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## Self-regulation in an evolutionary perspective

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*Original Citation:*

*Availability:*

This version is available <http://hdl.handle.net/2318/1852939> since 2022-04-08T21:32:47Z

*Publisher:*

Springer

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**Del Giudice, M. (2015). Self-regulation in an evolutionary perspective. In G. H. E. Gendolla, M. Tops & S. Koole (Eds.), Handbook of biobehavioral approaches to self-regulation (pp. 25-42). Springer.**

## **Chapter 2. Self-Regulation in an Evolutionary Perspective**

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**Keywords:** control theory; coping styles; discounting; feedback; feedforward; impulsivity; inhibition; life history theory; self-regulation; trade-offs.

**Abstract:** In this chapter I situate self-regulation in an evolutionary perspective, and explore the implications of an evolutionary approach for the study of individual differences in self-regulation. I review the two basic strategies of behavior control (feedback and feedforward control), compare their relative advantages and disadvantages, and highlight the role of trade-offs in the evolution of control systems. I then discuss how organisms shift the balance between feedback and feedforward control in a context- and task-specific manner, and outline an ecological theory of control strategies. I show how the same principles can be employed to understand stable individual differences in control strategies and impulsivity, characterized as “coping styles” in the biological literature. Finally I introduce the framework of life history theory, discuss how it provides a unifying perspective on the development of individual differences in self-regulation, and critically examine the association between life history strategies and self-regulation in humans and nonhuman animals.

## 2.1. Introduction

In this chapter I situate self-regulation in an evolutionary perspective, and explore the implications of an evolutionary approach for the study individual differences in self-regulation. I begin with an overview of the self-regulation continuum, from simple control mechanisms with no explicit goal representation to deliberate, self-directed executive processes like those found in human adults. In particular, I highlight the central role of inhibition and future orientation in the emergence of complex self-regulatory abilities, and introduce the construct of impulsivity. In the next section I review the two basic strategies of behavior control—feedback and feedforward control—and discuss their relative advantages and disadvantages from the standpoint of control theory. A central theme of the section is that self-regulation involves trade-offs at all levels—between speed and accuracy, robustness and flexibility, and so forth; organisms deal with those trade-offs by implementing multiple control systems that coexist in the brain and cooperate in the regulation of goal-directed behavior.

Next, I discuss how organisms shift the balance between feedback and feedforward control in a context- and task-dependent manner, and outline an ecological theory of control strategies. The goal is to understand how environmental and individual factors interact to determine the optimal self-regulation strategy in a given context. I then go on to show how the same principles can be employed to understand stable individual differences in control strategies and impulsivity (characterized as “coping styles” in the biological literature), and review some potential evolutionary explanations of adaptive individual variation. Finally I introduce the framework of life history theory, discuss how it provides a unifying perspective on individual differences in self-regulation, and conclude by critically examining the association between life history strategies and self-regulation in humans and nonhuman animals.

## 2.2. Self-Regulation: An Overview

### 2.2.1. The Self-Regulation Continuum

The term “self-regulation” has many possible meanings, and definitions vary across authors and research areas. While the existence of multiple definitions can be confusing, the different kinds of self-regulation described in the literature can be easily understood as regions along a continuum going from comparatively simple and mindless control mechanisms to complex, hierarchical, and deliberate mental processes.

In the broadest sense, the concept of self-regulation applies to all forms of goal-directed behavior (e.g., Carver & Scheier, 2011; Hofmann et al., 2012; Tops et al., 2010). It is important to realize that, by this definition, self-regulation does not require goals to be explicitly represented by the individual organism, even if the goal may be clearly discernible by an outside observer. When a bacterium moves toward higher concentrations of glucose by chemotaxis, its behavior is regulated by a clever system of feedback control that alternates straight line swimming and random tumbling. The *objective* goal of this behavior is obvious to an external observer—moving the bacterium toward glucose—even if the bacterium itself has no internal representation of the reason for its behavior; in fact, the bacterium does not even need to represent the direction in which it is swimming (Bechhoefer, 2005).

In Daniel Dennett’s terminology, such real but unrepresented goals can be understood as “free-floating rationales” (Dennett, 2009). Even in very simple organisms, natural selection tracks the causal regularities that affect survival and reproduction, since those organisms that—for whatever reason—are better at exploiting the causal structure of their environment are usually also better at surviving and reproducing. As a result of this selection process, evolution equips organisms with machinery that supports effective goal-directed performance (e.g., chemotaxis) with no need for the individual organism to possess any representation of the underlying goals and causal properties. As organisms evolve more sophisticated nervous systems, however, goals and reasons may begin to be actively represented, even if only partially and implicitly. For example, the firing rate of a neuronal group may implicitly encode the expected amount of food in a given direction of space. By gradual accumulation of function, evolution has provided humans with a remarkable ability to explicitly represent their goals (or at least some of them), communicate them to conspecifics, and employ those representations to build detailed plans as well as mental scenarios of their behavior and that of other people (see Dennett, 2009).

Self-regulation in the narrow sense concerns a subset of behaviors—broadly defined to include cognitive operations in addition to body movements—whose main function is to change the probability of later behaviors by the same organism (see Barkley, 2001). Some scholars refer to narrow-sense self-regulation as *self-control* (e.g., Carver & Scheier, 2011; Hofmann et al., 2012). The basic component of narrow-sense self-regulation is *inhibition*—the ability to override impulses and responses that conflict with current goals. Thus defined, inhibition does not require explicit goal representations, although it does require the existence of multiple interacting control systems within the same organism. Simple forms of inhibition can take place in absence of a control hierarchy; for example, control systems A and B—each equipped with their own goals—may reciprocally inhibit one another whenever their activation level crosses a certain threshold. Of course, when self-regulation processes become hierarchically organized (e.g., Carver & Scheier, 2011; Filevich et al., 2012; Kopp, 2012), higher-order systems may acquire the ability to flexibly inhibit lower-order systems in the service of higher-order goals. In the self-regulation literature, inhibition is usually framed in the context of hierarchical control systems (e.g., Carver & Scheier, 2011; Filevich et al., 2012).

At the far end of the continuum is the family of *executive functions*, an even narrower subset of regulatory processes that—in their most elaborate form—are only possessed by adult humans. Executive functions stand out because of their deliberate self-directedness (Barkley, 2001), and permit extremely high levels of flexibility and strategic planning (Diamond, 2013; Miyake et al. 2000). The standard taxonomy of executive functions includes *inhibition* (deliberate overriding of dominant or prepotent responses), *updating* (constant monitoring and rapid addition/deletion of working memory contents), and *shifting* (switching flexibly between tasks or mental sets). A broader, biologically plausible taxonomy of executive functions advanced by Barkley (2001) also includes *affective self-regulation* and *generativity* (the ability to mentally generate new combinations of behavioral units).

On the surface, executive functions look like a heterogeneous collection of cognitive processes. What they all share is a common theme of *future orientation*. In different ways, executive processes contribute to detach behavior from immediate, short-term goals in order to maximize the long-term outcomes for the individual (discussed in Barkley, 2001; Denckla, 1996). Executive functions can serve multiple adaptive roles including vicarious learning,

delayed reciprocity in social exchanges, flexible tool use, and self-defense against social manipulation. In adults, executive functions are usually covert (e.g., silent self-talk), possibly as an adaptation to social competition (see Barkley, 2001, for a detailed treatment).

### 2.2.2. Impulsivity

Both conceptually and empirically, inhibition and future orientation play a central role in the self-regulation continuum. Together, they allow the emergence of the full range of executive functions deployed by adult humans. Inhibitory functions allow individuals to interrupt ongoing actions, delay prepotent responses, and reduce attentional and motor interferences. Inhibition is a precondition for all other forms of executive control, and is required to protect ongoing executive processes from external and internal interferences (Barkley, 2001). Consistent with this view, psychometric studies show that inhibition can be regarded as the “general factor” of executive functioning, as it accounts for most of the shared variance between different executive abilities (Miyake & Friedman, 2012). The concept of future orientation can be understood in more rigorous terms as a function of *time discounting* (or *delay discounting*). In a nutshell, time discounting quantifies the extent to which preferences are affected by delays in the presentation of rewards. High discount rates are revealed by a strong preference for smaller immediate rewards over larger, delayed ones. Future orientation is reflected in low discount rates, and covaries with inhibitory abilities in both humans and nonhuman species (see Coppens et al., 2010; DeYoung, 2011).

Behavioral disinhibition and present orientation can be seen as partially overlapping facets of a broader trait—*impulsivity*. Impulsivity is arguably the most important dimension of individual variation in self-regulation, and can be described as the tendency to act without deliberation and without consideration of future consequences (Carver, 2005; DeYoung, 2011). The construct of *effortful control* is symmetrical to that of impulsivity, and refers to the ability to inhibit dominant responses while taking into account the long-term consequences of actions (see Rothbart, 2007).

In much psychological literature, impulsivity is treated by default as a dysfunctional, maladaptive aspect of personality and behavior. However, some authors have stressed how impulsivity can also bring important advantages, including the ability to make quick decisions and seize on unexpected opportunities (Block, 2002; Dickman, 1990). The adaptive potential of impulsivity has been examined in greater detail by evolutionary biologists<sup>1</sup>. A wealth of empirical and theoretical findings demonstrate that—depending on ecological circumstances, the structure of the environment, and the nature of specific tasks—present orientation and impulsive decision-making can often be highly adaptive, leading individuals to maximize the benefits of behavior in key areas such as mating, foraging, and exploration (e.g., Chittka et al., 2009; Coppens et al., 2010; Daly & Wilson, 2005; Green & Myerson, 1996; Sih & Del Giudice, 2012; Stephens et al., 2004).

## 2.3. Two Strategies of Behavior Control

Self-regulatory processes may reach a remarkable degree of sophistication and differentiation, especially in socially complex organisms like humans (Barkley, 2001). However, their internal logic ultimately boils down to two basic strategies of behavior control—*feedback*

*control* and *feedforward control*. Feedback and feedforward controllers are the building blocks of all regulatory systems, and their characteristics and limitations have been worked out in detail in the field of mathematical control theory (see Albertos & Mareels, 2010; Bechhoefer, 2005). In this section I provide a brief overview of feedback and feedforward systems from the standpoint of control theory.

### 2.3.1. Feedback Control

In feedback or closed-loop control, the current goal (or *control signal*) is compared with the actual state of the system (i.e., the system's *output*), and an *error signal* is obtained as a result. For example, the goal of a bird chasing a fly may be that of getting as close as possible to the fly; the distance between the bird and the fly at any given moment would then constitute the system output. The error signal is used to generate a goal-directed action, which alters the state of the system (the bird may change speed and/or trajectory). However, other causal factors (*disturbances*) may be acting on the system at the same time; for example, the fly may suddenly turn, or a change in wind speed may affect the bird's trajectory. The joint effect of goal-directed actions and disturbances determines the system output, which is then measured and compared to the current goal, closing the control loop (Figure 2.1). The critical feature of a feedback controller is that it tracks the system output in real time, progressively narrowing the gap between the goal and the state of the world through moment-to-moment self-correction.

As a rule, the system output is not *directly* available for comparison but has to be estimated or measured in some indirect way, for example through sensory organs and related neural pathways. Measurement processes—broadly defined to include sensory processes and the associated neural computations—inevitably introduce some error (or *noise*) in the feedback loop. Indeed, feedback systems face a fundamental trade-off between tracking speed and the ability to reject unwanted noise. If the output is measured with higher temporal resolution—thus increasing the ability to track rapid changes in the state of the system—more irrelevant noise will enter the feedback channel and get mixed up with the useful information. Conversely, effective filtering of unwanted noise inevitably reduces the tracking speed of the control system (Bechhoefer, 2005).

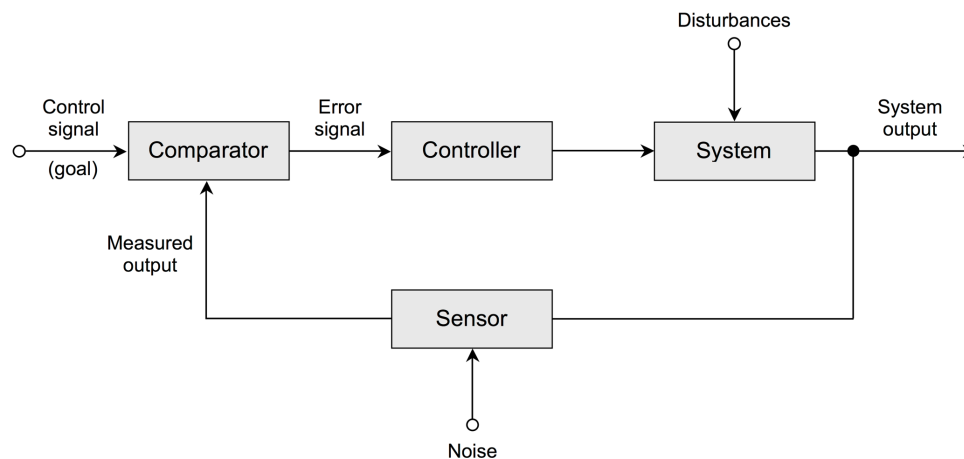


Figure 2.1. Schematic representation of a feedback (closed-loop) control system.

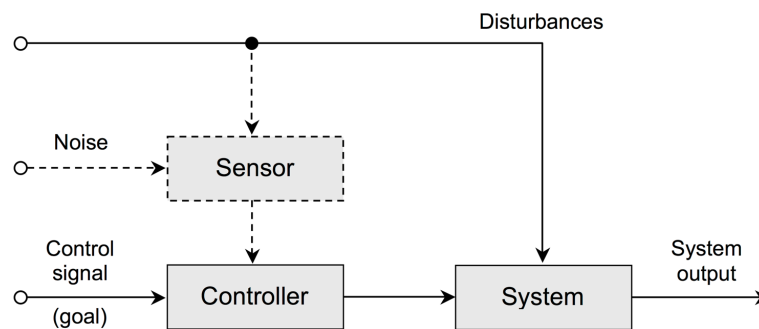
A powerful way to employ feedback controllers is to nest multiple feedback loops within one another, yielding a *feedback cascade*. In this type of hierarchical arrangement, the inner control loop regulates a lower-order variable (i.e., pursues a lower-order goal) in order to simplify the control actions performed by the controller in the outer loop (Albertos & Mareels, 2010). Nested feedback loops allow a complex control task to be split into smaller modular tasks, and permit high levels of flexibility and accuracy. For these reasons, feedback cascades are very popular in cognitive and neuropsychological models of self-regulation (see Carver & Scheier, 2011; Filevich et al., 2012; Kopp, 2012). A classic application of feedback loops is the TOTE model advanced in 1960 by Miller and colleagues. A TOTE unit (acronym of *Test-Operate-Test-Exit*) is an abstract feedback controller that executes an iterative “plan” until its goal is reached. In this model, the hierarchical plans that control an organism’s behavior are implemented by cascades of nested TOTE units working at different levels of abstraction (Miller et al., 1960).

The main strength of feedback control lies in its ability to respond to unknown or unanticipated disturbances. More generally, feedback control has an intrinsically self-correcting nature; for this reason, it does not require an accurate preexisting model of the system in order to function properly. However, feedback systems are also highly sensitive to noise and rely on accurate measurement of the system output, which may or may not be available in a given situation. Another crucial limitation of feedback control is that it depends on the ability to track real-time changes in the system. Sensory processing, neural computation, inertia in the system, and so forth introduce delays and response lags in the feedback loop. As the overall delay increases, the performance of feedback control deteriorates rapidly; beyond a certain threshold, delays in the feedback loop may destabilize the system and lead to erratic, uncontrolled behavior (Albertos & Mareels, 2010; Azuma & Hirose, 2008; Bechhoefer, 2005).

### **2.3.2. Feedforward Control**

While feedback control is an ubiquitous and powerful strategy, it also has important limitations. As deftly put by Albertos & Mareels (2010), “driving a car by feedback only would equate to driving using information only from the rear view mirror” (p. 213). In other words, feedback controllers can only respond to disturbances and changes in the system once they have occurred, but are unable to *anticipate* them. Returning to the car analogy, imagine a driver trying to keep her car on track by only looking in the rear view mirror. Every time the road turns, the car begins to veer off course; the backward-looking driver then notices the deviation in the mirror and responds by steering the car back on its trajectory (with some unavoidable delay). A forward-looking driver would see the turn approaching and could begin the steering movement in advance, resulting in a much smoother trajectory.

When disturbances can be anticipated (or ignored altogether), feedforward or open-loop systems may become highly effective means to control the behavior of a system. In feedforward control, the goal is combined with a model of the system that may also include the predicted effects of future disturbances; the results of this computation are then used to guide behavior, with no further feedback about the state of the system (Figure 2.2). For example, when a chasing bird gets close enough to the fly, it may “dive” toward the prey with a rapid anticipatory motion based on (a) the predicted position of the fly in the next fraction of a second and (b) a model of the motor actions required to reach that position at the right time.



*Figure 2.2.* Schematic representation of a feedforward (open-loop) control system. A feedforward controller may employ information about past and current conditions to predict the future state of the system (dashed box and arrows).

The simplest forms of open-loop control may skip the prediction step entirely; many protective reflexes—for example retracting one’s hand when it touches a hot object—are based on simple, “ballistic” open-loop mechanisms (see Albertos & Mareels, 2010). More complex instances of feedforward regulation may involve simulation of future events, strategic planning, and integration of preexisting knowledge about the rules that govern the system, the likelihood of potential outcomes, and the influence of contextual variables.

Just like feedback control, feedforward control has strengths as well as weaknesses. To begin with, feedforward control permits extremely fast execution once an action sequence is initiated. Other advantages of feedforward systems include their insensitivity to noise, their greater dynamic stability, and the fact that they do not require accurate, real-time measurement of the system output. On the other hand, feedforward regulation often requires an accurate model of the system, and enough information about the current state of the system so that future disturbances can be successfully predicted. Most crucially, feedforward systems—regardless of their complexity—are unable to respond to unanticipated events that occur while the planned action is unfolding (Albertos & Mareels, 2010; Bechhoefer, 2005).

### 2.3.3. Combining Feedback and Feedforward Control

It is apparent from the preceding discussion that feedback and feedforward systems have largely complementary sets of advantages and disadvantages. As a result, the design of self-regulation strategies involves a number of important trade-offs—between speed and accuracy, flexibility and robustness, predictive ability and computational simplicity, and so forth. The standard engineering solution to these trade-offs is to combine feedback and feedforward elements in the same control system, in order to exploit the strengths of both strategies and compensate for their weaknesses (Albertos & Mareels, 2010; Bechhoefer, 2005). For example, the predictive estimates employed in feedforward control can be used to compensate the delays



introduced by feedback loops and make the system more resistant to sensory noise (see Wolpert & Ghahramani, 2000).

There is considerable evidence that the brain controls behavior through the joint action of multiple control systems based on complementary principles (e.g., Tucker et al., 1995; Wolpert & Ghahramani, 2000; Wolpert et al., 2003). Control subsystems employing the same or different strategies can be combined in many different ways; in particular, hierarchical arrangements of higher- and lower-order controllers—as in feedback cascades—can achieve remarkable qualities of speed, accuracy, and flexibility (e.g., Albertos & Mareels, 2010; Carver & Scheier, 2011; Filevich et al., 2012). In addition, feedback and feedforward processes can be combined *sequentially* in time to increase behavioral flexibility and optimize learning. When a feedforward controller needs an accurate model of the system, feedback loops can be employed in the learning phase to build, update, and refine such a model—effectively “training” the feedforward controller and enhancing its future performance (this is known as *feedback-error learning*; see Wolpert & Ghahramani, 2000). For example, an initial phase of feedback control may facilitate slow, systematic exploration of a novel environment (Sih & Del Giudice, 2012); the context model built in the learning phase can then be used to make quick, effective decisions guided by feedforward processes.

#### 2.4. The Ecology of Control Strategies

While the overall performance of a control system can be improved by a mixture of feedback and feedforward processes, the optimal combination between the two strategies may change—sometimes dramatically—across different contexts and tasks. For example, Azuma and Hirose (2008) simulated a neural network performing a complex control task (riding a bicycle without falling) with different amounts of delay in the perception-action loop. As the delay increased, feedback control became more and more unstable and the optimal strategy shifted to feedforward prediction (see section 2.3). From a biological standpoint, brains can be expected to possess the ability to shift the balance between feedback and feedforward control depending on the current task and environmental conditions. Moreover, there is no reason why strategic flexibility should be limited to motor tasks: the general principles of feedback and feedforward control—and the resulting trade-offs—apply to all kinds of goal-directed behavior, from simple motor actions to complex social interactions (e.g., Carver & Scheier, 2011; Wolpert et al., 2003).

In the remainder of this section, I combine the principles of control theory with insights from evolutionary biology to derive some initial predictions about the ecology of control strategies. In order to understand how optimal strategies may vary across environments, the standard focus on control performance has to be supplemented with careful consideration of the organism’s needs and priorities. In general, whether a strategy is biologically adaptive in a given context does not only depend on its performance in terms of speed and accuracy, but also on the overall cost-benefit balance with respect to an individual’s fitness. A slower and/or less accurate strategy may be adaptive if it increases the organism’s chances of successful survival and reproduction. Furthermore, the costs and benefits of a strategy in a given environment may vary dramatically between different individuals (for example between males and females, old and young, well-fed and starving). Since environmental *predictability* has been singled out as a key determinant of the adaptiveness of control strategies (e.g., Tops et al., 2010), I will center my analysis on the distinction between predictable and unpredictable environments.

### 2.4.1. Unpredictable Environments

When the local environment is unpredictable and subject to sudden changes, feedback strategies have two important advantages over feedforward strategies. First, feedback control tracks the environment in real time, enabling flexible behavioral adjustment in response to changing conditions; and second, it works even when it is difficult or impossible to construct an accurate model of the environment (see also Tops et al., 2010). The benefits of feedback control are especially critical when an individual's goal is to prevent and/or avoid potential dangers in the environment. However, the preventive effectiveness of feedback strategies is greatest when dangerous events can be anticipated based on warning cues; since feedback processes are intrinsically backward-looking, they cannot successfully prevent events that occur too abruptly.

When the environment reaches very high levels of unpredictability, the potential benefits of feedback control decrease while the costs of continued vigilance increase accordingly. In such environments, it may be more advantageous to embrace unpredictability rather than attempt to control it—in other words, some individuals may shift from a risk-averse strategy focused on harm prevention to a high-risk strategy involving competition, bold exploration, and so forth (see Del Giudice et al., 2011; Ellis et al., 2012). Individual characteristics that favor risk-taking in unpredictable environments include sex, dominance status, and physical conditions. In particular, the males of most species—including humans—face stronger mating competition and more variable reproductive outcomes than females (see Geary, 2003; Kokko & Jennions, 2008). The result is stronger sexual selection for competitive traits such as risk-taking, dominance-seeking, and physical aggression (see Archer, 2009; Cross et al., 2011; Wilson et al., 2002).

By definition, risky decisions face individuals with unpredictable outcomes, as they may result in large gains as well as large losses (see Frankenhuis & Del Giudice, 2012). When individuals engage in high-risk courses of action, the immediate feedback they receive can be irrelevant or even misleading. In an all-out fight with a dangerous opponent, the best strategy is usually to keep fighting no matter what rather than backing down after the first blow. More generally, high-risk strategies often require outright *insensitivity* to threats and dangers to work successfully. For extreme risk-takers, informational insulation from signals of threat can be an asset, not a weakness (Del Giudice et al., 2011; Korte et al., 2005). Thus, it can be adaptive for them to suppress the activity of feedback control systems and rely on open-loop, “ballistic” strategies that deliberately ignore the immediate consequences of one's actions.

### 2.4.2. Predictable Environments

In predictable environments, feedforward strategies offer several potential benefits including robustness, decision speed, and enhanced sequential planning capabilities. It is important to keep in mind that open-loop self-regulation can take various forms that differ in their complexity and in their relation with impulsivity. First, there is the ballistic, impulsive sort of open-loop regulation involved in high-risk strategies. At moderate levels of complexity, feedforward control is driven by habits and rigid, inflexible behavioral routines (see Coppens et al., 2010). When coupled with detailed context models, however, open-loop control may enable careful, deliberate, future-oriented planning, which in turn requires active inhibition of competing short-term goals. While all these modes of self-regulation imply a primacy of feedforward

control, they differ widely in their functional implications. The most complex forms of feedforward regulation require a host of dedicated cognitive adaptations for planning and mental simulation, and might only make sense in long-lived species with complex social structures such as humans (Barkley, 2001). Moreover, the human ability to use language to transmit knowledge about the environment permits vicarious learning on an unprecedented scale, and maximizes the power of self-regulation based on explicit rules and expectations.

While feedforward control may function especially well in predictable environments, it is not necessarily the optimal strategy for all individuals. When harm prevention is a high priority it may be adaptive to shift to feedback strategies, which as a rule are better suited for dealing with unforeseen events—including dangerous ones. Closed-loop strategies sacrifice some of the speed and robustness of open-loop strategies in exchange for enhanced protection from harm. For example, higher female investment in offspring production and parental is expected to select for stronger risk aversion and harm avoidance in females (Archer, 2009; Campbell, 1999; Cross et al., 2011). As a result, females should have a stronger tendency than males to rely on feedback controls strategies even in predictable and comparatively safe contexts.

The superior ability of feedback control to deal with unexpected changes in the environment does not apply only to dangerous events. Closed-loop systems respond quickly to all sorts of novel circumstances, including the emergence of unforeseen *opportunities* (Sih & Del Giudice, 2012). While feedforward strategies are more robust, they cannot adjust to unexpected events—regardless of their positive or negative quality—and tend to suppress sensory input that does not conform to predictions (Tops et al., 2010; Tops & Boksem, 2010). Thus, an abundance of potential opportunities may tip the balance in favor of feedback strategies even in predictable environments.

Even more generally, feedback control may be adaptive in stable, predictable contexts because it supports systematic learning. As noted by Sih and Del Giudice (2012), feedforward strategies are associated with fast but shallow learning styles; in addition, they make it difficult to update one's cognitive models once they are formed because of their limited self-correction abilities. In contrast, stimulus-driven processes favor slower but more careful and systematic learning, and are associated with increased cognitive and behavioral flexibility—including the ability to quickly unlearn rules and associations that are no longer valid (Coppens et al., 2010). Thus, feedback strategies may be highly adaptive when the task is to learn the structure of a predictable environment with high accuracy and resolution. Once a sophisticated model of the environment has been constructed through feedback-driven exploration (Wolpert & Ghahramani, 2000), it can be exploited by feedforward control systems to enable quick and accurate decision-making. Developmentally, individuals growing up in predictable contexts may go through an initial phase of predominantly closed-loop regulation and increasingly shift toward open-loop control as they learn and mature.

### 2.4.3. Delayed Outcomes

In many important domains of behavior, the consequences of an action can only be evaluated at some distant point in the future. Accepting or rejecting a mate, deciding how many offspring to raise, choosing a nest site or a territory, stocking food reserves for the winter—what all these decisions have in common is that their outcomes take a long time to become manifest.

When decisions affect subsequent generations, their consequences may even extend beyond the lifespan of a single individual. When outcomes are delayed beyond a certain point, feedback control is simply not an option; while self-correction may be possible in the long term (e.g., building a new nest in the next breeding season), the only viable strategy in the short term is to base actions on feedforward models.

On the face of it, the last statement might seem paradoxical: how can an individual build a model of something it has never experienced before (and may never experience again)? The answer is, *it doesn't have to*. When fitness-relevant decisions recur over many generations, evolution can be expected to equip organisms with built-in implicit knowledge about the causal structure of the system (see Cosmides & Tooby, 1994). Such knowledge can inform model-based planning—thus enabling feedforward behavior control—even in cases where individual learning is difficult or impossible. From another perspective, feedback does not occur at the individual level but rather at the *population* level, as a consequence of natural selection—successful decision rules are retained (as individuals who make good decisions reproduce more) while unsuccessful ones are weeded out. This argument can be generalized to decisions in unstable and/or unpredictable contexts. While unpredictability makes it difficult to build a model of the environment, an organism may still rely on evolved feedforward strategies designed to maximize fitness in unpredictable conditions. As discussed above, such strategies may often involve high levels of impulsivity and risk-taking.

#### 2.4.4. Defensive Responses

A final topic to consider is the regulation of defensive responses. Shudo and colleagues (2003) developed a mathematical model to investigate optimal response strategies to unpredictable danger. In the model, a potentially dangerous event occurs, but assessing the actual severity of the danger takes a certain amount of time. Feedforward strategies are directly triggered by the event and immediately start a ballistic defensive response; in contrast, feedback strategies respond to the *consequences* of the event and adjust the strength of the response to the actual level of danger, thus maximizing control accuracy. Shudo and colleagues found that optimal response strategies always include a feedforward component. Mixed strategies can be favored if uncertainties in danger estimation are very large and delays in the feedback loop are sufficiently small; however, pure feedback control is never optimal. A similar logic applies to defensive reflexes such as hand retraction or the blink reflex (section 2.3). These results suggest that even individuals who rely on feedback strategies to prevent danger may suddenly switch to feedforward control *after* a dangerous event has occurred, in order to mount a quick and effective response.

### 2.5. From Control Strategies to Coping Styles

As detailed in the preceding sections, the trade-offs of behavior control explain both the existence of multiple control systems in the brain and the ability to shift between different strategies in a context- and task-sensitive way. The same trade-offs are likely to underlie the existence of stable individual differences in self-regulation styles. In the biological literature, patterns of individual differences in self-regulation are usually characterized as *coping styles*, as they emerge most reliably in response to stressful challenges involving unpredictable and/or potentially threatening events (Koolhaas et al., 1999).

The basic distinction in the biological literature is that between *reactive* and *proactive* coping styles. Reactive individuals show a primacy of feedback control; they are behaviorally flexible, high in cue dependency, and engage in thorough exploration of novel environments. Reactive individuals also tend to be shy, fearful, non-aggressive, risk-averse, future-oriented, and low in general activity. On the contrary, proactive individuals show a primacy of feedforward control; they are low in cue dependency, show rigid, inflexible behavioral routines, and are quick but superficial explorers. Proactive individuals also tend to be active, bold, aggressive, risk-prone, and impulsive (Coppens et al., 2010; Koolhaas et al., 1999, 2007; Réale et al., 2010; Sih & Del Giudice, 2012). Of course, the existence of stable coping styles does not mean that individuals are rigidly tied to a fixed control strategy regardless of the current situation. Instead, contextual and state-dependent variation in control strategies usually coexists with *average* differences in preferred strategy across individuals.

Individual differences in coping styles along the proactive-reactive axis have been documented in a broad range of species, including (but not limited to) monkeys, pigs, rodents, birds, and fish (see Carere et al., 2010; Koolhaas et al., 1999; Réale et al., 2010). The concept of coping styles overlaps significantly with those of *behavioral syndromes*, *behavioral types*, and *personality types*. Accordingly, there is a growing tendency to regard those labels as practically synonymous (e.g., Coppens et al., 2010; Sih & Del Giudice, 2012; for a different perspective see Uher, 2011).

### 2.5.1. The Evolution of Coping Styles

Why should members of the same population display stable individual differences in coping styles? Evolutionary biology provides several potential answers to this question; here I review some of the most common alternatives (see Wolf et al., 2013, for in-depth discussion). To begin with, small initial differences in individual conditions may be amplified and stabilized by self-reinforcing cycles if conditions and behavior are reciprocally connected. For example, larger individuals of a species could afford to explore more boldly because they are less threatened by predators. Bolder exploration may enable them to find more food, thus becoming even larger, and so on (see Luttbegg & Sih, 2010; Sih & Del Giudice, 2012).

Alternatively, individual differences may result from *adaptive developmental plasticity* (West-Eberhard, 2003; Schlichting & Pigliucci, 1998). Developmental plasticity is the ability of an organism to produce distinct phenotypes when exposed to different environments throughout its ontogeny. Since different control strategies are adaptive in different contexts (section 2.4), individuals may have evolved the ability to respond to early cues—for example, cues indicating that the environment is unpredictable, or that adult social competition is going to be especially intense—by adjusting their behavioral phenotype so as to match the predicted environmental conditions. As a result, individuals growing up in different conditions will go on developing different coping styles, possibly in interaction with individual variables such as sex, competitive ability, and so forth.

While developmental plasticity depends on early environmental inputs, there is ample evidence that coping styles also reflect genotypic differences between individuals (reviewed in Carere et al., 2010; van Oers & Sinn, 2013). Adaptive genotypic differences can be maintained in

a population for a number of distinct reasons. First, the costs and benefits associated with different coping styles may result in the same average fitness (*selective neutrality*). Second, genotypic differences may be maintained by *frequency dependent-selection* if the fitness of a given phenotype depends on its relative abundance in the population relative to other phenotypes. For example, proactive individuals may enjoy high reproductive success when a population is mostly composed of reactive individuals, but *not* when most other members of the population are also proactive. Third, spatial and temporal variation in environmental conditions and the associated selective pressures (*fluctuating selection*) may favor the maintenance of polymorphic alleles (see Del Giudice, 2012; Wolf et al., 2013). Studies of bird and mammal populations have provided initial evidence that selection on coping styles does indeed fluctuate across space and time, creating the conditions for the maintenance of adaptive genotypic variation (see Dingemanse & Réale, 2013).

Finally, unpredictable environmental fluctuations may favor the evolution of *diversified bet-hedging*. In bet-hedging strategies, each individual randomly develops one out of two or more phenotypes through a stochastic “switch” mechanism. Diversified bet-hedging spreads the risk of reproductive failure across a genetic lineage, since at least some individuals will end up with a well-matched phenotype regardless of the state of the environment. Specifically, bet-hedging reduces average individual fitness in the short term, but enhances the long-term reproductive success of the lineage by decreasing fitness variance across generations (see Starrfelt & Kokko, 2012). It should be noted that bet-hedging, developmental plasticity, and genotypic variation are not mutually exclusive alternatives; in fact, they can coexist in various combinations and proportions depending on the structure of environmental fluctuations, the costs of plasticity, and other ecological factors (see Wolf et al., 2013).

## 2.6. A Life History Perspective on Self-Regulation

### 2.6.1. Life History Strategies

Life history theory is a branch of evolutionary biology dealing with the way organisms allocate time and energy to the various activities that comprise their life cycle (see Ellis et al., 2009; Hill & Kaplan, 1999; Kaplan & Gangestad, 2005; Stearns, 1992). All organisms live in a world of limited resources; for example, the energy that can be extracted from the environment in a given amount of time is intrinsically limited. Time itself is a limited good; the time spent by an organism looking for mates cannot be used to search for food or care for extant offspring. Since all these activities contribute to an organism’s evolutionary fitness, devoting time and energy to one will typically involve both benefits and costs, engendering trade-offs between different fitness components. For example, there is a trade-off between bodily growth and reproduction because both require substantial energetic investment, and thus producing offspring reduces somatic growth. Natural selection favors organisms that schedule developmental tasks and activities so as to optimize resource allocation. Different allocation decisions result in different *life history strategies*.

The critical decisions involved in a life history strategy can be summarized by the fundamental trade-offs between *current* and *future reproduction*, between *quality* and *quantity of offspring*, and—in sexual species—between *mating* and *parenting effort* (see Ellis et al., 2009; Kaplan & Gangestad, 2005). By delaying reproduction, an organism can accumulate resources

and/or “embodied capital” (including skills and knowledge), thus increasing the quality and fitness of future offspring; however, the risk of dying before reproducing increases concomitantly. When reproduction occurs, the choice is between many offspring of lower quality and fewer offspring of higher quality. While intensive parental investment is a powerful way to increase the embodied capital (and long-term prospects) of one’s descendants, the fitness gains accrued through parenting must be weighed against the corresponding reduction in mating opportunities. Different life history strategies solve these problems in different ways by determining how organisms allocate effort among fitness-relevant traits. The same framework can be employed to describe life history differences between species and between individuals of the same species (Réale et al., 2010).

### 2.6.2. The Fast-Slow Continuum of Life History Variation

Because life history trade-offs are not functionally independent of one another, differences in life history strategies between and within species show a general pattern of trait covariation. Specifically, slow growth and late reproduction correlate with long lifespan, high parental investment, fewer offspring of higher quality, and low juvenile mortality. Conversely, fast growth and early reproduction correlate with high juvenile mortality, short lifespan, larger numbers of offspring and reduced parental investment in each. This is commonly referred to as the *fast-slow continuum* of life histories (Sæther, 1987; see Ellis et al., 2009; Figure 2.3). The fast-slow continuum has profound implications for the organization of behavior. A short lifespan, higher mortality, and early reproduction make it optimal to discount future rewards and to favor short-term gains over long-term benefits; future-oriented behavior is only favored in the context of slow strategies. Furthermore, organisms betting on future reproduction must maximize their chances of surviving and remaining healthy. This is best obtained through risk aversion—that is, avoidance of variable rewards in favor of surer outcomes, even at the price of a lower average payoff.

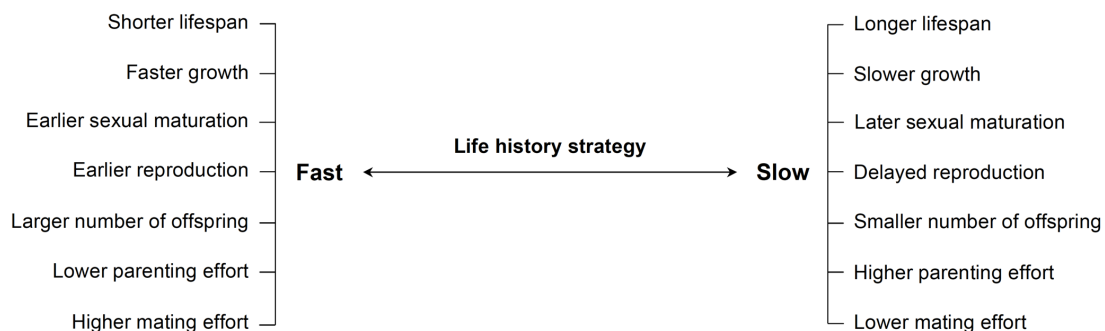


Figure 2.3. The fast-slow continuum of life history variation.

In most organisms, individual life histories are determined by a combination of genetic and environmental factors. Indeed, life history strategies often exhibit a remarkable degree of developmental plasticity. The key dimensions of the environment that affect the development of life history strategies are *resource availability*, *extrinsic morbidity-mortality*, and

*unpredictability*, as signaled by observable cues (see Ellis et al., 2009; Kuzawa & Bragg, 2012). Energetic stress causes the developing individual to shift toward a slower life history strategy; this translates into development of a more energy-sparing phenotype, including slower growth, delayed sexual maturation, and low fecundity. Extrinsic morbidity-mortality constitutes external sources of disability and death that are relatively insensitive to the adaptive decisions of the organism. Environmental cues indicating high levels of extrinsic morbidity-mortality cause individuals to develop faster life history strategies. Faster strategies in this context—a context that devalues future reproduction—function to reduce the risk of disability or death prior to reproduction. Moreover, high extrinsic morbidity-mortality means that investing in parental care has quickly diminishing returns, which favors reduced parental investment and offspring quantity over quality. In addition to average levels of extrinsic morbidity-mortality, unpredictable *variation* in environmental conditions over time and space also regulates life history development. On the timescale of human development, variable and unpredictable contexts tend to entrain faster life history strategies, thus acting in the same direction of environmental harshness (e.g., Belsky et al., 2012; Brumbach et al., 2009; Ellis et al., 2009). In summary, dangerous and unpredictable environments promote the development of fast life history strategies; conversely, safe and predictable environments tend to shift development toward slow life histories.

### **2.6.3. Life History Strategies and Individual Differences in Self-Regulation**

In recent years, it has become apparent that life history theory offers a unifying perspective on individual differences in self-regulation (Del Giudice, under review; Kruger et al., 2008; Réale et al., 2010; Sih & Del Giudice, 2012; Wolf et al., 2007). The logic of fast life history strategies promotes a focus on current rewards, a steep discounting of the future, and a tendency to take risks (especially in males). As a consequence, individual differences in impulsivity can be expected to overlap to a large degree with the fast-slow continuum of life history variation. This hypothesis is supported by a large amount of data showing that fast life history traits systematically correlate with higher impulsivity, both in humans and nonhuman animals (e.g., Kruger et al., 2008; Réale et al., 2010; Wang et al., 2009; reviewed in Del Giudice, under review).

In many nonhuman species, the association between impulsivity and life history strategies extends to individual differences in coping styles. Studies of coping styles in nonhuman animals show that feedforward regulation—characterized by reduced flexibility, low cue dependency, and quick but superficial exploration—is systematically associated with boldness and impulsivity in proactive, fast life history individuals. In contrast, feedback regulation—characterized by increased flexibility, cue dependency, and slow but thorough exploration—clusters with shyness and low impulsivity in reactive, slow life history individuals (Biro & Stamps, 2008; Careau et al., 2009; Carere et al., 2010; Coppens et al., 2010; Koolhaas et al., 1999; Réale et al., 2010). Sih and Del Giudice (2012) recently argued that the association between feedforward regulation, impulsivity, and fast life histories may be explained by a general trade-off between avoiding risk and acquiring larger rewards (the *risk-reward trade-off*). This argument converges with theoretical models advanced by Stamps (2007) and Wolf and colleagues (2007) in suggesting that basic life history trade-offs may underlie the structure of personality and cognition in nonhuman animals.



While the association between feedforward regulation and impulsivity has been replicated in various species (though with exceptions and qualifications; see Réale et al., 2010), there are reasons to doubt the generality of this pattern, at least where humans are concerned. As discussed in section 2.4, feedforward control can take many forms, ranging from simple and inflexible strategies to complex, highly structured strategies oriented toward long-term goals. My argument is that the association between feedforward regulation and impulsivity described in the animal literature only applies to simpler forms of feedforward control—ballistic responses and rigid, inflexible routines. Indeed, the more sophisticated forms of deliberate, future-oriented feedforward control are associated almost by definition with *low* impulsivity. The fact that most species do not engage in the kind of long-term planning typical of human adults may explain the apparent consistency of the animal literature, in which impulsivity is almost invariably associated with traits that indicate a primacy of feedforward regulation.

The idea that feedforward control can be associated with both high *and* low impulsivity is both theoretically plausible and consistent with the empirical data. For example, there is considerable evidence that motor inhibition can be achieved through reactive, stimulus-driven processes but also through proactive anticipatory processes; moreover, the two kinds of inhibition rely on partially distinct neural pathways (Aron, 2011). In the same vein, Tops and colleagues (2010) made an important distinction between *proactive impulsivity*, arising from a lack of feedback control on behavior, and *reactive impulsivity*, in which behavior is directly controlled by immediate emotional stimuli (see also Tops & Boksem, 2010). In a longitudinal study of executive functions in children, self-restraint in a delay of gratification task—a prototypical measure of future orientation—was associated with higher inhibition and *reduced* shifting ability, the latter being a key correlate of feedforward regulation (see Miyake & Friedman, 2012).

In humans, slow life history strategies may often involve a combination of effortful control (low impulsivity) and predominantly feedforward regulation, as indicated by reduced shifting ability and low dependency on immediate cues. Intriguingly, individuals who develop in safe, predictable environments may show an initial primacy of feedback regulation (supporting thorough, systematic learning; section 2.4) followed by a developmental shift toward increased feedforward control. This prediction is consistent with the idea that slow life histories entail higher investment in embodied capital, including accumulation of knowledge and skills. At the opposite end of the life history continuum, individuals who engage in high-risk behavioral strategies may develop a pattern of impulsivity coupled with relatively inflexible feedforward control. Because the costs and benefits of risk-taking differ systematically between the sexes, males should be more likely to develop a bias toward feedforward regulation in response to danger and unpredictability. In line with this prediction, human males consistently display more risk-taking than females, even if sex differences in impulsivity are very small (Cross et al., 2011).

In sum, the structure of individual differences in self-regulation is likely more complex than currently acknowledged in the coping styles literature. While simpler forms of feedforward control may be functionally associated with impulsivity and risk-taking, feedforward regulation can also be employed in the service of long-term goals and may require high levels of active inhibition. So far, this distinction has not been explored in the animal literature on coping styles; it is therefore unclear whether it only applies to humans or may extend to other species as well.

## 2.7. Conclusion

Self-regulation is a biological property of living organisms, and can only be fully understood in the light of evolution. In this chapter I approached the topic from a theoretical vantage point, leaving aside the issue of how self-regulatory processes are implemented at the neurobiological level. I started my analysis from the basic concepts of control theory, and showed how the logic of feedback and feedforward control can be combined with insights from evolutionary biology to outline an ecological theory of control strategies. I then discussed how life history theory offers a general framework for understanding individual differences in impulsivity and coping styles, and concluded with a critical examination of the relation between life history strategies and self-regulation in humans. In particular I argued that, at least in humans, a primacy of feedforward control may be associated with fast life history strategies and high levels of impulsivity, but also with *slow* life history strategies and high levels of effortful control. In total, I hope I have shown how an evolutionary perspective can enrich the study of self-regulation by fostering integration across levels of analysis and suggesting new, testable predictions to guide empirical research.

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### Footnotes

<sup>1</sup>In evolutionary biology *adaptive* and *maladaptive* denote the effects of traits and behaviors on fitness, that is, the differential replication of genes in subsequent generations. In psychology and the social sciences, the same terms usually denote the subjective and/or social desirability of a trait or behavior. Traits that promote health, subjective well-being, and mutually rewarding social relations are viewed as adaptive, whereas socially undesirable, distressing, or health-damaging traits are viewed as maladaptive. Since natural selection promotes reproductive success rather than happiness or health, biologically adaptive traits may or may not be socially desirable or conducive to health and well-being.