–2494.

89. Ros, I.G., Bhagavatula, P.S., Lin, H.-T., and Biewener, A.A. (2017). Rules to fly by: pigeons navigating horizontal obstacles limit steering by selecting gaps most aligned to their flight direction. Interface Focus *7*, 20160093.

90. Brace, N.L., Hedrick, T.L., Theriault, D.H., Fuller, N.W., Wu, Z., Betke, M., Parrish, J.K., Grünbaum, D., and Morgansen, K.A. (2016). Using collision cones to assess biological deconfliction methods. J. R. Soc. Interface *13*, 20160502.

91. Wiederman, S.D., Fabian, J.M., Dunbier, J.R., and O'Carroll, D.C. (2017). A predictive focus of gain modulation encodes target trajectories in insect vision. eLife *6*, e26478.

92. Nordstrom, K., Barnett, P.D., and O'Carroll, D.C. (2006). Insect detection of small targets in moving visual clutter. PLoS Biol. *4*, e54.

93. Card, G.A., and Dickinson, M.H. (2008). Visually mediated motor planning in the escape response of *Drosophila*. Curr. Biol. *18*, 1300–1307.

94. Borghuis, B.G., and Leonardo, A. (2015). The role of motion extrapolation in amphibian prey capture. J. Neurosci. *35*, 15430–15441.

95. Hosoya, T., Baccus, S.A., and Meister, M. (2005). Dynamic predictive coding by the retina. Nature *436*, 71–77.

96. Scott, S.H. (2008). Inconvenient truths about neural processing in primary motor cortex. J. Physiol. *586*, 1217–1224.

97. McNamee, D.A., and Wolpert, D.M. (2019). Internal models in biological control. Annu. Rev. Control Robot. Auton. Syst. *2*, 339–364.

98. Scott, S.H. (2012). The computational and neural basis of voluntary motor control and planning. Trends Cogn. Sci. *16*, 541–549.

99. Anderson, D.J., and Perona, P. (2014). Toward a science of computational ethology. Neuron *84*, 18–31.

100. Calhoun, A.J., Pillow, J.W., and Murthy, M. (2019). Unsupervised identification of the internal states that shape natural behavior. Nat. Neurosci. *22*, 2040–2049.

101. Brown, A.E., and De Bivort, B. (2018). Ethology as a physical science. Nat. Phys. *14*, 653–657.

102. Mathis, M.W., and Mathis, A. (2020). Deep learning tools for the measurement of animal behavior in neuroscience. Curr. Opin. Neurobiol. *60*, 1–11.

103. Gomez-Marin, A., Paton, J.J., Kampff, A.R., Costa, R.M., and Mainen, Z.F. (2014). Big behavioral data: psychology, ethology and the foundations of neuroscience. Nat. Neurosci. *17*, 1455–1462.

104. Domenici, P. (2002). The visually mediated escape response in fish: predicting prey responsiveness and the locomotor behaviour of predators and prey. Mar. Freshw. Behav. Physiol. *35*, 87–110.

105. Srinivasan, M.V., Lehrer, M., Kirchner, W.H., and Zhang, S.W. (1991). Range perception through apparent image speed in freely flying honeybees. Vis. Neurosci. *6*, 519–535.

106. Bhagavatula, P.S., Claudianos, C., Ibbotson, M.R., and Srinivasan, M.V. (2011). Optic flow cues guide flight in birds. Curr. Biol. *21*, 1794–1799.

107. Yilmaz, M., and Meister, M. (2013). Rapid innate defensive responses of mice to looming visual stimuli. Curr. Biol. *23*, 2011–2015.

108. Bialek, W. (2012). Biophysics: Searching for Principles (Princeton University Press).

109. Bialek, W., Cavagna, A., Giardina, I., Mora, T., Silvestri, E., Viale, M., and Walczak, A.M. (2012). Statistical mechanics for natural flocks of birds. Proc. Natl. Acad. Sci. USA *109*, 4786–4791.

110. Flierl, G., Grünbaum, D., Levin, S., and Olson, D. (1999). From individuals to aggregations: the interplay between behavior and physics. J. Theor. Biol. *196*, 397–454.