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1	Collective Decision-Making
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4	
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12	Abstract:
13	! "##\$%&'(\$)*\$%'+'", /0', 1 is the subfield of collective behaviour concerned with
14	how groups reach decisions. Almost all aspects of behaviour can be considered in
15	a decision-making context, but here we focus primarily on how groups should
16	optimally reach consensus, what criteria decision-makers should optimise, and
17	how individuals and groups should forage to optimise their nutrition. We argue
18	for deep parallels between understanding decisions made by individuals and by
19	groups, such as the decision-guiding principle of (/#2\$-+\$, +'&'('&3. We also review
20	relevant theory and empirical development for the study of collective decision
21	making, including the use of robots.
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25	We consider collective decision-making to be the subfield of collective
26	behaviour concerned with how groups reach decisions without centralised
27	leadership. Examples include nestsite selection by honeybees [1] and ants [2],
28	and consensus selection of food sources in shoaling fish [3]. Individuals in a
29	group can prefer to participate in a consensus decision, in which all individuals
30	seek to agree on the same outcome, either because the group is tightly
	functionally integrated, nnJlJMvggia sZı 'a srnigR.vl.rvMJig.gRRigahsArniia sZı MJrng.ll.ilalsArn

34 relatedness groups under appropriate conditions, selection on the group can 35 lead to group-level adaptations [4], so group members' behaviour is shaped as 36 part of a group-level decision-making mechanism. Within unrelated groups, 37 individuals' behaviour should maximise their own expected fitness, within the 38 context of the group [5]. Indeed inferring 'group cognition' abilities for unrelated 39 groups may be harder than previously appreciated; alternative explanations for 40 improved decision performance in fish shoals are that fish in larger groups have 41 improved individual-level abilities, and that larger groups are more likely to 42 contain better decision-makers who dominate collective decisions [6].

43 In this review we focus primarily on functionally-integrated decision-44 making systems for two reasons; first, as mentioned above, functional group 45 integration makes it appropriate to apply "4&'. /#'&3)&5\$"63 at the level of the group [7]. Second, parallels can be drawn between the behavioural rules of a 46 'superorganismal' group, and the behavioural rules of unitary individuals. We 47 48 consider such parallels to be illuminating. Our review can thus be read as 49 primarily presenting an 'economic' view of the behaviour of groups making 50 decisions, where decision outcomes result in gains or losses of quantities that co-51 vary with reproductive fitness. We place particular emphasis on the links 52 between collective decision-making, perceptual decision making and value-53 based decision-making, and on nutritional decision-making. We review 54 applicable theory, as well as the emerging use of robotics, for understanding 55 such systems.

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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 20<sup>th</sup> 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.

65 7'1, /#)\*\$&\$%&''', )&5\$"63, developed to understand optimal psychophysical
 66 decision-making by individuals, shows that there is an inherent decision-making

67 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 68 69 increasing the rate at which they incorrectly detect those events when they have 70 not happened. Yet in the group situation, Max Wolf and colleagues show how 71 introducing a quorum decision rule, typical of social insect colonies, allows the 72 group to simultaneously improve both rates [9]. Understanding how to correctly 73 set quorums, which may be sub-majority or super-majority according to the 74 accuracy of individuals, also shows that in fact group decisions are /#8/3+ more 75 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].

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84 In the preceding section group decision performance was considered in 85 terms of decision accuracy, or probability of making the correct response. Yet 86 consider the decision problem faced by a honeybee swarm selecting a new nest 87 site [12]. Obviously, it is advantageous for the collective of bees to choose the site 88 of highest possible quality. Imagine, for example, that there are two potential 89 nestsites available, both of equal but low quality. In this case it is best to wait and 90 postpone the decision until another option will be discovered. In contrast, if there are two alternatives having equal but high qualities, then the honeybees 91 92 should choose as quickly as possible, as a long decision making process is 93 accompanied by the consumption of resources and a prolonged absence of 94 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 +4\$\$\*-(/#2\$)&6/\*\$"99 [15] that underlies value-based decisions,
rather than a +4\$\$\*-/%26/%3)&6/\*\$"99 as discussed in the preceding section, and
considered in conventional two-alternative choice perceptual decisions [16].

104 Conceptualising value-based decisions shows, however, that there are 105 similarities between perceptual and value-based decision making [17,18], 106 although the usage of the term 'value' may vary with context [19]; value may 107 refer to stimulus intensity, or to reward magnitude. In fact, recent studies 108 demonstrate that for primates value-sensitivity represents an important feature 109 of perceptual decision making, underlining the significance of absolute values 110 (magnitudes) of input signals [20]. Teodorescu et al. showed in experiments with 111 human participants that increasing the magnitudes of two input signals while 112 keeping their difference or ratio constant leads to faster responses; this effect is 113 not predicted by influential decision models that optimise the speed-accuracy 114 trade-off. Using data from humans and monkeys, similar observations are 115 reported by Pirrone et al. [21] for the case of equal alternatives for both 116 perceptual decisions where 'value' represents the magnitude of an input signal, 117 and value-based decisions where 'value' denotes a reward. These results provide 118 evidence for a speed-value tradeoff in decision making and, given the suggested 119 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 120 121 principles of collective decision making in social groups. Speed-value trade-offs 122 should be as fundamental for groups as they are for individuals.

123 A speed-value tradeoff should play a key role in decision making that is 124 not about 'correct' or 'false' but rather requires a strategy to choose the best 125 alternative among available options. Therefore, it would be interesting to 126 investigate the link between speed-value tradeoffs and a recently published 127 model describing the optimal decision making strategy for value-based decisions [23], which may reflect the ultimate goal of maximising fitness and reproductive 128 129 success in realistic natural decision making scenarios, including collective 130 decision making of insect societies.

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134 Individuals on their own or within social groups frequently make foraging 135 decisions. Those decisions often aim at balancing the intake of different nutrients rather than maximising the gain in energy [24], as described by the : \$". \$6'%) 136 ; 6/. \$8"60 — a graphical approach pioneered by Stephen Simpson and David 137 138 Raubenheimer [24,25]. In this framework, the performances of animals or insect 139 colonies are evaluated by considering their actions in , 2&6', &)+4/%. The 140 geometric framework is important for functionally-integrated social insects 141 colonies as for single animals, as satisfying nutritional needs is crucial for both. 142 Thus, nutritional deficits may bias or shape decision making for both in a similar 143 way. The nutrient space is an N-dimensional space, which is spanned by N axes 144 each of which represents one nutrient required in the diet. Imagine, for example, 145 an animal or social insect colony that needs to consume proteins and 146 carbohydrates. Then, the nutrient space is two-dimensional. The performance of 147 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 148 149 coordinate plane. As the aim of the (super)organism is to reach a nutritional 150 target [25], a measure of distance between current state (a point in the diagram) 151 and target (another point) quantifies the effectiveness of their foraging 152 behaviour. When nutrients do not interact this required distance measure is 153 simply Euclidean distance [25].

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154 Although based mostly on laboratory experiments, considering two-155 dimensional problems such as choosing between proteins and carbohydrates, or 156 food and water, has led to important insights into how animals and social groups 157 forage and is empirically well motivated [24,26–29]. Given a)target intake the 158 animal or the insect colony has to fulfil an ongoing decision task by selecting 159 repeatedly among two alternatives, to bring their internal state as close as 160 possible to their target intake. Hence, behaviour that is guided by multiple 161 decisions can be tracked in nutrient space. Deficits in one or more nutrients 162 drive the motivations for deciding for or against an action that reduces a deficit. 163 Houston et al. analyse the optimal strategy for reducing expected deficit in 164 simple scenarios where food types contain differing ratios of required nutrients 165 [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.

170 The geometric framework has been studied in decentralised decision-171 making systems such as ant colonies [27] and slime molds [26]. Nutrition in ants 172 is particularly well studied and emphasises the insect group's cognitive ability to 173 integrate the different nutritional needs of workers and larvae [27], and the 174 flexibility to make decisions in dynamic environments [31], whilst also 175 highlighting the vulnerability to extreme nutritional imbalances [32]. 176 Considering the foraging decisions of ant colonies illustrates the social 177 dimension of nutrition [33] and has been related to social immunity [34]. This 178 link between nutrition and immunocompetence has also been observed in 179 honeybees [35].

Being central to all social groups, nutritional interactions may have 180 contributed to the evolution of social behaviour [36]. In this light, recent 181 182 observations in wasps [37] showing reductions in mushroom body investments 183 from solitary to social species indicate the intriguing connection between 184 'distributed cognition' [37], sociality and nutritional decision making by social 185 insect colonies in evolutionary contexts. It could be interesting to see what 186 effects imbalanced nutrition has on non-foraging decisions of social insects, such 187 as in the house hunting of honeybees. Here, the geometric framework could be 188 used to characterise the nutritional state of the colony, providing the link 189 between nutrient regulation at multiple organisation levels, social immunity, 190 cognitive abilities in general and collective decision making in particular.

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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 +8/6. )6"<"%", 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
- 200 identifying the rules that each agent should follow in order to obtain the desired
- 201 collective behaviour, a widespread approach has been to look at natural
- 202 processes that display the desired behaviour and adapt such processes to
- 203 implement multirobot systems.

204 While most works have an engineering scope a few robotics studies, 205 instead, aim at replicating the actual animal behaviour to investigate the veracity 206 of different assumptions, or validate the correctness of biological models (e.g., 207 [38,39]). Usually, to understand collective processes biologists use analytical and 208 computational models such as multiagent simulations, in order to identify 209 individual rules that lead to the observed group response. Through models, the 210 individual behaviour can be varied systematically to identify which are the relevant components or model parameters. In collective behaviour, the process 211 212 dynamics are principally determined by how information is acquired, processed 213 and transferred between individuals. In some cases, all relevant components and 214 realistic assumptions can be included in the mathematical model. However, when space, situatedness

229 with each other [41,43–45]. The first challenge of this research field concerns the 230 design of robots that are considered as groupmates by the animals. These studies 231 allow identification of the relevant perceptual components used by the animals 232 (e.g., robot-fish [46–48], robot-bee [49], robot-rat [50]). Once a robot is accepted 233 as a groupmate, controlling the robot's behaviour allows investigation of social 234 interactions and how animals respond to specific behaviours. These studies help 235 to identify individuals' cognitive abilities [45,51–53] as well as how (and what) 236 information is transferred within groups [54,55].

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239 As motivated in the Introduction, our review has focussed primarily on an 240 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 241 242 study of animal behaviour. Here we argue that for decisions in functionally-243 integrated groups, such as social insect colonies, optimality theory should also be 244 applied to collective behaviour. The economic, optimality theory, view is also 245 applied extensively to understanding animal behaviour in the various fields of 246 neuroscience and psychology. There, the additional focus on mechanisms 247 underlying behaviour opens up a new dimension of study. In studying individual 248 animal behaviour, behavioural ecology has traditionally ignored mechanism, 249 however there is a movement to integrate the study of mechanism with function 250 [56]. Collective behaviour is, of course, particularly amenable to observation of 251 mechanisms. Furthermore, through adopting modern robotics technology, 252 behavioural mechanisms can be elucidated through manipulation; this might be 253 of particular interest in functionally-integrated decision-making groups such as 254 social insect colonies. We argue that when drawing parallels between 255 mechanisms for collective behaviour and mechanisms for individual behaviour is 256 justified, doing so provides a particularly powerful research programme. 257 258 259 This work was funded by the European Research Council (ERC) under the

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Kopman V, Laut J, Polverino G, Porfiri M: Closed-loop control of 408 55. 409 zebrafish response using a bioinspired robotic-fish in a preference test. HJ **→**7"%→D, &\$69/%\$ 2013, **10:20120540**. 410 McNamara JM, Houston AI: Integrating function and mechanism. E6\$, \*+) 411 56. 412 C%"#)C("#=2009, **24**:670–675. 413 414 415 ¥ Wolf, Kurvers, Krause, Marshall (2016) - \*\* In this paper the authors 416 417 demonstrate how group decisions are always more accurate than 418 individual decisions, yet achieving this improvement requires that 419 quorum thresholds for decisions be set according to the accuracy of group 420 members, and optimal thresholds need not be simple majority rules. Marshall, Brown, Radford (2016) - \*\* In this review the authors note that 421 ¥ 422 when group members vary in individual decision accuracy, decision 423 theory shows how contributions to group decisions should be weighted 424 by the accuracies, or confidences, of group members. The authors review 425 the application of such theory to human collective decision-making and 426 note the potential for application of the theory to non-human animal 427 groups. ¥ Teodorescu, Moran, Usher (2016) - \*\* This paper demonstrates the 428

- 429 presence of magnitude sensitivity in decision making by individuals. The 430 authors show that the absolute value of a stimulus does matter in decision 431 making, as an increase of the absolute value reduces decision times, in 432 agreement with theoretical arguments [13,15]. The authors emphasise 433 that theoretical frameworks explaining decisions only based on the 434 accumulation of relative evidence cannot explain experimental findings 435 and they propose two alternatives to resolve this issue, one being based 436 on a drift diffusion model with value-dependent multiplicative noise and 437 the other one being related to a leaky competing accumulator model with 438 lateral inhibition.
- 439 ¥ Tajima, Drugowitsch, Pouget (2016) \*\* This paper derives the optimal
  440 strategy for decisions in which the decision-maker is rewarded by the
  441 value of the option chosen. Interestingly, the optimal strategy is
  442 equivalent to a process of integrating differences in evidence streams, but

with decision boundaries that collapse over time. Relating this optimal
strategy to behavioural observations and to models of collective decisionmaking (\$=1=[13]) should prove valuable.

- O'Donnell, Bulova, DeLeon, Khodak, Miller, Sulger (2015) \*\* In this paper 446 ¥ the authors study a distributed cognition hypothesis, building on social 447 448 communication instead of individual cognition. One prediction of this 449 model is that brain investment in social species is reduced. The authors 450 present data from observations in wasps, which support the distributed 451 cognition hypothesis. They conclude that evolution of eusociality in wasps 452 was accompanied by the reduction of central processing brain areas, which might be a significant feature of other types of social insects, too. 453
- 454 ¥ Frohnweiser, Murray, Pike and Wilkinson (2016) \* In this review the
  455 authors survey the use of robots for understanding animal cognition,
  456 including examples mentioned above. The authors argue that robotics
  457 could have an important impact on understanding of perception, spatial
  458 cognition, social cognition, and early cognitive development. Their
  459 highlighting of social interactions, such as between fish and honeybees, is
  460 particularly relevant to the study of collective decision-making.