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## Research

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# Motion-guided attention promotes adaptive communications during social navigation

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Animals are capable of enhanced decision making through cooperation, whereby accurate decisions can occur quickly through decentralized consensus. These interactions often depend upon reliable social cues, which can result in highly coordinated activities in uncertain environments. Yet information within a crowd may be lost in translation, generating confusion and enhancing individual risk. As quantitative data detailing animal social interactions accumulate, the mechanisms enabling individuals to rapidly and accurately process competing social cues remain unresolved. Here, we model how motion-guided attention influences the exchange of visual information during social navigation. We also compare the performance of this mechanism to the hypothesis that robust social coordination requires individuals to numerically limit their attention to a set of  $n$ -nearest neighbours. While we find that such numerically limited attention does not generate robust social navigation across ecological contexts, several notable qualities arise from selective attention to motion cues. First, individuals can instantly become a local information hub when startled into action, without requiring changes in neighbour attention level. Second, individuals can circumvent speed–accuracy trade-offs by tuning their motion thresholds. In turn, these properties enable groups to collectively dampen or amplify social information. Lastly, the minority required to sway a group's short-term directional decisions can change substantially with social context. Our findings suggest that motion-guided attention is a fundamental and efficient mechanism underlying collaborative decision making during social navigation.

## 1. Introduction

To survive organisms must adapt quickly and accurately to changes in their environment. Social organisms can enhance this process by disseminating cues among themselves in a manner that either dampens or amplifies local information [1–5]. The fluid manoeuvres observed in flocks of birds and schools of fish have long epitomized the speed at which such collective processes can occur [1–4,6–10]. The constituents of these groups can dampen directional errors by adopting the average decisions of their neighbours [8], while any abrupt movements by only a single startled individual can trigger rapid directional shifts across the ensemble [9]. Discerning how group members distinguish salient from spurious social information in a manner that harmonizes these opposing qualities remains a fundamental paradox [3,11]. Our objective is to discern what individual-level mechanism(s) can promote adaptive social communications during navigation, thereby complementing a group's capacity to collectively dampen or amplify information.

Numerous models have explored how social individuals may integrate local information [6,8,10,12–15]. These theoretical efforts are complemented by an equally diverse set of empirical findings supporting various alternatives [6,7,9,10,15–19]. Most models of collective behaviour assume that behavioral interactions change with distance (i.e. metric models) and that individuals integrate all available information within their sensory range [10,12,20–22]. This causes an

important sensory processing issue because by simply averaging across all available information group members invariably dampen out any novel signal or cue. It is therefore unlikely that this approach alone can catalyse collective adaptability across contexts without requiring higher-order cognitive computations, e.g. memory [21].

Recent work suggests that group members can resist disruptions more effectively by limiting their attention to a set of  $n$ -nearest neighbours (approx. 6 or 7 if  $n$  can only be a whole number), resulting in topological interactions that are particularly effective with regard to changes in separation distance [6]. We will refer to this mechanism as a numerical threshold, since the term topological has much broader cognitive implications related to visual object recognition and association [23]. It is hypothesized that such numerically limited attention is, in fact, essential to explain robust collective coordination [6]. While this mechanism suggests a mathematically elegant solution, it is unlikely to be cognitively tenable across taxa. Experimental evidence indicates that, in general, species ranging from fish to human children can only visually identify and track 3 or 4 discrete objects simultaneously [24–26]. Furthermore, a numerical limit does not address the sensory processing issue because all available information is still treated equitably.

We recently proposed an alternative mechanism based on Weber's Law to explore how selective visual attention can influence collective behaviour [14]. Visual motion cues are a primary feature in sensory processing [26–28], conveying information that directly impacts individual fitness, such as with navigation, foraging, courtship and predator avoidance [26,29–31]. The amount of information within a scene generally exceeds the capacity of the visual system, so neural selectivity compensates by sifting salient features from the scene to limit processing [26–29]. Both numerical and motion thresholds are features that can guide visual attention, although there is stronger evidence supporting selective attention to motion [28] and movement behaviour is an inherent component of social navigation. Here, we extend our previous efforts by modelling how these visual features can influence the flow of social information across a variety of conditions.

We proceed by drawing analogy to social foragers who are often dispersed and disorganized when searching for food within a patch, yet must remain vigilant to minimize competitive effects, conflict and predation risk [4,32,33]. These effects can lead to a range of social conditions, spanning from seemingly normal to disturbed group departures. However, regardless of context, group members must integrate competing movement cues from their neighbours in order to come to a directional consensus. Modelling this scenario allows us to address several pertinent questions. First, how does coupling individual attention to movement behaviour influence information transfer during social navigation? Second, can alternative visual features (numerical versus motion thresholds) provide a mechanism to catalyse adaptive social coordination across a wide range of ecological contexts? Specifically, can these attention mechanisms influence a social individual's ability to display prolonged resistance to environmental uncertainty, yet remain equally responsive to sudden disturbances? Last, if individual attention and behaviour can influence the flow of social information, how then will these factors influence collective coordination as group size increases?

## 2. Model

### (a) Visual interactions

Individuals are initialized with random positions  $\mathbf{x}_i$  and orientations  $\hat{\mathbf{v}}_i$ , as may be expected of social animals foraging within a patch. Social interactions in the model are first scaled by visual perception. This process begins by relating how the relative motion of a neighbour,  $\mathbf{v}_{j,i} = \mathbf{v}_j - \mathbf{v}_i$ , changes visually along an individual's line-of-sight,  $\mathbf{d}_{j,i} = \mathbf{x}_j - \mathbf{x}_i$ . Individual  $i$  'sees' neighbour  $j$  as an arc of angular size:

$$\Omega_{j,i} = 2 \tan^{-1} \left( \frac{r_L}{d_{j,i}} \right), \quad (2.1)$$

where  $r_L$  is the particle's radius and  $d_{j,i}$  is the intervening distance (e.g.  $d_{j,i} = |\mathbf{d}_{j,i}| - 2r_L$ ). Length units are scaled to body length  $L = (2r_L)$  and time is in generic units,  $t$ . At each time step, neighbours are sorted by increasing distance to reflect the group from the individual's perspective. Neighbour detection is limited by a minimal image size,  $\Omega_{\min}$ , and occlusion (see the electronic supplementary material, appendices S.1 and S.2). Each subject therefore sees the group as a set of apparent neighbours,  $A_i$ .

A neighbour's motion is perceived as

$$\mathbf{v}_{j,i} = \omega_{j,i} \cdot \hat{\mathbf{v}}_{j,i}, \quad (2.2)$$

where directional information is provided by  $\hat{\mathbf{v}}_{j,i} = \mathbf{v}_{j,i}/|\mathbf{v}_{j,i}|$  and weighted by  $\omega_{j,i} = f(\Omega_{j,i}, \hat{\mathbf{d}}_{j,i})$ .  $\omega_{j,i}$  essentially quantifies the speed at which an image  $\Omega_{j,i}$  moves along, or across, an individual's line of sight,  $\hat{\mathbf{d}}_{j,i}$ . The primary effect is that interactions are proportional to a neighbour's relative speed and decay exponentially with distance,  $d_{j,i}$ . A secondary effect is that individuals do not explicitly align with the heading of their neighbours ( $\hat{\mathbf{v}}_j$ ), but, rather, respond to how images move with respect to a neighbour's position (see the electronic supplementary material, appendix S.1).

### (b) Attention mechanisms

While the above equations characterize visual perception, we are primarily interested in how individuals identify influential neighbours from among competing visual stimuli. Here, individuals select influential neighbours based on one of two alternative mechanisms: the motion or number of apparent neighbours, as proposed by Lemasson *et al.* [14] and Ballerini *et al.* [6], respectively.

Individuals reacting to motion cues direct their attention towards any apparent image(s) whose relative speed exceeds some proportion of their optic flow [14]:

$$j \in N_i^+ \quad \text{if} \quad \frac{\omega_{j,i}}{\bar{\omega}} \geq m. \quad (2.3)$$

In this case, individual attention level at time  $t$  is defined by the number of influential neighbours,  $N_i^+ = |N_i^+|$ , optic flow is the average relative speed of all apparent neighbours,  $\bar{\omega}$ , and  $m$  is a motion-sensitive attention threshold. Equation (2.3) is based on a fundamental signal-to-noise property inspired by Weber's law, where the perception of a stimulus is a constant proportion  $m$  of the background physical intensity, given by  $\bar{\omega}$ . Here, the number of motion signals that stand out from the background drop as  $m$  increases continuously, which serves to narrow the individual's attention.

Alternatively, individuals reacting to a fixed number of neighbours limit their attention to their  $n$ -nearest apparent neighbours [6]:

$$N_i^+ = A_i\{1, 2, 3, \dots, n\}. \quad (2.4)$$

Here, the number of influential neighbours increases discretely in direct proportion with increasing values of  $n$  (e.g.  $N_i^+ = |N_i^+| = n$ ).

Parameters  $m$  and  $n$  are thresholds that control attention level and represent changes in the individual's internal state, e.g. hunger or fear [6,12–15,20–22]. Note that individuals are exposed to the same visual stimuli when adopting either the motion or numeric mechanism (equation (2.3) or (2.4), respectively).

### (c) Social navigation

The relative velocities of any influential neighbours that are selected by equation (2.3) or (2.4) are then averaged to adjust an individual's intended course:

$$v_i(t + \Delta t) = v_i(t) + \langle v_{j,i} \rangle(t). \quad (2.5)$$

Intended speed is bounded by  $v \in [0, 1]$  with a maximum turning arc of  $\Delta\hat{v}_i \in [-\pi/2, \pi/2]$ . These constraints ensure continued, yet limited motion. Individuals then move in their intended direction with some degree of uncertainty:

$$x_i(t + \Delta t) = x_i(t) + U(v_i, \eta, t)\Delta t. \quad (2.6)$$

Function  $U$  independently adjusts individual speed and direction according to a noise scalar,  $\eta$ ; a parameter generating disorientation, such as may arise from environmental turbulence or panic behaviour [12,14]. Speed is adjusted as  $v(t + \Delta t) \pm \eta \cdot v(t)$ , where  $\eta \in [0, 1]$  and heading  $\hat{v}(t + \Delta t)$  is rotated by  $\theta \in [-\eta \pi/2, \eta \pi/2]$ .

## 3. Measuring information transfer

We quantify information transfer by measuring how directional information is distributed and the accuracy with which it is transmitted at both the individual and group level. At the individual level, we select transmitter–receiver (T–R) pairs, each of which is chosen at random from within a group to measure pairwise coordination (one pair per group). Across replicate departures, receivers represent a typical member's attention level (how many neighbours one is responding to; equation (2.3) or (2.4); figure 1a), while transmitters represent social influence (the number of neighbours responding to one's motion, figure 1b). The median values of these metrics across replicates (attention,  $\tilde{N}^+$  and influence,  $\tilde{N}^-$ ) quantify how information is initially distributed in the communication networks that emerge.

Coordination between any given T–R pair begins by measuring their directional deviation from one another,  $\sigma = \cos^{-1}(\hat{v}_R \cdot \hat{v}_T)$ . The accuracy of all pairwise coordinations is then measured by the angular concentration in  $\sigma$  values across departure events:

$$\rho_\sigma = \sqrt{E[\cos \sigma]^2 + E[\sin \sigma]^2}, \quad (3.1)$$

where  $E$  is the expected value of  $\sigma$ . This statistic provides an individual-level distillation of the group-level order parameter [12,14,21]:

$$\rho(\hat{v}, t) = \frac{1}{G} \left| \sum_i \hat{v}_i(t) \right|, \quad (3.2)$$

which measures collective coordination at time  $t$  across all individuals in a group of size  $G = |G|$ . The final value of this metric at the end of each simulation is then averaged across departures,  $\rho_v = \overline{\rho(\hat{v}, t)}$ . Coordination improves from 0 to 1 in both  $\rho_\sigma$  and  $\rho_v$ . We initially focus on measuring information transfer among individuals,  $\rho_\sigma$ , yet directional agreement between any two individuals does not guarantee collective consensus. We therefore compare  $\rho_\sigma$  and  $\rho_v$  to confirm or deny such associations.

## 4. Simulations

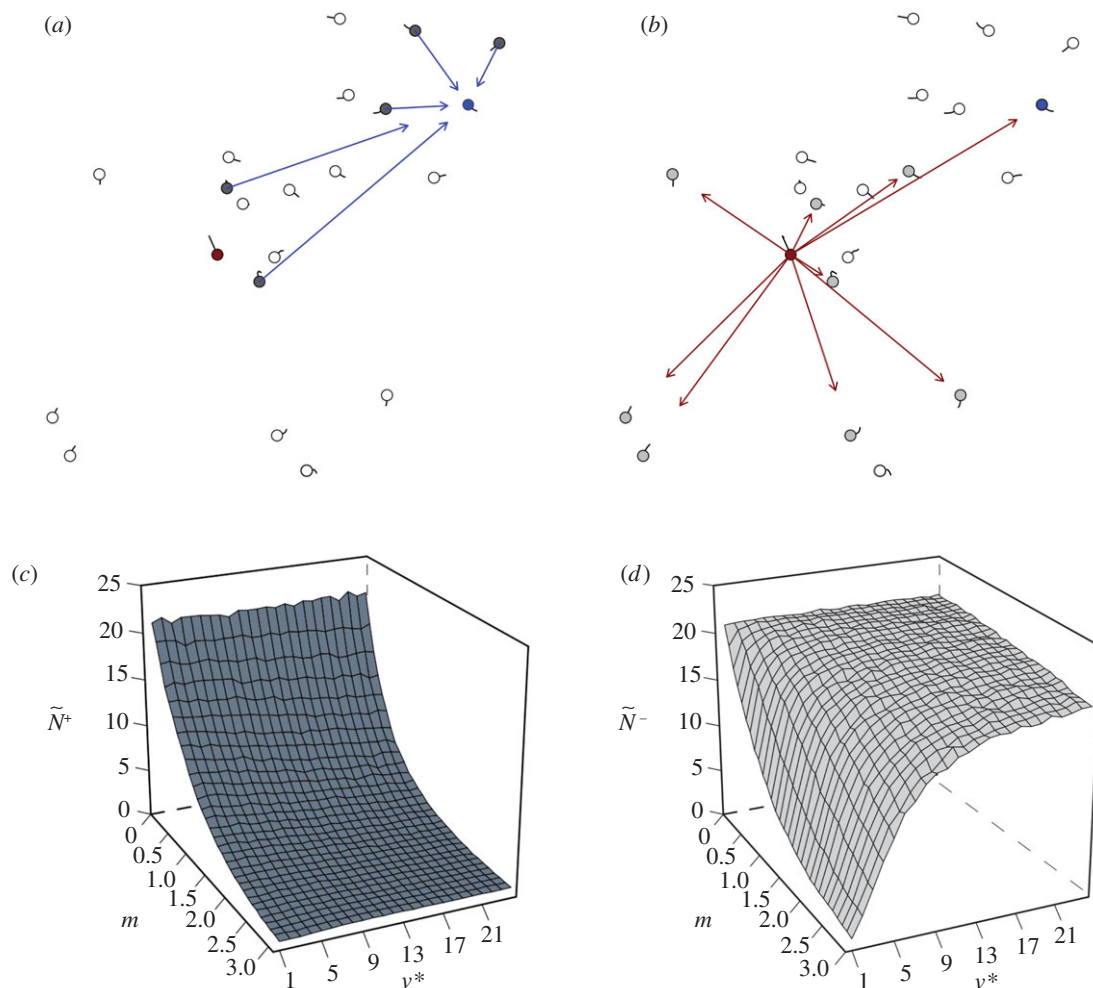
### (a) Motion-guided attention

The first objective is to quantify how coupling individual attention to neighbour motion cues can influence the transfer of social information through a group. Here, we focus on the motion threshold because it directly links attention and movement behaviour, whereas  $N_i^+$  is not directly affected by motion under the numerical mechanism and its effects have been explored elsewhere [6]. We measure information transfer between T–R pairs in moderately sized groups of 25 individuals; a size that enables interactions to realistically range from local to global and meets both theoretical and empirical expectations related to individual attention level ( $N_i^+ \approx 1-7$  neighbours) [6,18–20]. We then record how changes in the transmitter's motion cue relate to the receiver's direction. Transmitter speed in this case is presented in relation to the group average:  $v^* = v_T/\bar{v}$ . The influence of attention and motion on information transfer are measured by how changes in  $m$  and  $v^*$  influence the initial communication networks that emerge across all 25 group members (using  $\tilde{N}_i^+$  and  $\tilde{N}_i^-$ ), followed by the resulting T–R coordination patterns across time and replicate departures,  $\rho_\sigma$ . Corresponding simulations are conducted for the numerical mechanism (see the electronic supplementary material, appendix S.3).

### (b) Ecological context

For the second objective, we determine if either attention mechanism can catalyse adaptive social coordination across ecological contexts. We measure the performance of these two mechanisms using  $\rho_\sigma$  and  $\rho_v$  as a function of individual cost, e.g. the attention level required to generate the observed degree of coordination. Recall that incremental changes in the  $m$  and  $n$  thresholds have an inverse effect on individual attention (equations (2.3) and (2.4)). Therefore, comparisons are facilitated by translating changes in  $m$  and  $n$  into the resulting attention level,  $\tilde{N}_i^+$  (see the electronic supplementary material, appendix S.4).

Ecological context is defined as the combination of one's physical and social environment. We alter the physical environment by varying environmental noise ( $\eta$ ) and the initial nearest-neighbour distance ( $d_1$ ). These physical changes occur under two extreme social contexts: normal and disturbed patch departures. During normal departures all 25 individuals in a group behave similarly without any inherent movement biases, and both  $\rho_\sigma$  and  $\rho_v$  are recorded at  $t = 1000$  to measure navigational coordination over an extensive period (i.e. resistance to persistent environmental uncertainty). Under disturbed conditions, each group's transmitter ignores its neighbours and moves off rapidly in a random direction at speed  $v^*$ , following the 'leading according to need'



**Figure 1.** Snap shots of the initial communication networks that emerge when a single member, acting as a transmitter, ignores its neighbours and departs with motion cue  $v^*$ . Average attention level,  $\tilde{N}^+$ , reflects the median number of neighbours that influenced a receiver (ex. *a*, receiver in blue). Average transmitter influence,  $\tilde{N}^-$ , reflects the median number of neighbours that were influenced by its movement behaviour (ex. *b*, transmitter in red). The resulting attention/influence communication networks are defined by  $\tilde{N}^+$  (*c*) and  $\tilde{N}^-$  (*d*), respectively. The decay in attention level with  $m$  reflects the physical nature of dispersed neighbours, whose motion cues decay exponentially with distance ( $c$ ;  $m \propto d^{-2}$ ; see the electronic supplementary material, appendix S.1). There are 1000 replicates per parameter combination,  $\eta = 0.1$  and  $\tilde{d}_1 = 2L$ . Results are for motion-guided attention only (see the electronic supplementary material, appendix S.3 for corresponding figures related to communications under numerically limited attention).

hypothesis [22] (figure 1*a,b*). Here, the disturbance is dramatic ( $v^* = 10$ ) and mimics the initial moments of a reflexive startle response [34], as when an individual avoids an attack from a predator, neighbour aggression or responds to producer–scrounger dynamics [4,32,33]. In these scenarios  $\rho_\sigma$  and  $\rho_\nu$  are sampled at  $t = 100$  to measure how responsive individuals are to such sudden disruptions (see the electronic supplementary material, appendix S.5). Additionally, it is important to quantify whether pairwise coordination,  $\rho_{\sigma\sigma}$ , is either amplified or dampened by the remaining group members. For this, we control for social feedbacks by repeating the above simulations, but remove all group members save the selected T–R pairs to compare how  $\rho_{\sigma\sigma}$  changes in groups of 25 versus two.

### (c) Group size

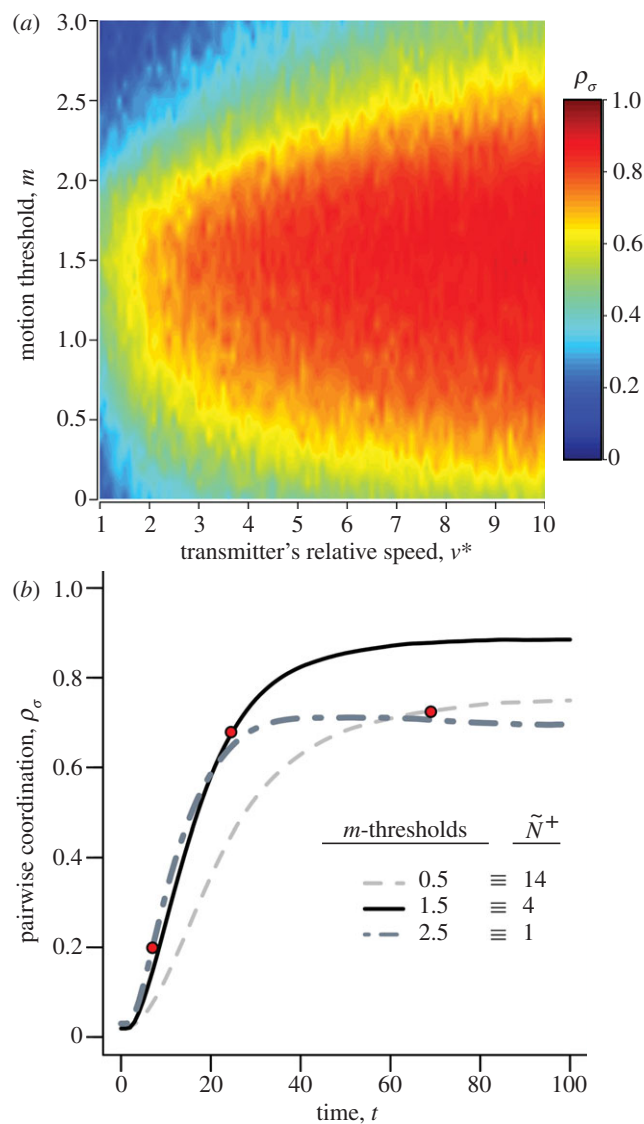
Lastly, we extend our analyses by exploring how the two attention mechanisms affect navigational coordination as group size increases (10–200 individuals) [4,12,22]. Here, attention thresholds ( $m$  or  $n$ ) and environmental conditions ( $\eta$ ,  $d_1$ ) are fixed at operable levels determined from the preceding analyses (see the electronic supplementary material, appendix S.8). In groups capable of self-organization, we

then measure how the strength of a cue ( $v^*$ ) influences the proportion of transmitters,  $P_T$ , necessary to sway a group’s ability to come to a directional consensus, e.g.  $\rho_\nu \sim f(P_T, v^*)$ . To measure this, we run simulations that are initiated with a single transmitter at  $t = 2$ . We then assume that some proportion  $P_T$  of the group members that are influenced by a transmitter will copy its behaviour and become transmitters themselves, thereby mimicking a visually contagious response. Transmitter departure ranges from subtle to dramatic and we constrain ourselves to short time periods under both departure scenarios ( $v^* : \{1, 10\}$ ;  $t = 100$  time steps).

## 5. Results

### (a) Motion-guided attention

Under motion-guided attention movement cues ( $v^*$ ) and attention threshold ( $m$ ) can interact to generate striking structural asymmetries in the communication networks that emerge (figure 1*c,d*). Average individual attention level is unaffected by changes in a particular neighbour’s motion cue,  $v^*$  (figure 1*c*). However, a transmitter’s  $v^*$  can range from having little influence across the group, to instantly



**Figure 2.** (a) Coordination accuracy between transmitter–receiver pairs (T–R,  $t = 100$ ) as a function of the transmitter's motion cue,  $v^*$ , and the receiver's motion threshold,  $m$ . (b) Time series of the average trends in T–R coordination during a social disturbance ( $v^* = 10$ ) for three attention levels. Red dots indicate the median time that receivers tracked their transmitter's motion through the crowd (i.e.  $T \in N_i^+$ ; equation (2.3)).  $v^*$  is limited to  $10L \cdot t^{-1}$  to reflect the saturation point seen in (a) and corresponds to the relative speeds displayed by startled fish [34]. Trend lines in (b) reflect median values that are all smoothed by the same exponential moving average. Parameter values and conditions match those in figure 1.

becoming public (figure 1*d*,  $v^* \rightarrow 20$ ), even when members are largely ignoring one another (corresponding to figure 1*c*,  $m \rightarrow 3.0$ ,  $\tilde{N}^+ \rightarrow 1$ ). Over time, weak directional cues (low  $v^*$ ) are generally dampened or ignored, while strong cues (high  $v^*$ ) are nearly always accurately transmitted, regardless of the average individual's attention level (figure 2*a*). Individuals can therefore tune their response to weaker cues either through social indifference (high  $m$  threshold, resulting in low attention levels), or unintentionally through collective averaging (low  $m$  threshold, resulting in high attention levels). The trade-off between these behavioural endpoints is that higher attention levels slow down response time because of collective dampening, but generate slightly better pairwise coordination (figure 2*b* and [14]). However, intermediate levels of attention can enhance both the speed and accuracy with which social information is transmitted, albeit at the price of increased

sensitivity to weaker motion cues (figure 2*a,b*). Information distribution and transmission patterns differ substantially when individuals adopt the numerical mechanism (see the electronic supplementary material, appendix S.3).

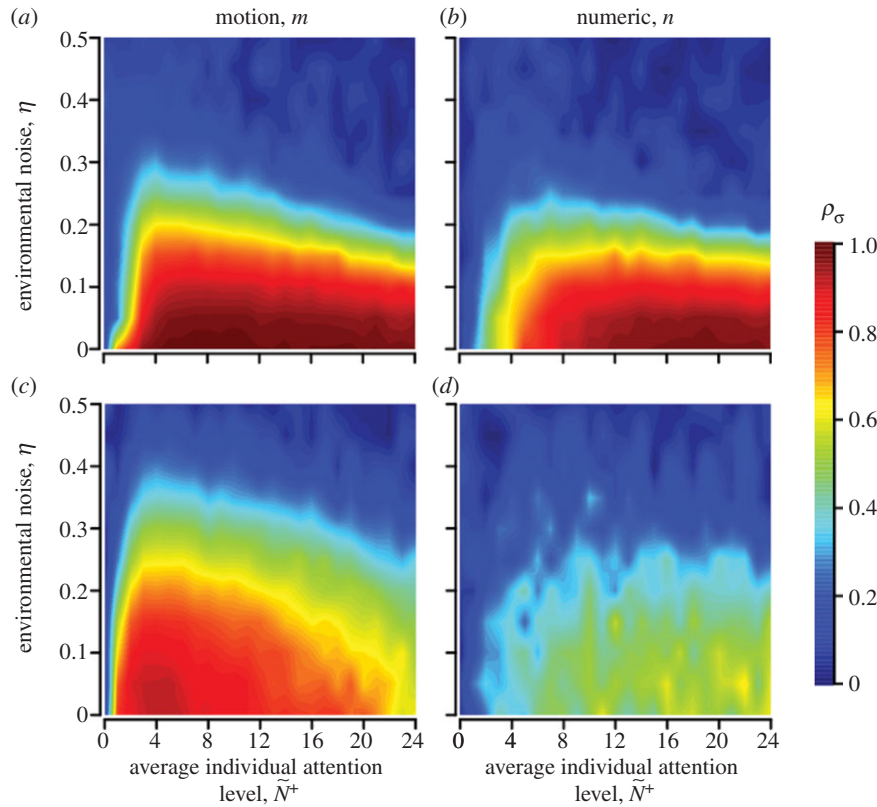
## (b) Ecological context

As environmental noise or panic levels increase, motion-guided attention enables individuals within a group to maintain directional coordination across contexts more effectively than when they adopt the numerical mechanism ( $\rho_\sigma$ , figure 3). During normal patch departures, individuals can achieve high levels of navigational performance at half the attention level required by those adopting numerically limited attention (figure 3*a,b*). Resistance to noise is not limited by  $n$  under the numeric mechanism because pairwise coordination accuracy peaks well before  $\tilde{N}^+ = G$  (figure 3*b*). Motion-guided attention also enables individuals to retain high levels of coordination accuracy during a sudden disturbance, suggesting a robust means to optimize social communications across large changes in context (figure 3*a,c*). Moreover, this rapid response occurs without requiring receivers to alter their internal state (i.e.  $m$ ). In contrast, coordination accuracy breaks down during a disturbance when individuals adopt the numerical mechanism (figure 3*b,d*). While both attention mechanisms can result in a receiver not responding to a transmitter's motion cue, missed or dampened cues are much more prevalent with the numerical mechanism (see the electronic supplementary material, movies S1 and S2 for example).

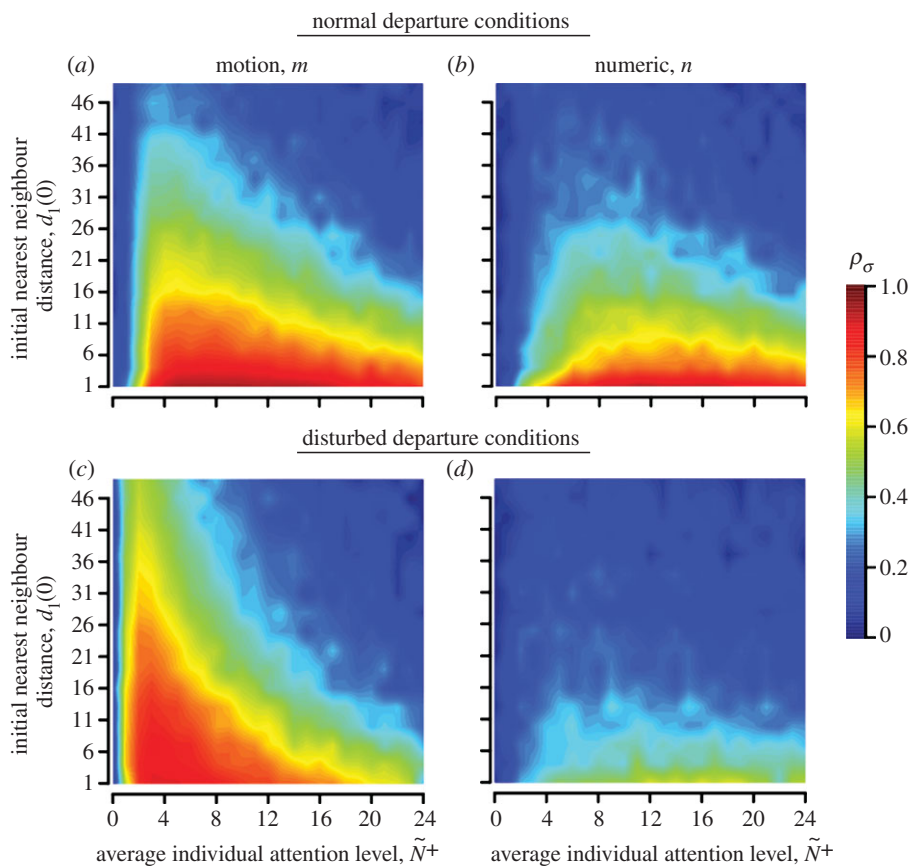
We find qualitatively similar patterns between the attention mechanisms within and across contexts when group dispersion levels vary from crowded to sparse ( $\rho_\sigma$ , figure 4). Additionally, coordination accuracy between T–R pairs within groups of 25 individuals is generally reflected at the group level across these ecological contexts, confirming collective coordination ( $\rho_v$ ; see the electronic supplementary material, appendix S.6). Lastly, social feedbacks play a critical role in amplifying information transfer through groups, which only occurs under the motion mechanism. The result is that pairwise coordination within full groups ( $G = 25$ ) can be substantially enhanced beyond what is observed in isolated pairwise interactions (see the electronic supplementary material, appendix S.7).

## (c) Group size

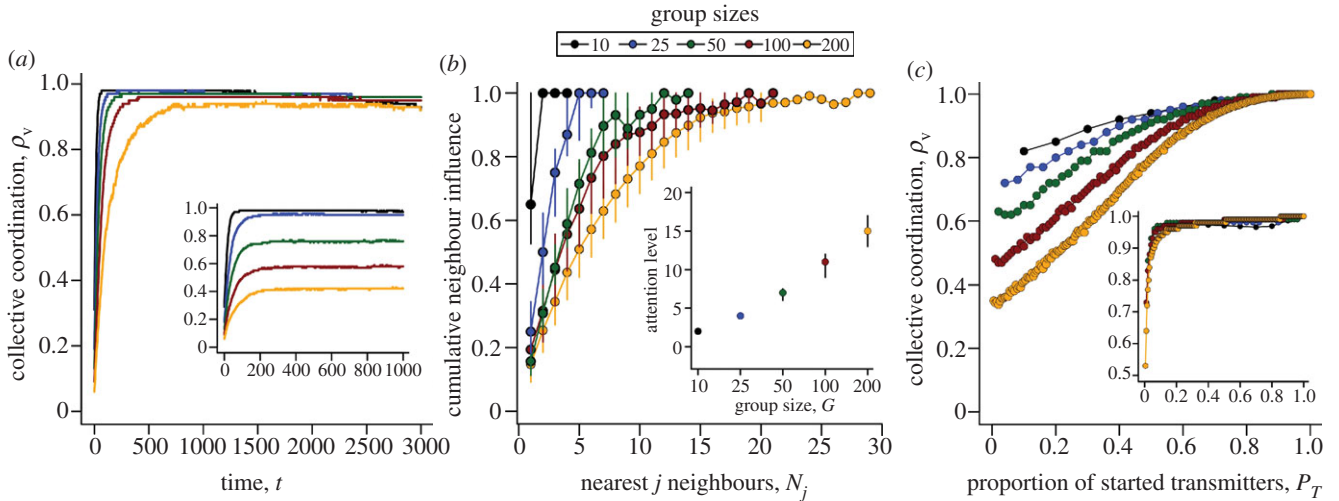
Under normal conditions motion-guided attention enables individuals to self-organize across a broad range of group sizes, albeit more slowly as group size increases (figure 5*a*). When the numerical mechanism is employed at  $n=7$ , the biological upper limit for this mechanism [24–26], larger groups fail to self-organize (see figure 5*a* inset and electronic supplementary material, appendix S.8). One reason for these differences in group-level coordination is that the motion mechanism enables individual attention to scale with group size, thereby enhancing social connectivity. However, a receiver's  $N_j$  nearest neighbours become less influential with increasing separation distance, regardless of the attention mechanism (as  $\omega_{j,i}$  decays in strength with increasing distance; see electronic supplementary material, appendix S.1). This results in distal neighbours having diminishing navigational influence as  $G$  and  $N_j$  increase, which is shown by the cumulative influence that each successive neighbour



**Figure 3.** Coordination accuracy between T–R pairs as a function of ecological context, environmental noise ( $\eta$ ) and attention. Individuals adopt either a motion threshold (*a,c*) or a numerical threshold (*b,d*). Under normal patch departures all individuals interact socially and move at similar speeds (*a,b*). During disturbed departures a startled transmitter ignores its neighbours and departs with a motion cue of  $v^* = 10$  (*c,d*). Coordination is shown as a function of individual attention level to facilitate comparison between the attention mechanisms (see the electronic supplementary material, appendix S.4 and movies S1–S3 for example). Simulations lasted 1000 and 100 time steps for normal and disturbed scenarios, respectively; 500 replicates per parameter combination; initial dispersion level is  $\tilde{d}_1 = 2L$  (see electronic supplementary material, table A1 and appendix S.2 for parameter values and rationale).



**Figure 4.** Coordination accuracy between T–R pairs as a function of ecological context, initial nearest-neighbour distance ( $\tilde{d}_1$  at  $t = 0$ ) and attention. Individual attention level is dictated by either a motion threshold, *m* (*a,c*), or a numerical threshold, *n*, (*b,d*). Additional parameter values match those in figure 3, albeit with noise fixed at  $\eta = 0.1$ .



**Figure 5.** The effects of group size, movement behaviour and attention mechanisms on collective coordination. Average trends in collective coordination in groups of 10–200 individuals over time when members adopt either motion (*a*; main) or numerical (*a*; inset) thresholds. (*b*) The cumulative influence of  $G$  and the  $N_j$  nearest influential neighbours on the magnitude of the typical receiver's response. Each successive influential neighbour provides additional movement information whose proportional contribution is given by  $\omega_{j,i} / \sum \omega_{j,j}$ . The sum of all influential motion weights is then averaged to scale the receiver's response to its social stimuli (equations (2.2) and (2.5)). Inset (*b*) shows the median receiver attention levels as a function of group size under a fixed motion threshold. Points and error bars represent 25, 50 and 75% quantiles. (*c*) Collective coordination across groups of varying size as a function of the number of transmitters and their motion cue, where  $v^* = 1$  (main) and 10 (inset). Starting values of  $\rho_v$  equate to those at  $t = 100$  in (*a*) for each group size. When  $v^* = 1$  transmitters have limited social influence, but their directional influence increases dramatically when  $v^* = 10$  (Note the lower limits in the  $y$ -axis.). Parameter values for all simulations:  $m = 1.5$ ,  $n = 7$  (*a*; inset only),  $d_1 = 2L$  at  $t = 0$ ,  $\eta = 0.1$ .

adds to a receiver's optic flow (figure 5*b*). So, although median attention levels rise with group size (figure 5*b*, inset), movement decisions remain locally biased and show little change in the proportion of influential neighbours across group sizes (figure 5*b*, inset; see the electronic supplementary material, movie S3).

Motion-guided attention also affects the proportion of group members necessary to sway a group's directional consensus during short time periods ( $t = 100$ ). When transmitters display a persistent directional bias, but move no faster than the average individual ( $v^* = 1$ ), it takes a greater proportion of them to successfully bias the group's direction as group size increases (figure 5*c*). This is because it simply takes larger groups longer to self-organize ( $\rho_v$  values at  $P_T = 0$  in figure 5*c* equate to those at  $t = 100$  in figure 5*a*). However, we see a dramatic shift in the influence that a minority of individuals can exert over a group during a sudden social disturbance across all group sizes ( $v^* = 10$ ; figure 5*c*, inset; see electronic supplementary material, movie S4). These dynamics are largely driven by the underlying pairwise interactions, which increase more rapidly (see the electronic supplementary material, appendix S.8, figure A-11).

## 6. Discussion

The central finding of this study is that motion-guided attention can catalyse adaptive social communications across a broad range of ecological contexts. This mechanism enables individuals to become temporary information hubs simply through their actions, without requiring a shift in the average receiver's attention level, thereby increasing both the speed and accuracy with which information is locally disseminated. In turn, these properties can substantially influence the

proportion of individuals necessary to sway a group's responsiveness to a social disturbance. Our results do not support the hypothesis that numerically limited interactions are essential to generate robust collective behaviour, particularly with regard to large changes in ecological context. As arguments for and against a numerical mechanism are nicely presented elsewhere [6,35], we will discuss how the motion mechanism may extend our understanding of coordinated social behaviour.

Motion-guided attention provides an intuitive means of generating adaptive communications in animal groups on the move. For instance, animals tend to optimize their travel speeds to balance ecological and energetic trade-offs [36]. The high energetic costs associated with bursts of motion would therefore minimize the risk of behavioral cascades from false alarms (type I errors), while enabling individuals to tune their attention to hedge their bets against type II errors (failing to respond to a neighbour's predator avoidance manoeuvre) [37]. Additionally, biasing social sensory processing according to the strength of any perceivable cues effectively removes distracting cues from the integration process, thereby reducing the dampening effects of weaker cues that can frequently arise simply through minor random motions. The result is that individuals sift energetically salient information from a scene while avoiding the associated costs, such as time lost for other activities (e.g. foraging–vigilance trade-offs [4,32,33,38]).

The simulation results also provide interesting parallels to recent laboratory studies. For instance, fish swimming in small groups of 2–30 individuals have been shown to primarily respond to their nearest 1–3 neighbours and these kinematic interactions appear largely driven by changes in individual speed [18,19]. Speed drives the interactions in the model when individuals adopt motion-guided attention. Likewise, motion-guided attention generates very similar

kinematic associations among nearest neighbours in similarly sized groups ( $G = 10$  and 25; figure 5b). Interestingly, as group size expands beyond the limits of the empirical data [18,19], the influence of one's nearest neighbours becomes progressively muted as group size increases. In the model, this occurs from local density effects over time, as groups compact and an individual's neighbours become more evenly distributed around it. While additional effects certainly play a role in local interactions (occlusion, collision avoidance), our results suggest a mechanism that may underlie both the limited interaction patterns observed in small groups [18,19] and the theoretical and empirical evidence supporting density-driven interactions in larger groups (i.e. attraction/avoidance of crowded horizons) [39,40]. The model also predicts that the role of minorities within a group can shift considerably when groups are exposed to different social contexts, which suggests that the quorum necessary to bias collective decision making may be equally affected (i.e. behavioural inter-dependencies and social context dictate the quorum; [1,2,41]). Our study focused on the short term, reflexive motions that may occur during rushed decisions [1], whereas time and the addition of social

cohesion may serve to shift the long-term leader–follower dynamics in social groups [12].

Selective attention is likely to be an important mechanism promoting collaborative decision-making processes in social organisms [13,14]. The basic properties of selective attention appear across a broad taxonomic range [26,37,42–44], which suggests a fundamental mechanism underlying basic social interactions in taxa spanning from bacteria to humans. These findings have broad inter-disciplinary potential, from re-evaluating vigilance trade-offs in foraging theory, advancing information exchange in distributed systems and expanding our biological understanding of dynamic networks.

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