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Review

Linking behavioural syndromes and cognition: a behavioural ecology perspective

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With the exception of a few model species, individual differences in cognition remain relatively unstudied in non-human animals. One intriguing possibility is that variation in cognition is functionally related to variation in personality. Here, we review some examples and present hypotheses on relationships between personality (or behavioural syndromes) and individual differences in cognitive style. Our hypotheses are based largely on a connection between fast–slow behavioural types (BTs; e.g. boldness, aggressiveness, exploration tendency) and cognitive speed–accuracy trade-offs. We also discuss connections between BTs, cognition and ecologically important aspects of decision-making, including sampling, impulsivity, risk sensitivity and choosiness. Finally, we introduce the notion of cognition syndromes, and apply ideas from theories on adaptive behavioural syndromes to generate predictions on cognition syndromes.

Keywords: animal personalities; behavioural syndromes; cognition; speed–accuracy trade-off

1. INTRODUCTION

Cognition refers to the mechanisms by which animals acquire, process, store and act on information from the environment. These include perception, learning, memory and decision-making [1]. Numerous studies of cognition have focused on quantifying and understanding species-specific cognitive abilities and learning tendencies [1]. In contrast, relatively little attention has been paid to individual variation within species [2]. The exception, of course, is in our own species, where it has long been obvious that individual humans differ in cognitive abilities and styles [3]. In recent years, however, there has been growing interest in individual differences in cognition in non-humans, and in their causes and consequences for fitness-related behaviours [4–6].

Recent years have seen a parallel surge of interest in individual differences within species in animal personalities. Although personalities in humans, a few primates and domesticated (including laboratory) animals have long been studied [7], recent work found individual differences in personality in a broad range of taxa, with mounting evidence that these differences are ecologically important [8–11]. For example, individuals often exhibit consistent differences in boldness, aggressiveness, activity, sociability and/or exploratory tendency [9,12]. Interestingly, behavioural tendencies associated with different ecological tasks are often correlated; for example, the same individuals that are more aggressive in competitive contests are also often bolder when predators are present, or poor at parental care or more likely to disperse from a home site [13–16]. Suites of correlated behaviours across contexts have been termed behavioural syndromes, where individuals have a behavioural type (BT); here, we will use personality and BT interchangeably.

The present paper focuses on the intriguing possibility that individual differences in animal cognition are related to BT and vice versa (also see [17]; figure 1). While differences in BT might be related to cognitive ability, we focus, in particular, on relationships between personality and ‘cognitive style’. By cognitive style, we mean the way individuals acquire, process, store or act on information, independent of cognitive ability [3]. For example, as will be discussed in more detail, some individuals might be consistently slower or more careful about how they collect and assess information than others. Or, some might rely more on a history of past information to guide decision-making, while others are quicker to use new information to guide decisions. We organize our ideas around the evolutionary view that both cognition and personality have been shaped by natural selection in past environments, and that both influence fitness in parallel ways. Our overarching hypothesis is that the fundamental aspect of cognition that relates closely with individual differences along the bold–aggressive–active–exploratory BT axis is individual variation in the speed–accuracy trade-off that underlies, at least in part, individual differences in various aspects of cognition.

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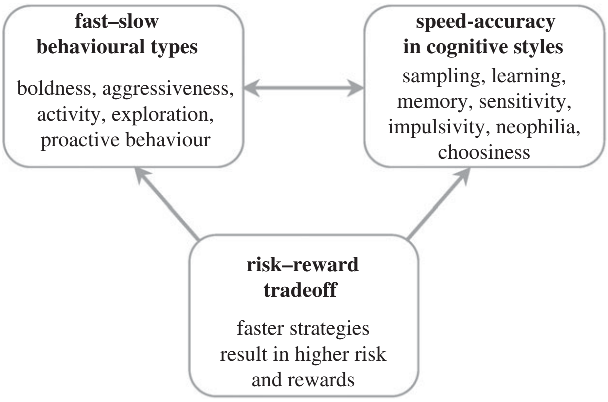

Figure 1. The general hypothesis on connections between fast–slow behavioural types and cognitive styles involving a speed–accuracy trade-off, both driven, in part, by their connection to a risk–reward trade-off that is fundamental for many behaviours.

2. FAST BEHAVIOURAL TYPES AND THE SPEED–ACCURACY TRADE-OFF

A central axiom in behavioural ecology is that many behaviours produce a risk–reward trade-off where a higher expression of the behaviour brings in more rewards (e.g. resources, mates), but at the cost of exposure to higher risk (e.g. predation risk). We hypothesize that this risk–reward trade-off can provide a first principles link between cognitive decision-making styles based on the speed–accuracy trade-off and several BT axes that fall on a 'fast–slow' gradient (figure 1). For personalities, many of the BT axes studied by behavioural ecologists (boldness, aggressiveness, activity, exploratory tendency, proactive–reactive) are associated with variation along a risk–reward axis [8,10]. Animals that are bolder, more aggressive, exploratory and/or proactive can potentially gather more rewards (food, mates), but take more risks along the way. These BTs essentially attack or otherwise move forward actively and often quickly without cautiously accounting for risks. Conversely, shy, unaggressive, less exploratory and/or reactive animals might be safer, but at least in the short-term, collect fewer rewards.

By definition, the speed–accuracy trade-off also falls along a fast–slow gradient. And, it can also often involve a risk–reward trade-off [18,19]. Fast animals take risks while gathering more short-term gains, whereas slow animals take time (sacrifice short-term gain) to make accurate inferences and decisions that are often safer (e.g. slow animals take the time to accurately assess predation risk), but relatively low in short-term gain rate. Note that contrary to the intuition that cognitive performance as measured by accuracy (e.g. percentage correct on tests) should be associated with higher fitness, because of the speed–accuracy trade-off neither speed alone nor accuracy alone is necessarily adaptive. While the most able individuals can be both fast and accurate [20], overall, a trade-off often exists where individuals that are fast are inaccurate, and those that are more accurate are slower (reflecting a need to collect and assess more information; [18,19]). Owing to this trade-off, a range of speeds and accuracies on cognitive tasks might represent alternative strategies (alternative cognitive styles) that yield similar overall fitness.

The general hypothesis that emerges from the earlier-mentioned considerations is that high scores on the fast–slow BT axes (boldness, aggressiveness, activity, proactive and exploratory tendency) are associated with speed as opposed to accuracy in cognitive styles (table 1). Factors (e.g. aspects of morphology, physiology, life history or condition) that lead animals to adopt a faster, more risk-prone lifestyle might tend to produce both faster BTs [8,10,21] and cognitive styles that emphasize speed over accuracy. Furthermore, BTs and cognitive styles might have direct cause–effect links going one or both ways. Having a faster BT (e.g. more bold, aggressive, active or exploratory) might favour adopting a faster cognitive style and vice versa. In the following sections, we discuss our rationale for each point in table 1 along with a selection of the existing literature. Many of these ideas are novel, and most of them rest on a relatively limited empirical base. Our intention is thus to stimulate further work to test our hypotheses, refine them and elucidate underlying causal mechanisms.

3. PERSONALITY AND INDIVIDUAL DIFFERENCES IN COGNITIVE STYLE

Here, we first address BTs and individual differences in learning and memory, distinguishing three stages of the learning process. We then discuss BTs and differences in assessment and decision-making, focusing on several major issues in cognitive ecology (optimal sampling, impulsivity, persistence, risk sensitivity and choosiness).

(a) *Personality, learning and memory*

We distinguish three steps in the process following the appearance of a new or altered situation that can result in a learned change in behaviour in response to that new situation. First, the animal must actually encounter the new or altered situation. After it encounters it, its experience can result in an updated assessment of the situation, and finally, the updated assessment can produce a learned alteration in behaviour. Personality can affect outcomes in each of these stages.

In step 1—encountering new situations (new stimuli, new tasks)—animals that are bolder or faster explorers should encounter new stimuli more quickly (particularly if they are neophilic), than individuals that are more fearful or neophobic. As a result, bold, exploratory animals may appear to be better at a cognitive task simply because they are quicker to encounter and do the task even if they are not better at learning the task after it is encountered [1]. Fast-exploring macaques were indeed quicker to try a new operant conditioning device and thus learned sooner. Fast-exploring corvids were less neophobic and thus learned more [22], and fast-exploring chickadees were faster at learning an acoustic discrimination task [23]. Along similar lines, guppies that evolved under a high-predation risk (that are presumably more fearful) were slower to sample and learn in a spatial memory task [24].

Step 2—assessing a new situation—can be thought about in terms of Bayesian updating, where the animal has a prior assessment of a situation that can be updated by new information. Animals that rely heavily on their prior assessments (and ignore new information) do not learn as much as those that

Table 1. A summary of hypotheses contrasting situations and traits for high speed–low accuracy versus low speed–high accuracy individuals. See the text for more explanation of each point.

	high speed–low accuracy	low speed–high accuracy
immediate reward rate	high	low
mortality risk	high	low
exposure to novel environments	common	rare
behavioural types	proactive fast-exploring bold aggressive asocial?	reactive slow-exploring cautious unaggressive sociable?
eco-cognitive behavioural types	insensitive not choosy more impulsive risk-prone neophilic	sensitive choosy less impulsive risk-averse neophobic
learning and memory		
sample/information collection	less	more
reversal learning	slow	fast
information storage	less	more
learn new activity-based tasks	fast	slow
learn new avoidance tasks	slow	fast
spatial map	shallow	complex
episodic memory	less	more

update more quickly and strongly. Proactive individuals are, essentially by definition, the ones that are relatively insensitive to new information, when compared with reactive, sensitive individuals. Proactive individuals (that are typically also bolder and more aggressive) are predicted to be particularly slow at reversal learning—learning that environments have changed in quality, or signals have changed in meaning. Several studies corroborate these expectations. Fast-exploring chickadees learned more slowly on reversal tasks [23], and proactive trout exhibited longer retention of conditioned responses [25].

Differences between proactive and reactive individuals in updating can also be reflected in their styles of memory formation. Proactive individuals that emphasize speed over accuracy might store less information if excess information slows decision-making [26,27]. In contrast, reactive, sensitive individuals might store more information in long-term memory (than insensitive proactive individuals), including more information that is not useful now, but could be useful later. Personality might also be related to the flipside of memory formation—forgetting. An interesting question is whether forgetting represents active (energetically costly) erasing of information (such as deleting old e-mail, a process that can take a substantial amount of time and mental energy) or masking of information (such as filing old e-mail in folders) behind new, more salient information [28]. In the latter case, information is forgotten in the sense that it no longer affects decision-making, but is still available to be relatively easily restored. Intriguingly, a recent study found that ‘rover’ flies that explore larger areas seem less able to restore old information than ‘sitter’ flies that are relatively stationary [29]. A plausible adaptive explanation is that fast-exploring rovers are more likely to be in novel environments that do not require reference to old information.

Finally, in step 3—personality can also affect how animals alter their behaviour in response to new assessments. Proactive individuals tend to form relatively inflexible routines where they either do not perceive or pay attention to new information (step 2) or new information is processed, but does not alter behaviour (step 3). A classic video that J. Koolhaas has shown in talks follows a proactive, young pig running a simple T-maze where going left (for example) leads to food. After the investigator has moved the food to the right arm, the pig runs left as usual, finds no food, presumably sees that there is no food, but at least in an anthropomorphic view seems unable to accept that new information. It runs back to the beginning, starts over and returns again to the left arm where, of course, there is still no food [30]. Although it is useful, in principle, to distinguish between steps 2 and 3, it can be difficult to separate the two steps empirically [31]. While the common view is that proactive individuals are generally relatively insensitive, the effect of other BTs on sensitivity and relative ability to learn tasks should be task- and context-dependent. For example, bold individuals might be quick to learn tasks that require high activity, but slow to learn tasks that require reduced activity. Indeed, fearful quail were faster than bold ones at an avoidance-learning task that required reduced activity, but slower at a maze-learning task that required higher activity [32].

Note that given that exploratory tendency can have conflicting effects on speed or ability to learn in different stages of the overall process, it should not be surprising to find that in some cases, exploratory tendency has no overall correlation with learning or problem solving ability [33]. Also note that while much of the earlier-mentioned discussion implicitly assumes that BT affects cognitive style, the causal pathway could go the other way. For example, Light *et al.*

[34] found that while high explorers tend to have high cognitive ability, when exposed to novel situations, individuals with high cognitive ability habituated more quickly and thus explored more.

Beyond individual learning *per se*, social learning tendencies might also relate to differences in BT. An obvious prediction is that more sociable animals (a BT) that are attracted to conspecifics might rely more on social learning while less sociable individuals who either avoid conspecifics or aggressively drive them away should rely more on individual as opposed to social learning. Furthermore, asocial individuals might be more likely to disperse from groups [35] and thus not only be alone, but also be in novel environments where rapid individual learning can be critical for survival [35]. These differences in cognitive style can translate into different social roles; for example, in house sparrows, the tendency to be a producer (to find food) rather than a scrounger (use social information) is positively associated with individual learning ability [36].

(b) *Personality and the cognitive ecology of assessment and decision-making*

We next consider how individual differences in personality and the speed–accuracy trade-off might relate to a series of cognition issues that behavioural ecologists have traditionally examined using the optimality approach.

(c) *Sampling*

While simple optimality theory assumes that animals are omniscient, behavioural ecologists have long recognized that real animals need to sample to assess their options [37–39]. Sampling embodies the speed–accuracy trade-off where making a quick decision after only brief sampling is faster but less accurate. If a quick decision (e.g. about coming out of refuge, accepting a potential mate, or attacking a competitor) is riskier, but can produce higher immediate rewards, then the speed–accuracy trade-off in sampling should fit the earlier-mentioned predictions that connect speed–accuracy and BTs along a risk–reward gradient. Animals that are bolder, more aggressive or faster explorers should sample less, and make faster, often less-accurate decisions.

The intuitive idea that fast BTs should be associated with fast decisions can be explored more rigorously using optimal sampling models [38,40,41]. These models often predict that animals should wait longer to make a decision (sample more) if the cost of waiting to make a decision is lower (e.g. if the animal is in good condition and can afford to wait) or if the cost of making a wrong decision is larger (e.g. if making a wrong decision can get you killed; [40]). Another key factor is the environment's rate of change. Sampling is less favoured if the environment is either stable or it changes so rapidly that new information is quickly out of date. Sampling is most favoured in environments that fluctuate at an intermediate rate. Individual differences in optimal sampling can arise if individuals differ in traits that influence the costs or benefits of sampling, or if they live in environments that differ in environmental stability.

In guppies, Burns & Rodd [24] found that fast explorers made rapid, inaccurate decisions in a spatial memory task, while slow explorers took longer to make choices, but were more accurate. While these differences could be seen simply as reflections of the different inherent tendencies of fast- versus slow-exploring BTs, here, the differences were also associated with differences in brain size (in particular, in the size of the telencephalon, a part of the brain that is plausibly related to spatial cognition). Slow explorers had larger brains and presumably higher spatial ability [24]. Fast explorers might make quick decisions, in part, because they lacked the spatial ability to gain as much from additional sampling. The inaccurate decisions made by fast explorers might then have been due both to the fact that they made decisions quickly (the speed–accuracy trade-off), and because of their lower spatial processing ability *per se*. Along similar lines, bold animals might come out of refuge more quickly (after less sampling for danger outside of refuge) either because boldness is inherently associated with a tendency to make quick decisions, or because bolder animals are often stronger, faster or more vigorous than fearful animals, so even if a bold individual makes an error and comes out of refuge when predators are present, this error is less costly for them than it is for a less vigorous, fearful animal [21,40].

Different BTs might also differ in optimal sampling tendencies because they experience different levels of environmental stability. In particular, the speed of exploration and sampling can fit together in a reinforcing feedback loop. The fact that fast explorers often move on to new options [42] can favour a shallow sampling strategy. While it can be important for fast explorers to quickly assess each new option at least cursorily, if they do not typically stay long, there is little benefit for them to sample carefully to more completely understand that option. In contrast, given that slow explorers tend to stay with a familiar option, they have incentives to sample more to accurately understand that option which further favours sticking with that option. Aggressiveness can also influence the stability of an individual's social environment that, in turn, influences the benefit of sampling. Aggressiveness is often positively related to dominance [43]. In cases where dominant individuals do not need to do as much social sampling (as subordinates do) to monitor conspecifics, this can result in an adaptive connection between aggressiveness and a fast, relatively inaccurate assessment strategy.

Differences between fast- and slow-exploring BTs in how much information they collect and accumulate could translate into fundamental differences in spatial and temporal cognition. In space, fast explorers might explore a wider area in a shallow way, while slow explorers might explore a smaller area more carefully. These differences can be extended to suggest that proactive, fast explorers might rely on a few salient landmarks over that larger area, while reactive, slow explorers might build a more information-rich, integrated map with multiple landmarks and locational cues about multiple aspects of the smaller area that they cover. If fast explorers have a relatively shallow understanding of their space, they might easily get lost if they lose sight of key landmarks. In contrast, somewhat paradoxically, slow explorers might be more capable of using their more complete map to plot novel pathways. In some species, the detailed information base of slow explorers might be reflected in better capabilities of episodic memory, 'mental time travel' and planning [1].

(d) *Impulsivity and persistence*

Impulsivity is the tendency to prefer immediate rewards (even if smaller) over delayed rewards (even if larger). Humans [44], several other mammals [45,46] and birds [47] tend to be highly impulsive in many situations. Intuitively, impulsiveness appears associated with speed over accuracy, and fast BTs: boldness, aggressiveness and proactive tendencies. Persistence might, at first glance, seem like the opposite of impulsiveness. High persistence in sampling and evaluating options before choosing a preferred one is associated with slow, careful, reactive individuals that are indeed low in impulsivity. The connection between proactive–reactive BTs and persistence, however, depends on the situation. When deciding when to quit an option (e.g. following a 'win–stay, lose–shift' rule), proactive individuals are expected to persist longer even after some losses (i.e. slow reversal learning). Proactive animals are relatively insensitive to change (ignore the losses), and instead follow set routines sometimes long after an option is no longer apparently rewarding. A cognitive bias that results in overpersistence is the 'sunk cost effect' (referred to in behavioural ecology as the Concorde fallacy [48]) where past use of an option (past investment) produces a tendency to stick with that option even after it is no longer optimal. The suggestion is that proactive individuals are more likely to fall victim to the Concorde fallacy. Note, however, that proactive persistence through a string of losses is not necessarily maladaptive. If the environment's signals are noisy (i.e. if a few losses are not good indicators of future losses), or if the environment changes frequently, so a string of losses is likely to shift back soon to wins, then 'overpersistence' in the short-term can be adaptive in the long-term.

(e) *Risk sensitivity*

By risk sensitivity, we mean sensitivity to variance in outcome. If all else is equal, risk-averse individuals prefer low variance options, whereas risk-prone ones prefer high variance options. Risk-insensitive individuals do not base their decisions on variance. In behavioural ecology, the term risk sensitivity usually refers to variance in rewards; e.g. being 100 per cent certain that you will have $100, as opposed to the variance of gambling where you have a 50 : 50 chance of getting either nothing or $200. Although people are often careful to note that risk in the sense of reward variance is not the same as predation or mortality risk, much of the logic underlying risk sensitivity can also apply to mortality risk.

Empirical studies show that risk sensitivity can depend on whether the variance is in rewards or time delays [49]. Humans and a few other tested animals tend to be risk-averse about rewards, but risk-prone about time delays. Note that the commonly seen tendency to be impulsive (discussed earlier) implies being risk-prone about time delays. The 'risky' option that includes both short and long delays is preferred over all medium-length delays, because the strong preference for short delays outweighs the dislike for long delays [41]. Risk sensitivity for rewards should depend on the individual's state. If the relationship between condition or reward rate (e.g. feeding rate) and fitness is sigmoid, then individuals in poor condition who have little to lose and everything to gain if they can increase their condition should be risk-prone, while those in excellent condition who have little to gain and everything to lose should be risk-averse. Work on humans and several other organisms corroborates these predictions [49,50]. A corollary prediction based on sexual selection theory is that in systems with strong sexual selection (e.g. strong male–male competition or female choice favouring high-quality males) males have more to gain from increasing their state or rank than females; thus males should be more risk-prone than females. This does, indeed, appear to be generally true in humans and a few other species [51].

How might BT relate to individual differences in risk sensitivity? The intuitive prediction is that risk-prone behaviour might be associated with impulsivity and bold, aggressive, proactive, fast-exploring BTs. Optimality theory corroborates this intuitive prediction with an interesting twist. While animals with fast BTs should generally be risk-prone, whether these are high- or low-condition animals depends on how condition (or state, in general) affects future risks [21]. If state does not affect future risk, then based on the logic in the previous paragraph, individuals in excellent condition should exhibit a cautious, unaggressive BT [52] and be risk-averse (avoid variability; [53]). If, however, fitness increases in an accelerating ('cup-up') fashion with increasing condition (e.g. if in a lek mating system, the males in best condition have extremely high mating success), the higher condition males should exhibit a fast (aggressive) BT and be risk-prone. Or, if being in superior condition reduces future variances in outcome, then individuals in excellent condition should be bold, aggressive and often prefer options that are inherently variable but less variable for high condition individuals [21]. Being in good condition can reduce variability if strong, vigorous animals are better at escaping predators, or if animals in excellent condition have high dominance rank and thus have less variance in their probability of gaining rewards [21].

(f) *Choosiness*

Behavioural ecologists have a long history of theoretical and empirical studies examining various fitness-related aspects of choice: e.g. diet choice [38,54], patch or habitat choice [55] and mate choice [56]. While much of the empirical literature has tested predictions about average preferences for a group of organisms (e.g. leading to conclusions about mate preferences for entire species), and some recent work has focused on individual differences in preferences [57,58], very few studies have looked at individual differences in *choosiness per se*. In almost all published studies, individuals appear to differ in choosiness—e.g. in a typical mate choice study, some females strongly prefer larger males, some weakly prefer larger males, some females appear indifferent about male size and a few prefer smaller males. Recent work suggests that individual differences in choosiness are repeatable [59,60].

How might BT be related to individual differences in choosiness? Although there are a plethora of models of choice, including both optimality models and sampling models (e.g. [61–63]), in general, because being choosy often requires one to reject several options before accepting one, less choosy animals make fast choices (after sampling only a few options) that might be less accurate, while more choosy animals take extra time to evaluate more options more carefully to make a better informed choice. That is, choosiness involves a speed–accuracy trade-off where we thus expect fast BTs (bold, aggressive, proactive) to be less choosy.

Optimality models predict that animals should generally be choosier if options are more different in quality, and if high-quality options are more abundant. Individual differences in choosiness could thus be adaptive if individuals differ systematically in their ability or tendency to discriminate differences in option quality, or if individuals differ in their access to high-quality options. Interestingly, these two considerations generate opposite predictions regarding the relationship between BT and choosiness. For the former, a key relevant aspect of cognition is stimulus or option generalizing in associative or discrimination learning [1]. If animals learn to associate stimulus X with a reward, how different can a new stimulus be and still be treated as being in the same category as X? To better discriminate between similar options, animals need to take more time to collect information, and animals might use multiple cues, as opposed to one primary cue. Both of these imply a speed–accuracy trade-off, not just in time taken to consider more options, but also time taken to evaluate each option. This logic predicts that fast BTs should be less choosy. In contrast, if fast BTs encounter more food or mates (by being bold, active or exploratory) or gain better access to high-quality foods or mates (by being aggressive and attaining higher dominance rank), then following the standard predictions of optimal diet or mate choice theory, fast BTs should be more choosy. If cautious, unaggressive individuals encounter few food items or possible mates, they do better to accept what they can get rather than be choosy and risk getting nothing. Finally, choosiness can be influenced by the tendency to prefer familiar options (where familiarity *per se* is a major choice criterion), which is related to neophobia. Slow BTs tend to be more neophobic and should thus be choosier.

4. COGNITIVE SYNDROMES

Key aspects of the concept of a behavioural syndrome include the existence, for a given BT axis (e.g. boldness), of consistent behavioural tendencies across time or contexts and correlations or carryovers across BT axes (e.g. between boldness and aggressiveness). Correlations among the fast–slow BTs include the observation that foraging activity in the absence of predators is often correlated with boldness when predators are present [64], with aggressiveness in contests [15,65], with mating tactics [66,67], with patterns of parental care [13] and with dispersal tendencies [16,35,68].

While consistent, individual differences in the fast–slow BTs and in sociability have received a great deal of attention, less attention has been given to the possibility that individuals might differ consistently in cognitive style: sampling style, persistence, impulsivity, risk sensitivity (or sensitivity, in general) or choosiness [69]. Consider, for example, the possibility that individual differences in sensitivity (response to stimuli or to changes in stimuli) might carry over across different tasks and contexts (figure 2). Fascinating questions that are seldom addressed include: (i) within a mating context, is sensitivity in mate choice (e.g. ability to discriminate mate quality) correlated to sensitivity in choosing optimal times or places to search for mates? (ii) Is sensitivity in mate choice correlated to sensitivity to courtship signals that results in successful mating? (iii) Going beyond mating, is sensitivity in the mating context correlated to social sensitivity in other contexts—e.g. in partner choice and adjustments to social situations in the context of cooperation or competition? And, (iv) going beyond social situations, is social sensitivity in one or more social situations correlated to sensitivity relative to habitat choice, or diet choice? Finally, is sensitivity correlated to other aspects of personality? The coping style literature suggests that sensitivity is negatively related to boldness and aggressiveness [70]. An alternative hypothesis is that extreme BTs (either very bold or very shy individuals, very aggressive or very unaggressive ones) are generally less sensitive and less plastic, while some individuals with intermediate BTs might be most sensitive and plastic.

Should sensitivity in different contexts be positively or negatively correlated? If individuals vary in general sensitivity, then sensitivity should be positively correlated across different tasks or situations. If, however, sensitivity is costly; e.g. if it requires sampling and assessment, or if it draws on a finite pool of attention [71], then we might expect negative correlations between sensitivity in different tasks. For example, sensitivity towards potential mates might draw attention away from, and thus reduce sensitivity towards food or predators.

Similar issues (that have also seldom been studied) arise for choosiness. For example, for female choice (a major area of interest in behavioural ecology), interesting questions include: whether females are repeatable in their choosiness across trials in the same basic situation, and whether they are consistent in their degree of mate choosiness across different situations (e.g. involving different types of focal male traits, or different male abundances). Going beyond mating *per se* to other ecological contexts, are the same individuals that are choosier than others about mates also relatively choosy about other social partners, about food choices or about aspects of habitat use, etc? In humans, we believe that people differ in choosiness about their foods or wines, or about music or movies, or about clothes or other accoutrements, or about mating

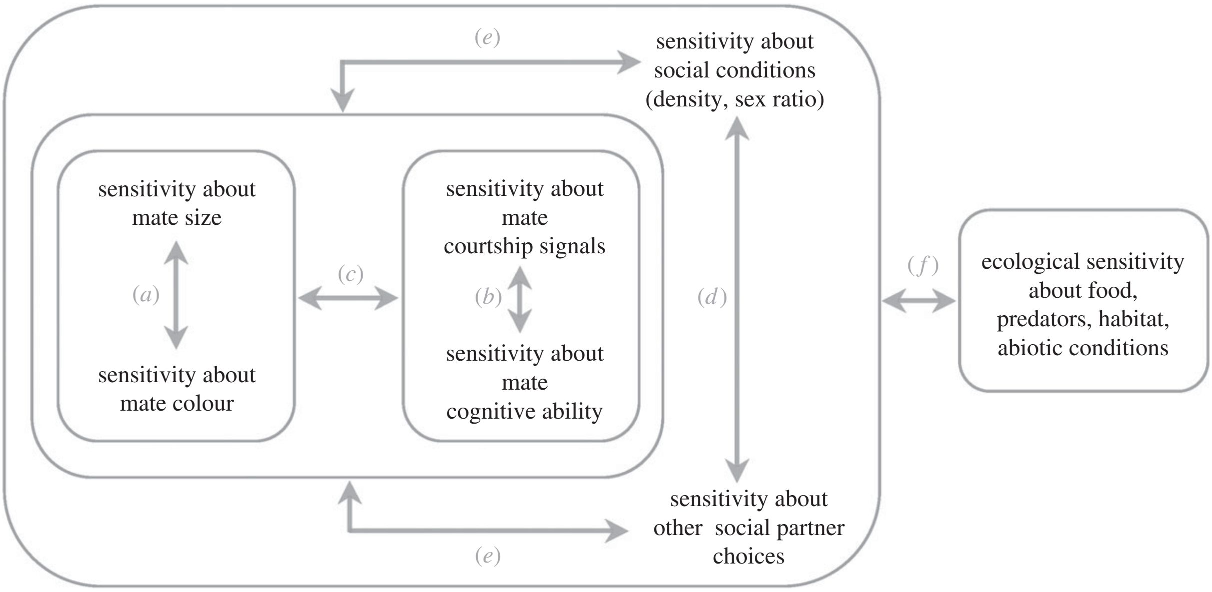

Figure 2. A sensitivity syndrome. Double arrows represent possible correlations between sensitivities, including correlations between sensitivity for: (*a*) different mate morphological traits; (*b*) different mate behavioural traits; (*c*) morphological and behavioural traits; (*d*) different social situations beyond mating *per se*; (*e*) mating and other social variables; (*f*) social and ecological conditions. A general sensitivity syndrome predicts positive correlations; however, if sensitivity requires time or energy that draws from a limited budget, then the result could be some negative correlations.

partners. The question that has received little attention is—is choosiness correlated across these different contexts? As with sensitivity, if there is a general choosiness syndrome, then choosiness might be positively correlated across situations [59,60]; however, given that choice takes time and energy (to gather information and evaluate choices), it is also conceivable that choosiness might be negatively correlated across contexts. In either case, as with other BT-related correlations, a choosiness syndrome could result in suboptimal behaviour. An individual that is generally very choosy across many situations will likely be too choosy in some situations. Or, an individual that only has enough discrimination ability to be choosy in one or a few situations might be inappropriately non-selective in another situation.

What about correlations across tasks for the different aspects of cognition often studied by cognitive psychologists—e.g. following Shettleworth [1], what correlations might exist between *styles* related to: habituation, associative, recognition, and discrimination learning, memory, spatial cognition, timing, numerical competence, tool use, social learning, communication and language? Do individuals exhibit cognition syndromes featuring consistent cognitive styles that carry over across some of these categories of cognition? To emphasize, although a growing literature exists on individual differences in cognitive *abilities* across different tasks [3–6], the focus here is on carryovers in cognitive style, not on cognitive ability. For example, does knowing how a given individual handles an associative learning task allow us to predict how it handles timing tasks or how it builds and uses spatial maps? Following a general theme of this study, a hypothesis is that how an individual handles the speed–accuracy trade-off might carry over across tasks. Individuals that emphasize speed over accuracy (or vice versa) in associative learning might also be quick but inaccurate in their discrimination among options. They might be fast, shallow explorers that do not build dense, multi-cue spatial maps, and they might have broad social networks with relatively weak bonds with social partners. Because speed uses little of the organism's cognitive or time budget, it should be possible for an organism to exhibit a fast style in all cognitive tasks. However, following a second theme of the paper, the existence of a limited overall time, energy or attention budget suggests an asymmetry in the correlation structure. Accuracy that takes time, energy or attention will likely face a 'limited budget' constraint that results in some negative correlations between ability to be accurate in multiple tasks.

The issue of correlations across multiple categories of cognition relates to the modularity of cognition—the notion that the mind consists of independent, domain-specific processing modules [1,72]. Strong domain-specificity implies that a given module is specialized to operate only on a specific type of information [73], whereas a weaker version of modularity suggests that although different cognitive tasks may have specialized information-processing modules, they also share cognitive resources (e.g. memory). While there is some confusion and controversy over the definition of cognitive modularity [74], some evidence suggests different rules of operation for different tasks; e.g. for song learning versus food location learning [75] with perhaps separate modules for processing spatial information, timing, non-verbal number systems and the representations that are implicit in imitation. Selection might favour numerous distinct, cognitive modules, in particular, if information processing is functionally incompatible across different tasks.

Correlations in cognitive style (e.g. tendency to favour speed versus accuracy) across different cognitive tasks could arise because modularity is weak (e.g. different 'modules' engage in cross-talk or draw from a common central processing unit or resource). Alternatively, even if modularity is strong, cognitive styles can be correlated across contexts if selection has favoured parallel adaptive cognitive styles in different tasks. The main point is that the existence of cognitive modules with weak or even strong, mechanistic domain-specificity is not incompatible with the notion of cognition syndromes. A similar point has been discussed for genetic/neuroendocrine mechanisms underlying behavioural correlations. Behavioural correlations across contexts might exist because behaviour in the different contexts is governed by shared mechanisms; however, even if different mechanisms govern different behaviours, correlations can exist if they are favoured by correlational selection [12,76]. Given that modules have presumably also been shaped by natural selection (i.e. the degree of cognitive modularity is adaptive), an exciting integrative approach would be to examine the joint evolution of cognitive modularity and cognitive syndromes.

5. THE ROLE OF FEEDBACK LOOPS IN EXPLAINING SYNDROME PATTERNS

As a growing list of empirical studies suggested patterns, the behavioural syndromes field began exploring general theory to explain or even predict patterns. One interesting, novel question that arose is: why do personalities exist [8,21,76,77]? Given that behavioural carryovers across time or contexts are sometimes associated with suboptimal behaviours, why do these carryovers exist at all? Analyses of this issue acknowledge that animals are obviously behaviourally plastic. For example, as conditions change, almost all individuals adjust their aggression levels, typically in an adaptive way. The existence of BTs, however, often limits each individual's range of plasticity that can result in suboptimal behaviour. If, for example, individuals with a bold or aggressive BT are sometimes bolder or more aggressive than they should be, and if individuals with a shy BT sometimes miss the opportunities that they could have otherwise had, why should animals, including humans, exhibit consistent BTs? Along similar lines, why should aggressiveness with conspecifics be correlated to boldness with predators? Why not be completely plastic and exhibit the optimal behaviour in all circumstances? The analogous question for cognition is if cognitive styles have trade-offs, why have a cognitive style? If it is sometimes best to assess and decide quickly, but in other situations, it is best to assess and decide slowly and carefully, why might individuals exhibit a tendency to maintain a consistent cognitive style across situations? Again, we recognize that animals probably often switch their sampling and decision-making styles to better match the task, but why might they do so within the limits of a general cognitive style?

Several models of adaptive personalities emphasize the importance of state variables and positive feedback loops between BT and the state variables in developing and maintaining a style [21,76]. The logic for these models is simple. While behaviour has the potential to be highly plastic, it should be less plastic if it is 'anchored' to a less plastic state variable. Stable differences in BT emerge if state and behaviour reinforce each other in a positive feedback loop. For BTs, stochastic, state-dependent dynamic programming models have focused on individual condition (vigour, strength, size) as a key state variable [21]. Being bold or aggressive brings in energy that increases individual condition. If animals in superior condition can then be bold or aggressive with less cost (e.g. if fast prey can escape predators) or greater benefit (e.g. if large, strong competitors win contests), this favours further bold or aggressive behaviour that continues to bring in the energy to maintain high condition and so on. Conversely, if low-condition animals suffer higher costs or lower benefits of being bold or aggressive, then they should be cautious and unaggressive, which results in low energy intake that keeps them in poor condition, which keeps them cautious and unaggressive as a 'best of a bad job' BT. Note that this line of reasoning generates the opposite of the common prediction that animals with high assets (high reproductive value, high energy) should be cautious and unaggressive to protect their assets (the 'asset protection principle' [52]), whereas animals with low assets should be bold and aggressive because they have nothing to lose [53]. Whether animals that are in excellent condition should be bold/aggressive or cautious/unaggressive should depend on the relative importance of these two lines of logic [21]. Most interestingly, under a range of ecological conditions, the two forces counteract each other. Under those conditions, the model predicts that animals should not exhibit consistent differences in BT [21].

The models also make intuitively clear predictions on when differences in initial state (e.g. vigour when young) should affect the individual's BT later in life [78]. When the positive feedback loop between state and behaviour dominates, then differences in early state (e.g. due to genetic differences in vigour, or differences in maternal effects or parental care) can determine later BT [21]. Individuals who start in better condition are bolder and more aggressive, gain more energy and gain an ever-greater advantage over individuals that begin in relatively poor condition. In contrast, when the logic of the asset protection principle dominates, then early differences in state erode. Individuals that started in poor condition take chances (are bold or aggressive) and assuming they survive, catch up to individuals that began in better condition but did not take chances to maintain their head start. Thus, the existence of an 'early developmental window' where early experiences shape later BTs is not a developmental constraint, but is instead an adaptive outcome that emerges only when positive feedback loops are important [21].

Note that when positive feedback loops are present, animals might often take risks that seem excessive early in life; the rationale is that early condition will later kick in a positive feedback loop where high condition allows the animal to successfully be bold or aggressive and further increase in condition and so on. Similar logic can explain condition-dependent play or other practice behaviours in young animals. For example, meerkat pups that are in good condition invest more time than others in foraging behaviours that do not actually yield immediate rewards, presumably because they can afford to take time to develop skills that will be important in later success [79]. Whether this tendency to accept high risks or inefficiencies in the short-term for future gains is adaptive or not depends on short- and long-term costs and benefits, on the strength of the positive feedback loop, and on the time available for long-term future benefits to be enjoyed.

To emphasize, the strength of this modelling approach is that it predicts both: (i) when we should versus should not see consistent differences in BT; (ii) when we should versus should not see an early developmental window where early experiences determine later BT; (iii) when animals should versus should not take risks early on for long-term benefits; and (iv) it predicts when the correlation between condition and boldness or aggressiveness should be positive versus negative. That is, rather than simply explain why animals often exhibit BTs, the models make novel predictions on factors that influence the nature of these BTs.

All of the earlier-mentioned issues have parallels for cognition—replacing BT with cognitive style, and condition with a relevant cognitive state variable. For example, the state variable(s) might be the individual's skill level for using tactic A versus B on a cognitive task. In keeping with the speed–accuracy trade-off, tactic A might involve quick collecting and processing of adequate information, whereas tactic B involves processing larger amounts of more complex information gathered slowly. Use of tactic A can increase the skill level for A, which then favours continued use of A, which further increases skill at A and so on. The same could apply for tactic B. If there is a trade-off where specializing on using either tactic reduces skill in the other tactic, then this further reinforces specializing on one tactic, thus resulting in a stable, consistent cognitive style for that task. Analysing why animals might use the same cognitive style (e.g. fast/superficial versus slow/accurate assessment styles) for different cognitive tasks would require explicit assumptions about relationships between relevant state variables and cognitive styles and abilities for the different cognitive tasks. If skills compete for cognitive resources, it might favour the use of simple heuristics that require less information and less information processing for each of multiple tasks. The main point is that adaptive dynamic models perhaps, using stochastic dynamic programming methods, can potentially generate novel, explicit predictions on cognition syndromes.

Beyond explaining behavioural syndromes *per se*, and cognitive syndromes *per se*, a higher-level challenge is to explain potential correlations between these syndromes (figure 1). Across-syndrome correlations might arise because both fast–slow BTs and fast/inaccurate versus slow/accurate cognitive styles share an adaptive connection via their shared risk–reward trade-off. Alternatively, the cause–effect relationship between behavioural and cognitive syndromes could go one way, or the other, but without positive feedbacks loops. Individuals that have a fast BT might require having a fast cognitive style that rapidly collects and processes the information needed to be successful. Individuals with a fast cognitive style might not collect deep enough information to support a slow, careful BT. Finally, there is the possibility of feedback loops between behavioural and cognitive syndromes where having a fast BT favours individuals developing a fast cognitive style that, in turn, feeds back to favour the fast BT. Further models and data on interconnections between otherwise separate syndromes should prove exciting.

6. FUTURE DIRECTIONS

- We suggest the broad, general hypothesis that fast BTs might often be associated with speed over accuracy as a cognitive style (table 1). Using optimality thinking, however, to sharpen our logic on why BTs might be related to fast–slow cognitive styles revealed some contrary predictions. More explicit theory and experimental tests should prove useful in moving this field forward.
- In particular, theory (based on analogous theory on adaptive personalities) integrating adaptive and mechanistic approaches with feedback loops can make explicit predictions on how BTs might relate to cognition.
- Beyond further tests of the basic idea that fast BTs might exhibit fast cognitive styles, we need more empirical data on how multiple BTs might relate to multiple aspects of cognition, and how both of these influence individual differences in choice of behavioural strategies, performance and ultimately fitness. These studies can help us to understand how these types of traits fit together in an integrated package.

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