Co-Evolution of Pursuit and Evasion I: Biological and Game-Theoretic Foundations[*]

Geoffrey F. Miller[†]and **Dave Cliff**

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School of Cognitive and Computing Sciences
University of Sussex, Brighton BN1 9QH, U.K.
Email: `geoffm@cogs.susx.ac.uk`, `davec@cogs.susx.ac.uk`
Phone: +44 273 606755 ext. 3102
Fax: +44 273 671320

Abstract

Animals often chase each other about. These pursuit-evasion contests require the continuous dynamical control of complex sensory-motor behavior, and give rise to some of the most common and challenging co-evolutionary arms races in nature. This paper argues for the importance and fruitfulness of studying pursuit-evasion scenarios using evolutionary simulation methods, and reviews the relevant literatures; in a companion paper, our simulation methods and results will be presented. We first review the biological ubiquity of pursuit-evasion contests, the *protean* (adaptively unpredictable) behavior that often evolves in evasion strategies (e.g. when prey zig-zag to evade predators), and the relevant neuroethology of capture by predators and escape by prey. The *differential game theory* relevant to analyzing pursuit-evasion games is then reviewed, including the proven optimality of *mixed strategies* (corresponding to protean behavior) in many such games, and the difficulty of deriving analytical solutions in realistically complex games. Previous work on evolving pursuit-evasion tactics in simulation and in real robots is then reviewed, and directions for further research are identified. We conclude with some possible engineering applications and scientific implications of pursuit, evasion, and their co-evolution.

Keywords: pursuit-evasion contests; co-evolution; protean behavior; differential game theory, mixed strategies; neuroethology;

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[†] Address after 1 Jan. 1995: Department of Psychology, University of Nottingham, Nottingham NG7 2RD, U.K. `geoffrey.miller@psychology.nottingham.ac.uk`

1 Introduction

Suppose that adaptive behavior research turns out to be wildly successful over the next few years, so robots can be built to perform various useful tasks in public spaces, such as cleaning, transport, security, and entertainment. At first, such robots will probably be expensive, slow-moving, and delicate. This raises two serious problems. The *biophilic baby* problem is that human infants and children show an innate and rather brutal curiosity about things that behave like animals (see Kellert & Wilson, 1993). so the more lifelike our robots, the more motivated children will be to chase them, hug them, poke them, dissect them, and throw them about. The *technophilic teenager* problem is that young entrepeneurs have economic motivations to steal anything that is both publicly accessible and expensive; a converse technophilic teenager problem is that young people sometimes show Luddite-like tendencies to damage and deface public machinery and vehicles. Unless precautions are taken, we can expect a thriving black market in graffiti-covered, battered, half-functioning robots. These problems can be ameliorated by one simple principle: autonomous agents must have at least the escape and evasion abilities of the common house pet. If they don't, they will not last long performing their tasks in public. Although the importance of evasion tactics has long been recognized in military applications, our whimsical alarmism about the perils facing public robots should make clear that the problems of pursuit and evasion are quite general.

Contests of pursuit and evasion are among the most common, challenging, and important adaptive problems that confront mobile animals, and are some of the most important potential applications for robots and other artificial autonomous agents. In a typical contest of this sort, a predator chases a prey animal around until the prey is eaten or the predator gives up. More symmetrically, two members of the same species may fight over a territory or resource, alternating between attack and defense tactics analogous to pursuit and evasion tactics. Pursuit and evasion behaviors, like attack and defense behaviors, tend to co-evolve against one another, resulting in some of the most intense and sustained evolutionary arms races in nature. Although pursuit-evasion contests have been relatively neglected in research on the simulation of adaptive behavior, they have five major features that render them interesting and relevant.

First, problems of pursuit and evasion are common, because conflicts of interest over approach and avoidance are common. Agents that mutually benefit from being close together can mutually approach, and agents that mutually benefit from being far apart can mutually avoid one another. But quite often, one agent (e.g. a predator or parasite) would benefit from an encounter and the other (e.g. a prey animal or host) would not, so the potential beneficiary tends to end up chasing the potential victim. Section 2.1 discusses this logic in more detail.

Second, pursuit and evasion contests are difficult, because dynamic, stochastic, continuous-space, continuous-time games are difficult. Pursuit and evasion require highly robust forms of adaptive behavior and have particularly important fitness consequences. Animals that pursue or evade must maintain complex sensory-motor coordination with respect to both a physical environment and a hostile animate opponent. Pursuit-evasion contests also require continuous, real-time, dynamical control, in the face of an opponent that will ruthlessly exploit any delay, uncertainty, or error. Natural or artificial behavior-control systems that are slow, brittle, easily confused, or error-prone do not survive long in pursuit-evasion scenarios. For these reasons, traditional artificial intelligence methods may prove particularly poor as models of pursuit-evasion behaviors (imagine the famously slow robot "Shakey" trying to evade a fast predator), and newer reactive, behavior-based, bottom-up approaches (e.g. Braitenberg, 1984; Brooks, 1989; Beer, 1990; Maes, 1990; Wilson, 1991) may prove particularly apt.

Third, pursuit and evasion are scientifically interesting, because they evolve against one another in an ongoing, open-ended, frequency-dependent way, so pursuit-evasion contests often give rise to co-evolution within or between species. Because pursuit-evasion scenarios may be the simplest and most common cases of behavioral co-evolution, their investigation may illuminate behavioral arms races in general (see Futuyama & Slatkin, 1983). Such sustained co-evolution reinforces all of the challenges discussed in the previous paragraph: temporary adaptive advantage is continually eroded under co-evolution as new tactics arise. Co-evolution probably drives the evolution of both special perceptual capacities to entrain, track, and predict animate motion, and special motor capacities to generate complex, robust, unpredictable behavior (Miller & Freyd, 1993). Understanding both perception and motor control may thus depend on appreciating the role of pursuit-evasion contests in behavioral evolution. Moreover, pursuit-evasion co-evolution is the simplest situation that can favor "protean" (adaptively unpredictable) behavior, as when prey animals zig-zag unpredictably to escape predators (see e.g. Chance, 1957; Chance & Russell, 1959; Driver & Humphries, 1988). Further, because effective pursuit may often require prediction and 'mind-reading', while effective evasion may require the use of unpredictable or deceptive tactics (Driver & Humphries, 1988), such contests raise issues of signaling, communication, and tactical deception (Dawkins & Krebs, 1978; Harper, 1993; Krebs & Dawkins, 1984), and may provide a natural bridge from the evolution of basic sensory-motor control to the evolution of social psychology and 'Machiavellian intelligence' (Byrne & Whiten, 1988; Miller, 1993). Some complex social, sexual, communicative, and political behavior could be viewed as pursuit-evasion contests carried out on more abstract levels, with respect to state spaces involving social information, status, resources, kinship, and sexual relationships.

Fourth, pursuit-evasion contests have received serious attention from at least three scientific disciplines: behavioral biology, neuroethology, and game theory. Animal behavior studies have revealed the ubiquity and importance of pursuit-evasion tactics, anti-predator behaviors, and fighting skills (Driver & Humphries, 1988; Endler, 1991). The centrality of such behaviors is revealed by the fact that pursuit-evasion games are the most common form of animal play behavior (Fagen, 1981; Symons, 1978); such play facilitates learning sensory-motor coordination through "developmental arms races" between play-mates. Neuroethology (e.g. Camhi, 1984; Hoyle, 1984) has spent much effort understanding neural systems for pursuit ("approach") and evasion ("avoidance"), including: explorations of specific circuits for rapid startle and escape behaviors (e.g. Camhi, 1988; Krasne & Wine, 1987; Eaton, 1984); the role of the (very fast) tecto-spinal pathway in mediating the pursuit behavior of vertebrate predators such as salamanders, frogs, cats, and owls (e.g. Alstermark, Gorska, & *et al*, 1987; Meredith, Wallace, & Stein, 1992; Westby, Keay, Redgrave, Dean, & Bannister, 1990); and the specific attunement of sensory cells to patterns of animate motion relevant to pursuit and evasion (e.g. Arbib & Cobas, 1991; Ewert, 1987; Nakayama, 1985; Perrett, Harries, Mistlin, & Chitty, 1990). The possibilities for computational neuroethology (Beer, 1990; Cliff, 1991) and behavioral modelling in this area are obvious. Game theorists have also studied pursuit-evasion contests intensely for several decades, because of their importance in tactical air combat (e.g. telling pilots how to evade guided missiles) and other military applications (see Yavin & Pachter, 1987). "Differential game theory" (Isaacs, 1965) has developed a vocabulary for analyzing the structure and complexity of pursuit-evasion games, and a number of formal results concerning optimal strategies for particular pursuit-evasion games. We will review the relevant animal behavior studies, neuroethology, and game theory at length in the following sections.

Fifth, the study of pursuit-evasion behaviors has many scientific implications and practical applications. A better understanding of the evolutionary, behavioral, and cognitive dynamics of pursuit-evasion contests would have wide implications for animal behavior, neuroethology, comparative psychology, and evolutionary psychology (Miller & Freyd, 1993). Better methods for evolving pursuit-evasion behaviors would have many applications in robotics, video games, virtual environments, and any other technology where real or simulated mobile agents come into behavioral conflict with other agents.

Because pursuit-evasion contests are a major new area of investigation for simulation of adaptive behavior, which we hope will excite much further research, this paper lays out the biological and game-theoretic foundations in some detail: this is essentially a review paper. A companion paper (Cliff & Miller, 1994) will appear in a forthcoming issue of this journal, and will explore the evolution of pursuit and evasion in a variety of games under various conditions. Briefly, such work extends previous work in evolutionary robotics (Cliff, Harvey, & Husbands, 1993) to investigate: (1) whether co-evolution between simulated robots engaged in pursuit-evasion contests can lead to the more and more complex pursuit and evasion tactics over generations; (2) whether the use of continuous recurrent neural networks as control systems allows the emergence of more interesting and dynamic perceptual, predictive, pursuit and evasion abilities; (3) whether the incorporation of random-activation units in the control system allows the evolution of adaptively unpredictable tactics; and (4) whether changes in the relative physical speed and neural processing speed of pursuers and evaders influences the pursuit and evasion tactics that evolve. These two papers extend and expand a previous report on this work (Miller & Cliff, 1994).

2 Biological foundations

2.1 The generality of pursuit-evasion problems

We use the term "fitness affordances" (FAs) to denote things that have particular statistically expected consequences for the fitness (survival or reproduction) of organisms of a particular age, sex, condition, and species (see Miller, 1993; Miller & Freyd, 1993; Todd & Wilson, 1993). Positive FAs such as food, mates, shelter, or offspring have a positive expected effect on the replication of one's genes; negative FAs such as poisons, predators, parasites, and physical dangers have a negative expected effect. FAs are objective features of the environment insofar as their potential fitness effects exist regardless of whether the organism facing them knows or cares of their existence, but FAs are relational insofar as their biological significance exists only in relation to organisms with particular modes of survival and reproduction (e.g. what is food to one species is poison to another in a perfectly objective and yet perfectly relational way). Most FAs are spatially localized (at some scale), and only impose their fitness effects on organisms immediately present. As suggested by Marler and Hamilton (1966), animals do not usually bother perceiving anything other than what we are calling fitness affordances, because, by definition, only fitness affordances can affect reproductive success. Even more stringently, animals should bother perceiving only those fitness affordances whose impact on reproductive success can be modified by individual behavior (e.g. although cosmic rays can affect reproductive success by inducing mutations, their affects cannot be modified through animal behavior, so there is no point in perceiving them.) The term 'fitness affordance' was inspired by J. J. Gibson's (1966, 1979) term "affordance", but emphasizes the evolutionary consequences of affordances rather than their available sensory cues.

Mobility allows animals to actively approach and exploit positive FAs, and to actively avoid negative FAs. But very often, FAs are themselves mobile animals with their own fitness interests, which may turn the problem of approach into a problem of pursuit, or the problem of avoidance into one of evasion. For example, if the Roadrunner is a positive FA (e.g. "prey") for the Coyote, whereas the Coyote is a negative FA (e.g. "predator") for the Roadrunner, then the Roadrunner may attempt to move away from the Coyote, while the Coyote may attempt to move towards the Roadrunner. Whenever there are recognized conflicts of interest over fitness effects between mobile animals, we may predict manifest conflicts of movement. If the conflict of movement is sustained across some expanse of space and time, there is a pursuit-evasion conflict, such as the Coyote chasing the Roadrunner around Arizona all day long. Thus, interactions between two mobile agents that have conflicting expected fitness effects on one another will create a pursuit problem for one agent and an evasion problem for the other.

The above scenario, where the roles of pursuer and evader are pre-determined by the FA relationships, and fixed for the duration of the interaction, could be called an asymmetric pursuit-evasion contest. More symmetric sorts of pursuit-evasion contests can unfold when similar animals both seek access to a positive FA, such as a territory or resource, that is worth more if enjoyed alone. Animals of the same species often fight over food, nest sites, and mates. In symmetric contests, the roles of pursuer and evader can switch back and forth rapidly as the animals take offensive or defensive roles (as in the Game of Tag simulated by Reynolds (1994)). In both symmetric and asymmetric contests, the immediate behavioral conflict can result in a co-evolutionary arms race between pursuit and evasion tactics, if the agent-types in question encounter each another with reasonable frequency and with significantly opposed fitness consequences across generations.

2.2 Typical pursuit and evasion behaviors

Pursuit is fairly simple: animals are usually observed to move towards the remembered, observed, or predicted location of the target. Evasion is more complex. For example, animal escape behavior in asymmetric pursuit-evasion contests generally breaks down into three phases: (1) directional fleeing if a predator (or other negative, mobile FA) is threatening but still distant; (2) erratic zig-zagging if the predator begins catching up; and (3) convulsive 'death-throes' if caught. Directional fleeing is about as simple as directional chasing, but the last two tactics, zig-zagging and convulsing, are examples of a more interesting type: protean behavior.

Animals generally evolve perceptual and cognitive capacities to entrain, track, and predict the movements of other biologically-relevant animals such as prey, predators, and potential mates (Camhi, 1984; Miller & Freyd, 1993). Such predictive abilities mean that unpredictable behavior will inevitably be favored in many natural pursuit-evasion situations. For example, if a rabbit fleeing from a fox always chose the single apparently shortest escape route, the very consistency of its behavior would make its escape route more predictable to the fox, its body more likely to be eaten, its genes less likely to replicate, and its fitness lower. Predictability is punished by hostile animals capable of prediction. This is the basic logic behind the theory of protean behavior: the effectiveness of almost any behavioral tactic can be enhanced by endowing it with characteristics that cannot be predicted by an evolutionary opponent (Driver & Humphries, 1988). An arms race between perceptual capacities for predicting animate motion, and motor capacities for generating protean behavior, will generally result from evolutionarily recurring pursuit-evasion contests (Miller & Freyd, 1993).

Along with directional fleeing, protean escape behaviors are probably the most widespread and successful of all behavioral anti-predator tactics, being used by virtually all mobile animals on land, under water, and in the air. Driver and Humphries (Driver & Humphries, 1988) review examples from hundreds of species, including insects, fish, birds, and mammals. Human proteanism is obvious in any competitive sport: good boxers use unpredictable feints and attacks, and good rugby players use unpredictable jinks. Predators can also exploit unpredictability to confuse prey, as when weasels do "crazy dances" to baffle the voles that they stalk, or when Australian aborigine hunters do wild dances to mesmerize the kangaroos that they hunt (Driver & Humphries, 1988). Of course, proteanism is typically used at one level of behavioral description (e.g. the trajectory through the environment), and is consistent with maintenance of orderly behavior at other levels (e.g. posture, locomotor gait, obstacle avoidance, perceptual scanning).

The case of protean escape from bats by insects has been particularly well-studied (for review see (May, 1991)). Roeder (1962) observed that "the variety of unoriented manoeevers released [in moths] by high intensity ultrasonic stimulation [e.g. from bats] continues to defy any attempt at orderly description." These flight patterns may include passive dives with wings folded, powered dives, erratic flight movements, looping, and tight turns (May, 1991). Whereas bats can easily predict the aerial trajectories of passive ballistic objects, the moth's erratic tumbling make them much more unpredictable and harder to catch. Some species of moths (presumably evolved in bat-free areas) cannot perform this protean behavior, and do rather poorly against bats. In an experimental study using both types of moths, Roeder and Treat (1961) found an average 40% higher escape rate for tumbling over non-tumbling per bat encounter; this translates into a 40% selective advantage for unpredictable tumbling. The intensity of selection on evasive behaviors is also revealed in their speed. The neural systems for initiating protean escape are astonishingly fast: a cricket can detect the sound of a predator and effectively alter the rhythmic motor signals to its wings to initiate erratic escape in under 60 milliseconds (May, 1991).

Even if erratic zig-zagging fails, another form of proteanism, convulsive behavior, may succeed. Sudden, unpredictable, vigorous "death-throes", alternating with puzzling passivity ("playing dead") is often effective at allowing prey to escape from predators (Driver & Humphries, 1988). Indeed, the adaptive significance of convulsive behavior was first recognized by M. R. A. Chance (Chance, 1957; Chance & Russell, 1959), who initiated the study of protean behavior with his analysis of "audiogenic seizures" in laboratory rats. (When lab technicians accidentally jangle their keys, lab rats have a peculiar tendency to go into convulsions, but if the rats are provided with hiding places in their cages, they simply run and hide when keys are jangled; thus, the convulsions are facultative defensive behaviors rather than pathological oddities.) Adaptive convulsions can also occur in more abstract state-spaces, as when cuttlefish and octopi undergo rapid color changes to defeat the search images (perceptual expectations) of their predators. Additional confusion effects may arise from group flocking and mobbing behaviors that include unpredictable movements, complex motion dynamics, and confusing coloration (zebra stripes or shiny scales on fish); Werner and Dyer (1993) found such confusion effects when simulating the evolution of herding behavior by prey under predation pressure. Unpredictability can also be exploited by divergence between individuals, as when animals within a species evolve "aspect diversity" (polymorphic coloration or behavior) through "apostatic selection" (Clarke, 1962) that favors low-frequency traits (e.g. because predators' use of search images penalizes common appearances). Indeed, apostatic selection may be a general feature of pursuit-evasion arms races: novel and unexpected tactics may be favored at a variety of levels.

Co-evolution itself can be viewed as a pursuit-evasion contest, operating between lineages rather than between individuals. From this perspective, sexual recombination makes sense as a protean strategy which unpredictably mixes up genes so as to "confuse" pathogens (Hamilton, Axelrod, & Tanese, 1990). Indeed, this proteanism argument is one of the leading explanations for the the evolution of sex (Ridley, 1993). Despite proteanism's importance, it has been long overlooked in biology, because complex order rather than useful chaos was assumed to be the defining feature of Darwinian adaptations (see Miller, 1993).

2.3 The neuroethology of pursuit and evasion

The study of fast pathways for escape and attack forms is one of the major successes of neuroethology (see Beer, Ritzmann, & McKenna, 1993; Camhi, 1984; Ewert, 1980; Ewert, Capranica, & Ingle, 1983; Guthrie, 1980; Kandel, 1976; Hoyle, 1984; Huber & Markl, 1983; Roeder, 1967). Neuroethologists like to study neural circuits for such behaviors because the relevant neurons are so large, the axons are so thick, the circuits are so easy to identify, and the behaviors are so fast, robust, and well-tuned (e.g. see Roeder, 1948; Eaton, 1984). In the tube worm *Myxicola infundibulum* for example, most axons (nerve fibers) are less than 5 μm in diameter, but the median giant fiber for escape can reach 1700

μm in diameter, occupying most of the cross-section of the nerve cord (Guthrie, 1980). Unusually in this case, methodological convenience reflects adaptive importance: large, fast neurons arranged in reliably wired circuits make not only easy work for the scientists, but adaptive sense for the animals. Although circuits for fast attack and escape are probably different from those used for sustained pursuit and evasion, the neuroethology of the former illustrates some relevant principles of speed, robustness, co-evolution, and adaptive specialization.[1]

2.3.1 Escape reflexes

Escape circuits are among the best-studied systems in neuroethology (see Eaton, 1984). Unexpected stimuli often provoke startle, escape, or withdrawal in animals, and these reflexes are generally mediated by specialized 'fast pathways' (Guthrie, 1980). As far back as 1836, Ehrenberg had identified very large cells in the ventral nerve cords of lobsters and crayfish which were later shown to mediate their escape behaviors. Particularly well-understood are the quick withdrawl of the worm's head, the tail-flip escape of the crayfish, the escape turn of the cockroach, and the sudden dart of the fish. Aside from whole-body escape, animals with limbs usually have specialized circuits for limb-withdrawl from painful or threatening things. Fast pathways generally use a few large neurons with polarized inputs, long, thick, heavily insulated, low-resistance axons, widely distributed outputs, and electrical rather than chemical synapses. Such neural adaptations permit conduction velocities a couple orders of magnitude faster than normal. Escape reflexes also recruit attention, increase activation, and release hormones, in preparation for sustained evasion if necessary.

Even in colenterates such as sea anemones and jellyfish, there appear to be separate fast pathways for withdrawl reflexes (Guthrie, 1980; MacFarlane, 1969). Similar circuits for gill-withdrawl in sea slugs (*Aplysia*) have been studied by Kandel (1976). The escape-reflex nerve fibers ('third-order giant fibers') of the squid *Loligo* are so thick (700 μm) that they have been widely used in studies of the ionic mechanisms of nerve-fiber conduction. The common earthworm *Lumbricus* has an escape reflex mediated by medial, lateral, and segmental giant fibers and by giant motor neurons, which contact longitudinal body muscles to withdraw the head from danger. The medial giant fibers can attain conduction velocities of up to 45 meters per second, as fast as the myelinated escape-reflex fibers of frogs and fish (Guthrie, 1980). Darwin noted that the worm's escape reflex rapidly habituates to light or touch, and shows a higher threshold for activation during active locomotion.

The American cockroach *Periplaneta americana* escapes from toad predators (such as *Bufo marinus*) by sensing toad-induced air accelerations with their anal cerci (rear-facing sense organs), turning from the predator, and running away (see chapter 4 of (Camhi, 1984), (see also Camhi, 1980). The sedentary toads generally wait for insects to walk by before striking with their tongues, so a single brief escape suffices; there is rarely sustained pursuit. The cockroach's seven pairs of giant interneurons (GI) mediate the escape behav-

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[1] For further relevant readings in neuroethology, see the journals: *Aggressive Behavior; Animal Behavior; Behavioral Neuroscience; Biological Cybernetics; Brain, Behavior, and Evolution; J. Comparative Physiology A: Sensory, Neural and Behavioral Physiology; J. Experimental Biology,* and *J. Neuroscience.*

ior, which averages an extremely fast 41 milliseconds (ms) latency (Plummer & Camhi, 1981), but which can occur in an astonishing 11 ms in response to a stronger-than-normal air stimulus (Camhi & Nolen, 1981). The hundreds of wind-receptive hairs on the cerci are directionally tuned and several of the giant interneurons code for predator direction to guide the escape turning behavior (Dowd & Comer, 1988; Liebenthal, Uhlmann, & Camhi, 1994; Westin, Langberg, & Camhi, 1977). This direction information triggers consistent changes in interleg coordination and turning, which have been analyzed with high-speed video, (Camhi & Levy, 1988; Nye & Ritzmann, 1992). Under certain conditions, the same giant interneurons that trigger escape running can trigger escape flying instead (Ritzmann, Tobias, & Fourtner, 1980). The entire system is essentially innate, hard-wired, and fully functional in hatchlings, though there is some plasticity to compensate for injury to various components of the system (see chapter 4 of Camhi, 1984). The cockroach's escape system works much like a Braitenberg (1984) vehicle to implement a very rapid predator-avoidance, and could provide a model for further simulation and robotics work.

The escape circuits of the American crayfish *Procambarus clarkii* have also been well-studied (Krasne & Wine, 1987; Edwards, 1991; Olson & Krasne, 1981; Wiersma, 1947) (see also chapter 8 of Camhi, 1984). This animal lives in streams, eats detritus, and is attacked by various large fish. Touches to the crayfish's rear will trigger an abdominal flexion mediated by lateral giant interneurons that somersaults the animal upward and forward; touches to the front will trigger a different kind of abdominal flexion or 'tailflip' mediated by medial giant interneurons that shoots the animal backwards (Wine & Krasne, 1972). In each case, the giant interneurons have rectifying electrical synapses onto large (F1) motor neurons, which, in conjunction with 'segmental giant' cells, activate 'fast flexor muscles'. The escape is an all-or-nothing, highly stereotyped response, which cancels out all other ongoing locomotor activity, requires the coordination of muscles in several abdominal segments, and begins within 20 ms of stimulation. The circuitry underlying this escape behavior has been studied in great detail (Krasne & Wine, 1987; Olson & Krasne, 1981); Stork, Jackson, and Walker (1992) have simulated its evolution from swimming locomotion circuits.

In most teleosts (body fishes), Mauthner cells of the reticulospinal network (Diamond, 1971) mediate a two-stage escape called a 'C-start': turn rapidly, then accelerate axially (Eaton & Emberley, 1991). Within 100 ms, a C-starting fish will have moved around one body length away from the threatening stimulus, and will be pointed in roughly the right direction for further evasion. Rapid escape is especially important for fish attacked by plunge-diving birds such as gannets and kingfishers (Guthrie, 1980), whose appearance is unpredictable, rapid, and lethal. The Mauthner cells as studied in the goldfish *Carassius auratus* guide the basic decision to turn left or right during escape; the exact escape heading is modulated by parallel circuits to produce variations from 15 to 135 degrees change in orientation (Eaton, Didomenico, & Nizzanov, 1988a, 1988b; Foreman & Eaton, 1993). The C-start is fast (initiated within 10 ms), highly ballistic, and is not corrected for threat location once initiated; however, fish seem to avoid facing towards static obstacles during C-starts, so C-starts may be modulated by some environmental information (Eaton & Emberley, 1991). Although Mauthner cells (M-cells) are important in triggering C-starts, (Nissanov, Eaton, & Didomenico, 1990) found that M-cell stimulation alone produces a much weaker and less variable C-start. The M-cells seem to determine an initial left-or-right direction of response and a rough stage-1 escape angle; a second group of neurons fires later and modulates the onset time and direction of the stage-2 swimming behavior. Interestingly, Mauthners have also been implicated in pursuit and prey capture (Canfield & Rose, 1993): in predatory fish, M-cells fire and the fish do C-start-like flexions during the terminal stage of prey capture. Thus, Mauthners are important for both capture of prey and escape from predators; (Canfield & Rose, 1993) suggest that "Group competition between predators and their prey may have facilitated a 'neural arms race' for M-cell morphology and physiology" (p. 611).

Rats sometimes attempt to wrest food away from other rats that are feeding; the feeding rats protect the food by rapid contralateral dodges (Whishaw & Gorny, 1994). The details of the evasive dodge are sensitive to the expected time required to finish eating the contested food item: rats estimated time required to complete eating and adjusted the size and direction of their evasive maneuvers to gain this time. Such evasion behaviors may be mediated by the nucleus gigantocellularis (NGC), which is known to be important in nociceptive, escape, and avoidance behavior (Roberts, 1992). In other mammals, various other fast pathways function in escape and startle behavior (Gogan, 1970; Shapovalov, 1972).

The only known 'command neurons' (neurons capable of triggering an entire behavior by themselves) (Kupferman & Weiss, 1978) have been found in escape circuits: these include the medial and lateral giant interneurons of the crayfish, and the Mauthner cells of fish and larval amphibians. However, most vertebrate behaviors are released by command systems rather than single command neurons, so it is much easier to study the neuroethology of invertebrate escape, evasion, and pursuit behaviors.

Of course, escape reflexes are only one possible response to predation threats. Some animals such as *Aplysia* and squid have special circuits for releasing ink or other obscurants during their escape behavior (Carew & Kandel, 1977; Kandel, 1976). Other animals use startle displays such as eye spots to counter-threaten predators; some play dead to avoid releasing the cues of evasive movement that tend to attract predators' attention.

2.3.2 Attack circuits

Ewert (1980, 1984, 1987) and colleagues examined visually guided capture of prey by toads. Toads generally sit motionless until something moves into their field of view; if it's small and moving in the direction of its long axis, they attack; if it's big, they run away (Ewert, 1980; Lettvin, Maturana, McCulloch, & Pitts, 1959). In toads, the TP3 cells of the thalamic pretectal area and the T5(1) and especially the T5(2) cells of the optic tectum are responsive to worm-like moving stimuli; the T5(2) cells appear necessary and sufficient for visual recognition of prey (Ewert & Burghagen, 1979; Ewert, 1980, 1984; Ingle, 1991). If the target shows apparent escape behavior, especially strong pursuit behavior is released (Guthrie, 1980). If the target is too large to be prey, the TP region inhibits the tectal prey-catching system. The toad's tectum is organized in a spatially organized retinotopic map of prey positions, to guide striking behavior. Arbib and colleagues (Arbib & Cobas, 1991; Liaw & Arbib, 1993) have simulated this system in considerable detail, with a neural network that detects the location and heading of looming predators and determines an escape direction. Specific attunement of visual cells to patterns of animate motion relevant to pursuit and evasion have been found in primates as well (Nakayama, 1985; Perrett et al., 1990). For an interesting contrast to vertebrate prey-catching systems, see Ewert's (1980) discussion of prey-catching by the arthropod backswimmer *Notonecta glauca*, which hangs on the underside of pond water surfaces and has tactile senses tuned to the circular waves produced by prey that have fallen in.

Similar principles and circuits underlie audition-guided attack behaviors. In the barn owl (*Tyto alba*), much work has been done on the auditory homolog of the visual tectum: the mesencephalicus lateralis dorsalis (MLD), which lies just below the optic tectum and appears to mediate prey capture by sound (Knudsen, 1981, 1982). In echolocating bats, cortical maps seem to code for target parameters such as reflectivity, range, velocity, and angular position (Altes, 1989).

Retinotopic tectal maps are evolutionarily conservative systems found in many vertebrates, and are generally tuned to detecting and locating small, moving, prey-like stimuli (Ewert, 1980; Ingle, 1991; Wurtz & Albano, 1980). Even in mammals where the striate cortex is used for target identification, the superior colliculus is still used for target localization to guide oriented behavior: a cortical identification system co-exists with a subcortical localization system (Ewert, 1980). The visual or auditory representation of prey location in the tectum guides prey-directed movement via the very fast tecto-spinal pathway in vertebrates (e.g. Alstermark et al., 1987; Meredith et al., 1992; Westby et al., 1990).

Pursuit behavior in insects has also been studied in the context of mating and courtship (e.g. Land, 1993). Male flies often 'shadow' females at a short distance (e.g. Collett & Land, 1975), and chase other flies more aggressively (e.g. Land & Collett, 1974). In many species of fly, it is only the males that engage in high-speed aerobatic chases, and in several such species, the males have gender-specific optical anatomy which facilitate such behaviors (e.g. Land, 1981, pp.553–555) (Gilbert & Strausfeld, 1991).

2.3.3 From attack and escape to pursuit and evasion

There appears to have been an arms race with respect to speed between the final strikes by predators to capture prey and the escape responses of prey. We have already seen how the cockroach can initiate escape turns in as little as 11 ms. Although cuttlefish orient themselves slowly and carefully to their prey, the final capture strike by their two long tentacles takes about 30 ms (Messenger, 1968). Most such behaviors are too fast to be subject to feedback or correction during their execution. This makes generalization from the neuroethology of open-loop (ballistic) attack and escape to closed-loop (feedback-driven) pursuit and evasion problematic. Some work has been done on the transition from open-loop escape to closed-loop evasion behavior in crayfish (Wine & Krasne, 1982) and cockroaches (Camhi & Nolen, 1981), but the neuroethology of sustained pursuit and evasion requires more research. Such neuroethology will require analysis of less stereotyped, more protean behaviors mediated by larger numbers of smaller cells.

The only sustained research program in neuroethology focused on pursuit and evasion (rather than simple attack and escape) has been the work by Kenneth D. Roeder, Asher E. Treat, and their colleagues and followers on interactions between bats and moths (see e.g. Dunning & Roeder, 1965; Roeder, 1962, 1967; Roeder & Treat, 1961) (for reviews see Guthrie, 1980; Huber & Markl, 1983; May, 1991). Insectivorous bats use pulse-modulated ultrasound in the 20 to 120 KHz range for echolocating the flying insects that they eat. Such bats hunt prey in three phases: a searching phase with 10 or so chirps per second, an approach phase after detecting prey with more frequent chirps and with the head aimed at the prey, and a terminal phase with around 200 chirps per second, ending if successful with the prey captured in the wing or tail membranes. The latter two stages usually last less than one second (Griffin, Webster, & Michael, 1960).

Noctuid moths (Roeder, 1962; Roeder & Treat, 1961), green lacewings (L. A. Miller, 1983), and other bat prey have paired auditory organs specially attuned to detecting bat ultrasound, and initiating evasion maneuvers. Noctuid moths can register most bat cries from 35 meters away, whereas bats can only detect echoes from moths around 6 meters away, giving the moths a considerable safety factor (L. A. Miller, 1983), despite the bats' flying approximately twice as fast (Guthrie, 1980). Moth evasion behavior is of three basic types: negative phonotaxis (flying away) when bat cries are soft, slow, and distant; passive nose dives that deny bats information about wingbeat rate, heading, and species type (as favored by lacewings (see L. A. Miller, 1983)); and active evasion maneuvers (as favored by noctuid moths). Moths that can hear ultrasound and take evasive maneuvers show about a 40% selective advantage over experimentally deafened moths (Roeder, 1962); normal green lacewings likewise have a 47% selective advantage over deafened lacewings (L. A. Miller, 1983). The proteanism of prey responses to echolocation has been noted by (Roeder, 1975) (who termed evasion ability 'evitability') and (L. A. Miller & Olesen, 1979). Moths can also emit ultrasonic 'jamming signals' that confuse bats during the terminal phase of capture (Fullard, Fenton, & Simmons, 1979). Pursuit and evasion behavior per se only occur when a bat in the approach or terminal phase of predation interacts with a prey insect using active evasive maneuvers. Even against actively evading insects, bats are often successful (Simmons & Kick, 1983).

Still, little is known about the neural circuitry that underlies the pursuit and evasion behaviors, as opposed to the reflexive attack and escape behaviors, or the echolocation. Moiseff and colleagues (1978) found that a pair of specialized cells (interneuron-1) in the cricket *Teleogryllus oceanicus* responds to bat ultrasound signals from ears on the cricket's forelegs and contracts dorsal longitudinal muscles on the side away from the sound, thereby steering the cricket away from the sound source. Roeder (1970) speculated that the moth's protean evasion behavior was mediated by the A2 fibers carrying ultrasound information from the ears to the brain, and by the brain's output of inhibition to the thoracic ganglia, tending to shut down the ganglias' steering control over the wings. The result would be a loss of synchrony and rhythmicity in wing-beats, leading to erratic flight; however, this account remains untested. Nor is much know about how bats perform their stunningly fast and agile mid-air pursuit maneuvers. The auditory cortex of bats may have neurons that code for target range (O'Neill & Suga, 1979) and perhaps for reflectivity, velocity, and angular position as well (Altes, 1989), but the rest of the circuit for controlling pursuit flight remains obscure. The reasons for this ignorance are largely methodological: it is very difficult to do intracellular recording while animals are making wild evasive moves or violent attacks.

Psychologists have also studied manual tracking tasks and smooth pursuit eye movements in humans and other primates. Tracking and visual pursuit are often important components in behavioral pursuit of evasive animals, but very little of this work has used ecologically valid stimuli or evolutionary theory for guidance. There is a huge gap between the study of reflexive attack and evasion in invertebrates, and the study of conscious, artificial pursuit and tracking tasks by human subjects. In general then, neuroethology has investigated attack and escape circuits in a wide range of animals, but much remains to be discovered about the more flexible and dynamic behaviors or pursuit and evasion. We hope that simulation and robotics research will inspire renewed neuroethological efforts in this area.

3 Game-theoretic foundations

3.1 Differential pursuit-evasion game theory

Game theory (von Neumann & Morgenstern, 1944) is concerned with the formal analysis of situations called "games" where: (1) players can choose different strategies that determine their actions under particular conditions; (2) conditions and outcomes unfold through the interactions of the players' strategies; and (3) players have preferences among outcomes, i.e. payoffs exist (see (Rapoport, 1966) for a non-technical introduction; see (Fudenberg & Tirole, 1991) for a recent textbook). In brief, players are agents that can make choices, implement strategies, and receive payoffs.

Traditional game theory focused on games with discrete moves (e.g. chess), but in the 1950s, Isaacs (1951, 1965) wondered whether game theory could be used to model pursuit-evasion situations such as aerial combat, where moves unfold continuously over time, and control systems can vary continuously in the strategies they implement. Isaacs had two basic insights. First, pursuit-evasion contests do require game theory rather than simple optimality theory, because the optimal pursuit strategy for one player (e.g. a guided missile) depends on the evasion strategy adopted by the other player (e.g. an aircraft), and vice-versa. This chicken-and-egg problem is precisely what game theory is good at analyzing. Second, the continuous nature of pursuit-evasion contests can be modeled using differential equations that specify how state conditions (such as player positions and velocities) change incrementally as a function of players' strategies and previous state conditions: pursuit and evasion moves become continuous trajectories through a state-space. Isaacs (1951, 1965) developed the "Tenet of Transition" which specifies that players must optimize (find the minimax solution for) the transitions between states leading towards a goal-state, which can be represented as optimizing the temporal derivatives of the relevant state variables. For example, pursuers try to minimize the time until capture and evaders try to maximize it. Applying the tenet of transition, pursuers at each moment in time should try to maximize the rate of their instantaneous approach towards the capture-state, and evaders should try to minimize it. If a solvable set of differential equations can be written that specify the continuous effect of strategies on state-conditions, then the optimal pursuit and evasion strategies can be found by applying the tenet of transition.

Isaacs' ideas have proven enormously fruitful (see Basar & Olsder, 1982; Grote, 1975; Isaacs, 1965; Yavin & Pachter, 1987), and initiated a sort of Cold War arms race between American and Russian game theorists concerned with applications to aerial combat tactics. The *Journal of Guidance, Control, and Dynamics* is a major venue for differential pursuit-evasion game theory; Rodin's (1989) recent bibliography of the pursuit-evasion differential game theory literature contains about 1200 entries. Aside from differential game theory, there are also large and relevant literatures on control theory (see Brogan, 1991), missile guidance, aircraft control, aerial tactics, and sports tactics.

Differential pursuit-evasion games are defined by a set of controls (what each player can do), a set of dynamics (that maps from the control variables onto the state variables of the game, and from state variables at one moment in time to the next moment), and a set of termination conditions (state conditions that determine when successful capture or evasion happens). For example, in a classic case analyzed by Berkovitz (1975), a pursuer and an evader move with equal and constant speed in a plane, and control the direction of their velocity vector (which thus becomes their control variable). These two velocity vectors give rise to a system of first-order differential state equations that determine how the players move over time. The pursuer wants to minimize time to capture the evader and the evader wants to maximize time until capture, with capture defined as proximity within some small distance. Both players know the present state of the game (e.g. both of their positions and velocity vectors) but at each time-point they make separate and simultaneous decisions about what to do next. The available strategies are therefore functions that map from current states of the game (i.e. the positions and velocity vectors of both players) onto velocity-vector decisions about what direction to move next. In all differential games, strategies determine trajectories through the relevant state-space; in pursuit-evasion games, strategies determine trajectories through physical space. From each player's perspective, the game becomes a problem of optimal spatio-temporal control with respect to the opponent and the environment. Indeed, control theory can be viewed largely as the solution of one-player differential games (Isaacs, 1975); differential game theory addresses the more complex multi-player cases.

In classic "asymmetric" games (e.g. missile vs. aircraft), the roles of pursuer and evader are pre-determined and fixed. But in "symmetric" games (e.g. aircraft vs. aircraft), both players can collect payoffs for successful pursuit and successful evasion. Symmetric pursuit-evasion contests have been analyzed as "two-target games" (Getz & Pachter, 1981; Merz, 1985). The symmetric contests in some of our initial experiments (Cliff & Miller, 1994) resemble various two-target games such as a coplanar tail-chase aerial combat game (Merz & Hague, 1977), a deterministic planar dogfight game (Getz & Pachter, 1981), a stochastic dogfight game (Yavin, 1986, 1987), and a 3-D dogfight game (Greenwood, 1992); see (Grimm & Well, 1991) for review. The classic "game of two cars" is also symmetric: two players with fixed speeds and limited turning radii move in the same plane and attempt to capture each other somehow (Isaacs, 1965; Merz, 1976, 1985; Merz & Hague, 1977; Meyer & Trigeiro, 1991).

3.2 The optimality of mixed strategies

The key to formal analysis in game theory is for games to be reduced from descriptive form (e.g. rules and heuristics) or "extensive form" (i.e. decision-tree form) to "normal form" (i.e. a joint payoff matrix that lists game outcomes given all possible strategies for all players). Some games in normal form have "minimax solutions" (a.k.a. "saddle points") that minimize each player's expected loss regardless of what the opponent does to maximize their expected gain; minimax solutions, if they exist, are jointly optimal for rational players. In games of perfect information, players are precisely and continuously aware of all moves made by other players, so that deception, confusion, and uncertainty are impossible. All games of perfect information have one or more saddle points corresponding to "pure" deterministic optimal strategies (though finding them may often be difficult, as in chess).

However, games of imperfect information (e.g. games where deception is possible) may have multiple saddle points or no saddle points. In such cases, "mixed strategies" (probability distributions across pure strategies) may be optimal. Perhaps the most important and interesting result from von Neumann and Morgenstern (1944) was that every two-player, zero-sum game of incomplete information with multiple saddle points has an optimal strategy that is mixed rather than pure:

> "One important consideration for a player in such a game is to protect himself against having his intentions found out by his opponent. Playing several different strategies at random, so that only their probabilities are determined, is an effective way to achieve a degree of such protection. By this device the opponent cannot possibly find out what the player's strategy is going to be, since the player does not know it himself. Ignorance is obviously a good safeguard against disclosing information directly or indirectly." (von Neumann & Morgenstern, 1944, p.146)

The logic of mixed strategies is simple (see Rapoport, 1966). If a player's choice sometimes remains unknown to others after the move is made, the game is one of imperfect information. This can result from the move being hidden, or the other players' sensors being insufficient to register all moves with complete accuracy. Typically, games lose their saddle points when they are no longer games of perfect information, such that the first player's minimax solution does not correspond to the second player's minimax solution. For example, the popular children's game Rock, Paper, Scissors involves a circular pattern of dominance among the pure strategies (Rock beats Scissors, Scissors cut Paper, Paper smothers Rock), so there is no saddle point, and one's optimal (minimax) strategy against a rational opponent is to choose each move with one-third probability. In general, mixed strategies randomize moves to confuse opponents and keep them guessing. (But the task of determining the optimal mixed strategy is usually very difficult for games with many pure strategies and complex interactions.)

Because many pursuit-evasion games are ones of incomplete information with multiple saddle points, mixed strategies have often proven useful in such games. Mixed strategies are optimal for a pursuit-evasion game with rectilinear movement on a planar grid (Ermolov, Kryakovskii, & Maslov, 1986). In some more complex continuous cases, the optimal strategies for both pursuer and evader are also mixed. Forte and Shinar (e.g. Forte & Shinar, 1988, 1989; Shinar, Forte, & Kantor, 1992) have shown that in aerial combat scenarios, mixed strategies yield much better performance than any previously known guidance law, and did so for both pursuers and evaders. Moreover, Bernhard and Colomb (1988) showed that the use of mixed strategies by both players can be optimal even when only one player has incomplete information. Other results by Bugnon and Mohler (1988), Imado (1993), and Linder (1991) also illustrate the utility of mixed strategies in pursuit-evasion games. Indeed, some aircraft use systems for "electronic jinking" (Forte & Shinar, 1988) to generate unpredictable flight paths, by analogy to gazelles jinking erratically to evade a predator. Such game-theoretic results support the protean behavior hypothesis of Driver and Humphries (1988) that erratic zig-zagging by animals is truly stochastic behavior that derives its utility from its unpredictability. We might expect then that in any pursuit-evasion game with incomplete information and complex dynamics, unpredictable pursuit and evasion strategies will evolve.

Evolutionary game theory (Maynard Smith, 1982) has also recognized the optimality of mixed strategies in many contests between animals. Animals can be considered players in the game-theoretic sense because they make choices, implement behavioral strategies, and receive fitness payoffs contingent on their interactions with other animals' strategies. Mixed strategies can be implemented as behavioral polymorphisms across individuals in a population or as protean behavior within each individual. However, evolutionary game theory has focused mostly on single-step games (such as sex-ratio determination or the Hawk-Dove game: see (Maynard Smith, 1982)) and discrete-step games (such as the iterated prisoner's dilemma (Axelrod, 1984)). The literature on differential pursuit-evasion games has been strangely overlooked despite its obvious relevance to predator-prey interactions and territorial fights, so the importance of protean evasion behavior has been neglected. Dynamic programming methods (e.g. Houston & McNamara, 1987, 1988) may prove more useful in analyzing pursuit-evasion contests, since they can optimize stochastic dynamic strategies, even in two-player games (e.g. Clark & Ydenberg, 1990). However, such methods require the specification of a fairly well-defined strategy set, and Miller and Todd (1991) have argued that genetic algorithms can evolve strategies in a more open-ended fashion than dynamic programming. Evolutionary game theory and dynamic programming should prove useful adjuncts to differential game theory as ways of analyzing simple pursuit-evasion conflicts, but the next section suggests that simulated evolution may be required to deal with complex cases.

3.3 Reasons to simulate pursuit-evasion games

Games are characterized by various dimensions of complexity: (1) the number of players, ranging from one-player cases (covered by control theory) to classic two-player cases to more difficult multi-player cases; (2) the number of moves, ranging from "static" games of one discrete move per player (e.g. Rock, Paper, Scissors) to games with multiple discrete moves per player (e.g. chess), to differential games with continuous moves (e.g. air combat); (3) the continuity of the strategy space, with discrete spaces (e.g. in two-alternative forced-choice games) simpler than continuous spaces (e.g. in spatio-temporal control problems); (4) the payoff structure, with zero-sum games usually simpler than non-zero-sum games; (5) the information structure, with games of complete information much simpler than games of incomplete information. Moreover, in differential games with continuous dynamics, the complexity and noisiness of the dynamics has a major influence on the tractability of the game. Anything that complicates the differential state equations complicates the game analysis. Finally, formal application of game theory requires the complete specification of a strategy space. Such a complete specification may not be possible if the strategies are emergent properties of human heuristics, animal brains, or evolved robot control systems, and if the emergent strategies can vary continuously along a number of dimensions, thereby making the game difficult to represent in extensive (decision-tree) form or normal (payoff matrix) form. These problems suggest that differential pursuit-evasion games are difficult to analyze even under the best circumstances, and that the introduction of realistic complexity renders most of them formally intractable.

To avoid these complexities, differential game theory usually assumes that the pursuit-evasion game is one of perfect information between two players with fixed and predetermined roles (one "pursuer" and one "evader"), deterministic dynamics and constant speeds, and a zero-sum payoff structure. Mathematically adept researchers can relax one or two of these assumptions at a time to derive results for special and simplified cases, but relaxing all the assumptions at once makes the game hopelessly complex. For example, the classic two-cars game emphasizes positional advantage and neglects vehicle dynamics; on the other hand, symmetric differential-turning games (e.g. Kelley, 1975) emphasize relative heading, energy management, and turning while neglecting positional advantage. Some recent work attempts to analyze more difficult asymmetric and symmetric games with noise-corrupted environments (Yavin, 1987), uncertain environments (Corliss, Leitmann, & Skowronski, 1987), or uncertain dynamics (Galperin & Skowronski, 1987). Yet even with bounded uncertainties in dynamics, the classical game-theoretic concepts of optimality, value, and saddle point may be irrelevant (Galperin & Skowronski, 1987). Pursuit-evasion games that cannot be reduced to differential state-space equations cannot be analyzed using the traditional methods of differential game theory. For example, without a linear and deterministic mapping from control to state variables (e.g. from a player's sensors to its effectors), it is impossible to construct tractable differential equations that relate player strategies directly to changes in the game's state-space. A recent complexity-theoretic analysis of differential pursuit-evasion games by (Reif & Tate, 1993) illustrates the difficulties of developing control systems for robots and autonomous vehicles playing such games.

Another important assumption, rarely mentioned in game theory, is that strategies can be implemented instantaneously, without time-lags, computational costs, or speed-accuracy trade-offs. That is, decision dynamics are assumed to be much faster than behavioral dynamics. For real animals and robots, this assumption is unrealistic. Indeed, the basic assumption in game theory that unpredictability is only useful given incomplete information assumes that decision-making happens so much faster than action, that the dynamics of information-processing are irrelevant to the dynamics of action. But if we view both cognition and action as dynamical processes operating on similar time scales (Miller & Freyd, 1993), then the utility of unpredictability becomes more apparent. The terms "perfect" and "imperfect" information conflate the objective information structure of the game (e.g. the state-information available in the world) with the sensory and information-processing capacities of the players. If the latter are limited, then confusion, uncertainty, deception, and protean behavior may prove relevant even if the objective information structure of the game is "perfect". The great size and speed of escape circuits and muscles in many animals, as reviewed in the previous section on neuroethology, suggests that the speed of both neural processing and motor movement has been under intense selection in pursuit-evasion contests.

In recognition of these problems, some game theorists have recently shifted to numerical and simulation methods to derive near-optimal strategies for more complex pursuit-evasion games (e.g. Jarmark, 1987; Moritz, Polis, & Well, 1987; Rodin, Lirov, Mittnik, McElhaney, & Wilbur, 1987; Tolwinski, 1989). For example, Rodin et al. (1987) used artificial intelligence (AI) methods to simulate players in an air combat maneuvering scenario. Each player derives tactical maneuvers using a world-model based on sensor inputs, an inference engine linked to a database (containing player parameters and capabilities and an environment model), and a knowledge base (containing a basic set of pursuit-evasion algorithms). The inference engine updates tactical plans every time an opponent's actual trajectory deviates from its expected trajectory. Clearly, unexpected behavior increases problem complexity and processing time. Rodin et al. (1987) emphasized the "transparency" of the system; i.e. the ability to explain its decisions and solutions in plain English. But such AI methods for controlling autonomous agents tend to become hopelessly slow as the dynamics of agents and environments become more complex and noisy, and the transparency requirement places unnecessary constraints on the types of control systems that can be used. We need simulation methods that yield reactive, robust, dynamic pursuit-evasion strategies, rather than slow, brittle, hand-designed AI systems.

Differential game theory provides a framework for describing the important features of pursuit-evasion contests, and a set of normative results concerning optimal strategies in simple cases. However, it cannot generally provide optimal strategies for realistically complex pursuit-evasion problems, nor can it show how strategies can be implemented in a real control system subject to limited sensory capacities, sensory and motor noise, component failure, and constraints on processing speed and accuracy. Evolutionary simulation methods can fulfill these goals and can complement game-theoretic approaches, because adaptive pursuit-evasion strategies can be evolved in contest scenarios that defy formal analysis. Others have recognized this, and so we next review previous simulation work related to pursuit-evasion issues.

4 Review of Previous Simulation and Robotics Work

4.1 Simple Evolution of Pursuit or Evasion

Themes of pursuit and evasion are implicit in much of the recent work in artificial life and simulation of adaptive behavior. Classic problems of obstacle avoidance and of foraging and navigation can be viewed as degenerate special cases of evasion and pursuit, respectively, with the "opponents" consisting of inanimate, non-moving obstacles, food items, or other goal objects. Much of the work on simulation of collective behavior involves dynamical interactions with other agents that may be similar to the those arising in pursuit-evasion contests. For example, the cooperative behaviors of following, flocking, and aggregation are similar to pursuit behaviors; others such as disperson and collision-avoidance are more similar to evasion behaviors (e.g. Mataric, 1993). (But note that selection for cooperation rarely favors deception or protean behavior.)

Previous simulation work has usually examined the origins and effects of pursuit-evasion tactics with neither player evolving or with one player evolving; these will be reviewed in order. Given very simple, fixed rules for individual movement, Schmieder (1993) examined the different pursuit-evasion dynamics that result when a number of simulated males and females are attracted or repulsed by one another with varying strengths, and with varying degrees of mutual knowledge about one another's movements. Other artificial life simulations have successfully used pre-programmed predators that impose selection for simple evasion behaviors (e.g. Ackley & Littman, 1992; Werner & Dyer, 1993), or have simply modelled pursuit and evasion behaviors in simulated animals with hand-designed systems (e.g. Edwards, 1991; Liaw & Arbib, 1993; Terzopoulos, Tu, & Grzeszczuk, 1994).

Stork et al. (1992) modelled the evolution of the crayfish escape reflex, a very fast and efficient method of evasion that has been well-studied by neuroethologists (e.g. Krasne & Wine, 1987). Artificial neural networks that were first selected for swimming behavior, and then for escape behavior, performed more poorly and had less optimal designs than networks selected directly for escape behavior. Similar 'non-optimality' (in the form of redundant neuronal connections) is also present in the real networks generating escape behavior in crayfish. Stork et al.'s results add weight to the claim that the non-optimality is the result of evolutionary pre-adaptation; this work highlights the evolutionary continuity between locomotion, evasion, and escape behaviors, and the risks of getting caught in local optima when evolving the latter from the former.

Grefenstette's (1992, 1990) SAMUEL system, resembling a classifier system, evolved robust rule-based strategies for simulated agents with noisy, coarse-grained sensors and effectors, including both effective evasion rules given one or two pre-programmed pursuers (in the 'predator-prey' problem), and effective pursuit rules given a randomly moving evader (in the 'cat-and-mouse' problem). However, SAMUEL uses high-level sensory input (e.g. direct heading, bearing, speed, and range information), symbolic condition-action rules operating in discrete time-slices (e.g. 2 to 20 decisions per contest), and fairly domain-specific genetic operators (such as Lamarckian rule deletion, generalization, and specialization).

Koza's (1991, 1992) genetic programming work includes a number of pursuit-evasion simulations. His Pac-Man scenario (Koza, 1992) required both evasion (of pre-programmed "monsters") and pursuit (of sluggishly moving "fruit"); control systems evolved through genetic programming that were capable of prioritizing these activities appropriately. Some Pac-Man controllers that evolved were skillful enough to eat the monsters after eating a special "pill" that made the monsters vulnerable, so to some extent the roles or pursuer and evader could be switched in this scenario. Koza (1992) also investigated the evolution of pursuit-evasion strategies in Isaacs' (1965) "squad car game", where a police squad car pursues a slower pedestrian evader on a discrete grid. Most relevantly, Koza (1991) used genetic programming to evolve LISP S-expression controllers for both players in a differential pursuit-evasion game. His game had pre-determined and fixed roles for pursuer and evader, constant speeds for both agents, and perfect information. Agents were randomly placed in a planar world, controlled their directions (velocity vectors) based on simple inputs concerning the current heading of the opponent, and received fitness payoffs for effective pursuit or evasion. This game has a single optimal pursuit strategy (move directly towards the evader) and a single optimal evasion strategy (move directly away from the pursuer). Given an optimal evader as the "environment", genetic programming was successful in evolving a near-optimal pursuer within a few generations (e.g. 51 generations of 500 individuals each); likewise, near-optimal evaders evolved given fixed optimal pursuers as the environment. However, Koza's pursuit-evasion game was very simple: it required mapping a single input (current angle of opponent) onto a single output (direction to move in), given perfect information and trivial movement dynamics, and it had a known optimal solution from differential game theory. Co-evolution between pursuer and evader did not occur. Nevertheless, Koza's work represents an important fore-runner and inspiration for our research.

4.2 Co-Evolution of Pursuit and Evasion

The only previous simulation work explicitly aimed at investigating the co-evolution of pursuit and evasion tactics was Craig Reynolds' (Reynolds, 1994) study of the Game of Tag. One player is designated "It" and pursues the other player(s) until one of them is tagged and thereupon becomes "It". Pursuit and evasion roles can shift back and forth fluidly, as in animal play behavior (Fagen, 1981; Symons, 1978). Reynolds used genetic programming to evolve vehicle steering systems for playing this game; the less time spent being "It" during a series of 4 games against each of 6 competitors from the same population, the higher an individual's fitness. During 7 long runs with populations around 1000, a variety of different pursuit and evasion controllers evolved, often exploiting the particular weaknesses of their competitors, and sometimes approaching the performance of a known optimal controller. The Game of Tag was an ingenious choice of task because it allows co-evolution within a single population, but clearly distinguishes between pursuit and evasion roles; this overcame some of the problems we encountered in trying to use symmetric pursuit-evasion games within populations (see Cliff & Miller, 1994)). But, as Reynolds acknowledges, his methods greatly simplified the game and the evolutionary process. The vehicles had constant speed, zero momentum, zero turning radius, perfect information about opponent position, and operated in a featureless planar environment; more realistic physics and obstacles would probably make the pursuit-evasion behaviors more difficult and interesting. Also, the tree-like control programs were usually required to have as their first branch point a very convenient conditional "If It, then A (pursue) otherwise B (evade)"; when this requirement was relaxed (as in Reynolds' run G), evolution did not work very well. One of our aims in these papers was to explore the co-evolution of pursuit and evasion under harder conditions.

Sims (1994a) investigated the co-evolution of behavioral tactics using a sophisticated open-ended method for evolving 3D body forms, neural circuits, sensors, and effectors.

Individuals from two species played a competitive game where each player attempts to capture a cube and keep it from the opponent. The simulations used realistic physics with gravity, collisions, friction, and momentum. A fascinating variety of tactics evolved for falling, crawling, rolling, and reaching towards the cube, for blocking or pushing away opponents, and for covering or wrapping securely around the cube. This work shows the feasibility of co-evolving complex and diverse behavioral tactics in simulations with realistic physics and open-ended body and brain development methods. Sims' system could be easily extended to studying pursuit-evasion games, since it has already been used to evolve walking, jumping, and swimming capacities (Sims, 1994b).

Other simulation work has evolved forms of pursuit and evasion, or approach and avoidance, without explicitly selecting for them. Yeager's (1994) "PolyWorld" system managed to evolve some simple pursuit-evasion tactics in simulated creatures controlled by neural networks, including running away or fighting back when attacked, and following other creatures in order to attack them. Although not very sophisticated, these behaviors did evolve simply through the ecological interactions such as predation that were permitted in PolyWorld, without any explicit selection for pursuit or evasion abilities. Yeager's work demonstrates not only that pursuit-evasion contests emerge spontaneously given mobile creatures with conflicts of interest, but also that genetically encoded neural networks can evolve to generate adaptive pursuit and evasion behaviors in such contests.

4.3 Pursuit and Evasion by Robots

There is a huge literature on mobile robot control, largely focused on problems of navigation and path-following in unrealistically friendly environments free of anything that requires sustained pursuit or protean evasion (e.g. Brooks, 1989; Cliff et al., 1993; Harvey, Husbands, & Cliff, 1994). Even work on avoiding moving obstacles (e.g. the asteroid avoidance problem (Latombe, 1991) assumes that the obstacles are following predictable courses, which allows long-term path-planning (Canny, 1987; Tychonievich, Zaret, Mantegna, Evans, Muhle, & Martin, 1987). However, many potential robot tasks are essentially pursuit-evasion problems. The same fitness affordance theory that confirms the generality of pursuit-evasion problems for animals also applies to robots, where fitness can be interpreted in economic rather than reproductive terms (see McFarland, 1991). Pursuit and evasion by robots may require control systems more predictive than reactive control (e.g. Brooks, 1986; Arkin, 1989) allows, but much faster and more robust than traditional symbolic planning (e.g. Latombe, 1991) allows.

Yamauchi and Beer (1994) evolved dynamical neural networks for obstacle avoidance in simulation and found that these networks, when downloaded into real robots, functioned fairly well as evasion circuits for avoiding mobile human pursuers. Sharma and Aloimonos (1992) discussed the advantages of developing active vision in mobile robots for pursuing moving targets. The system called 'Mousebuster' developed by (Buttazzo, Allotta, & Fanizza, 1993) uses vision and prediction methods to track and catch fast unpredictable objects such as mice; this real-time system could catch objects moving on a plane at velocities of up to 0.7 meters per second.

Various "Robot Sumo" contests have been run (e.g. at the BEAM Robot Olympics (Tilden, 1992)), in which two robots subject to restrictions on size, weight, and degree of agression[2] try to push one another outside the boundaries of a circular pad, under either radio control or autonomous control. Robot Sumo is a symmetric pursuit-evasion game in which each agent strives for a more central position and for a better application of a centrifugal force vector to the other.

Arkin, Carter, and MacKenzie (1993) reviewed previous work on how robots can avoid moving obstacles, and developed motor schemas for dodging and escape in their reactive mobile robot. Dodging avoids ballistic projectiles by side-stepping; escaping avoids pursuers by moving directly away from the projected point of collision. Both forms of reactive active avoidance use a simple vector extrapolation method to detect expected collisions with moving obstacles. This sort of predictive perception turns the robot from a purely reactive system into a slightly anticipatory system. Avoidance of active and passive obstacles, movement towards goals, and wandering behavior are integrated by summing and normalizing the different velocity vectors specified by the motor schemas for each behavior. Simulation indicated thast these dodging and evading behaviors were sufficient to deal with multiple moving obstacles under noisy conditions. Implementation on Denning MRV-2 and MRV-3 mobile robots, which used 24 ultrasonic sensors for threat detection, also proved successful. This work by Arkin and colleagues shows that bottom-up, reactive control systems can be extending to do predictive evasion without sacrificing speed or robustness.

In addition to the robotics literature proper, there is also an enormous amount of technical military research on pursuit and evasion control systems for guided missiles, aircraft, and autonomous vehicles (i.e. tanks).[3]

4.4 General Simulations of Co-evolution and Mixed Strategies

Other simulated evolution work has demonstrated the adaptiveness of mixed strategies and protean behavior. Koza (1992) used genetic programming to evolve random-number generation programs under "entropy-driven evolution"; this direct selection for randomness is analogous to the indirect selection for unpredictable evasion that occurs in pursuit-evasion contests. Nowak (1993) showed that generous tit-for-tat (GTFT), a stochastic strategy, could evolve and thrive in evolutionary simulations of the prisoner's dilemma; GTFT cooperates even after a defection at some non-zero random rate (e.g. one-third of the time), and its unpredictability is the key to its success.

Benhamou and Bovet (1989, 1991) (Bovet & Benhamou, 1988) have used mathematical models to explore the spatio-temporal dynamics of animal movement, with particular attention to the utility of random-walk patterns in foraging. They developed a first-order correlated random walk model (rather than zero-order, to account for animals' head-tail difference and tendency to go forwards), and modelled search paths as a series of steps of particular length, with changes of direction after each step randomly drawn from nor-

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[2] In BEAM Class A Sumo, competitor robots may not attack the opponent's hardware. In BEAM Class B, damaging aggressive attack is encouraged, subject to certain constraints which limit the potential danger to nearby humans.

[3] The following journals contain relevant robotics work: *Advanced Robotics; IEEE Int. Conf. on Robotics and Automation; IEEE Transactions on Automatic Control; Int. J. Robotics and Automation; Proceedings of the SPIE; Robotica;* and *Robotics and Autonomous Systems.*

mal distribution wrapped around a circle, with a null mean corresponding to forwards movement. Varying the step-length and the variance of the direction-change distribution results in changes of a formal measure of movement "sinuosity" S , which can in turn be used to calculate an expected diffusion path length for foraging. Optimal sinuosity values can evolve for optimal foraging in environments with different food distributions. Although Benhamou and Bovet (1989) did not discuss the utility of this sort of movement unpredictability in pursuit and evasion, their sinuosity measure, or other similar measures, could be useful in analyzing the movement dynamics of pursuing and evading animals. Killeen (1992) has also developed a framework for the dynamical analysis of animate motion based on fields of approach and avoidance vectors.

Other simulation work has shown the utility of co-evolution in evolving strategies for game-like interactions. Work by Hillis (1990) on the co-evolution of sorting strategies and test sets can be viewed as an abstract version of a one-play pursuit-evasion contest, in which the sorting strategies 'pursue' optimal sorts while the test sets 'evade' the strengths of particular sorting algorithms. Co-evolution of strategies for the simple and iterated prisoner's dilemma has been particularly well-studied, e.g. by Axelrod (1989), J. H. Miller (1989), and Nowak and colleagues (1992, 1992). Co-evolution has also been simulated successfully in Holland's (1992) ECHO system, Koza's (1991, 1992) genetic programming research, Ray's (1992) TIERRA system, Werner and Dyer's (1993) Bioland system, and Yeager's (1994) Polyworld. Angeline and Pollack (1993) demonstrated the utility of co-evolution in genetic algorithms for solving complex problems. Chapter 6 of Kauffman (1993) explores the dynamics of co-evolution in great detail using simulation on N-K fitness landscapes.

4.5 Directions for Further Research

This work on co-evolution, along with Koza's demonstration of entropy-driven evolution through selection for randomness, and previous research on evolution of pursuit and evasion strategies, gave us hope that a co-evolutionary pursuit-evasion scenario could lead to the evolution of protean behaviors. In the companion paper (Cliff & Miller, 1994), we review our simulation methods and results, in which a genetic algorithm evolves pursuit and evasion strategies implemented as dynamical neural networks in simulated robots.

Simple demonstrations that effective pursuit and evasion abilities can evolve in simulation will not prove of much scientific interest (although they may have important engineering applications.) We already know from neuroethology and animal behavior that pursuit-evasion contests result in exquisitely adapted sensors, effectors, neural circuits, and behaviors. To go beyond this, we must address develop and test specific hypotheses about the co-evolutionary dynamics of pursuit-evasion contests, the typical neural mechanisms underlying pursuit-evasion behaviors, the trade-offs between pursuit-evasion capacities and other behavioral capacities, and so forth. For example, researchers could develop hypotheses about variables that might influence the evolution of pursuit-evasion behaviors, manipulate these variables in simulation, and observe the results using relevant measurement tools. In our work, we are currently manipulating the relative physical speed and the relative neural processing speed of pursuers versus evaders, to explore where in this 2D space of parameters various sorts of behaviors (such as dodging, feinting, and proteanism) will prove adaptive. Other variables to manipulate could include the structure of the physical environment (including obstacles) and the number of pursuers and evaders interacting at a time.

More generally, pursuit-evasion co-evolution could be used as a test bed for developing better genetic algorithms, better neural development schemes, better body designs, better sensors, etc. The basic requirements of effective pursuit and evasion – continuous robust dynamical control with respect to a hostile opponent – seem relevant to a variety of other adaptive behaviors. Pursuit-evasion contests could also prove more useful than spatial navigation tasks for testing the speed and robustness of various sorts of learning algorithms. Whatever control or learning methods have been shown effective for inanimate environments should now be tested against environments containing animate opponents.

Finally, pursuit-evasion contests typically result in both morphological and behavioral adaptations. Endler (1991) reviews a variety of such antipredator adaptations that include both bodily and behavioral components, including hiding, use of inconspicuous resting places, polymorphism (varied appearance across individuals), polyethism (varied behavior across individuals), camouflage, cryptic immobility, release of ink, blood, or other smoke screens, dropping off of distractors (e.g. wriggling tails), resemblance to inedible or distasteful objects, confusion effects arising from the interaction of body color patterns and movement patterns, modes of locomotion different from predators, startle, bluff, and threat displays, re-direction of attack towards less vulnerable body parts, physical toughness, slimy-ness, or spiny-ness, or safe passage through the predator's gut. A similar list could be compiled of predator adaptations; for example, many predators solve the pursuit problems not just by evolving more sophisticated neural circuits, but by enlarging their 'catch area' with larger mouths, webs, traps, or cooperative hunting methods (see Driver & Humphries, 1988). Behavioral challenges do not always require purely neurological solutions. Extensions of Sims' (1994a, 1994b) methods for morphogenesis and neurogenesis could prove useful for investigating the evolution of these sorts of integrated bodily, sensory, and behavioral systems for pursuit and evasion.

Exploring the co-evolution of predictive pursuit and creative evasive also opens the way for understanding more abstract psychological arms races. Miller (1993) has postulated that the evolution of the human brain was driven primarily by runaway sexual selection (see Cronin, 1991; Ridley, 1993), elaborating mental capacities for creative language, art, music, dance, and conceptual play. Under this hypothesis, cognitive mechanisms for mate choice can be viewed as pursuit systems that tend to track, predict, and habituate to various courtship behaviors, while the courtship behaviors themselves can be viewed as evasion systems that try to avoid being predictable and boring through generating creative, witty, humorous, and interesting novelty. Thus, creativity may be more of a neophilic, centrifugal, exploratory, evasive capacity, than a goal-directed, centripetal, convergent, pursuit capacity. The human brains' recent technological and scientific achievements can be viewed as spin-offs from mental adaptations for generating protean courtship displays to keep potential mates interested in pursuing our unpredictable trajectories of thought and feeling. Thus, even our most cherished cognitive abilities can be understood as the outcome of an unusual sexual-selective form of a pursuit-evasion contest.

5 Applications and Implications

By pursuing rather than evading the complexities of pursuit-evasion contests, we may reap significant engineering and scientific benefits. These are reviewed in turn.

5.1 Applications in Robotics

Many traditional robot control tasks are degenerate special cases of pursuit-evasion problems: collision-avoidance is evasion of non-moving obstacles, goal-directed navigation and homing behavior are pursuit of a non-moving target region, and grasping can be pursuit of a non-moving target object. Clearly, the avoidance, pursuit, or manipulation of active mobile agents radically increases the difficulty of such tasks, and their robust solution may require co-evolutionary design methods, where robot control systems evolve against pursuer or evader agents. Even where a robot's operating environment is expected to contain only static or passively moving objects, co-evolution of grasping and movement tactics against animate opponents might increase the robustness, speed, smoothness, and generality of control systems, because the opponents would evolve to exploit any instabilities or weaknesses in the control system. For example, a legged robot that is harried by a hostile predator that keeps trying to trip it up will probably evolve more robust walking abilities than one that merely clambers over passive obstacles. The co-evolution of evasion tactics through interaction with simulated animal, human or vehicle pursuers may help to solve the potentially catastrophic biophilic baby and technophilic teenager problems. Pursuit and evasion capacities have other obvious applications in computer animation, video games, and virtual environments, aside from less savory military uses.

5.2 Applications in Scientific Methodology

Some engineering applications shade over into scientific applications because they raise the possibility of developing new research methods. Artificial animals capable of realistic pursuit and evasion could be used as reliable experimental stimuli in further neuroethological studies of perception and behavior in a variety of animal species. Further, perceptual systems evolved for pursuit could be useful in automated recording of animal movements in laboratory or natural situations. One could imagine developing small autonomous robots whose goal is to videotape rather than eat a target species; such automata would make much easier the study of elusive animals in hard-to-reach natural habitats such as mountains, deep ocean, or rainforest canopies. Once the elusive subject is discovered, such robots could alert a scientist by radio and be switched over to remote control via a teleoperation system, for more detailed interactive study of the target species.

5.3 Implications for Scientific Research

The scientific benefits of a better understanding of pursuit and evasion would extend to game theory, animal biology, evolutionary psychology, and neuroethology. There are many open questions in the biology of pursuit and evasion that bear on general issues in animal behavior.

For example, the debate in adaptive behavior research over representational versus dynamical approaches to animal cognition might be illuminated by closer study of pursuit and evasion circuits. Many biologists have cited predator-prey interactions to argue for the special attunement of perceptual systems and internal representations to biologically relevant stimuli and situations; others have cited such interactions to argue for the importance of robust dynamical control. Miller and Freyd (1993) saw no necessary conflict between these positions, and have suggested that pursuit-evasion contests demand 'dynamic mental representations' (Freyd, 1987) that have both a dynamical structure and a representational function.

Another major issue is how unpredictable protean behavior could be generated. Options include stochastic neurons, emergent chaotic effects in recurrent neural networks, sensitivity to sensory input noise, output noise that emerges from unpredictable interactions between motor output and environment (as postulated by Roeder, 1970)), or noise that emerges when translating information between sensory and motor cognitive maps that use different coding schemes (as observed by (Liaw & Arbib, 1993)). It is easy to generate noisy behavior, but hard to know how animals actually do so. Simulations that compare different noise-generation methods might identify different trajectory characteristics that could be used to understand how animals produce proteanism.

The co-evolution of pursuit and evasion also raise challenges for motion perception, motor control, action selection, and learning. For example, a motion perception system sufficient for detecting inanimate motion may not suffice for detecting the unpredictable motion of a camouflaged animal. A motor control system sufficient for clambering over passive obstacles may not resist being tripped by a clever predator. An action selection system robust enough under normal conditions may be confused by startle displays, playing dead, jinking, feinting, or counter-attacks. Learning effective pursuit and evasion may be especially difficult because of the complexity of temporal credit assignment, and the continuity of decisions and behaviors. It will be difficult to construct models of adaptive behavior that are good enough to perform effective pursuit and evasion, but not so good that they could never be fooled by counter-measures, as animals often are.

Pursuit-evasion contests naturally lead to some important varieties of social behavior and communication such as herd defense, pack-hunting, and alarm calls. The coordination of one's own behavior with respect to a single hostile opponent and an inanimate environment is challenging enough; the additional difficulties of robust coordination with respect to co-evaders or co-pursuers boggle the mind. The cooperative behavior of thousands of ants may be easier to model than conflicts between a dozen partially-cooperating predators and a dozen partially-cooperating prey. By analogy, the statistical mechanics of billions of gas molecules is easier than the three-body problem in celestial mechanics.

Biologists need to do more descriptive studies of pursuit and evasion trajectories in a wider array of species, with new techniques such as high-speed film, computer movement analysis, and statistical analysis (e.g. time series methods). Perhaps only when simulation research over-reaches what is known about the dynamics of animal behavior will biologists feel forced to make their data catch up with our simulations. More optimistically, perhaps this paper will inspire more collaboration between behavioral biologists and simulation researchers.

Implications also arise for our understanding of the general relationship between agents and environments. For those seeking a general theory of environmental complexity (e.g. Wilson, 1991; Todd & Wilson, 1993), the addition of animate agents capable of unpredictable pursuit and evasion in the environment represents a significant conceptual challenge. For example, an environment that contains creatures with continuous-time dynamical noisy recurrent networks as their control systems would be difficult to model as an environmental finite state machine, as proposed in (Wilson, 1991). As in sexual selection (Miller, 1993; Miller & Todd, 1993) and other forms of "psychological selection" (Miller, 1993; Miller & Freyd, 1993), pursuit-evasion contests break down the distinction between environment complexity and agent complexity, because agents become the most important selective forces in each other's environments.

6 Conclusions

Pursuit and evasion behaviors are common because conflicts of interest over approach and avoidance are common, and they are difficult because dynamic, stochastic, continuous-space, continuous-time games are difficult. This paper has argued that the exploration of pursuit-evasion contests is the next logical step in the simulated evolution of adaptive behavior, after the development of basic capacities for avoiding inanimate obstacles and approaching inanimate goals. Pursuit-evasion contests are ideal arenas for investigating adaptive behavior at many levels over many time-scales, from the robust dynamical control of movement to the long-term co-evolution of behavioral strategies in social groups of cooperating agents.

Like the blind men studying the elephant, behavioral biology, neuroethology, and game theory have focused on quite different aspects of pursuit-evasion contests. Much is known about the how animals look when they're chasing each other, how simple neural circuits in animals do reflexive escape and attack behaviors, and how optimal strategies work in overly simplified differential games. But we do not yet have a realistic, integrated theory about how the co-evolution of pursuit and evasion happens in nature, or how it could happen in engineering applications. We believe the best way forward is to use evolutionary simulation methods that can track the emergence of complex sensory, neural, and motor systems using detailed measurement techniques and experimental comparisons across relevant variables (see Cliff & Miller, 1994). If such work is done with a thorough understanding of ideas and results already contributed by biology, game theory, and previous simulation and robotics work, if will be more likely to promote the fruitful interdisciplinary study of pursuit, evasion, and their co-evolution.

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