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Speed–accuracy tradeoffs in animal decision making

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The traditional emphasis when measuring performance in animal cognition has been overwhelmingly on accuracy, independent of decision time. However, more recently, it has become clear that tradeoffs exist between decision speed and accuracy in many ecologically relevant tasks, for example, prey and predator detection and identification; pollinators choosing between flower species; and spatial exploration strategies. Obtaining high-quality information often increases sampling time, especially under noisy conditions. Here we discuss the mechanisms generating such speed–accuracy tradeoffs, their implications for animal decision making (including signalling, communication and mate choice) and the significance of differences in decision strategies among species, populations and individuals. The ecological relevance of such tradeoffs can be better understood by considering the neuronal mechanisms underlying decision-making processes.

Accuracy and time as measures of decision quality

We all too commonly assume that animals will give their best when confronted with a discrimination test (see Glossary); the accuracy that animals display has sometimes been taken to reflect the limit of their ability, and these 'limits' have, in turn, been used as arguments for the evolution and ecology of biological signals. Crucially, animals have no interest *per se* in excelling at the experimenter's task; typically, they are only interested in getting rewards and avoiding punishments, and will devise strategies to achieve this. When it takes a long time to solve a difficult task, and the potential costs of errors are low [1,2], the best solution from the perspective of an animal might be to 'guess' the solution quickly [3–5], a strategy that is likely to result in low decision accuracy.

It is probable, then, that there will often be a relationship between the difficulty of the task, and the speed and accuracy with which it is solved [6–8] (Figure 1). Given that information from both the environment and sensory systems is inherently noisy, animals must often continue sampling for some time, until a threshold of neuronal activity is reached and the decision taken. This process has been likened to a jury taking time to deliberate and weigh the evidence before reaching a verdict [9]. In biology, decision making can sometimes take extended periods as, for example, when honeybee swarms take several days to gather information about suitable new nest sites before reaching a consensus [10]. The need for

rapid decisions might mean that accuracy suffers, but when accuracy is of prime importance, such as when avoiding hidden predators [1,11,12], substantial time might need to be invested to ensure the coast is clear. In other biologically relevant decisions, error penalties are low, such as pollinators choosing between rewarding flowers and their Batesian mimics, such as species of nectarless orchids [13].

Speed–accuracy tradeoffs (SATs) can occur at several mechanistic levels and over multiple timescales. Sampling of noisy conditions can take place within individual receptor cells, central nervous processing systems or, in some cases, distributed across many individuals (as in social insects or human societies). Here we focus first on experimental work on the physiology of sense organs and subsequent neuronal processing, which lays the foundation for the biological decision-making processes in the subsequent section. We describe how individuals place a

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Glossary

Animal personality: the complex of behavioural and cognitive attributes that characterise an individual animal consistently over time.
Aposematism: evolution of distinctive warning signals by resistant (often toxic) prey species to discourage predation.
Batesian mimicry: evolution of a susceptible prey species to resemble (mimic) a resistant (model) prey species to discourage predation.
Categorisation: the grouping together of objects based on some unifying property and independently of individual features, for example 'dogs' or 'tables.'
Consensus: a decision supported by all members of a group (cf quorum below).
Discrimination: the ability to distinguish different sensory stimuli and generate different behavioural responses to them.
Odorant: a chemical compound with a smell, or odour, which can be detected by olfactory receptors.
Photoreceptor: a light-sensitive cell, which generates, via a process of phototransduction, an electrical signal related to the number of photons absorbed.
Quorum: the minimum (threshold) number of individuals necessary to reach a decision.
Quorum sensing: the process of detecting the quorum (threshold) number of individuals required to make a decision.
Recruitment: in social animals, the process by which animals inform other individuals of the need to perform a particular task and solicit them to engage in it.
Speed–accuracy tradeoff (SAT): in many motor or perceptual discrimination tasks, a tradeoff exists between the precision or accuracy on the one hand and the speed of performing the task on the other.
Telencephalon: the anterior portion of the forebrain, whose hemispheres generally contain 'higher-order' brain functions, giving rise to the cortex in mammals.
Visual search: involves actively scanning the environment for a defined 'target,' typically within an array of 'distractors' that differ from the target in visual appearance. Requires attention.
Waggle dance: a repetitive stereotyped motor pattern used by honeybees to symbolically encode both spatial (distance and direction) information about a food source to other individuals.

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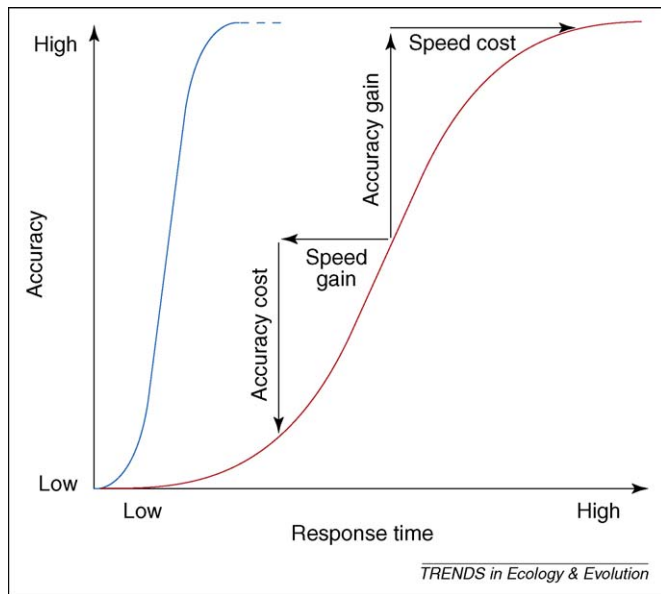
Figure 1. Relationship between speed and accuracy in discrimination tasks. For most decision tasks (e.g. a perceptual discrimination of at least moderate difficulty), there is an inverse relationship between response speed and accuracy (red curve) over a range of response times. Accuracy can be improved by investing more time in the decision process or, conversely, decisions can be made more quickly but at the cost of making a higher number of errors: that is a SAT. If the discrimination being tested is perceptually very easy (blue curve), then potential SATs will not be evident, because the subject will be performing with high accuracy over any realistic range of reaction times.

selective emphasis on either speed or accuracy in fundamental processes such as foraging, avoiding predators and communication. Finally, we expand our focus to 'personality' differences in terms of SATs, and the question of how many individuals can contribute to effective group decision making.

Tradeoffs in sensory processes: psychophysics and physiology

Although SATs are likely to affect many, if not all, sensory modalities (including hearing and echolocation, temperature sensing and electroreception), the best-studied modalities are vision and olfaction, and we discuss the mechanistic properties of these pathways insofar as they might affect SATs in natural decision making.

Vision
Successful vision depends on swiftly detecting and accurately apprehending visual change, for example, discovering an approaching predator in tall savannah grass, or a pollinator searching for flowers against green foliage. Although the optics of insect compound eyes have relatively poor spatial resolution [14], they can have excellent temporal resolution, exceeding our own by an order of magnitude. Furthermore, during movement, spatial information can be considered in the temporal domain: during visual scanning, fine spatial detail will result in high-frequency temporal variation in photoreceptor responses [15]. This implies that the acquisition of spatial detail in a visual scene depends on sampling time; if this is the case, then SATs are to be expected. In fact, this has been found when bees have to detect and discriminate flowers using colour [16]. Bees choosing

rapidly are more error prone than are conspecifics choosing more slowly [4,17], but all individuals improve their choice accuracy (and typically increase their response time) if errors are penalised [4,18]. These effects depend on task difficulty: they are found where target and distractor colours are similar (and where more information can be extracted from longer integration times) but not when colours are clearly distinguishable [8].

Efficiency requires photoreceptors to make the most of available light levels, and nocturnal animals can push their visual systems remarkably far in such situations, but at the cost of speed [19]. Compared to their fast-flying diurnal cousins, nocturnal bees and wasps have 'slow' photoreceptors that are unsuitable for fast visual pursuit, but make the most of the low light levels available through temporal summation (at the cost of speed). Diurnal pollinators also fly more slowly in dim light conditions, which increases photoreceptor sampling time and facilitates flower detection [20]. However, although behavioural strategies can be adapted to either speed or accuracy of visual sampling, the ultimate limits on speed are determined by the species-typical endowment of photoreceptor properties. This is because of the relatively high cost of fast neural processing and the consequent selection pressure to minimise these costs [21].

Although the fastest insect photoreceptors can outperform vertebrate cones when judged by frequency response, there is no doubt that the primate visual system is extremely efficient in the rapid identification and classification of visual scenes [22]. However, as task difficulty increases, such as when searching for hard-to-find objects, SATs are the rule [23]. Motion detection by primates is particularly well understood in terms of SATs in the decision-making process, and models based on neurophysiological data reliably predict variations in response speed and accuracy with task difficulty [9].

When processing stimuli indicating predation threat, mammals appear to use one of two neuronal circuits. The first, an evolutionary ancient, subcortical pathway where sensory information is processed in the amygdala and directly triggers behavioural fear responses, is fast but inaccurate [1]. The second, a more recently evolved cortical system, accumulates information about predation threat more slowly but with greater accuracy [1]. This shows that SATs can occur within, as well as across, different neuronal mechanisms in the same animal.

However, the interaction between neural processing systems of different speed is not always this straightforward. In some instances of rapid visual categorisation by humans, for example, deciding whether an animal is present in a natural scene, the expected SAT seems not to apply [24] and, in some perceptual decisions about briefly presented abstract patterns, might even be reversed [25]. Early visual processing sometimes appears capable of extracting maximal information from short sampling times [26], whereas longer time windows might introduce interference from higher-lever cortical systems (top-down processing), thus obscuring the typical SAT. The extent to which such complications might apply to natural decision making, in non-human primates and other animals, remains to be determined.

Olfaction

Traditionally, olfaction has not been considered a fast sense, but recent studies indicate that rodents are capable of identifying odorants with a single sniff [27–30]. Behavioural measures suggest rodents can make olfactory discriminations within 200 ms, and neurophysiological data indicate that much of the information about odorant identity can be extracted in as little as 50 ms [29,31]. Given the apparent speed of odour identification and discrimination, is there a SAT in early olfactory processing? This issue is not simple to resolve, because performance (discrimination of the same odour pairs) depends substantially on the experimental procedure [29,32,33], as well as the motivation of the animal, and its consequent behavioural strategy, which is often simply to opt for 'just good enough' [5].

Mice trained to sample for a variable time interval (until the possibility of a reward was cued by a buzzer) showed a SAT, where discrimination accuracy depended on both the difficulty and sampling time available [30]. Tellingly, mice free to pace themselves opted for a short sniffing time and performed less accurately. It is likely that the mice were not pushing their olfactory system to its limits, given that there was a 50% chance of a reward regardless. This suggests the interesting possibility for future experiments of attempting to control voluntary sampling time by manipulating potential payoffs.

Extensive electrophysiological analysis and modelling of odour processing in insects suggest that (based on temporal coding) improved olfactory discrimination accuracy should be possible with longer sampling times, but also that significant information is present relatively early after odour onset [34]. This suggests that SATs in the olfactory domain will be common. Few behavioural studies have yet attempted to disentangle accuracy, speed and motivation. A recent study that controlled odorant exposure time and discrimination difficulty found a SAT for honeybee olfactory discrimination, with highest-concentration odorants identified with high accuracy following 200 ms exposure, but performance accuracy still increasing up to 1 s exposure for the lowest concentrations [7].

Adaptive decision making by individuals in the field

Whereas the preceding sections dealt with sensory–neural mechanisms that might generate SATs in information acquisition, our focus now turns to how individuals might flexibly adjust their emphasis on either speed or accuracy in their natural lives.

Avoiding predation

One context in which choice accuracy has great biological value is predator detection: here, costs of errors are potentially extreme [1,11]. The cost of the time taken to ascertain a threat could be substantial, because predators can be cryptic and often use behavioural tactics to minimise detection [35]. Complete certainty about the absence of a predator, however, can perhaps only be ascertained by near-constant searching, which would interfere with other activities. Thus, a crucial question is when to stop a search for a cryptic predator when the threat is at least reasonably low [1]. In mammalian visual search, the question of the optimal time to terminate a search for a predator has been well explored both on a psychophysical and neurobiological level, as well as in terms of theoretical (optimality) considerations [1] (Figure 2). However, the predictions arising
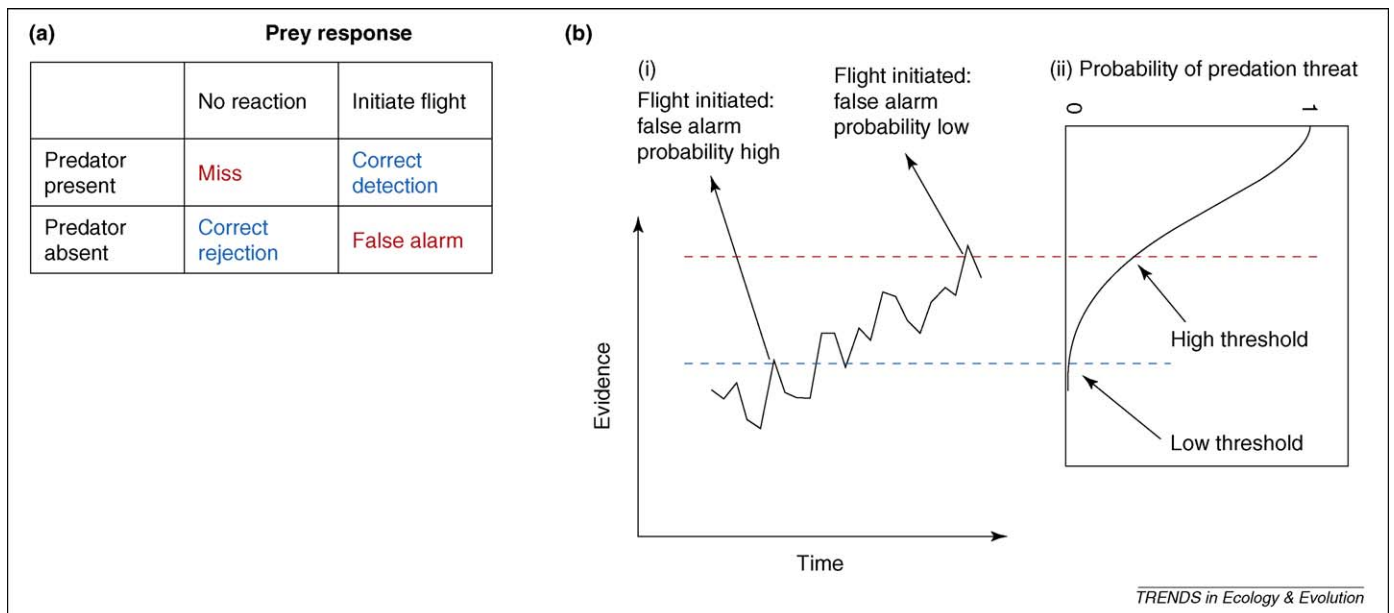

Figure 2. Model of relationship between perceptual sampling time and decision accuracy in a predator avoidance response, based on signal detection theory and sequential analysis [1,9]. In signal detection theory, there are four types of response, with two categories of error shown in red and two types of correct decision shown in blue (a). The frequency of these responses changes depending on the response threshold (b). The probability that a predation threat is present can range from 0 (definitely absent) to 1 (definitely present [bii]). The actual sensory 'evidence' in the CNS of an animal (e.g. differences in neuronal spiking frequencies in relevant brain regions) will accumulate over finite sampling times and is inherently noisy (bi) [1,9]. The cumulative sum of 'sensory evidence' at any point in time represents a decision variable, which can be compared with a threshold evidence level required for the initiation of avoidance behaviour. If the threshold is set at a low level (blue dashed line), then less time is needed for accumulation of the sensory evidence, but the accuracy of this evidence will be poor. This will result in regular false alarms, in which avoidance responses are triggered when the actual probability (bii) of predation is extremely low. Raising the threshold level (red dashed line) improves the accuracy of the sensory evidence accumulated, reducing the likelihood of false alarms, but at the cost of slowing down decision speed and increasing the (potentially fatal) risk of missing a predator.

from this work remain to be tested in biologically realistic settings.

Recent empirical work addressed the SATs faced by flower-visiting insects when foraging under predation threat. Some species of crab spiders (e.g. *Misumena vatia*) can match the colour of the flower on which they wait to ambush unsuspecting insect pollinators [35,36]. However, insects not only learn to avoid flowers that harbour spiders [37] but will also adopt specific changes in flight behaviour to facilitate detection of cryptic predators and minimise risk [11,38]. Bees that have previously encountered cryptic crab spiders fly slower and scan the flowers for nearly twice the time needed to detect a conspicuous predator.

Natural guppy (*Poecilia reticulata*) populations are exposed to variable predation risk and, in high-predation environments, one might expect fish to be more cautious when deciding where to look for mates. In a recent study, wild-caught male guppies from high-predation streams were compared with those from low-predation streams in terms of their speed and accuracy in spatial memory tasks, using a three-chamber maze where the reward was access to females [39]. Males began each trial in the middle chamber, and the authors recorded the time taken to make a choice (i.e. when the fish entered either the rewarded or unrewarded chamber). Males from a predator-infested background were significantly slower in making decisions, whereas those from safer environments would make quicker, and potentially inaccurate, decisions [39]. It remains to be established whether these behavioural patterns are genetically determined or result from prolonged experience of predation risk.

Foraging and prey choice
When deciding what to eat, there is a range of conditions in which either speed or accuracy could be advantageous [40–42]. In pollinating insects, the cost of visiting the 'wrong' flower species can be relatively marginal, if error penalties are simply lower nectar rewards than from the targeted species [3,4,43]. Elsewhere, error costs can be considerably higher, such as predators choosing between toxic and edible prey, where choice accuracy is of prime importance [44]. These considerations have important implications for the evolution of signals used by foragers to decide whether to choose certain prey items.

The literature on bee colour discrimination provides an example of the potential pitfalls of considering discrimination accuracy independent of decision time. When extensively trained, the colour discrimination of bees is on a par with that of humans for coloured stimuli within the spectral ranges of both species [45], so that extremely fine colour differences are distinguishable. Colour discrimination has important implications for floral signal evolution: flowers competing for pollinator services often strive to generate unique and memorable signals, so that they are distinguishable from competitors, ultimately promoting pollinator constancy [46]. Some scholars have claimed that the high accuracy of bee colour discrimination means there is no selective pressure for competing flower species to diverge in colour beyond what is just above the discrimination threshold of a pollinator [47]. However, flower colour discrimination in the field can be poorer than demonstrated in the laboratory by more than an order of magnitude [48], suggesting that selection pressure on flowers to diverge in colour might result in highly distinguishable signals. This apparent contradiction can be resolved when one considers that fine discrimination comes with large time costs [7,8], in fact, potentially higher than the costs of visiting unrewarding or poorly rewarding flowers [3]. In such cases, an adaptive foraging strategy could be one that is fast and error prone [3,4]. However, we would be mistaken to assume that errors reflect an actual inability to discriminate. Indeed, this might explain why unrewarding orchids manage to persist as mimics of sympatric, rewarding model flowers [43], even though the mimicry is sometimes only superficial [13]. Depending on the rarity of orchid encounters and the degree of spatial intermingling of flower species, the time costs of avoiding errors simply exceed those of any actual errors. More research is needed to ascertain whether this is the case.

Errors can be substantially more costly when prey is potentially hazardous, such as unpalatable butterflies, stinging insects or venomous snakes. Sometimes, these are easily distinguishable from palatable prey by high-contrast 'warning' (i.e. aposematic) colouration, but there are also many perfectly edible animals that mimic sympatric unpalatable ones with aposematic colouration [49,50]. Although evolution textbooks tend to focus on near-perfect examples of such mimicry as striking examples of biological adaptation, there are many mimics whose similarity with a noxious model is only superficial: take, for example, the familiar yellow-and-black hoverflies, whose flight behaviour, body shape and, in many cases, colour pattern details make them easily distinguishable from their wasp models to the trained eye (Figure 3). It is unlikely that such imperfect mimicry results from cognitive or sensory limitations of predators that are unable to discriminate model from mimic. However, reliably assessing that a yellow-and-black insect is a defenceless fly takes time and, indeed, perhaps sufficient time for the fly to escape before the predator reaches a decision [44]. A testable prediction is that a predator pressed for time should avoid time-costly discriminations between defended models and inaccurate edible mimics, and instead adopt a 'safety first' policy of avoiding all prey with similar appearance [44].

Cannibalistic fish (e.g. *Pimephales promelas*) seeking to spare their own offspring or kin, including eggs, face a special challenge [51]: discrimination (often by chemosensory cues) can be difficult and probably requires extensive sampling time, perhaps driving adults to alternative diets at times when errors are particularly likely. However, this possibility awaits experimental support.

Communication
SATs are likely to affect the transmission of information in many communication systems. One process where the quality of information transmission is likely to increase with sampling time is the intricate 'dance communication' in honeybees (*Apis* spp.). In addition to collecting information about suitable forage in the outside world, these bees also collect information on the 'dance floor,' an area of wax comb inside the hive where successful foragers perform a figure-
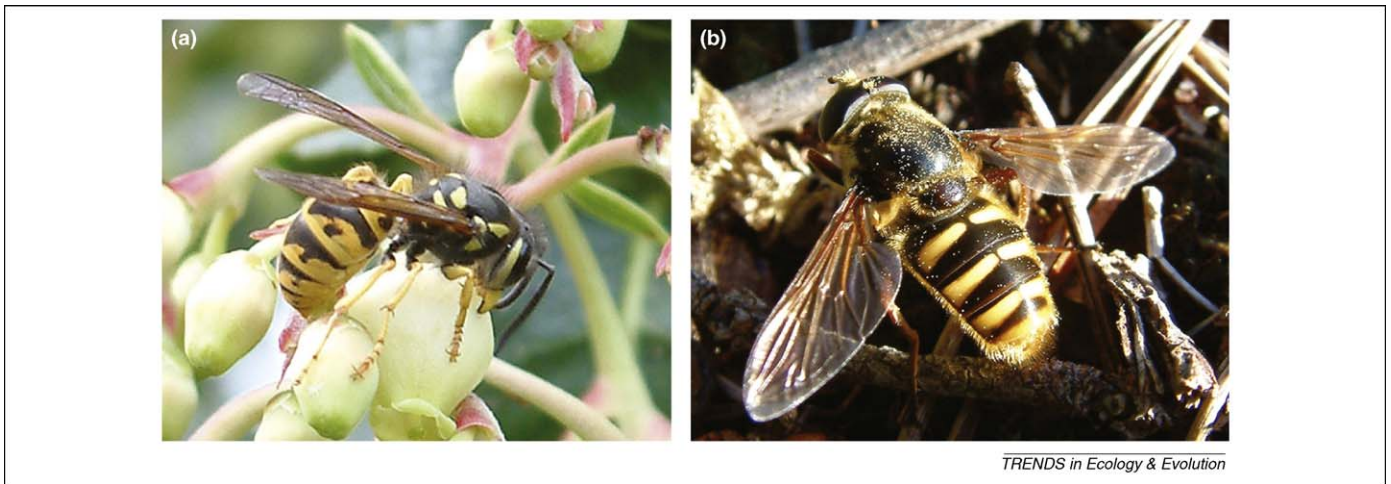
Figure 3. Imperfect mimicry in aposematic visual appearance. Many well-defended insects, such as the wasp *Vespula germanica*, have a warning colouration with alternating stripes of highly contrasting colours **(a)**. Such colouration is mimicked by hoverflies, such as *Sericomyia silentis* **(b)**. When images are large and inspection time unlimited, the mimicry is often only superficial in terms of body shape and specific detail of colour pattern. However, the reader is encouraged to print these images at life size and ask an observer whether they can decide between the wasp and fly, by presenting them, for example, for less than a second. We suggest that such imperfect mimicry persists because the temporal costs of making an accurate identification gives the flies the extra time needed to escape [44]. Reproduced, with permission, from Tom Ings.

of-eight-shaped 'waggle dance' to indicate the distance and direction of food sources to waiting bees [52,53]. Followers must interpret the duration and orientation of the waggle runs performed by the dancer to determine how far and in which direction to fly when leaving the nest. However, an individual dancer will vary somewhat in the orientation and duration of waggle runs between subsequent dance circuits when advertising the same location [52]. Information transmission will also be affected by noise: recruits need to keep track of the movements of the dancer in complete darkness, detecting tactile cues with their antennae. This means that a previously uninformed recruit needs to experience several dance circuits before it can hope to find a distant food source [54]. It remains to be tested whether the precision with which a new recruit locates a target depends on the amount of sampling inside the hive. A crucial challenge will be for the recruit to decide when to stop collecting information and to act on it: an early departure with information of limited accuracy might result in a wasted flight of several kilometres, whereas excessive sampling could constrain the time available for actual foraging. Similar tradeoffs are likely to affect other communication systems, such as mate quality assessment in bird or cricket song.

Interindividual differences and group decision making

Whereas the previous section focussed on within-individual adjustments of speed or accuracy in natural decision making, here we broaden the perspective to differences among individuals and to cases where groups of individuals need to arrive at a consensus when deciding between a variety of options.

Personality differences

SATs are typically assessed using a particular individual (or animal group [10,55]), tested under conditions selected to emphasise either decision speed or accuracy. However, there might also be between-subject differences, so that some individuals consistently make 'fast-and-sloppy' decisions, whereas others might be more meticulous and slow.

Indeed, personality differences between 'impulsive' and 'reflective' subjects are well known in human subjects [2,56]. In natural guppy populations tested in a spatial memory task, there was a continuum from 'hasty' individuals with a consistently high error rate to other individuals whose decisions were approximately twice as accurate but two log units slower [39]. Such 'careful' individuals had a relatively enlarged telencephalon, the brain region involved in spatial memory in fish. This raises the question of whether individuals with poor spatial memory choose a fast-and-inaccurate strategy because rapid spatial exploration might produce rewards more swiftly than would retrieving error-prone spatial memories [39].

Such interindividual differences have also been demonstrated in several social bee species, both in visual flower discrimination [4,18] and the olfactory domain [17]. This diversity of bee 'personalities' could benefit the colony, because each hive is likely to encounter a variety of conditions that favour either foraging speed or accuracy [4]. Because each bee can decide where to visit flowers depending on its own experience of foraging success, a prediction is that workers should distribute themselves adaptively across foraging locations that differ in reward variability [57]. More experiments are needed to explore whether each personality chooses an environment where its individual speed–accuracy strategy works best. On a more general scale, we also need to understand better the genetic and sensory–neural differences underpinning individual variation in SATs.

Consensus building in social decisions

It has been pointed out that, within social insect colonies, individuals might constitute the 'receptor cells' of the superorganism [58], and individual differences in judging the environment could contribute to adaptive decision making within the group. In such cases, sampling occurs on (at least) two levels: first, individuals collect information about the environment; second, this information is then integrated across many individuals; hence, such processes can take

extensive time. One example is house hunting in *Tem-nothorax* ant colonies, a regular task for these ants because they nest in friable rock crevices. Scouts that find potentially suitable new nest sites return to the old nest to recruit 'second opinions.' If recruits are impressed by the new location, they will also return to the old nest to recruit more ants. Once a threshold (quorum) number of ants accumulate in a new site, scouts switch to collecting workers and brood from the old nest [55]. Quorum sensing enables colonies to evaluate the merits of several potential nest sites simul-taneously before committing to any of them [59], and vary-ing the quorum threshold enables colonies to adapt decision taking to the urgency of the situation. Colonies use low-quorum thresholds and hence make faster, more error-prone decisions when their original nest is destroyed, or they are in a harsh environment [55]. However, colonies use high-quorum thresholds to achieve slower, more accurate decisions when there is no urgency, for example, when the original nest remains intact but they are looking for a better site [60]. Quorum sensing enables the colony to solicit multiple opinions, thereby smoothing out potential individ-ual errors in assessing nest-site quality, and provides flexi-bility for the decision process to change over time [61]. An especially extended consensus-building process (up to sev-eral days) operates when honeybee swarms select a new home, integrating conflicting information from multiple scouts with divergent 'opinions,' a process that is also likely to be affected by SATs [10].

Conclusion

Although SATs are not inevitable in sensory discrimi-nation and decision making [25,62,63], they are likely to affect more behavioural processes and sensory modalities than those described here. We suspect that mate choice will be a key area, as it has been known for some time that an inverse relationship exists between the time available to choose a mate and the 'choosiness' of the animals in selecting a partner [64]. Whether this represents a SAT

sensu stricto is unclear, because it is unknown whether a poor choice under time pressure is an error or a 'deliberate' compromise in the absence of alternatives. Nonetheless, there is already extensive information about how long individual potential mates are sampled for and how many are assessed sequentially or simultaneously [64–67], which would make integration into a formal SAT framework straightforward in future work [68,69].

Doubtless there are other biological processes where such tradeoffs are relevant (Box 1), such as studies of animal counting [6], the precision of motor skills [70], aggressive encounters or predator hunting. Other cases might be information transmission in animal communi-cation, and perhaps even processes such as subcellular signalling [71], the specificity and speed of immune responses or the speed of embryonic development [72,73] (especially the developing nervous system). In future stu-dies of tradeoffs in decision making, consideration of the neuronal mechanisms that underlie decision making will be fundamental to understanding specific temporal dynamics and precision levels. In some cases, tradeoffs are generated by the necessity of single mechanisms to accumulate 'evidence' over time [9]; in other cases, animals have both fast, low-accuracy and slow, high-accuracy mechanisms available, which can each be used adaptively according to current conditions [1,2,16]. Finally, in the natural lives of animals, several tasks will have to be scheduled within their daily routines. To understand how they allocate emphasis to either speed or accuracy across tasks requires information about their current priorities, which might often be difficult to obtain. The tightly controlled experimental studies reported here do not yet fully capture the complexity of decision making in the wild, but results from such studies can now be verified in the field. Behavioural ecologists and neuroscientists are encouraged to expand the bridge between their disciplines, to establish a more integrated view of how animals process information and ultimate reasons for these strategies.

Box 1. Outstanding questions

- What role do SATs have in motor control of predation? For example, ambush predators, such as mantids, generate fast movements, which, once initiated, are probably not subject to feedback control. However, are SATs present in the decision process leading to a strike? If so, what ecological conditions might favour speed or accuracy?
- If animals optimise their foraging strategies by taking into account time costs as well as reward benefits, how important is the accuracy with which an animal can estimate time? Should we expect all animals exhibiting flexible foraging strategies to be able to estimate time interval durations?
- Can imperfect mimicry (e.g. reward-less orchids or Batesian mimicry) be explained by discounting the potentially high cost of accuracy in the field?
- How is the balance between speed and accuracy calibrated to task requirements, both by experience in ontogeny and by evolution in phylogeny? How far can current models, based on simple integra-tion of sensory evidence and flexible decision thresholds, explain these processes at both the individual and species level?
- How important is accuracy in communication systems, and how does this vary with ecological conditions? For example, how long should a female bird listen to a male singing to establish whether his repertoire indicates that he is a good potential mate?

- Neural coding of information faces fundamental metabolic constraints, because the cost of increasing signalling speed rises more steeply than do the benefits of increased information rate. What role does the metabolic cost of neural information have in SATs?
- To what extent do SATs hold in cases where perceptual discrimina-tion, or even classification, can be accomplished extremely rapidly? Can the presence (or absence) of SATs in fast perceptual recogni-tion inform us about the dynamics of the underlying perceptual processes? Could there be ecologically relevant conditions in which conflict between fast, automatic perceptual systems and slower cognitive systems reverse the typical relationship between speed and accuracy?
- Can SATs be demonstrated in sensory modalities and behavi-oural contexts other than those described in the main text? For example, is discrimination between social insect nest mates and intruders using contact chemoreception subject to a SAT? Do strong relationships exist between speed and accuracy in tasks involving distance olfaction, for example, perception of spatial patterns of odorant concentration used in pigeon homing over long distances? For how long should spiders assess potential prey identity using vibratory signals on their web before attacking?

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