

Decision-making theories: linking the disparate research areas of individual and collective cognition

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Abstract In order to maximize their fitness, animals have to deal with different environmental and social factors that affect their everyday life. Although the way an animal behaves might enhance its fitness or survival in regard to one factor, it could compromise them regarding another. In the domain of decision sciences, research concerning decision making focuses on performances at the individual level but also at the collective one. However, between individual and collective decision making, different terms are used resulting in little or no connection between both research areas. In this paper, we reviewed how different branches of decision sciences study the same concept, mainly called speed-accuracy trade-off, and how the different results are on the same track in terms of showing the optimality of decisions. Whatever the level, individual or collective, each decision might be defined with three parameters: time or delay to decide, risk and accuracy. We strongly believe that more progress would be possible in this domain of research if these different branches were better linked, with an exchange of their results and theories.

A growing amount of literature describes economics in humans and eco-ethology in birds making compromises between starvation, predation and reproduction. Numerous studies have been carried out on social cognition in primates but also birds and carnivores, and other publications describe market or reciprocal exchanges of commodities. We therefore hope that this paper will lead these different areas to a common decision science.

Keywords Optimality · Primates · Insects · Diffusion Model · Delay · Risk · Speed-accuracy · Trade-off

Introduction

In order to maximize their fitness, animals have to deal with different environmental and social factors that affect their everyday life. Although the way an animal behaves might enhance its fitness or survival in regard to one factor, it could compromise them regarding another (McNamara and Houston 1996, 2009; Johnson 2003; Raubenheimer et al. 2009). For instance, a small bird such as a blue tit has to search for food throughout most of the daylight hours during the winter season. This intense foraging activity allows the bird to satisfy its daily requirements and avoid starvation but results in a higher exposure to risks of predation. First, the bird's foraging movements increase the probability of being detected by predators, and second, the increase in body mass can make it more difficult to take off after foraging. The bird therefore has to make some compromises or trade-offs between the risk of starvation and the risk of predation (McNamara and Houston 1996; Zimmer et al. 2011; Higginson et al. 2012). This is just one example of the many trade-offs made by animals for their survival. Strong literature also exists concerning

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reproduction and parental investment (Parker et al. 2002; Johnstone and Hinde 2006; Boos et al. 2007; Hinde et al. 2010).

In the domain of decision sciences, most research concerning decision making focuses on performances at the individual level in animals, including humans (Gould 1974; Powell and Ansic 1997; Nagengast et al. 2010, 2011b; Feher da Silva and Baldo 2012). The main aim of these studies is to assess whether or not choices made by animals are rational (Cohen 1981; Wood et al. 2007; Feher da Silva and Baldo 2012), in terms of the optimality of a decision. Indeed, taking the right decision requires the prior collecting of information about all possible options but this requires time, which is often limited (Franks et al. 2003; Dall et al. 2005; Czaczkes et al. 2011). Numerous studies have examined this trade-off between the speed of the decision and its accuracy and have tried to determine whether the decision is optimized in such a way that the benefit obtained by the subject concerned is simultaneously optimized against costs (Nagengast et al. 2011a). For instance, monkeys (*Macaca mulatta*) were tested in a task presenting a subject with moving dots on a screen (Britten et al. 1993; Roitman and Shadlen 2002; Cook and Maunsell 2002). Some of these dots moved together in one specific direction, while the others moved randomly. The subject was expected to identify the direction of dots moving together by making an eye movement in this direction. When he was right, the subject obtained a food reward (see Table 1 for details). Here, the risk for the subject was to fail to obtain the reward by making a wrong choice. The rate of rewards was of course not evaluated on the basis of one trial but was calculated by considering the subjects' choices over several trials. The rate of rewards could therefore decrease according to the time taken by the subject to make his decision. However, the likelihood of making mistakes increases with the haste of wanting to achieve something rapidly, resulting in mistakes that make the wait longer than expected and explaining the adage 'More haste, less speed' (Kagel et al. 1986; Green and Myerson 1996; Myerson et al. 2001). Thus, the subject has to take both the decision time and its accuracy into consideration, that is, the number of correct choices throughout the experiment. Results of this study in monkeys showed that the trade-off between the time needed to take a decision (moving the eye) and the accuracy of this decision (moving the eye in the right direction) was optimal. It allows the subject to obtain a maximum number of rewards over a succession of trials. It is now commonly accepted that this speed-accuracy trade-off should be found in most of species and should affect 'many, if not all, sensory modalities' (Bogacz 2007; Couzin 2009; Marshall et al. 2009; Chittka et al. 2009).

The particular speed-accuracy trade-off is studied not only at the individual level but also at the collective one

(Franks et al. 2003; Latty and Beekman 2011a; Ward et al. 2011; Sueur et al. 2012). Although living in groups provides some benefits for group members such as the limitation of the predation risks (Janson and Goldsmith 1995; Hill and Lee 1998) and the sharing of information about the environment (Franks et al. 2002; Danchin et al. 2005), it also has costs such as the facilitation of disease transmission (Nunn et al. 2006; MacIntosh et al. 2012). Thus, sociality may lead to new conflict of interests and can consequently result in the necessity of collective trade-offs (Parrish and Edelman-Keshet 1999; Conradt and Roper 2009). Group members have to make compromises between the time taken to make a decision and its accuracy: Is it the good direction to move? Will the most of animals be satisfied with this decision? etc. If animals do not reach a consensus, then the group may split and animals lose the advantages of group living (Conradt and Roper 2005; Sueur 2011a, 2012; Conradt 2011). While many models try to explain how group members might solve this issue, only few experimental studies have been carried out. One of these studies is about collective decisions in ants (*Temnothorax albipennis*; Franks et al. 2003; Marshall et al. 2006). In this experimental set-up, ants had to switch to a new nest. They were given the choice between a close but inadequate new location and a distant but more adequate one, and this choice was made in either normal or risky environmental conditions. Results showed that ants adapt their choices according to the environmental conditions. The use of a quorum response, in which a minimum number of animals are required to reach the decision-making threshold, enabled ants to optimize their decisions. They chose the inadequate nest when conditions were harsh (taking a rapid but less accurate decision) and the adequate nest when conditions were favourable (a decision that took longer but was more accurate) (Table 1). This shows that ants were able to make trade-offs between the speed and the accuracy of decisions and to decide efficiently according to the risk involved in each situation. Experimental studies have shown similar speed-accuracy trade-offs in fish shoals (*Gambusia holbrooki*, Ward et al. 2011) during a task of collective vigilance in the presence of an artificial predator and in an acellular slime mould (*Physarum polycephalum*, Latty and Beekman 2011b) during foraging decisions in different risky situations (Table 1). These different examples show how the speed-accuracy trade-off rule seems to be common to many, if not all, kingdoms of life.

The examples cited above also illustrate how optimality of decisions is studied, at both the individual and the collective levels. At the collective level, group members might be compared to the 'receptor cells' of an organism and analogous decentralized principles should rule the coordination of entities, neural cells or animal group members

Table 1 Examples of speed-accuracy trade-offs in individual or collective decisions

	Publications	Species	Decision	Measure of speed	Measure of accuracy	Measure of risk incurred
Individual	Roitman and Shadlen (2002)	Rhesus macaques (<i>M. mulatta</i>)	Identify the direction of moving dots	Time for eye movement, no. of neuron impulses per sec	Rate of rewards	No reward
	Britten et al. (1993)					
	Dufour et al. (2007)	Chimpanzees (<i>P. troglodytes</i>)	Wait a given time lag	Delay to exchange or not the initial food item	Rate of rewards	No reward
	Pelé et al. (2010)	Long-tailed macaques (<i>M. fascicularis</i>)				
	Pelé et al. (2011)	Tonkean macaques (<i>M. tonkeana</i>)				
		Capuchin monkeys (<i>C. apella</i>)				
	Dyer and Chittka, (2004)	Bumblebees (<i>B. terrestris</i>)	Choose the right coloured flower	Response time (to discriminate flowers)	Correct choices according to colour similarity	No reward/punishment (aversive quinine solution)
	Latty and Beekman (2011b)	Slime mould (<i>Physarum polycephalum</i>)	Selecting the highest-quality food item	Time to select one item	Quality of food	Hunger and light exposure
Collective	Franks et al. (2002, 2003)	Ants (<i>T. albigennis</i>)	Choose a new nest	Delay to choose a new nest	Chosen nest	Harsh conditions (high wind and humidity)
	Ward et al. (2011)	Fishes (<i>Gambusia holbrooki</i>)	Choosing the good direction (arm of a Y-maze)	Time to choose a direction	Good direction (arm without predator replica)	Predator encounter
	Sueur et al. (2010, 2011b)	Tonkean macaques	Choose a direction to move	Time to move in one direction, time to initiate	Group cohesion, success of initiation	Group splitting and wrong direction

including humans (Couzin 2009; Chittka et al. 2009). However, the two levels are regularly separated with individual cognition on one side and collective phenomena on the other, with little or no connections made between them (Marshall et al. 2009; Sueur 2011a). The cognitive abilities of other individual animals are mostly compared to those of humans in terms of neuroscience, psychology or economics, whereas collective phenomena are compared to self-organization, or processes already highlighted in physical or chemical sciences. Different terms are used resulting in little or no connection between both research areas. On the one hand, we are talking about the time animals take to respond, while on the other, we are talking about the speed of the decision. In one case, we are talking about risk, that is, when actions may lead to different possible outcomes, whereas in the other, we are talking about decision accuracy. In the end, however, both areas of research investigate equivalent issues, and their comparison should help to further study of decision behaviour (Marshall et al. 2009; Sueur 2011a).

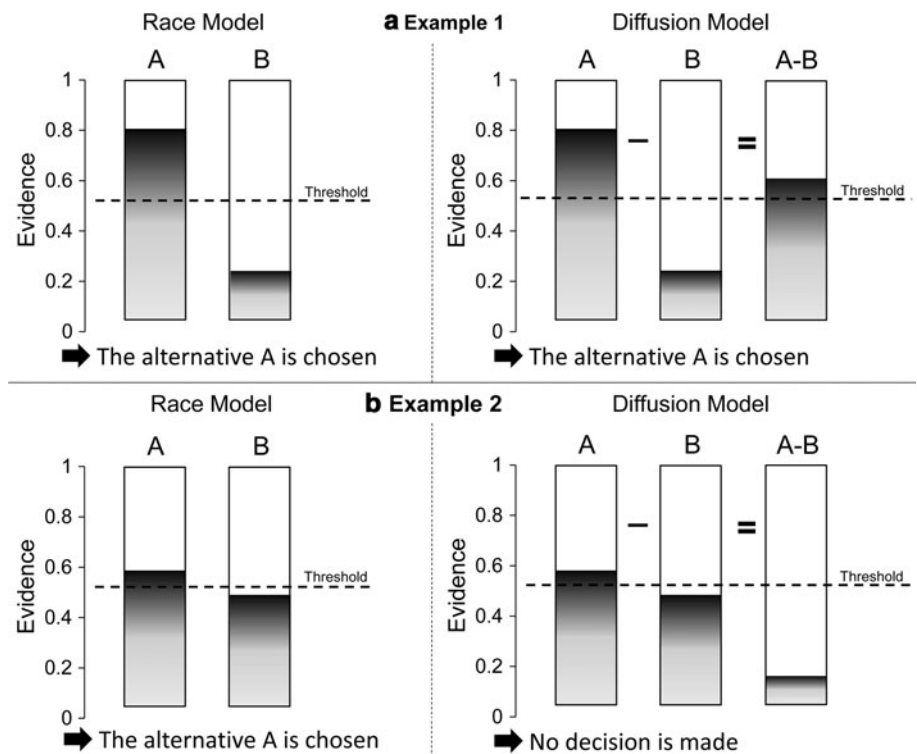
Here, we attempt to merge individual and collective cognition by showing the correspondences between them. First, we will describe the Diffusion Model, which is the origin of the optimality concept in decision sciences (Bogacz 2007). Then, we will compare two examples of decision making by describing two processes, one at the individual level and another at the collective one.

The Diffusion Model: the origin of decision-making theory

Let us consider a subject who has to choose between two alternatives A and B (see Fig. 1). One simple solution is to choose the alternative for which the evidence (i.e. the level of choice or the motivation) exceeds a threshold. In our example, A is then called the winning alternative, whatever the value of the evidence for B, which is called the losing alternative. If the two values are comparable, the value of the winning alternative would be globally higher than that of the losing alternative, and our focal subject will choose the winning alternative whatever the difference between the values of both alternatives. This simple model is called the Race Model. However, the Diffusion Model stipulates that ‘a choice should be made as soon as the difference between the evidence supporting the winning alternative and the evidence supporting the losing alternative exceeds a threshold. The Diffusion Model implements an optimal test called the sequential probability ratio test (SPRT, Wald and Wolfowitz 1948; Kulldorff et al. 2011) which optimizes the speed of decision making for a required accuracy. The direct comparison between the Race Model and the Diffusion Model may allow us to understand this concept of optimization.

Let us consider that the value of the evidence of the winning alternative is the same for both models, Race and

Fig. 1 Two examples (a and b) of conflicts between two alternatives and the outcome decision according to the Race Model and the Diffusion Model. **a** The alternative A is chosen whatever the model. **b** The alternative A is chosen only in the Race Model; a decision according to the Diffusion Model requires a higher threshold and therefore requires more time to reach this threshold



Diffusion. In the Race Model, the speed of decision making will always be the same whatever the value of the evidence for the losing alternative (Fig. 1). By contrast in the Diffusion Model, the speed of the decision for an equal value of evidence for the winning alternative will be different according to the value of the evidence for the losing alternative, since the threshold is based on the difference between both values. In these conditions, if the evidence for the losing alternative is weak (e.g. no real need to satisfy it now), the difference between both values will be high, resulting in the threshold being easily reached and the decision being taken quickly (Fig. 1a). However, if the value of evidence for the losing alternative is equivalent to that of the winning alternative (e.g. needs to satisfy motivations corresponding to either alternatives, or little environmental information allowing to determine the better alternative), there is a conflict between both alternatives, and the threshold will not be reached quickly. The consequence is that decision making will be slow (Fig. 1b). This adaptive ability does not exist in the Race Model and makes the Diffusion Model possible to take these conflicts between two alternatives into account and then optimize the decision (Bogacz 2007; Marshall et al. 2009). This model was developed by Turing and colleagues to break the Enigma code developed by the Germany Navy during the Second World War (Wainer and Savage 2012; Randell 2012). The mathematical framework they developed comprised three components: (1) a method to quantify the value of evidence for the alternatives under consideration and to choose the best alternative, (2) a method to update this value and therefore modify the choice of the best alternative over time after considering multiple pieces of evidence (such as new environmental information) and other alternatives, and (3) a final decision rule to identify which alternative is the best when a threshold is reached. The Diffusion Model was then applied to decision making in brain sciences, including research to ascertain whether monkeys can identify the direction of moving dots (Roitman and Shadlen 2002; Cook and Maunsell 2002). Indeed, it has been shown that some neurons within the cerebral cortex are able to measure evidence of the different alternatives before inhibitory connections for certain values of these evidences are used to identify and reach a threshold, thereby achieving an optimal decision. The study in ants (Franks et al. 2003) also showed that the Diffusion Model can be applied at the collective level in order for ant colonies to achieve optimal decision making when choosing a new nest. Some behaviours in ants, such as tandem running, were shown to function in a similar way to the inhibitory connections found in monkeys' brains and then lead by a quorum threshold to optimal decisions (Marshall et al. 2009).

The speed-accuracy trade-off is also well illustrated by the study of Chittka, Dyer and colleagues (Chittka et al.

2003; Dyer and Chittka 2004; Burns and Dyer 2008) where bumblebees (*Bombus terrestris*) have to discriminate between artificial flowers with different colours to obtain a reward. The risk or cost of making errors could be increased by introducing a punishment (aversive quinine solution), resulting in slower but more accurate decisions. A variant of the experiment exposed foraging bees to controlled predation risk (from robotic crab spiders), and results showed that bees exposed to predation reduced their foraging efficiency and increased their inspection time (Ings and Chittka 2008). Lihoreau and colleagues used a radio tracking system (Lihoreau et al. 2012, 2013) to show that bees in natural conditions are able to estimate the shortest possible route to visit all flowers and prioritize flowers offering the greater rewards. This optimization, as illustrated in the studies of Chittka, Dyer or Lihoreau and their colleagues, might be explained by a simple heuristic model in which bees learned the best alternative. For instance, bees compared the length of the route they had just travelled to the shortest route previously experienced. If the recently travelled route is shorter, the bee will be more prone to repeat it in future foraging bouts. This learning is reinforced by positive feedback in the memory of the bee (Lihoreau et al. 2013). In the same way, Latty and Beekman (2011a) assume that pseudopods of slime mould may represent each alternative, and movements of biomass inside tubes of these pseudopods may be functionally analogous to inhibitory connections in the brains of monkeys (see Table 1 for a comparison).

What is very important to understand here is that contrary to other models, the Diffusion Model is the only one to explain speed-accuracy trade-off, since the decision accuracy is directly dependent upon the time needed to pool the different information data required to take a decision. This statement results from ecologically motivated theories about evolutionary processes that optimize decision speed and accuracy and therefore increase fitness and/or to decrease risk (Bogacz 2007). Even Shepard wrote in his paper about universality of principles (1994) that 'natural selection has favoured the ability to make decisions not only accurately but also swiftly' generalizing the theory of speed-accuracy trade-off. Although we cannot suggest that the Diffusion Model is universal or that it is the only model explaining speed-accuracy trade-off or decision making, it does implement the sequential probability ratio test (SPRT), and as every model implementing this test, it can therefore be used to explain speed-accuracy trade-off and decision making. The SPRT makes use of the Neyman and Pearson (1933) lemma which is familiar to statisticians and makes it possible to select the most powerful test/model. By creating varying parameters of this model, we can fit theoretical to behavioural data and even if the data fitting does not allow to imply that the model is

correct, it at least enables us to make predictions or to discard certain parameterizations of the model. Chittka et al. (2009) suggested that speed-accuracy trade-offs or other trade-offs are generated by the necessity of single mechanisms to accumulate evidence over time and to choose the best alternative through the SPRT (Gold and Shadlen 2007). The Diffusion Model covers different other models such as the Usher and McClelland (2001) model for neural decision making or the quorum threshold model for collective decision making (Seeley and Visscher 2004; Sumpter and Pratt 2009; Sueur et al. 2010) and therefore proves to be useful in understanding individual or collective cognition (Couzin 2009). It can be argued that other models exist, and this is indeed true. However, other models do not implement SPRT and then do not explain speed-accuracy trade-off, ignoring all discussions about decision optimality. While the Race Model is based on the threshold reaching of one alternative (accuracy), others might be based on decision speed such as ‘choose the best alternative after x samples’ or ‘choose the best alternative after some fixed time’ but here, again, these models do not permit the optimization of the decision speed for a required accuracy (Bogacz 2007). This speed-accuracy trade-off has to be taken into account since it exists in many ecologically relevant tasks, as suggested by Chittka et al. (2009).

Application of the Diffusion Model to individual and collective decision making

The Diffusion Model developed by Turing and colleagues was successfully applied to decision making in animals (Britten et al. 1993; Roitman and Shadlen 2002; Cook and Maunsell 2002; Marshall et al. 2009; Sueur et al. 2010; Ward et al. 2011). Here, we will illustrate how this model, and thus the speed-accuracy trade-off, could be generalized to decision-making processes by presenting two examples, both in non-human primates, one at the individual level and the second at the collective one. These two examples are presented in Table 1 along with the aforementioned examples: moving dots in monkeys (Britten et al. 1993; Roitman and Shadlen 2002), the choice of a new nest in ants (Franks et al. 2003), collective vigilance in fish shoals (Ward et al. 2011), foraging decisions in slime mould (Latty and Beekman 2011a) and in bees (Dyer and Chittka 2004; Ings and Chittka, 2008).

Our first example concerns delay of gratification in non-human primates. Pelé and colleagues explored the abilities of chimpanzees (*Pan troglodytes*, Dufour et al. 2007), macaques (*M. fascicularis*, *M. tonkeana*, (Pelé et al. 2010, 2011)) and capuchin monkeys (*Cebus apella*, Ramseyer et al. 2006; Pelé et al. 2011) to wait for a returned reward by involving animals in food exchange tasks. Subjects had

to return a piece of cookie after a given time lag to obtain a larger one from a human experimenter. If the subject dropped or ate the small piece of cookie, it did not receive the larger reward. This experimental setting can easily be compared to the situation in the wild where an animal that is searching for food has to choose between a small but immediate amount of food and a bigger, but delayed one (due to a greater distance, for example). Besides, as the delay for the outcome increases, the subject’s return expectation may decrease. One reason would be that the risk of not receiving the bigger food amount increases with time. Thus, when waiting for more, an animal needs to evaluate expected outcomes and decide how long it may be worth waiting. This experimental set-up reflects a natural situation where taking too long to decide, waiting before foraging or searching for too long for new food sources may result in a higher risk of being detected by a predator or finding that the food resource has already been depleted by competitors (Dyer and Chittka 2004; Pelé et al. 2010).

The second example concerns collective movements in Tonkean macaques (Sueur et al. 2009, 2010; Sueur and Deneubourg 2011). Macaques perform activities in different areas: some are devoted to rest, others to socializing or foraging. Animals have then to move together from one place to another. In most cases (90 % of collective moves), movements are initiated by one animal who starts to walk and who is either followed or not (Sueur and Petit 2008). If it is not followed, the animal comes back within the group, and it, or another group member attempts another initiation some minutes later. If the initiator is followed, all group members go to a new location and carry out the activity designated by the initiator. This kind of initiation was found not only in other primate species (white-faced capuchins, *Cebus capucinus*, Petit et al. 2009; rhesus macaques, *M. mulatta*, Sueur and Petit 2008, 2010; brown lemurs, *Lemur fulvus*, Jacobs et al. 2008) but also other species (domestic geese, *Anser domesticus*, Ramseyer et al. 2009; sheep, *Ovis aries*, Pillot et al. 2010; Przewalski horses, *Equus ferus przewalskii*, Bourjade et al. 2009). Here, the time chosen to initiate a movement appears important since it might lead to a successful initiation (i.e. a reward) or to an unsuccessful one (potential risk) (King 2010). In the other cases in group movement in Tonkean macaques (about 10 %), not just one, but two directions are proposed by different group members. The decision to be taken concerns not only the time chosen to move, but also the direction. There are hence more conflicts between animals, that is to say, more risks of splitting. Thus, group members need to evaluate the best direction to follow and decide as a body to avoid group division (Bourjade and Sueur 2010; King 2010).

In the two examples described above, animals have to take the most accurate decision between different

alternatives, under a certain risk and within a certain amount of time. The question is to know whether animals in both of these examples demonstrate a speed-accuracy trade-off to optimize their decisions.

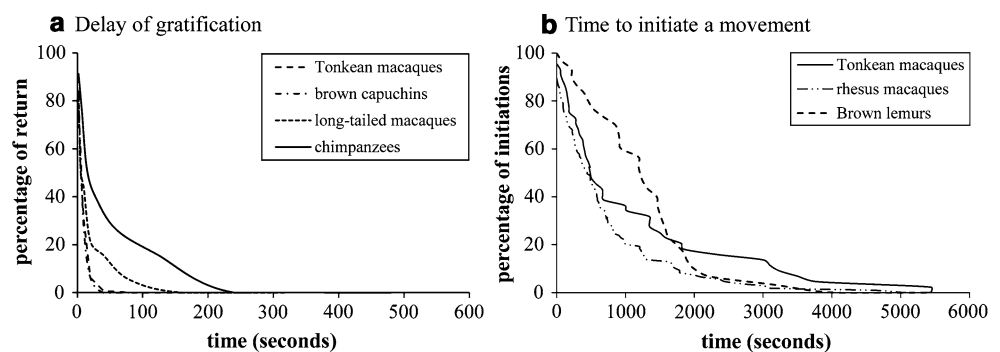
Temporal discounting: the decision changes over time

The ability of non-human primates to maximize pay-off was investigated in exchange tasks where time intervals and reward quantities were controlled (Ramseyer et al. 2006; Pelé et al. 2010, 2011). For each trial, the experimenter first offered a small piece of cookie (2 cm²), then presented the subject with a larger-sized piece, measuring around twice the size of the initial item. Then, increasing time lags were tested, ranging from a few seconds to several minutes. Subjects demonstrated high percentages of return for the time lags of a few seconds (Fig. 2a). However, as time lags became longer, subjects appeared to change their mind and refused the exchange with the experimenter by eating the initial piece of cookie (Fig. 2a). The authors proposed that as the wait for an outcome increases, the subject's expectations for a reward may decrease (Dufour et al. 2007; Pelé et al. 2010, 2011). We can see the speed-accuracy trade-off in this experimental set-up in two ways: either animals wait too long to reach a decision and once this time is over they have not obtained the larger reward or animals cannot maintain a long waiting time because natural selection has favoured a threshold or temporal discounting in order to decrease risk of predation or of food depletion by competitors. Authors have shown that primates achieve both spatial and temporal knowledge of their environment through the use of mental maps or anticipation (Menzel 1991; Byrne 2000; Janson and Byrne 2007; Sueur 2011b). Sometimes they have to decide whether to forage immediately for a close but low nutritive food resource or to forage for a more distant but rich food resource, with the risk that this food resource could already be depleted and an increased risk of meeting a predator. It has been shown that temporal discounting—whereby the subjective value of benefits declines with time—may affect decision making when current and future outcomes are in

conflict (Stevens et al. 2005). Thus, temporal discounting appears as a possible response to the risk associated with waiting for delayed rewards (Kagel et al. 1986). In the task of delayed gratification, there was no risk of subjects losing their reward. We nevertheless observed temporal discounting, meaning that animals, namely non-human primates, interpreted it as a risky situation and then chose not to exchange after a certain delay (McCoy and Platt 2005; Ramseyer et al. 2006; Dufour et al. 2007; Pelé et al. 2011). The tendency of animals to prefer immediate gratification instead of waiting for greater rewards has been described as impatience, impulsiveness or lack of self-control (Fawcett et al. 2012). Stephens (2002) identified two costly reasons to wait for a delayed reward: the interruption risk (risk of losing the next food item because of a competitor) and the termination risk (risk that an entire foraging sequence is cut short because of a predator). Animals are therefore uncertain about the risk of interruption, and they progressively lower estimates of rewards as time passes (Kagel et al. 1986). However, Fawcett et al. (2012) reviewed and proposed several possibilities under which patience is ecologically rational: fruit ripening, extractive foraging, caching for the winter, patch leaving, sequential mate search, etc. Then, both strategies—waiting or not waiting—might be met in the same population according to animals' strategies, temperaments or physical conditions (McNamara and Houston 1996; Lee 2005; Platt and Huettel 2008; Wolf and Weissing 2012).

In Tonkean macaques, the time an animal waits before initiating a movement could be compared to the time subjects spend waiting to receive the biggest piece of cookies. Indeed, if a group member initiates a movement immediately after the beginning of a new activity, it takes the risk to not be followed. On the other hand, if an group member waits too long before initiating a movement, it might deplete its energetic reserves or another group member might initiate its own movement in an undesired direction. Waiting too long before initiating may thus appear risky (Bourjade and Sueur 2010; King 2010). Hence, the decision to initiate should also be dependent on time and might be ruled by temporal discounting, as

Fig. 2 Temporal discounting **a** delay of gratification in four primate species. Curves of Tonkean macaques and brown capuchins are overlapping. **b** Time to initiate a movement in three primate species. In both instances, the probability to display a behaviour (percentage of return or of initiations) decreases exponentially with time



illustrated by a number of initiations decreasing over time. The same result was found in rhesus macaques (Sueur 2010) and brown lemurs (Jacobs et al. 2008) (Fig. 2b).

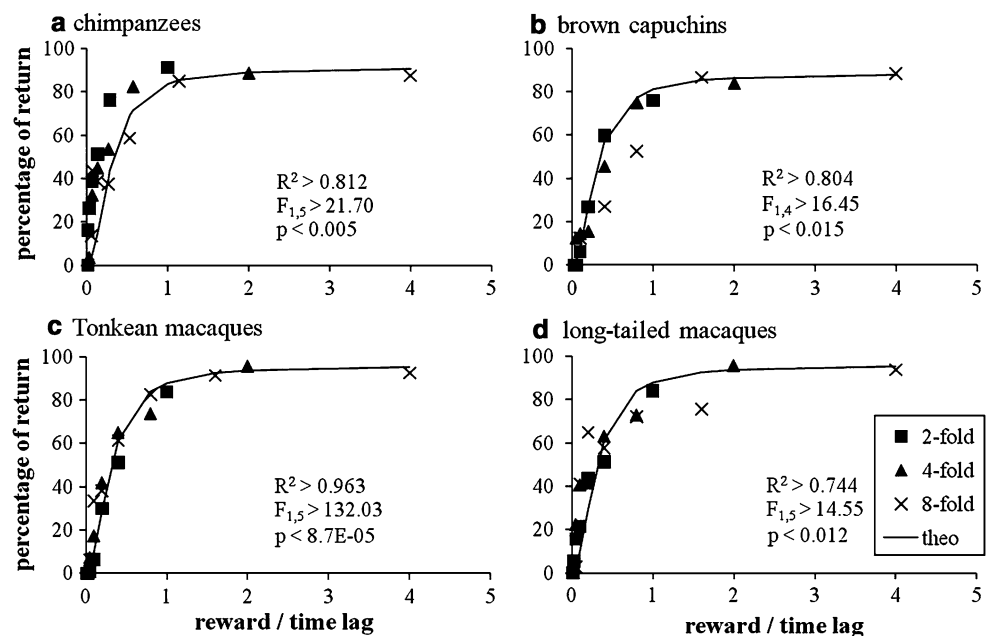
In both examples, the time accorded to decision-making process by animals (wait or not, initiate a movement or not) has been analysed following an exponential law (Fig. 2):

$$V = R \cdot e^{-k \cdot D} \quad (1)$$

where V is the present, discounted value of a reward R (bigger cookie or successful initiation) available after a delay D . The parameter k determines the rate at which the value decreases with the delay; a higher k value is associated with steeper discounting (Green and Myerson 1996; Sueur and Deneubourg 2011). The exponential function means that for each time step a subject has to wait, there is a constant probability of a risk occurring, possibly leading to the loss of the reward. These kinds of functions allow us to generalize decision-making theory and formulate hypotheses that take accuracy, risk and decision time into account (Shepard 1994; Bogacz 2007). Then, the more time animals spend deciding, the higher the risk of losing the reward will be. Again, this temporal discounting may be considered as an adaptive response to choosing between different alternatives, that is, now or later, which both imply a certain level of risk (Kagel et al. 1986). Figure 2 presents the potential differences we observed between species and between our two examples, namely delay of gratification and movement initiation. These differences may be due to some divergences in evaluating the risk according to the situation.

These results are directly comparable to the choice of a new nest site by ants (Franks et al. 2003) and the results observed in monkeys when following moving dots on a screen (Britten et al. 1993; Roitman and Shadlen 2002). For instance, by removing the nest of the ant colony, the experimenter exposed all subjects—including the brood—to harsh environmental conditions, forcing the scouts to find a new site as quickly as possible. Time is crucial in this type of situation, since other ants that protect the brood by immediately huddling around it also have to protect themselves. Franks and colleagues (Franks et al. 2003; Marshall et al. 2006, 2009) showed that the distribution of decision times in ants also follows an exponential law. Under highly risky conditions (i.e. harsh conditions), ants mostly prefer to decide quickly between two alternatives (inadequate vs. adequate new nest), even if the choice does not initially appear to be accurate. Even when choosing the inadequate shelter, ants are at least in a new nest and the brood is safe for a while. This nonlinear law was also underlined in the brains of monkeys, as illustrated in the moving dots task (Britten et al. 1993; Roitman and Shadlen 2002; Marshall et al. 2009). The majority of decisions made by monkeys were reached quickly and only a few were taken after a longer period of time had elapsed. Thus, the question still remains of why some decision times are long despite the inherent risk of waiting. This variance in the time taken for decision making might depend on the environmental conditions as well as on individual characteristics (for a same individual over time or between individuals). It could also be an adaption to potential changes

Fig. 3 Percentage of returns of the original food item according to the ratio ‘reward/time lag’ (size of the given reward compared to the initial reward divided by time lag of returns, in sec^{-1}) in four primate species. The curves are similar to a theoretical threshold function (black line) whatever the size of the reward (from twofold to eightfold the size of the original food item), suggesting an adjustment time according to the potential outcome, that is to say a speed-accuracy trade-off. Observed curves were compared to the theoretical curve using a curve estimation test



of environment which could benefit the animal if it waits longer.

Speed-accuracy trade-off: when the speed of the decision changes according to the outcome and/or the degree of risk involved in the situation

The studies described above showed that the choice of one alternative rather than another may change over time, because the degree of risk may increase with time. There remains the question of how a subject changes its behaviour depending on the importance of the outcome and the degree of risk associated with the situation (Chittka et al. 2003; Nagengast et al. 2010, 2011a). According to the speed-accuracy trade-off paradigm, animals should adjust their behaviour, and specifically temporal discounting, according to the outcome and/or the degree of risk. For instance, in ants, the steepness of the exponential distribution of decision times (k value in the Eq. 1, see above) depends on the different environmental conditions (Franks et al. 2003; Marshall et al. 2009). The harsher the conditions, the steeper the curve, and the quicker the decision is taken. Franks and colleagues considered this switch between the different risky situations as an adaption to a changing environment and as an optimization of decisions by preferring speed in some situations at the cost of accuracy, and the opposite (Franks et al. 2003). In the same way, when slime mould was exposed to harsh conditions (hunger and light exposure as stressors), it made faster but inaccurate decisions by selecting the worst possible food alternative (Latty and Beekman 2011a). For bumblebees, when an aversive quinine solution is introduced in distractor flowers (Chittka et al. 2003), the risk or cost of making errors is increased, and bees take slower but more accurate decisions.

In their delayed gratification tasks, Pelé and colleagues (Dufour et al. 2007; Pelé et al. 2010, 2011) tested the effect of quantity on the period of time that animals were prepared to wait. The experimenter presented the subject with different sizes of reward: not only twofold as previously described, but also fourfold and eightfold the original size. Results showed that the larger the reward was; the longer the subjects were capable of waiting. Thus, non-human primates appear to be able to adjust the time spent waiting to the size of the reward. The analysis of their giving up times (i.e. the time at which subjects gave up waiting before the end of the trial) suggested that subjects anticipated the duration they would have to wait for and decided accordingly whether to wait or not (Dufour et al. 2007). Non-human primates were therefore capable of taking into account both the size of reward and the duration of the time lag to decide to whether to exchange or not. Moreover, animals simultaneously analyse both the necessary time lag

and the size of reward when making decisions. Animals did not only process the time lags and the sizes of reward as separate data, but also pretty much make a relationship between the two evidences, following a same threshold rule and adapting their time lags according to the size reward (see Fig. 3). This shows how speed-accuracy trade-off governs decision making in animals, at least in these four studied species.

As explained above, in 10 % of cases, Tonkean macaques have not only conflicts about the time to move but also about the direction to follow, making consensus more difficult to reach (Sueur and Deneubourg 2011). In these situations, Tonkean macaques use a sequence of quorum decisions to choose the direction to follow (Sueur et al. 2010, 2011b). Before all moving in the same direction, animals first wait until a certain number of group members have shown their preferences to go in one direction or the other. This corresponds to the decision process related to the time of movement. When this first threshold is reached, they use a second threshold based on the difference of group members in both directions. This corresponds to the decision process for the direction that should be followed. However, the second threshold is very sensitive since a

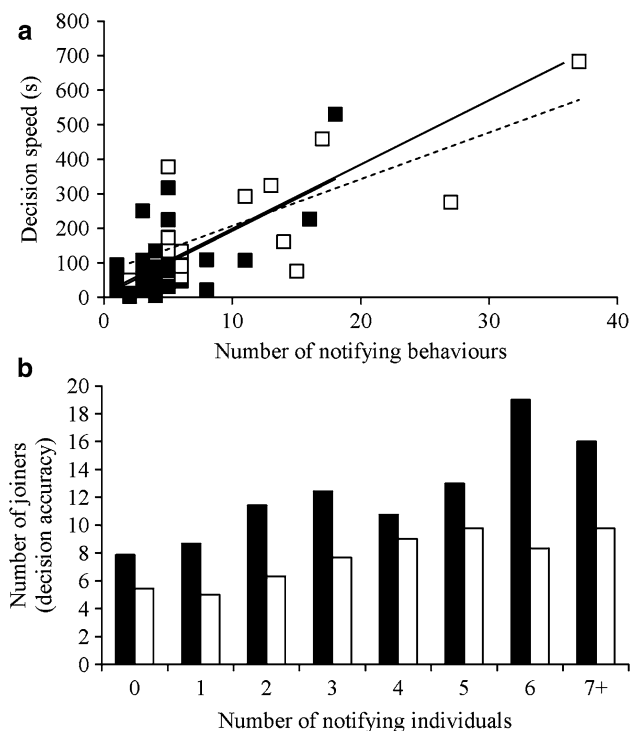


Fig. 4 **a** Decision speed according to the number of notifying behaviours in Tonkean macaques [group 1 (white square): $R^2 = 0.42$; group 2 (black square): $R^2 = 0.52$]. **b** Decision accuracy (number of joiners to a movement) according to the number of notifying individuals [group 1 (white square): $R^2 = 0.72$; group 2 (black square): $R^2 = 0.82$]. All relationships are linear and analysed using curve estimation tests

difference of only one animal may tip the balance in one direction. Such quorum responses do not only keep the group cohesive but also allow group members to pool information about each possible direction and to satisfy the needs of a majority of individuals (Franks et al. 2002; Sueur et al. 2010). Since group members wait until a certain number of group members show their preferences before moving, they make the decision more accurate: this takes longer, but more animals showing their preferences (Fig. 4a) and more animals joining the movement, meaning that they are satisfied by the decision (Fig. 4b). This threshold response surely allows animals to adapt their decisions according to environmental contexts and is reminiscent of experiment on ants. Mechanisms are similar in both species: first, some group members ('notifying individuals' in macaques and scouts in ants) try to recruit some partners in one direction by showing specific behaviours (voting behaviours in macaques and tandem running in ants). Then, a threshold is reached, and mechanisms change from this slow recruitment to a faster one of social amplification. Ants recruit their partners by carrying while the process of adhesion in macaques is a mimetism based on social relationships. The first slow mechanism described in both species makes it possible to find the best alternative by comparing values of evidence. If the value of the threshold is high, and the risk factor is low, the decision time will be short. Then, when the threshold is reached, a faster mechanism is set off. Here again, this quorum threshold allows to increase the decision accuracy (Wolf et al. 2013).

Biases and optimization of decisions

We have reviewed different situations here, in which animals are led to make the most accurate decision between different alternatives, with a given risk factor and within a given time. We show that despite several differences between the studied situations (the value of the outcome, or the risk incurred when making the wrong choice), animals demonstrate a speed-accuracy trade-off to optimize their decisions. Nevertheless, the speed-accuracy trade-off is not a systematic rule, and biases in the decision-making process can be highlighted (Cohen 1981; Bateson et al. 2002; Wood et al. 2007; Latty and Beekman 2011b). Indeed, the decision-making mechanism might change from the threshold answer we described here (i.e. the Diffusion Model) to a survival mechanism. Let us consider an animal moving within its home range. At a given time, in a specific location, this animal encounters a predator. The probability that this animal will encounter the predator a second time at the same location should be very weak, according to movement patterns described in several species (i.e.

Brownian and Lévy walks; Viswanathan et al. 1996; Edwards et al. 2007; Sueur 2011b; Sueur et al. 2011a). However, this animal will display a behavioural bias by not returning to this specific area. Indeed, even if the probability of encountering the predator again is very weak, the risk of being eaten if the predator is present is high. The mechanism of threshold based on the Diffusion Model is still used by the individual, but the alternative of the area where the possibility of encountering a predator exists displays too high a risk to be chosen as a winning alternative (the threshold in favour of this alternative will be never reached). This biased decision might be considered as superstition (Foster and Kokko 2009; Abbott and Sherratt 2011), and Beck and Forstmeier (2007) qualified it as an inevitable by-products of an adaptive learning strategy. If a subject receives a negative stimulus each time it displays a specific behaviour, then this subject will stop performing the behaviour concerned. Conversely, if an animal is rewarded each time it displays a specific behaviour, its probability to perform this behaviour again will increase. However, the number of times a subject will perform this behaviour will depend on the risk or the gain associated with the decision.

Conclusion

In this paper, we reviewed how different branches of decision sciences study the same concept, mainly called speed-accuracy trade-off, and how the different results are on the same track in terms of showing the optimality of decisions (Bogacz 2007; Marshall et al. 2009). We believe that more progress would be possible in this domain of research if these different branches were better linked, with an exchange of their results and theories. For instance, we have highlighted in this paper how different species, at different levels, reach optimal decisions by making trade-offs between the time they have to decide, the risk underlying the decision and its accuracy, showing that these three variables are closely linked one to the other.

The decision-making system described in this paper, the Diffusion Model, can be used to explain many decision-making processes found in animals, both at an individual and collective level. In our opinion, optimal decisions, described here through the Diffusion Model, are not the same as rational decisions. The last section, 'Biases and optimization of decisions', could help to understand this difference between rationality and optimality. While models of rationality often imply a boundless knowledge and no time limit to decide, the Diffusion Model is different. A trade-off is made between speed and accuracy after considering the risk of each alternative. Animals do not need to have all the information about each alternative,

but simply need enough information to reach the threshold. This decision strategy is simple and fits with the heuristic model of Gigerenzer (Todd and Gigerenzer 2000; Gigerenzer 2002, 2003) allowing fast, frugal but optimal decisions, contrary to rationality that may not be the best at promoting fitness, because it costs too much in time and resources. Step 2 of the Diffusion Model (a method to update information and values of evidence and therefore modify the choice of the best alternative over time after considering multiple pieces of evidence and other alternatives) is reminiscent of the heuristic principles for decision making, in which a simple process of elimination enables individuals to choose the best alternative through updating and confronting information (Todd and Gigerenzer 2000). Different models may illustrate this heuristic model in human collective behaviour. Pedestrian behaviour or crowd disasters are explained by simple rules. Helbing et al. (2000) first proposed a simple generalized force model considering collective phenomenon of escape panic as self-driven many-particle systems. Then, Moussaïd et al. (2011) combined this physics-inspired model to a cognitive science approach allowing pedestrians, guided by visual information, to apply two simple cognitive procedures to adapt their walking speeds and directions. Collective phenomena are self-organized and did not rely on boundless knowledge but only on local interactions (Helbing et al. 2000; Couzin and Krause 2003; Moussaïd et al. 2011; Helbing 2012) such as those observed in ants (Franks et al. 2003), fish (Ward et al. 2011) or primates (Jacobs et al. 2008; Sueur et al. 2009). As heuristics, the paradigm of speed-accuracy-risk is robust when confounded with environmental changes and could be applied to any species, in any ecological conditions. This assumption needs, however, to be verified by extending research on decision making to other species and in other contexts. McNamara, Houston and colleagues (McNamara and Houston 1990; Houston et al. 1993; Houston and McNamara 1999; Kokko et al. 2002) studied several trade-offs that animals have to make such as between food and predation, between time and energy or between reproduction and predation. They showed that several species are able to make these trade-offs such as lions, tits, newts or parasite wasps. We can greatly develop our understanding of decision systems if we compare all these data, confronting empirical to empirical but also theoretical to empirical data. This can be done by using a widely used methodology scoring the time, the accuracy and the risk of a decision. A growing amount of literature describes economics in humans (Farmer and Foley 2009; Glimcher 2009), and eco-ethology in birds making compromises between starvation, predation and reproduction (Zimmer et al. 2011; Higginson et al. 2012; Grodzinski and Johnstone 2012; Meunier and Kölliker 2012). Numerous studies have been carried out on social

cognition in primates (Addessi et al. 2011a; Pelé et al. 2011; Addessi et al. 2011b; Fletcher et al. 2012) but also birds (Mettke-Hofmann et al. 2002; Dufour et al. 2012; Krama et al. 2012) and carnivores (Topal et al. 2009; Leonardi et al. 2012), and other publications describe market or reciprocal exchanges of commodities (Fruteau et al. 2009; van de Waal et al. 2012; Wei et al. 2012). We therefore hope that this paper will lead these different areas to a common decision science.

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