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Collective decision-making

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Collective decision-making is the subfield of collective behaviour concerned with how groups reach decisions. Almost all aspects of behaviour can be considered in a decision-making context, but here we focus primarily on how groups should optimally reach consensus, what criteria decision-makers should optimise, and how individuals and groups should forage to optimise their nutrition. We argue for deep parallels between understanding decisions made by individuals and by groups, such as the decision-guiding principle of *value-sensitivity*. We also review relevant theory and empirical development for the study of collective decision making, including the use of robots.

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Introduction

We consider collective decision-making to be the subfield of collective behaviour concerned with how groups reach decisions without centralised leadership. Examples include nestsite selection by honeybees [1] and ants [2], and consensus selection of food sources in shoaling fish [3]. Individuals in a group can prefer to participate in a consensus decision, in which all individuals seek to agree on the same outcome, either because the group is tightly functionally integrated, as is the case with a social insect swarm or colony containing a single queen [1,2], or because group members prefer to remain within an unrelated group, for example to avoid predation risk [3]. Within high-relatedness groups under appropriate conditions, selection on the group can lead to group-level adaptations [4], so group members' behaviour is shaped

as part of a group-level decision-making mechanism. Within unrelated groups, individuals' behaviour should maximise their own expected fitness, within the context of the group [5]. Indeed inferring 'group cognition' abilities for unrelated groups may be harder than previously appreciated; alternative explanations for improved decision performance in fish shoals are that fish in larger groups have improved individual-level abilities, and that larger groups are more likely to contain better decision-makers who dominate collective decisions [6].

In this review we focus primarily on functionally-integrated decision-making systems for two reasons; first, as mentioned above, functional group integration makes it appropriate to apply *optimality theory* at the level of the group [7]. Second, parallels can be drawn between the behavioural rules of a 'superorganismal' group, and the behavioural rules of unitary individuals. We consider such parallels to be illuminating. Our review can thus be read as primarily presenting an 'economic' view of the behaviour of groups making decisions, where decision outcomes result in gains or losses of quantities that co-vary with reproductive fitness. We place particular emphasis on the links between collective decision-making, perceptual decision making and value-based decision-making, and on nutritional decision-making. We review applicable theory, as well as the emerging use of robotics, for understanding such systems.

Quorums and confidence

Groups can realise superior decision performance to individuals for a variety of reasons. The simplest argument is based on the 'wisdom of the crowds', recognised since the early 20th Century; for example a group decision realised by pooling independent individual assessments will be more accurate than an individual group member, under certain reasonable assumptions [8]. Inevitably, further refinements of group decision-making are possible; here we mention two recent developments.

Signal detection theory, developed to understand optimal psychophysical decision-making by individuals, shows that there is an inherent decision-making trade-off between true positive rate and false positive rate; a decision-maker cannot improve the rate at which they detect events of interest, without also increasing the rate at which they incorrectly detect those events when they have not happened. Yet in the group situation, Wolf *et al.* show how introducing a quorum decision rule, typical of social insect colonies, allows the group to simultaneously

improve both rates [9]. Understanding how to correctly set quorums, which may be sub-majority or super-majority according to the accuracy of individuals, also shows that in fact group decisions are *always* more accurate than individual decisions [10**].

Still further improvement is possible on group decision-making, by accounting for the unavoidable variation in individual decision accuracy. Decision theory shows how to optimally weight individuals' contributions to group decisions according to their accuracy, or 'confidence'; this theory has been applied successfully to human groups and may be fruitfully applied to other animal groups [11**].

Value-based decisions

In the preceding section group decision performance was considered in terms of decision accuracy, or probability of making the correct response. Yet consider the decision problem faced by a honeybee swarm selecting a new nest site [12]. Obviously, it is advantageous for the collective of bees to choose the site of highest possible quality. Imagine, for example, that there are two potential nest-sites available, both of equal but low quality. In this case it is best to wait and postpone the decision until another option will be discovered. In contrast, if there are two alternatives having equal but high qualities, then the honeybees should choose as quickly as possible, as a long decision making process is accompanied by the consumption of resources and a prolonged absence of shelter, and does not lead to any further advantage.

Precisely such an adaptive value-sensitive decision making mechanism has been analysed in a model of the stop-signalling behaviour of honeybees [12], whose decision dynamics change adaptively as a function of quality of available options [13,14]. In case of equal, high quality options a lower cross-inhibition strength is sufficient to break decision deadlock compared to higher cross-inhibition strengths required for lower quality options [13]. This has led to the proposal of a *speed-value tradeoff* [15] that underlies value-based decisions, rather than a *speed-accuracy tradeoff* as discussed in the preceding section, and considered in conventional two-alternative choice perceptual decisions [16].

Conceptualising value-based decisions shows, however, that there are similarities between perceptual and value-based decision making [17,18], although the usage of the term 'value' may vary with context [19]; value may refer to stimulus intensity, or to reward magnitude. In fact, recent studies demonstrate that for primates value-sensitivity represents an important feature of perceptual decision making, underlining the significance of absolute values (magnitudes) of input signals [20**]. Teodorescu *et al.* showed in experiments with human participants that increasing the magnitudes of two input signals while keeping their difference or ratio constant leads to faster

responses; this effect is not predicted by influential decision models that optimise the speed-accuracy trade-off. Using data from humans and monkeys, similar observations are reported by Pirrone *et al.* [21] for the case of equal alternatives for both perceptual decisions where 'value' represents the magnitude of an input signal, and value-based decisions where 'value' denotes a reward. These results provide evidence for a speed-value tradeoff in decision making and, given the suggested similarities between decision making in the brain and collective decision making in social insects (*e.g.* see [7,22]) may provide new insights into the underlying principles of collective decision making in social groups. Speed-value trade-offs should be as fundamental for groups as they are for individuals.

A speed-value tradeoff should play a key role in decision making that is not about 'correct' or 'false' but rather requires a strategy to choose the best alternative among available options. Therefore, it would be interesting to investigate the link between speed-value tradeoffs and a recently published model describing the optimal decision making strategy for value-based decisions [23**], which may reflect the ultimate goal of maximising fitness and reproductive success in realistic natural decision making scenarios, including collective decision making of insect societies.

Nutrition and decision making

Individuals on their own or within social groups frequently make foraging decisions. Those decisions often aim at balancing the intake of different nutrients rather than maximising the gain in energy [24], as described by the *Geometric Framework*—a graphical approach pioneered by Stephen Simpson and David Raubenheimer [24,25]. In this framework, the performances of animals or insect colonies are evaluated by considering their actions in *nutrient space*. The geometric framework is important for functionally-integrated social insects colonies as for single animals, as satisfying nutritional needs is crucial for both. Thus, nutritional deficits may bias or shape decision making for both in a similar way. The nutrient space is an N-dimensional space, which is spanned by N axes each of which represents one nutrient required in the diet. Imagine, for example, an animal or social insect colony that needs to consume proteins and carbohydrates. Then, the nutrient space is two-dimensional. The performance of the animal or social insects can then be evaluated by plotting the deficits in proteins and in carbohydrates on the axes of a two-dimensional Cartesian coordinate plane. As the aim of the (super) organism is to reach a nutritional target [25], a measure of distance between current state (a point in the diagram) and target (another point) quantifies the effectiveness of their foraging behaviour. When nutrients do not interact this required distance measure is simply Euclidean distance [25].

Although based mostly on laboratory experiments, considering two-dimensional problems such as choosing between proteins and carbohydrates, or food and water, has led to important insights into how animals and social groups forage and is empirically well motivated [24,26–29]. Given a target intake the animal or the insect colony has to fulfil an ongoing decision task by selecting repeatedly among two alternatives, to bring their internal state as close as possible to their target intake. Hence, behaviour that is guided by multiple decisions can be tracked in nutrient space. Deficits in one or more nutrients drive the motivations for deciding for or against an action that reduces a deficit. Houston *et al.* analyse the optimal strategy for reducing expected deficit in simple scenarios where food types contain differing ratios of required nutrients [30]; the optimal strategy requires decision-makers to reach a switching line and then move along this by ingesting food items in the required ratio. This is hard for animals to do without incurring switching costs, which change the optimal strategy [29], but could be more readily achieved by a social insect colony, or similar, regulating nutrient intake via a population of foragers.

The geometric framework has been studied in decentralised decision-making systems such as ant colonies [27] and slime molds [26]. Nutrition in ants is particularly well studied and emphasises the insect group's cognitive ability to integrate the different nutritional needs of workers and larvae [27], and the flexibility to make decisions in dynamic environments [31], whilst also highlighting the vulnerability to extreme nutritional imbalances [32]. Considering the foraging decisions of ant colonies illustrates the social dimension of nutrition [33] and has been related to social immunity [34]. This link between nutrition and immunocompetence has also been observed in honeybees [35].

Being central to all social groups, nutritional interactions may have contributed to the evolution of social behaviour [36]. In this light, recent observations in wasps [37**] showing reductions in mushroom body investments from solitary to social species indicate the intriguing connection between 'distributed cognition' [37**], sociality and nutritional decision making by social insect colonies in evolutionary contexts. It could be interesting to see what effects imbalanced nutrition has on non-foraging decisions of social insects, such as in the house hunting of honeybees. Here, the geometric framework could be used to characterise the nutritional state of the colony, providing the link between nutrient regulation at multiple organisation levels, social immunity, cognitive abilities in general and collective decision making in particular.

Robots and collective behaviour

For several decades, solutions from nature have been taken as a source of inspiration for the design of robotic

systems. This is particularly true for the field of *swarm robotics*, where a large number of autonomous robots coordinate with each other to perform a common task. In these decentralised systems, each individual gathers and exchanges information with the environment and peers in a local range; the large number of individuals and nonlinear interactions lead to a coordinated collective response of the swarm. Given the difficulties in identifying the rules that each agent should follow in order to obtain the desired collective behaviour, a widespread approach has been to look at natural processes that display the desired behaviour and adapt such processes to implement multirobot systems.

While most works have an engineering scope a few robotics studies, instead, aim at replicating the actual animal behaviour to investigate the veracity of different assumptions, or validate the correctness of biological models (*e.g.* [38,39]). Usually, to understand collective processes biologists use analytical and computational models such as multiagent simulations, in order to identify individual rules that lead to the observed group response. Through models, the individual behaviour can be varied systematically to identify which are the relevant components or model parameters. In collective behaviour, the process dynamics are principally determined by how information is acquired, processed and transferred between individuals. In some cases, all relevant components and realistic assumptions can be included in the mathematical model. However, when space, situatedness³ and the physical environment are determining factors in the process, implementing collective behaviour models on robots presents advantages which should not be overlooked [38,40,41]. Working with a physical device imposes constraints that force the designer to consider the limited capabilities of each individual (in terms of sensors and actuators), the effect of noise, and the mechanistic process of information transfer. As a result, a robot implementation reduces the possibility of oversimplifying the model and can provide insights into biological mechanisms. In particular, the embodiment and situatedness of a physical device influence group motion and alter the environmental perceptions of groupmates. As a consequence the dynamics of the communication topology are affected, and this can have a bearing on the collective dynamics (*e.g.* [42]).

Finally, a research area that is receiving growing attention is experimentation in *mixed societies*, composed of animals and robots that interact with each other [41,43,44,45*]. The first challenge of this research field concerns the design of robots that are considered as groupmates by the animals. These studies allow identification of the relevant

³ In robotics, situatedness refers to the extent to which a robot is embedded in the environment that can be sensed and modified through the robot's sensors and actuators [41].

perceptual components used by the animals (*e.g.* robot-fish [46–48], robot-bee [49], robot-rat [50]). Once a robot is accepted as a groupmate, controlling the robot's behaviour allows investigation of social interactions and how animals respond to specific behaviours. These studies help to identify individuals' cognitive abilities [45*,51–53] as well as how (and what) information is transferred within groups [54,55].

Conclusions

As motivated in the Introduction, our review has focused primarily on an economic view on collective decision-making. The economic view is a staple of behavioural ecology, and motivates the tools of optimal decision theory for the study of animal behaviour. Here we argue that for decisions in functionally-integrated groups, such as social insect colonies, optimality theory should also be applied to collective behaviour. The economic, optimality theory, view is also applied extensively to understanding animal behaviour in the various fields of neuroscience and psychology. There, the additional focus on mechanisms underlying behaviour opens up a new dimension of study. In studying individual animal behaviour, behavioural ecology has traditionally ignored mechanism, however there is a movement to integrate the study of mechanism with function [56]. Collective behaviour is, of course, particularly amenable to observation of mechanisms. Furthermore, through adopting modern robotics technology, behavioural mechanisms can be elucidated through manipulation; this might be of particular interest in functionally-integrated decision-making groups such as social insect colonies. We argue that when drawing parallels between mechanisms for collective behaviour and mechanisms for individual behaviour is justified, doing so provides a particularly powerful research programme.

Conflict of interest statement

The authors declare that there is no conflict of interest regarding the manuscript.

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