

Self-regulation in an Evolutionary Perspective

3

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1 3.1 Introduction

2 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 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.

25 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.

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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.

3.2 Self-regulation: An Overview 45

3.2.1 The Self-regulation Continuum 46

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 and Scheier 2011; Hofmann

59 et al. 2012; Tops et al. 2010). It is important to re- 107
 60 realize that, by this definition, self-regulation does 108
 61 not require goals to be explicitly represented by 109
 62 the individual organism, even if the goal may be 110
 63 clearly discernible by an outside observer. When 111
 64 a bacterium moves toward higher concentrations 112
 65 of glucose by chemotaxis, its behavior is regu- 113
 66 lated by a clever system of feedback control that 114
 67 alternates straight-line swimming and random 115
 68 tumbling. The *objective* goal of this behavior is 116
 69 obvious to an external observer—moving the 117
 70 bacterium toward glucose—even if the bacterium 118
 71 itself has no internal representation of the reason 119
 72 for its behavior; in fact, the bacterium does not 120
 73 even need to represent the direction in which it is 121
 74 swimming (Bechhoefer 2005). 122

75 In Daniel Dennett's terminology, such real but 123
 76 unrepresented goals can be understood as "free- 124
 77 floating rationales" (Dennett 2009). Even in very 125
 78 simple organisms, natural selection tracks the 126
 79 causal regularities that affect survival and repro- 127
 80 duction, since those organisms that—for what- 128
 81 ever reason—are better at exploiting the causal 129
 82 structure of their environment are usually also 130
 83 better at surviving and reproducing. As a result 131
 84 of this selection process, evolution equips organ- 132
 85 isms with machinery that supports effective goal- 133
 86 directed performance (e.g., chemotaxis) with no 134
 87 need for the individual organism to possess any 135
 88 representation of the underlying goals and causal 136
 89 properties. As organisms evolve more sophisti- 137
 90 cated nervous systems, however, goals and rea- 138
 91 sons may begin to be actively represented, even 139
 92 if only partially and implicitly. For example, the 140
 93 firing rate of a neuronal group may implicitly 141
 94 encode the expected amount of food in a given 142
 95 direction of space. By gradual accumulation of 143
 96 function, evolution has provided humans with 144
 97 a remarkable ability to explicitly represent their 145
 98 goals (or at least some of them), communicate 146
 99 them to conspecifics, and employ those represen- 147
 100 tations to build detailed plans as well as mental 148
 101 scenarios of their behavior and that of other peo- 149
 102 ple (see Dennett 2009). 150

103 Self-regulation in the narrow sense concerns a 151
 104 subset of behaviors—broadly defined to include 152
 105 cognitive operations in addition to body move- 153
 106 ments—whose main function is to change the 154

probability of later behaviors by the same organ- 107
 108 ism (see Barkley 2001). Some scholars refer to 108
 narrow-sense self-regulation as *self-control* (e.g., 109
 Carver and Scheier 2011; Hofmann et al. 2012). 110
 The basic component of narrow-sense self-reg- 111
 ulation is *inhibition*—the ability to override im- 112
 pulses and responses that conflict with current 113
 goals. Thus defined, inhibition does not require 114
 explicit goal representations, although it does re- 115
 quire the existence of multiple interacting con- 116
 trol systems within the same organism. Simple 117
 forms of inhibition can take place in absence of 118
 a control hierarchy; for example, control systems 119
 A and B—each equipped with their own goals— 120
 may reciprocally inhibit one another whenever 121
 their activation level crosses a certain threshold. 122
 Of course, when self-regulation processes be- 123
 come hierarchically organized (e.g., Carver and 124
 Scheier 2011; Filevich et al. 2012; Kopp 2012), 125
 higher-order systems may acquire the ability to 126
 flexibly inhibit lower-order systems in the ser- 127
 vice of higher-order goals. In the self-regulation 128
 literature, inhibition is usually framed in the con- 129
 text of hierarchical control systems (e.g., Carver 130
 and Scheier 2011; Filevich et al 2012). 131

At the far end of the continuum is the family 132
 of *executive functions*, an even narrower subset 133
 of regulatory processes that—in their most elabo- 134
 rate form—are only possessed by adult humans. 135
 Executive functions stand out because of their 136
 deliberate self-directedness (Barkley 2001), and 137
 permit extremely high levels of flexibility and 138
 strategic planning (Diamond 2013; Miyake et al. 139
 2000). The standard taxonomy of executive func- 140
 tions includes *inhibition* (deliberate overriding 141
 of dominant or prepotent responses), *updating* 142
 (constant monitoring and rapid addition/dele- 143
 tion of working memory contents), and *shifting* 144
 (switching flexibly between tasks or mental sets). 145
 A broader, biologically plausible taxonomy of 146
 executive functions advanced by Barkley (2001) 147
 also includes *affective self-regulation* and *gen- 148
 erativity* (the ability to mentally generate new 149
 combinations of behavioral units). 150

On the surface, executive functions look like a 151
 heterogeneous collection of cognitive processes. 152
 What they all share is a common theme of *future 153
 orientation*. In different ways, executive pro- 154

cesses 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).

3.2.2 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 and 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.¹ 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 and Wilson 2005; Green and Myerson 1996; Sih and Del Giudice 2012; Stephens et al. 2004).

3.3 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

¹ 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.

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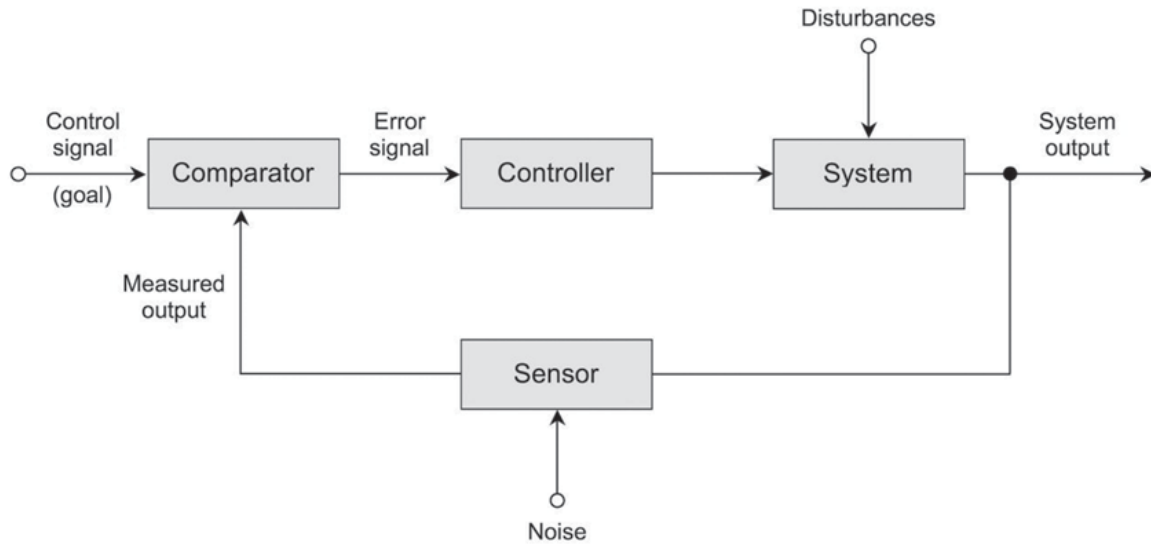


Fig. 3.1 Schematic representation of a feedback (closed-loop) control system

233 logic ultimately boils down to two basic strate- 261
 234 gies of behavior control—*feedback control* and 262
 235 *feedforward control*. Feedback and feedforward 263
 236 controllers are the building blocks of all regula- 264
 237 tory systems, and their characteristics and limita- 265
 238 tions have been worked out in detail in the field 266
 239 of mathematical control theory (see Albertos and 267
 240 Mareels 2010; Bechhoefer 2005). In this section, 268
 241 I provide a brief overview of feedback and feed- 269
 242 forward systems from the standpoint of control 270
 243 theory. 271

244 3.3.1 Feedback Control

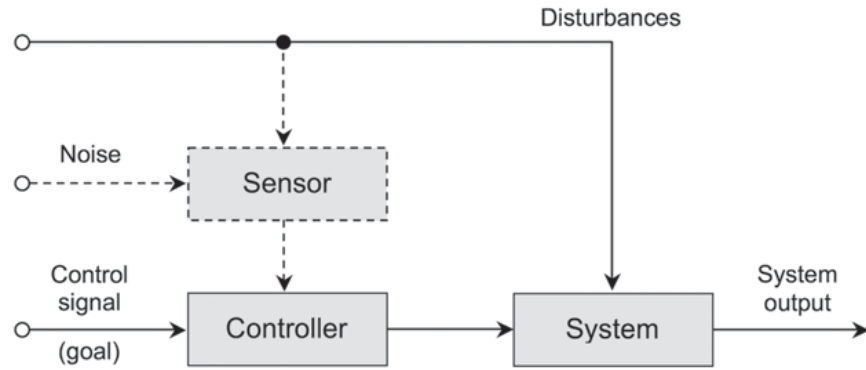
245 In feedback or closed-loop control, the current 272
 246 goal (or *control signal*) is compared with the ac- 273
 247 tual state of the system (i.e., the system's *output*), 274
 248 and an *error signal* is obtained as a result. For 275
 249 example, the goal of a bird chasing a fly may be 276
 250 that of getting as close as possible to the fly; the 277
 251 distance between the bird and the fly at any given 278
 252 moment would then constitute the system output. 279
 253 The error signal is used to generate a goal-directed 280
 254 action, which alters the state of the system 281
 255 (the bird may change speed and/or trajectory). 282
 256 However, other causal factors (*disturbances*) 283
 257 may be acting on the system at the same time; for 284
 258 example, the fly may suddenly turn, or a change 285
 259 in wind speed may affect the bird's trajectory. 286
 260 The joint effect of goal-directed actions and dis-

turbances determines the system output, which is 261
 then measured and compared to the current goal, 262
 closing the control loop (Fig. 3.1). The critical 263
 feature of a feedback controller is that it tracks 264
 the system output in real time, progressively nar- 265
 rowing the gap between the goal and the state of 266
 the world through moment-to-moment self-cor- 267
 rection. 268

As a rule, the system output is not *directly* 269
 available for comparison but has to be estimated 270
 or measured in some indirect way, for example, 271
 through sensory organs and related neural path- 272
 ways. Measurement processes—broadly defined 273
 to include sensory processes and the associated 274
 neural computations—inevitably introduce some 275
 error (or *noise*) in the feedback loop. Indeed, 276
 feedback systems face a fundamental trade-off 277
 between tracking speed and the ability to reject 278
 unwanted noise. If the output is measured with 279
 higher temporal resolution—thus increasing the 280
 ability to track rapid changes in the state of the 281
 system—more irrelevant noise will enter the 282
 feedback channel and get mixed up with the use- 283
 ful information. Conversely, effective filtering of 284
 unwanted noise inevitably reduces the tracking 285
 speed of the control system (Bechhoefer 2005). 286

A powerful way to employ feedback control- 287
 lers is to nest multiple feedback loops within 288
 one another, yielding a *feedback cascade*. In this 289
 type of hierarchical arrangement, the inner con- 290
 trol loop regulates a lower-order variable (i.e., 291

Fig. 3.2 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*)



292 pursues a lower-order goal) in order to simplify
 293 the control actions performed by the controller
 294 in the outer loop (Albertos and Mareels 2010).
 295 Nested feedback loops allow a complex control
 296 task to be split into smaller modular tasks, and
 297 permit high levels of flexibility and accuracy. For
 298 these reasons, feedback cascades are very popular
 299 in cognitive and neuropsychological models
 300 of self-regulation (see Carver and Scheier 2011;
 301 Filevich et al. 2012; Kopp 2012). A classic ap-
 302 plication of feedback loops is the TOTE model
 303 advanced in 1960 by Miller and colleagues. A
 304 TOTE unit (acronym of *Test-Operate-Test-Exit*)
 305 is an abstract feedback controller that executes an
 306 iterative “plan” until its goal is reached. In this
 307 model, the hierarchical plans that control an or-
 308 ganism’s behavior are implemented by cascades
 309 of nested TOTE units working at different levels
 310 of abstraction (Miller et al. 1960).

311 The main strength of feedback control lies in
 312 its ability to respond to unknown or unanticipated
 313 disturbances. More generally, feedback control
 314 has an intrinsically self-correcting nature; for this
 315 reason, it does not require an accurate preexisting
 316 model of the system in order to function prop-
 317 erly. However, feedback systems are also highly
 318 sensitive to noise and rely on accurate measure-
 319 ment of the system output, which may or may not
 320 be available in a given situation. Another crucial
 321 limitation of feedback control is that it depends
 322 on the ability to track real-time changes in the
 323 system. Sensory processing, neural computation,
 324 inertia in the system, and so forth introduce de-
 325 lays and response lags in the feedback loop. As
 326 the overall delay increases, the performance of
 327 feedback control deteriorates rapidly; beyond a
 328 certain threshold, delays in the feedback loop
 329 may destabilize the system and lead to erratic, un-

controlled behavior (Albertos and Mareels 2010; 330
 Azuma and Hirose 2008; Bechhoefer 2005). 331

3.3.2 Feedforward Control 332

333 While feedback control is a ubiquitous and pow- 333
 334 erful strategy, it also has important limitations. 334
 335 As deftly put by Albertos and Mareels (2010), 335
 336 “driving a car by feedback only would equate 336
 337 to driving using information only from the rear 337
 338 view mirror” (p. 213). In other words, feedback 338
 339 controllers can only respond to disturbances and 339
 340 changes in the system once they have occurred, 340
 341 but are unable to *anticipate* them. Returning to 341
 342 the car analogy, imagine a driver trying to keep 342
 343 her car on track by only looking in the rear view 343
 344 mirror. Every time the road turns, the car begins 344
 345 to veer off course; the backward-looking driver 345
 346 then notices the deviation in the mirror and re- 346
 347 sponds by steering the car back on its trajectory 347
 348 (with some unavoidable delay). A forward-look- 348
 349 ing driver would see the turn approaching and 349
 350 could begin the steering movement in advance, 350
 351 resulting in a much smoother trajectory. 351

352 When disturbances can be anticipated (or 352
 353 ignored altogether), feedforward or open-loop 353
 354 systems may become highly effective means to 354
 355 control the behavior of a system. In feedforward 355
 356 control, the goal is combined with a model of the 356
 357 system that may also include the predicted effects 357
 358 of future disturbances; the results of this compu- 358
 359 tation are then used to guide behavior, with no 359
 360 further feedback about the state of the system 360
 361 (Fig. 3.2). For example, when a chasing bird gets 361
 362 close enough to the fly, it may “dive” toward the 362
 363 prey with a rapid anticipatory motion based on 363
 364 (a) the predicted position of the fly in the next 364

365 fraction of a second and (b) a model of the motor
366 actions required to reach that position at the right
367 time.

368 The simplest forms of open-loop control may
369 skip the prediction step entirely; many protec-
370 tive reflexes—for example, retracting one's
371 hand when it touches a hot object—are based on
372 simple, “ballistic” open-loop mechanisms (see
373 Albertos and Mareels 2010). More complex in-
374 stances of feedforward regulation may involve
375 simulation of future events, strategic planning,
376 and integration of preexisting knowledge about
377 the rules that govern the system, the likelihood of
378 potential outcomes, and the influence of contex-
379 tual variables.

380 Just like feedback control, feedforward control
381 also has strengths as well as weaknesses. To
382 begin with, feedforward control permits extreme-
383 ly fast execution once an action sequence is ini-
384 tiated. Other advantages of feedforward systems
385 include their insensitivity to noise, their greater
386 dynamic stability, and the fact that they do not
387 require accurate, real-time measurement of the
388 system output. On the other hand, feedforward
389 regulation often requires an accurate model of the
390 system, and enough information about the current
391 state of the system so that future disturbances can
392 be successfully predicted. Most crucially, feed-
393 forward systems—regardless of their complexi-
394 ty—are unable to respond to unanticipated events
395 that occur while the planned action is unfolding
396 (Albertos and Mareels 2010; Bechhoefer 2005).

397 3.3.3 Combining Feedback and 398 Feedforward Control

399 It is apparent from the preceding discussion that
400 feedback and feedforward systems have largely
401 complementary sets of advantages and disadvan-
402 tages. As a result, the design of self-regulation
403 strategies involves a number of important trade-
404 offs—between speed and accuracy, flexibility
405 and robustness, predictive ability and computa-
406 tional simplicity, and so forth. The standard engi-
407 neering solution to these trade-offs is to combine
408 feedback and feedforward elements in the same
409 control system, in order to exploit the strengths

of both strategies and compensate for their weak- 410
nesses (Albertos and Mareels 2010; Bechhoefer 411
2005). For example, the predictive estimates 412
employed in feedforward control can be used to 413
compensate the delays introduced by feedback 414
loops and make the system more resistant to sen- 415
sory noise (see Wolpert and Ghahramani 2000). 416

417 There is considerable evidence that the brain
418 controls behavior through the joint action of
419 multiple control systems based on complemen-
420 tary principles (e.g., Tucker et al. 1995; Wolpert
421 and Ghahramani 2000; Wolpert et al. 2003).
422 Control subsystems employing the same or dif-
423 ferent strategies can be combined in many dif-
424 ferent ways; in particular, hierarchical arrange-
425 ments of higher- and lower-order controllers—as
426 in feedback cascades—can achieve remarkable
427 qualities of speed, accuracy, and flexibility (e.g.,
428 Albertos and Mareels 2010; Carver and Scheier
429 2011; Filevich et al. 2012). In addition, feedback
430 and feedforward processes can be combined *se-*
431 *quentially* in time to increase behavioral flexibil-
432 ity and optimize learning. When a feedforward
433 controller needs an accurate model of the system,
434 feedback loops can be employed in the learning
435 phase to build, update, and refine such a model—
436 effectively “training” the feedforward control-
437 ler and enhancing its future performance (this is
438 known as *feedback-error learning*; see Wolpert
439 and Ghahramani 2000). For example, an initial
440 phase of feedback control may facilitate slow,
441 systematic exploration of a novel environment
442 (Sih and Del Giudice 2012); the context model
443 built in the learning phase can then be used to
444 make quick, effective decisions guided by feed-
445 forward processes.

446 3.4 The Ecology of Control Strategies

447 While the overall performance of a control sys-
448 tem can be improved by a mixture of feedback
449 and feedforward processes, the optimal combi-
450 nation between the two strategies may change—
451 sometimes dramatically—across different con-
452 texts and tasks. For example, Azuma and Hirose
453 (2008) simulated a neural network performing a
454 complex control task (riding a bicycle without

455 falling) with different amounts of delay in the
 456 perception–action loop. As the delay increased,
 457 feedback control became more and more unsta-
 458 ble and the optimal strategy shifted to feedfor-
 459 ward prediction (see Sect. 3.3). From a biological
 460 standpoint, brains can be expected to possess the
 461 ability to shift the balance between feedback and
 462 feedforward control depending on the current
 463 task and environmental conditions. Moreover,
 464 there is no reason why strategic flexibility should
 465 be limited to motor tasks: The general principles
 466 of feedback and feedforward control—and the
 467 resulting trade-offs—apply to all kinds of goal-
 468 directed behavior, from simple motor actions
 469 to complex social interactions (e.g., Carver and
 470 Scheier 2011; Wolpert et al. 2003).

471 In the remainder of this section, I combine the
 472 principles of control theory with insights from
 473 evolutionary biology to derive some initial pre-
 474 dictions about the ecology of control strategies. In
 475 order to understand how optimal strategies may
 476 vary across environments, the standard focus on
 477 control performance has to be supplemented with
 478 careful consideration of the organism's needs
 479 and priorities. In general, whether a strategy is
 480 biologically adaptive in a given context does not
 481 only depend on its performance in terms of speed
 482 and accuracy but also on the overall cost–benefit
 483 balance with respect to an individual's fitness. A
 484 slower and/or less accurate strategy may be adap-
 485 tive if it increases the organism's chances of suc-
 486 cessful survival and reproduction. Furthermore,
 487 the costs and benefits of a strategy in a given en-
 488 vironment may vary dramatically between differ-
 489 ent individuals (for example, between males and
 490 females, old and young, well fed and starving).
 491 Since environmental *predictability* has been sin-
 492 gled out as a key determinant of the adaptiveness
 493 of control strategies (e.g., Tops et al. 2010), I will
 494 center my analysis on the distinction between
 495 predictable and unpredictable environments.

496 3.4.1 Unpredictable Environments

497 When the local environment is unpredictable and
 498 subject to sudden changes, feedback strategies
 499 have two important advantages over feedforward

500 strategies. First, feedback control tracks the envi-
 501 ronment in real time, enabling flexible behavioral
 502 adjustment in response to changing conditions;
 503 and second, it works even when it is difficult
 504 or impossible to construct an accurate model of
 505 the environment (see also Tops et al. 2010). The
 506 benefits of feedback control are especially criti-
 507 cal when an individual's goal is to prevent and/
 508 or avoid potential dangers in the environment.
 509 However, the preventive effectiveness of feed-
 510 back strategies is greatest when dangerous events
 511 can be anticipated based on warning cues; since
 512 feedback processes are intrinsically backward-
 513 looking, they cannot successfully prevent events
 514 that occur too abruptly.

515 When the environment reaches very high
 516 levels of unpredictability, the potential benefits
 517 of feedback control decrease while the costs of
 518 continued vigilance increase accordingly. In such
 519 environments, it may be more advantageous to
 520 embrace unpredictability rather than attempt to
 521 control it—in other words, some individuals may
 522 shift from a risk-averse strategy focused on harm
 523 prevention to a high-risk strategy involving com-
 524 petition, bold exploration, and so forth (see Del
 525 Giudice et al. 2011; Ellis et al. 2012). Individual
 526 characteristics that favor risk taking in unpredict-
 527 able environments include sex, dominance status,
 528 and physical conditions. In particular, the males
 529 of most species—including humans—face stron-
 530 ger mating competition and more variable repro-
 531 ductive outcomes than females (see Geary 2003;
 532 Kokko and Jennions 2008). The result is stron-
 533 ger sexual selection for competitive traits such
 534 as risk taking, dominance seeking, and physical
 535 aggression (see Archer 2009; Cross et al. 2011;
 536 Wilson et al. 2002).

537 By definition, risky decisions face individu-
 538 als with unpredictable outcomes, as they may
 539 result in large gains as well as large losses (see
 540 Frankenhuus and Del Giudice 2012). When in-
 541 dividuals engage in high-risk courses of action,
 542 the immediate feedback they receive can be ir-
 543 relevant or even misleading. In an all-out fight
 544 with a dangerous opponent, the best strategy is
 545 usually to keep fighting no matter what rather
 546 than backing down after the first blow. More gen-
 547 erally, high-risk strategies often require outright

548 *insensitivity* to threats and dangers to work suc-
 549 cessfully. For extreme risk takers, informational
 550 insulation from signals of threat can be an asset,
 551 not a weakness (Del Giudice et al. 2011; Korte
 552 et al. 2005). Thus, it can be adaptive for them to
 553 suppress the activity of feedback control systems
 554 and rely on open-loop, “ballistic” strategies that
 555 deliberately ignore the immediate consequences
 556 of one’s actions.

557 3.4.2 Predictable Environments

558 In predictable environments, feedforward strate-
 559 gies offer several potential benefits including ro-
 560 bustness, decision speed, and enhanced sequen-
 561 tial planning capabilities. It is important to keep
 562 in mind that open-loop self-regulation can take
 563 various forms that differ in their complexity and
 564 in their relation with impulsivity. First, there is
 565 the ballistic, impulsive sort of open-loop regula-
 566 tion involved in high-risk strategies. At moder-
 567 ate levels of complexity, feedforward control
 568 is driven by habits and rigid, inflexible behav-
 569 ioral routines (see Coppens et al. 2010). When
 570 coupled with detailed context models, however,
 571 open-loop control may enable careful, deliberate,
 572 future-oriented planning, which in turn requires
 573 active inhibition of competing short-term goals.
 574 While all these modes of self-regulation imply
 575 a primacy of feedforward control, they differ
 576 widely in their functional implications. The most
 577 complex forms of feedforward regulation require
 578 a host of dedicated cognitive adaptations for plan-
 579 ning and mental simulation, and might only make
 580 sense in long-lived species with complex social
 581 structures such as humans (Barkley 2001). More-
 582 over, the human ability to use language to trans-
 583 mit knowledge about the environment permits vi-
 584 carious learning on an unprecedented scale, and
 585 maximizes the power of self-regulation based on
 586 explicit rules and expectations.

587 While feedforward control may function espe-
 588 cially well in predictable environments, it is not
 589 necessarily the optimal strategy for all individu-
 590 als. When harm prevention is a high priority it
 591 may be adaptive to shift to feedback strategies,
 592 which as a rule are better suited for dealing with

unforeseen events—including dangerous ones. 593
 Closed-loop strategies sacrifice some of the 594
 speed and robustness of open-loop strategies in 595
 exchange for enhanced protection from harm. For 596
 example, higher female investment in offspring 597
 production and parental is expected to select for 598
 stronger risk aversion and harm avoidance in fe- 599
 males (Archer 2009; Campbell 1999; Cross et al. 600
 2011). As a result, females should have a stronger 601
 tendency than males to rely on feedback control 602
 strategies even in predictable and comparatively 603
 safe contexts. 604

The superior ability of feedback control to 605
 deal with unexpected changes in the environ- 606
 ment does not apply only to dangerous events. 607
 Closed-loop systems respond quickly to all sorts 608
 of novel circumstances, including the emer- 609
 gence of unforeseen *opportunities* (Sih and Del 610
 Giudice 2012). While feedforward strategies are 611
 more robust, they cannot adjust to unexpected 612
 events—regardless of their positive or negative 613
 quality—and tend to suppress sensory input that 614
 does not conform to predictions (Tops et al. 2010; 615
 Tops and Boksem 2010). Thus, an abundance of 616
 potential opportunities may tip the balance in 617
 favor of feedback strategies even in predictable 618
 environments. 619

Even more generally, feedback control may be 620
 adaptive in stable, predictable contexts because 621
 it supports systematic learning. As noted by Sih 622
 and Del Giudice (2012), feedforward strategies 623
 are associated with fast but shallow learning 624
 styles; in addition, they make it difficult to up- 625
 date one’s cognitive models once they are formed 626
 because of their limited self-correction abilities. 627
 In contrast, stimulus-driven processes favor 628
 slower but more careful and systematic learn- 629
 ing, and are associated with increased cognitive 630
 and behavioral flexibility—including the ability 631
 to quickly unlearn rules and associations that 632
 are no longer valid (Coppens et al. 2010). Thus, 633
 feedback strategies may be highly adaptive when 634
 the task is to learn the structure of a predictable 635
 environment with high accuracy and resolution. 636
 Once a sophisticated model of the environment 637
 has been constructed through feedback-driven 638
 exploration (Wolpert and Ghahramani 2000), it 639
 can be exploited by feedforward control systems 640

641 to enable quick and accurate decision making.
 642 Developmentally, individuals growing up in pre-
 643 dictable contexts may go through an initial phase
 644 of predominantly closed-loop regulation and in-
 645 creasingly shift toward open-loop control as they
 646 learn and mature.

647 3.4.3 Delayed Outcomes

648 In many important domains of behavior, the con-
 649 sequences of an action can only be evaluated at
 650 some distant point in the future. Accepting or
 651 rejecting a mate, deciding how many offspring
 652 to raise, choosing a nest site or a territory, stock-
 653 ing food reserves for the winter—what all these
 654 decisions have in common is that their outcomes
 655 take a long time to become manifest. When deci-
 656 sions affect subsequent generations, their conse-
 657 quences may even extend beyond the lifespan of
 658 a single individual. When outcomes are delayed
 659 beyond a certain point, feedback control is sim-
 660 ply not an option; while self-correction may be
 661 possible in the long term (e.g., building a new
 662 nest in the next breeding season), the only viable
 663 strategy in the short term is to base actions on
 664 feedforward models.

665 On the face of it, the last statement might
 666 seem paradoxical: How can an individual build
 667 a model of something it has never experienced
 668 before (and may never experience again)? The
 669 answer is, *it does not have to*. When fitness-
 670 relevant decisions recur over many generations,
 671 evolution can be expected to equip organisms
 672 with built-in implicit knowledge about the causal
 673 structure of the system (see Cosmides and Tooby
 674 1994). Such knowledge can inform model-based
 675 planning—thus enabling feedforward behavior
 676 control—even in cases where individual learn-
 677 ing is difficult or impossible. From another
 678 perspective, feedback does not occur at the in-
 679 dividual level but rather at the *population* level,
 680 as a consequence of natural selection—suc-
 681 cessful decision rules are retained (as individu-
 682 als who make good decisions reproduce more)
 683 while unsuccessful ones are weeded out. This
 684 argument can be generalized to decisions in un-
 685 stable and/or unpredictable contexts. While un-

predictability makes it difficult to build a model 686
 of the environment, an organism may still rely 687
 on evolved feedforward strategies designed to 688
 maximize fitness in unpredictable conditions. 689
 As discussed above, such strategies may often 690
 involve high levels of impulsivity and risk 691
 taking. 692

3.4.4 Defensive Responses 693

A final topic to consider is the regulation of de- 694
 fensive responses. Shudo et al. (2003) developed 695
 a mathematical model to investigate optimal re- 696
 sponse strategies to unpredictable danger. In the 697
 model, a potentially dangerous event occurs, but 698
 assessing the actual severity of the danger takes 699
 a certain amount of time. Feedforward strate- 700
 gies are directly triggered by the event and im- 701
 mediately start a ballistic defensive response; in 702
 contrast, feedback strategies respond to the *con-* 703
sequences of the event and adjust the strength of 704
 the response to the actual level of danger, thus 705
 maximizing control accuracy. Shudo and col- 706
 leagues found that optimal response strategies 707
 always include a feedforward component. Mixed 708
 strategies can be favored if uncertainties in dan- 709
 ger estimation are very large and delays in the 710
 feedback loop are sufficiently small; however, 711
 pure feedback control is never optimal. A similar 712
 logic applies to defensive reflexes such as hand 713
 retraction or the blink reflex (Sect. 3.3). These 714
 results suggest that even individuals who rely on 715
 feedback strategies to prevent danger may sud- 716
 denly switch to feedforward control *after* a dan- 717
 gerous event has occurred, in order to mount a 718
 quick and effective response. 719

3.5 From Control Strategies 720 to Coping Styles 721

As detailed in the preceding sections, the trade- 722
 offs of behavior control explain both the exist- 723
 ence of multiple control systems in the brain and 724
 the ability to shift between different strategies 725
 in a context- and task-sensitive way. The same 726
 trade-offs are likely to underlie the existence of 727

728 stable individual differences in self-regulation
729 styles. In the biological literature, patterns of in-
730 dividual differences in self-regulation are usually
731 characterized as *coping styles*, as they emerge
732 most reliably in response to stressful challenges
733 involving unpredictable and/or potentially threat-
734 ening events (Koolhaas et al. 1999).

735 The basic distinction in the biological litera-
736 ture is that between *reactive* and *proactive* coping
737 styles. Reactive individuals show a primacy of
738 feedback control; they are behaviorally flexible,
739 high in cue dependency, and engage in thorough
740 exploration of novel environments. Reactive in-
741 dividuals also tend to be shy, fearful, nonaggres-
742 sive, risk-averse, future-oriented, and low in gen-
743 eral activity. On the contrary, proactive individu-
744 als show a primacy of feedforward control; they
745 are low in cue dependency, show rigid, inflexible
746 behavioral routines, and are quick but superficial
747 explorers. Proactive individuals also tend to be
748 active, bold, aggressive, risk-prone, and impul-
749 sive (Coppens et al. 2010; Koolhaas et al. 1999,
750 2007; Réale et al. 2010; Sih and Del Giudice
751 2012). Of course, the existence of stable coping
752 styles does not mean that individuals are rigidly
753 tied to a fixed control strategy regardless of the
754 current situation. Instead, contextual and state-
755 dependent variation in control strategies usually
756 coexists with *average* differences in preferred
757 strategy across individuals.

758 Individual differences in coping styles along
759 the proactive–reactive axis have been document-
760 ed in a broad range of species, including (but not
761 limited to) monkeys, pigs, rodents, birds, and
762 fish (see Carere et al. 2010; Koolhaas et al. 1999;
763 Réale et al. 2010). The concept of coping styles
764 overlaps significantly with those of *behavioral*
765 *syndromes*, *behavioral types*, and *personality*
766 *types*. Accordingly, there is a growing tendency
767 to regard those labels as practically synonymous
768 (e.g., Coppens et al. 2010; Sih and Del Giudice
769 2012; for a different perspective see Uher 2011).

770 3.5.1 The Evolution of Coping Styles

771 Why should members of the same population
772 display stable individual differences in coping

773 styles? Evolutionary biology provides several 773
774 potential answers to this question; here I review 774
775 some of the most common alternatives (see Wolf 775
776 et al. 2013, for in-depth discussion). To begin 776
777 with, small initial differences in individual con- 777
778 ditions may be amplified and stabilized by self- 778
779 reinforcing cycles if conditions and behavior are 779
780 reciprocally connected. For example, larger indi- 780
781 viduals of a species could afford to explore more 781
782 boldly because they are less threatened by preda- 782
783 tors. Bolder exploration may enable them to find 783
784 more food, thus becoming even larger, and so on 784
785 (see Luttbeg and Sih 2010; Sih and Del Giudice 785
786 2012).

787 Alternatively, individual differences may 787
788 result from *adaptive developmental plasticity* 788
789 (West-Eberhard 2003; Schlichting and Pigliucci 789
790 1998). Developmental plasticity is the ability of 790
791 an organism to produce distinct phenotypes when 791
792 exposed to different environments throughout its 792
793 ontogeny. Since different control strategies are 793
794 adaptive in different contexts (Sect. 3.4), individ- 794
795 uals may have evolved the ability to respond to 795
796 early cues—for example, cues indicating that the 796
797 environment is unpredictable, or that adult social 797
798 competition is going to be especially intense— 798
799 by adjusting their behavioral phenotype so as to 799
800 match the predicted environmental conditions. 800
801 As a result, individuals growing up in different 801
802 conditions will go on developing different cop- 802
803 ing styles, possibly in interaction with individual 803
804 variables such as sex, competitive ability, and so 804
805 forth.

806 While developmental plasticity depends on 806
807 early environmental inputs, there is ample evi- 807
808 dence that coping styles also reflect genotypic 808
809 differences between individuals (reviewed in 809
810 Carere et al. 2010; van Oers and Sinn 2013). 810
811 Adaptive genotypic differences can be main- 811
812 tained in a population for a number of distinct 812
813 reasons. First, the costs and benefits associated 813
814 with different coping styles may result in the 814
815 same average fitness (*selective neutrality*). Sec- 815
816 ond, genotypic differences may be maintained 816
817 by *frequency-dependent selection* if the fitness of 817
818 a given phenotype depends on its relative abun- 818
819 dance in the population relative to other pheno- 819
820 types. For example, proactive individuals may 820

821 enjoy high reproductive success when a popula- 864
 822 tion is mostly composed of reactive individuals, 865
 823 but *not* when most other members of the popula- 866
 824 tion are also proactive. Third, spatial and tempo- 867
 825 ral variation in environmental conditions and the 868
 826 associated selective pressures (*fluctuating selec-* 869
 827 *tion*) may favor the maintenance of polymorphic 870
 828 alleles (see Del Giudice 2012; Wolf et al. 2013). 871
 829 Studies of bird and mammal populations have 872
 830 provided initial evidence that selection on cop- 873
 831 ing styles does indeed fluctuate across space and 874
 832 time, creating the conditions for the maintenance 875
 833 of adaptive genotypic variation (see Dingemans 876
 834 and Réale 2013).

835 Finally, unpredictable environmental fluctu- 878
 836 ations may favor the evolution of *diversified* 879
 837 *bet hedging*. In bet-hedging strategies, each in- 880
 838 dividual randomly develops one out of two or 881
 839 more phenotypes through a stochastic “switch” 882
 840 mechanism. Diversified bet hedging spreads the 883
 841 risk of reproductive failure across a genetic lin- 884
 842 eage, since at least some individuals will end up 885
 843 with a well-matched phenotype regardless of the 886
 844 state of the environment. Specifically, bet hedg- 887
 845 ing reduces average individual fitness in the short 888
 846 term, but enhances the long-term reproductive 889
 847 success of the lineage by decreasing fitness vari- 890
 848 ance across generations (see Starrfelt and Kokko 891
 849 2012). It should be noted that bet hedging, devel- 892
 850 opmental plasticity, and genotypic variation are 893
 851 not mutually exclusive alternatives; in fact, they 894
 852 can coexist in various combinations and propor- 895
 853 tions depending on the structure of environmen- 896
 854 tal fluctuations, the costs of plasticity, and other 897
 855 ecological factors (see Wolf et al. 2013).

856 3.6 A Life History Perspective 900 857 on Self-regulation 901

858 3.6.1 Life History Strategies 904

859 Life history theory is a branch of evolutionary 905
 860 biology dealing with the way organisms allo- 906
 861 cate time and energy to the various activities that 907
 862 comprise their life cycle (see Ellis et al. 2009; 908
 863 Hill and Kaplan 1999; Kaplan and Gangestad 909

2005; Stearns 1992). All organisms live in a 864
 world of limited resources; for example, the en- 865
 ergy that can be extracted from the environment 866
 in a given amount of time is intrinsically limited. 867
 Time itself is a limited good; the time spent by 868
 an organism looking for mates cannot be used to 869
 search for food or care for extant offspring. Since 870
 all these activities contribute to an organism’s 871
 evolutionary fitness, devoting time and energy to 872
 one will typically involve both benefits and costs, 873
 engendering trade-offs between different fitness 874
 components. For example, there is a trade-off 875
 between bodily growth and reproduction because 876
 both require substantial energetic investment, 877
 and thus producing offspring reduces somatic 878
 growth. Natural selection favors organisms that 879
 schedule developmental tasks and activities so 880
 as to optimize resource allocation. Different al- 881
 location decisions result in different *life history* 882
strategies. 883

The critical decisions involved in a life history 884
 strategy can be summarized by the fundamental 885
 trade-offs between *current* and *future reproduc-* 886
tion, between *quality* and *quantity of offspring*, 887
 and—in sexual species—between *mating* and 888
parenting effort (see Ellis et al. 2009; Kaplan and 889
 Gangestad 2005). By delaying reproduction, an 890
 organism can accumulate resources and/or “em- 891
 bodied capital” (including skills and knowledge), 892
 thus increasing the quality and fitness of future 893
 offspring; however, the risk of dying before re- 894
 producing increases concomitantly. When re- 895
 production occurs, the choice is between many 896
 offspring of lower quality and fewer offspring of 897
 higher quality. While intensive parental invest- 898
 ment is a powerful way to increase the embod- 899
 ied capital (and long-term prospects) of one’s 900
 descendants, the fitness gains accrued through 901
 parenting must be weighed against the corre- 902
 sponding reduction in mating opportunities. Dif- 903
 ferent life history strategies solve these problems 904
 in different ways by determining how organisms 905
 allocate effort among fitness-relevant traits. The 906
 same framework can be employed to describe life 907
 history differences between species and between 908
 individuals of the same species (Réale et al. 909
 2010). 910



Fig. 3.3 The fast–slow continuum of life history variation

911 **3.6.2 The Fast–Slow Continuum** 912 **of Life History Variation**

913 Because life history trade-offs are not functionally independent of one another, differences in
914 life history strategies between and within species show a general pattern of trait covariation.
915 Specifically, slow growth and late reproduction correlate with long lifespan, high parental investment,
916 fewer offspring of higher quality, and low juvenile mortality. Conversely, fast growth and early reproduction
917 correlate with high juvenile mortality, short lifespan, larger numbers of offspring, and reduced parental investment
918 in each. This is commonly referred to as the *fast–slow continuum* of life histories (Sæther
919 1987; see Ellis et al. 2009; Fig. 3.3). The fast–slow continuum has profound implications for
920 the organization of behavior. A short lifespan, higher mortality, and early reproduction make it
921 optimal to discount future rewards and to favor short-term gains over long-term benefits; future-oriented
922 behavior is only favored in the context of slow strategies. Furthermore, organisms betting on future reproduction
923 must maximize their chances of surviving and remaining healthy. This is best obtained through risk aversion—that is,
924 avoidance of variable rewards in favor of surer outcomes, even at the price of a lower average payoff.

940 In most organisms, individual life histories are determined by a combination of genetic and
941 environmental factors. Indeed, life history strategies often exhibit a remarkable degree of developmental
942 plasticity. The key dimensions of the environment that affect the development of life

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

982 3.6.3 Life History Strategies and 983 Individual Differences 984 in Self-regulation

985 In recent years, it has become apparent that life
986 history theory offers a unifying perspective on
987 individual differences in self-regulation (Del
988 Giudice [under review](#); Kruger et al. 2008; Réale
989 et al. 2010; Sih and Del Giudice 2012; Wolf
990 et al. 2007). The logic of fast life history strate-
991 gies promotes a focus on current rewards, a steep
992 discounting of the future, and a tendency to take
993 risks (especially in males). As a consequence,
994 individual differences in impulsivity can be ex-
995 pected to overlap to a large degree with the fast-
996 slow continuum of life history variation. This
997 hypothesis is supported by a large amount of data
998 showing that fast life history traits systematically
999 correlate with higher impulsivity, both in humans
1000 and nonhuman animals (e.g., Kruger et al. 2008;
1001 Réale et al. 2010; Wang et al. 2009; reviewed in
1002 Del Giudice [under review](#)).

1003 In many nonhuman species, the association
1004 between impulsivity and life history strategies
1005 extends to individual differences in coping styles.
1006 Studies of coping styles in nonhuman animals
1007 show that feedforward regulation—characterized
1008 by reduced flexibility, low cue dependency, and
1009 quick but superficial exploration—is system-
1010 atically associated with boldness and impulsiv-
1011 ity in proactive, fast life history individuals. In
1012 contrast, feedback regulation—characterized by
1013 increased flexibility, cue dependency, and slow
1014 but thorough exploration—clusters with shyness
1015 and low impulsivity in reactive, slow life history
1016 individuals (Biro and Stamps, 2008; Careau et al.
1017 2009; Carere et al. 2010; Coppens et al. 2010;
1018 Koolhaas et al. 1999; Réale et al. 2010). Sih and
1019 Del Giudice (2012) recently argued that the as-
1020 sociation between feedforward regulation, im-
1021 pulsivity, and fast life histories may be explained
1022 by a general trade-off between avoiding risk and
1023 acquiring larger rewards (the *risk-reward trade-*
1024 *off*). This argument converges with theoretical
1025 models advanced by Stamps (2007) and Wolf
1026 et al. (2007) in suggesting that basic life history
1027 trade-offs may underlie the structure of personal-
1028 ity and cognition in nonhuman animals.

1029 While the association between feedforward 1029
regulation and impulsivity has been replicated 1030
in various species (though with exceptions and 1031
qualifications; see Réale et al. 2010), there are 1032
reasons to doubt the generality of this pattern, at 1033
least where humans are concerned. As discussed 1034
in Sect. 2.4, feedforward control can take many 1035
forms, ranging from simple and inflexible strate- 1036
gies to complex, highly structured strategies ori- 1037
ented toward long-term goals. My argument is 1038
that the association between feedforward regula- 1039
tion and impulsivity described in the animal lit- 1040
erature only applies to simpler forms of feedfor- 1041
ward control—ballistic responses and rigid, in- 1042
flexible routines. Indeed, the more sophisticated 1043
forms of deliberate, future-oriented feedforward 1044
control are associated almost by definition with 1045
low impulsivity. The fact that most species do not 1046
engage in the kind of long-term planning typical 1047
of human adults may explain the apparent consis- 1048
tency of the animal literature, in which impulsiv- 1049
ity is almost invariably associated with traits that 1050
indicate a primacy of feedforward regulation. 1051

1052 The idea that feedforward control can be as- 1052
sociated with both high *and* low impulsivity is 1053
both theoretically plausible and consistent with 1054
the empirical data. For example, there is con- 1055
siderable evidence that motor inhibition can be 1056
achieved through reactive, stimulus-driven pro- 1057
cesses but also through proactive anticipatory 1058
processes; moreover, the two kinds of inhibi- 1059
tion rely on partially distinct neural pathways 1060
(Aron 2011). In the same vein, Tops et al. (2010) 1061
made an important distinction between *proac-* 1062
tive impulsivity, arising from a lack of feedback 1063
control on behavior, and *reactive impulsivity*, in 1064
which behavior is directly controlled by immedi- 1065
ate emotional stimuli (see also Tops and Boksem 1066
2010). In a longitudinal study of executive func- 1067
tions in children, self-restraint in a delay of grati- 1068
fication task—a prototypical measure of future 1069
orientation—was associated with higher inhibi- 1070
tion and *reduced* shifting ability, the latter being 1071
a key correlate of feedforward regulation (see 1072
Miyake and Friedman 2012). 1073

1074 In humans, slow life history strategies may 1074
often involve a combination of effortful control 1075
(low impulsivity) and predominantly feedfor- 1076

ward 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; Sect. 3.4) 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.

3.7 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 not only 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.

References

- Albertos, P., & Mareels, I. (2010). *Feedback and control for everyone*. Heidelberg: Springer.
- Archer, J. (2009). Does sexual selection explain human sex differences in aggression? *Behavioral and Brain Sciences*, *32*, 249–266. doi:10.1017/S0140525×09990951.
- Aron, A. R. (2011). From reactive to proactive and selective control: Developing a richer model for stopping inappropriate responses. *Biological Psychiatry*, *69*, e55–e68. doi:10.1016/j.biopsych.2010.07.024.
- Azuma, Y., & Hirose, A. (2008). Influence of neural delay in sensorimotor systems on the control performance and mechanism in bicycle riding. *Neural Information Processing*, *12*, 43–51. doi:10.1007/978-3-540-69158-7113.
- Barkley, R. A. (2001). The executive functions and self-regulation: An evolutionary neuropsychological perspective. *Neuropsychology Review*, *11*, 1–29. doi:10.1023/A:1009085417776.
- Bechhoefer, J. (2005). Feedback for physicists: A tutorial essay on control. *Reviews of Modern Physics*, *77*, 783–836. doi:10.1103/revmodphys.77.783.
- Belsky, J., Schlomer, G. L., & Ellis, B. J. (2012). Beyond cumulative risk: Distinguishing harshness and unpredictability as determinants of parenting and early life history strategy. *Developmental Psychology*, *48*, 662–673. doi:10.1037/a0024454.
- Biro, P. A., & Stamps, J. A. (2008). Are animal personality traits linked to life-history productivity? *Trends in Ecology and Evolution*, *23*, 361–368. doi:10.1016/j.tree.2008.04.003.
- Block, J. (2002). *Personality as an affect-processing system*. Mahwah: Lawrence Erlbaum.

- 1174 Boyce, W. T., & Ellis, B. J. (2005). Biological sensi- 1233
 1175 tivity to context: I. An evolutionary-developmental 1234
 1176 theory of the origins and functions of stress reactiv- 1235
 1177 ity. *Development and Psychopathology*, *17*, 271–301. 1236
 1178 doi:10.1017/S0954579405050145. 1237
 1179 Brumbach, B. H., Figueredo, A. J., & Ellis, B. J. (2009). 1238
 1180 Effects of harsh and unpredictable environments in 1239
 1181 adolescence on development of life history strategies: 1240
 1182 A longitudinal test of an evolutionary model. *Human 1241*
 1183 *Nature*, *20*, 25–51. doi:10.1007/s12110-009-9059-3. 1242
 1184 Campbell, A. (1999). Staying alive: Evolution, culture 1243
 1185 and women's aggression. *Behavioral and Brain Sci-* 1244
 1186 *ences*, *22*(2), 203–252. 1245
 1187 Careau, V., Bininda-Emonds, O. R. P., Thomas, D. W., 1246
 1188 Réale, D., & Humphries, M. M. (2009). Exploration 1247
 1189 strategies map along fast-slow metabolic and life-his- 1248
 1190 tory continua in murid rodents. *Functional Ecology*, 1249
 1191 *23*, 150–156. doi:10.1111/j.1365-2435.2008.01468.x. 1250
 1192 Carere, C., Cremaschi, D., & Fawcett, T. W. (2010). 1251
 1193 Covariation between personalities and individual dif- 1252
 1194 ferences in coping with stress: Converging evidence 1253
 1195 and hypotheses. *Current Zoology*, *56*(6), 728–740. 1254
 1196 Carver, C. S. (2005). Impulse and constraint: Perspec- 1255
 1197 tives from personality psychology, convergence with 1256
 1198 theory in other areas, and potential for integration. 1257
 1199 *Personality and Social Psychology Review*, *9*, 312– 1258
 1200 333. doi:10.1207/s15327957pspr0904_2. 1259
 1201 Carver, C. S., & Scheier, M. F. (2011). Self-regulation 1260
 1202 of action and affect. In K. D. Vohs & R. F. Baumeister 1261
 1203 (Eds.), *Handbook of self-regulation: Research, the-* 1262
 1204 *ory, and applications* (2nd ed., pp. 3–21). New York: 1263
 1205 Guilford. 1264
 1206 Chittka, L., Skorupski, P., & Raine, N. (2009). Speed- 1265
 1207 accuracy tradeoffs in animal decision making. *Trends 1266*
 1208 *in Ecology and Evolution*, *24*, 400–407. doi:10.1016/j. 1267
 1209 tree.2009.02.010. 1268
 1210 Coppens, C. M., de Boer, S. F., & Koolhaas, J. M. (2010). 1269
 1211 Coping styles and behavioural flexibility: Towards 1270
 1212 underlying mechanisms. *Philosophical Transactions 1271*
 1213 *of the Royal Society B*, *365*, 4021–4028. doi:10.1098/ 1272
 1214 rstb.2010.0217. 1273
 1215 Cosmides, L., & Tooby, J. (1994). Origins of domain 1274
 1216 specificity: The evolution of functional organization. 1275
 1217 In L. Hirschfeld & S. Gelman (Eds.), *Mapping the 1276*
 1218 *mind: Domain specificity in cognition and culture* 1277
 1219 (pp. 85–116). New York: Cambridge University Press. 1278
 1220 Cross, C. P., Copping, L. T., & Campbell, A. (2011). Sex 1279
 1221 Differences in impulsivity: A meta-analysis. *Psycho-* 1280
 1222 *logical Bulletin*, *137*, 97–130. doi:10.1037/a0021591. 1281
 1223 Daly, M., & Wilson, M. (2005). Carpe diem: Adaptation 1282
 1224 and devaluing the future. *The Quarterly Review of 1283*
 1225 *Biology*, *80*, 55–60. doi:10.1086/431025. 1284
 1226 Del Giudice, M. (2012). Sex ratio dynamics and fluctu- 1285
 1227 ating selection on personality. *Journal of Theoretical 1286*
 1228 *Biology*, *297*, 48–60. doi:10.1016/j.jtbi.2011.12.004. 1287
 1229 Del Giudice, M. (under review). An evolutionary life 1288
 1230 history framework for psychopathology. 1289
 1231 Del Giudice, M., Ellis, B. J., & Shirtcliff, E. A. (2011). 1290
 1232 The Adaptive Calibration Model of stress respon- 1291
 sivity. *Neuroscience & Biobehavioral Reviews*, *35*, 1233
 1562–1592. doi:10.1016/j.neubiorev.2010.11.007. 1234
 Denckla, M. B. (1996). A theory and model of executive 1235
 function: A neuropsychological perspective. In G. R. 1236
 Lyon & N. A. Krasnegor (Eds.), *Attention, memory,* 1237
and executive function (pp. 263–277). Baltimore: Paul 1238
 H. Brookes. 1239
 Dennett, D. (2009). Darwin's "strange inversion of 1240
 reasoning". *Proceedings of the National Academy 1241*
of Sciences USA, *106*, 10061–10065. doi:10.1073/ 1242
 pnas.0904433106. 1243
 DeYoung, C. G. (2011). Impulsivity as a personality 1244
 trait. In K. D. Vohs & R. F. Baumeister (Eds.), *Hand-* 1245
book of self-regulation (2nd ed., pp. 485–504). New 1246
 York: Guilford. 1247
 Diamond, A. (2013). Executive functions. *Annual 1248*
Review of Psychology, *64*, 135–168. doi:10.1146/ 1249
 annurev-psych-113011-143750. 1250
 Dingemanse, N. J., & Réale, D. (2013). What is the 1251
 evidence that natural selection maintains variation in 1252
 animal personalities? In C. Carere & D. Maestripieri 1253
 (Eds.), *Animal personalities: Behavior, physiology,* 1254
and evolution (pp. 201–220). Chicago: Chicago Uni- 1255
 versity Press. 1256
 Ellis, B. J., Figueredo, A. J., Brumbach, B. H., & 1257
 Schlomer, G. L. (2009). The impact of harsh versus 1258
 unpredictable environments on the evolution and 1259
 development of life history strategies. *Human Nature*, 1260
20, 204–268. doi:10.1007/s12110-009-9059-3. 1261
 Ellis, B. J., Del Giudice, M., Dishion, T. J., Figueredo, A. 1262
 J., Gray, P., Griskevicius, V., Hawley, P. H., Jacobs, W. 1263
 J., James, J., Volk, A. A., & Wilson, D. S. (2012). The 1264
 evolutionary basis of risky adolescent behavior: Impli- 1265
 cations for science, policy, and practice. *Developmen-* 1266
tal Psychology, *48*, 598–623. doi:10.1037/a0026220. 1267
 Filevich, E., Kühn, S., & Haggard, P. (2012). Intentional 1268
 inhibition in human action: The power of 'no'. *Neu-* 1269
roscience and Biobehavioral Reviews, *36*, 1107–1118. 1270
 doi:10.1016/j.neubiorev.2012.01.006. 1271
 Frankenhuis, W. E., & Del Giudice, M. (2012). When 1272
 do adaptive developmental mechanisms yield mal- 1273
 adaptive outcomes? *Developmental Psychology*, *48*, 1274
 628–642. doi:10.1037/a0025629. 1275
 Geary, D. C. (2003). Sexual selection and human life his- 1276
 tory. *Advances in Child Development and Behavior*, 1277
30, 41–101. doi:10.1016/S0065-2407(02)80039-8. 1278
 Green, L., & Myerson, J. (1996). Exponential versus 1279
 hyperbolic discounting of delayed outcomes: Risk 1280
 and waiting time. *American Zoologist*, *36*, 496–505. 1281
 doi:10.1093/icb/36.4.496. 1282
 Hill, K., & Kaplan, H. (1999). Life history traits in 1283
 humans: Theory and empirical studies. *Annual Review 1284*
of Anthropology, *28*, 397–430. 1285
 Hofmann, W., Schmeichel, B. J., & Baddeley, A. 1286
 D. (2012). Executive functions and self-regula- 1287
 tion. *Trends in Cognitive Sciences*, *16*, 174–180. 1288
 doi:10.1016/j.tics.2012.01.006. 1289
 Kaplan, H. S., & Gangestad, S. W. (2005). Life his- 1290
 tory theory and evolutionary psychology. In D. M. 1291

- 1292 Buss (Ed.), *Handbook of evolutionary psychology*
1293 (pp. 68–95). Hoboken: Wiley.
- 1294 Kokko, H., & Jennions, M. (2008). Parental invest-
1295 ment, sexual selection and sex ratios. *Journal of*
1296 *Evolutionary Biology*, *21*, 919–948. doi:10.1111/j.1420-
1297 9101.2008.01540.x.
- 1298 Koolhaas, J. M., Korte, S. M., de Boer, S. F., Van der
1299 Vegt, B. J., Van Reenen, C. G., Hopster, H., De Jong,
1300 I. C., Ruis, M. A., & Blockhuis, H. J. (1999). Coping
1301 styles in animals: Current status in behavior and stress
1302 physiology. *Neuroscience and Biobehavioral Reviews*,
1303 *23*, 925–935. doi:10.1016/S0149-7634(99)00026-3.
- 1304 Koolhaas, J. M., de Boer, S. F., Buwalda, B., & van
1305 Reenen, K. (2007). Stress: A multidimensional
1306 approach of ultimate and proximate mechanisms.
1307 *Brain, Behavior and Evolution*, *70*, 218–226.
1308 doi:10.1159/000105485.
- 1309 Kopp, B. (2012). A simple hypothesis of executive
1310 function. *Frontiers in Human Neuroscience*, *6*, 159.
1311 doi:10.3389/fnhum.2012.00159.
- 1312 Korte, S. M., Koolhaas, J. M., Wingfield, J. C., & McE-
1313 wen, B. S. (2005). The Darwinian concept of stress:
1314 Benefits of allostasis and costs of allostatic load and
1315 the trade-offs in health and disease. *Neuroscience*
1316 *and Biobehavioral Reviews*, *29*, 3–38. doi:10.1016/j.
1317 neubiorev.2004.08.009.
- 1318 Kruger, D. J., Reischl, T., & Zimmerman, M. A. (2008).
1319 Time perspective as a mechanism for functional devel-
1320 opmental adaptation. *Journal of Social, Evolutionary,*
1321 *and Cultural Psychology*, *2*(1), 1–22.
- 1322 Kuzawa, C. W., & Bragg, J. M. (2012). Plasticity in
1323 human life history strategy: Implications for con-
1324 temporary human variation and the evolution of
1325 genus. *Homo. Current Anthropology*, *53*, S369–S382.
1326 doi:10.1086/667410.
- 1327 Luttbeg, B., & Sih, A. (2010). Risk, resources and state-
1328 dependent adaptive behavioural syndromes. *Philo-*
1329 *sophical Transactions of the Royal Society B*, *365*,
1330 3977–3990. doi:10.1098/rstb.2010.0207.
- 1331 Miller, G. A., Galanter, E., & Pribram, K. H. (1960).
1332 *Plans and the structure of behavior*. New York: Holt,
1333 Rinehart & Winston.
- 1334 Miyake, A., & Friedman, N. P. (2012). The nature and
1335 organization of individual differences in execu-
1336 tive functions: Four general conclusions. *Current*
1337 *Directions in Psychological Science*, *21*, 8–14.
1338 doi:10.1177/0963721411429458.
- 1339 Miyake, A., Friedman, N. P., Emerson, M. J., Witzki, A.
1340 H., Howerter, A., & Wager, T. D. (2000). The unity
1341 and diversity of executive functions and their con-
1342 tributions to complex “frontal lobe” tasks: A latent
1343 variable analysis. *Cognitive Psychology*, *41*, 49–100.
1344 doi:10.1006/cogp.1999.0734.
- 1345 Réale, D., Garant, D., Humphries, M. M., Bergeron, P.,
1346 Careau, V., & Montiglio, P.-O. (2010). Personality and
1347 the emergence of the pace-of-life syndrome concept
1348 at the population level. *Philosophical Transactions*
1349 *of the Royal Society B*, *365*, 4051–4063. doi:10.1098/
1350 rstb.2010.0208.
- Rothbart, M. K. (2007). Temperament, development
1351 and personality. *Current Directions in Psycho-*
1352 *logical Science*, *16*, 207–212. doi:10.1111/j.1467-
1353 8721.2007.00505.x.
- 1354 Sæther, B.-E. (1987). The influence of body weight on
1355 the covariation between reproductive traits in Euro-
1356 pean birds. *Oikos*, *48*(1), 79–88.
- 1357 Schlichting, C. D., & Pigliucci, M. (1998). *Phenotypic*
1358 *evolution: A reaction norm perspective*. Sunderland:
1359 Sinauer.
- 1360 Shudo, E., Haccou, P., & Iwasa, Y. (2003). Optimal
1361 choice between feedforward and feedback control
1362 in gene expression to cope with unpredictable dan-
1363 ger. *Journal of Theoretical Biology*, *223*, 149–160.
1364 doi:10.1016/S0022-5193(03)00081-X.
- 1365 Sih, A., & Del Giudice, M. (2012). Linking behavioural
1366 syndromes and cognition: A behavioural ecology
1367 perspective. *Philosophical Transactions of the Royal*
1368 *Society of London B*, *367*, 2762–2772. doi:10.1098/
1369 rstb.2012.0216.
- 1370 Stamps, J. A. (2007). Growth-mortality tradeoffs and
1371 ‘personality traits’ in animals. *Ecology Letters*, *10*,
1372 355–363. doi:10.1111/j.1461-0248.2007.01034.x.
- 1373 Starrfelt, J., & Kokko, H. (2012). Bet-hedging-
1374 a triple trade-off between means, variances and
1375 correlations. *Biological Reviews*, *85*, 742–755.
1376 doi:10.1111/j.1469-185X.2012.00225.x.
- 1377 Stearns, S. C. (1992). *The evolution of life histories*.
1378 Oxford: Oxford University Press.
- 1379 Stephens, D. W., Kerr, J., & Fernández-Juricic, E. (2004).
1380 Impulsiveness without discounting: The ecologi-
1381 cal rationality hypothesis. *Proceedings of the Royal*
1382 *Society of London B*, *271*, 2459–2465. doi:10.1098/
1383 rspb.2004.2871.
- 1384 Tops, M., & Boksem, M. A. S. (2010). Absorbed in the
1385 task: Personality measures predict engagement during
1386 task performance as tracked by error negativity and
1387 asymmetrical frontal activity. *Cognitive, Affective, and*
1388 *Behavioral Neuroscience*, *10*, 441–453. doi:10.3758/
1389 CABN.10.4.441.
- 1390 Tops, M., Boksem, M. A. S., Luu, P., & Tucker, D. M.
1391 (2010). Brain substrates of behavioral programs asso-
1392 ciated with self-regulation. *Frontiers in Psychology*, *1*,
1393 152. doi:10.3389/fpsyg.2010.00152.
- 1394 Tucker, D. M., Luu, P., & Pribram, K. H. (1995).
1395 Social and emotional self-regulation. *Annals of*
1396 *the New York Academy of Sciences*, *769*, 213–239.
1397 doi:10.1111/j.1749-6632.1995.tb38141.x.
- 1398 Uher, J. (2011). Individual behavioral phenotypes:
1399 An integrative meta-theoretical framework. Why
1400 “behavioral syndromes” are not analogs of “person-
1401 ality”. *Developmental Psychobiology*, *53*, 521–548.
1402 doi:10.1002/dev.20544.
- 1403 van Oers, K., & Sinn, D. L. (2013). Quantitative and
1404 molecular genetics of animal personality. In C. Carere
1405 & D. Maestripieri (Eds.), *Animal personalities:*
1406 *Behavior, physiology, and evolution* (pp. 149–200).
1407 Chicago: Chicago University Press.
- 1408 Wang, X. T., Kruger, D. J., & Wilke, A. (2009). Life
1409 history variables and risk-taking propensity. *Evolu-*
1410

- 1411 *tion and Human Behavior*, 30, 77–84. doi:10.1016/j.
1412 *evolhumbehav*.2008.09.006.
- 1413 West-Eberhard, M. J. (2003). *Developmental plasticity*
1414 *and evolution*. New York: Oxford University Press.
- 1415 Wilson, M., Daly, M., & Pound, N. (2002). An evolu-
1416 tionary psychological perspective on the modulation
1417 of competitive confrontation and risk-taking. In D.
1418 W. Pfaff, A. P. Arnold, A. M. Etgen, S. E. Fahrbach
1419 & R. T. Rubin (Eds.), *Hormones, brain and behavior*
1420 (pp. 381–408). San Diego: Academic.
- 1421 Wolf, M., van Doorn, G. S., Leimar, O., & Weissing,
1422 F. J. (2007). Life-history trade-offs favour the evolu-
1423 tion of animal personalities. *Nature*, 447, 581–585.
1424 doi:10.1038/nature05835.
- Wolf, M., van Doorn, G. S., Leimar, O., & Weissing, F. 1425
J. (2013). The evolution of animal personalities. In C. 1426
Carere & D. Maestripieri (Eds.), *Animal personalities:* 1427
Behavior, physiology, and evolution (pp. 252–276). 1428
Chicago: Chicago University Press. 1429
- Wolpert, D. M., & Ghahramani, Z. (2000). Computa- 1430
tional principles of movement neuroscience. *Nature* 1431
Neuroscience, 3, 1212–1217. doi:10.1038/81497. 1432
- Wolpert, D. M., Doya, K., & Kawato, M. (2003). A 1433
unifying computational framework for motor control 1434
and social interaction. *Philosophical Transactions* 1435
of the Royal Society B, 358, 593–602. doi:10.1098/ 1436
rstb.2002.1238. 1437