Speeding Up Social Waves. Propagation Mechanisms of Shimmering in Giant Honeybees

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Abstract

Shimmering is a defence behaviour in giant honeybees (Apis dorsata), whereby bees on the nest surface flip their abdomen upwards in a Mexican wave-like process. However, information spreads faster than can be ascribed to bucket bridging, which is the transfer of information from one individual to an adjacent one. We identified a saltatorial process that speeds up shimmering by the generation of daughter waves, which subsequently merge with the parental wave, producing a new wave front. Motion patterns of individual "focus" bees (n = 10,894) and their shimmering-active neighbours (n = 459,558) were measured with high-resolution video recording and stereoscopic imaging. Three types of shimmering-active surface bees were distinguished by their communication status, termed "agents": “Bucket-bridging” agents comprised 74.98% of all agents, affected 88.17% of their neighbours, and transferred information at a velocity of \( v = 0.317 \pm 0.015 \) m/s. “Chain-tail” agents comprised 9.20% of the agents, were activated by 6.35% of their neighbours, but did not motivate others to participate in the wave. “Generator agents” comprised 15.82% of agents, showed abdominal flipping before the arrival of the main wave front, and initiated daughter waves. They affected 6.75% of their neighbourhood and speeded up the compound shimmering process compared to bucket bridging alone by 41.5% to \( v = 0.514 \pm 0.019 \) m/s. The main direction of shimmering was reinforced by 35.82% of agents, whereas the contribution of the complementing agents was fuzzy. We discuss that the saltatorial process could enable the bees to instantly recruit larger cohorts to participate in shimmering and to respond rapidly to changes in flight direction of preying wasps. A third, non-exclusive explanation is that at a distance of up to three metres from the nest the acceleration of shimmering could notably contribute to the startle response in mammals and birds.

Introduction

Shimmering [1–9] in giant honeybees (Apis dorsata) is one of the most sophisticated communication behaviours in insects. Shimmering takes place at the nest surface [1,3–9], which constitutes a matrix of densely clustered individuals arranged in a multi-layered stratum, forming the bee curtain [10] around a central, flat comb (Fig. 1A). In shimmering, individual bees flip their abdomens upwards, producing wave-like patterns (Movies S1, S2, S3, S4, S5, S6), which propagate across the nest surface in about one second, also affecting sub-surface layers [7–8]. Giant honeybees show this collective behaviour in response to threatening enemies, in particular to predatory wasps [6]. It is commonly accepted that colony defence is the primary goal of shimmering [6,11–12].

Some of the mechanisms of shimmering have been clarified [6–9,11–14], but it is not fully understood how the waves propagate [7–9]. Shimmering has been described as a Mexican-wave-like process [15], following the principles of bucket-bridging [7,9] to transfer information along a chain of agents, such as passing a bucket of water from one person to another to extinguish a fire in the old days. The bucket-bridging hypothesis of shimmering [7,9,12] predicts that surface bees are affected one-by-one continuously and linearly along a propagation line according to three principles: the first principle is that propagation is directed, whereby a surface bee is stimulated to participate in shimmering by her neighbour bees in those angular sectors where shimmering cohorts show maximal activity [9]. The second principle of bucket-bridging is that shimmering activity proceeds steadily from one agent to the next in a linear fashion [7,9]. The third principle is that information is transmitted in parallel chains of agents (for a summary of abbreviations and definitions, see Glossary S1). Theoretically, if information generated at a certain spot propagates in parallel queues at exactly the same velocity, the frontline of the wave would represent a single row of shimmering bees. Any deviation from this parallel propagation will broaden the wave front. The directivity in propagation based on these three principles was addressed in the directed-trigger hypothesis of bucket bridging [9].

Although shimmering is a collective, synchronized and cascading behaviour, each agent is seemingly free to decide whether to participate in shimmering or not. Furthermore, agents that do participate flip their abdomens at variable strengths and angles of up to 120°. The starting point of shimmering depends on the position of the threatening cue [11–12], from where it spreads into all directions, similar to mechanical analogues of water or sound waves [16–17]. However, shimmering does have different ways to propagate [9,11–12]. Apart from bucket-bridging [7–9], shimmering
waves appear to “jump” from specific sites to others [11–13], typically in increments of ten to fifteen surface bees, in a saltatoric process.

Here, we investigated the contribution of both, bucket-bridging [9] and saltatoric processes, to shimmering. The main characteristics of wave propagation were determined on the single bee level regarding recruitment, velocity and directionality, and three functional types of information transfer were distinguished. We found that the saltatoric process is associated with the generation of subordinate or daughter waves. By merging of daughter and parental waves, shimmering waves are speeded up by a factor of two to five, likely reinforcing the anti-predatory impact of shimmering [6].

Materials and Methods

Experimental conditions

Site and recording. The shimmering behaviour of giant honeybees was studied under field conditions during two expeditions to Nepal. The recording setup (see below) was established at three sites on the campus of the Tribhuvan University in Rampur (February 2009: nest A) and at the border of the Chitwan National park (February 2009: nest B [Fig. 1A]; November 2010: nest C). Two synchronized cameras were used to record black-and-white images with a resolution of 2,352×1,728 pixels (px), whereby one pixel covered approximately 0.30 mm in real-world coordinates. Therefore, the characteristic abdomen width of 6 mm of a giant honeybee was imaged by roughly 20 px. The cameras captured 60 frames per s (fps), resolving the abdomen-flipping phase of an individual bee of 200 ms within 12 frames (for further details see [6–9,12–13]).

Nests were also filmed with a high-definition video camera (Panasonic HVX 200) at 50 fps and a resolution of 1,280×720 px from distances between 1.5–10 m, whereby the camera angle always covered the whole nest. Nest B was used for an automated in-depth analysis of the data recorded for approximately 11,000 focus bees and 460,000 neighbour bees (see below). The validity of the results from nest B was confirmed by manual analysis of selected aspects from other nests (see Results). This confirmation, together with our previous experience with many other nests [5–9,11–13] made us confident that the parameters used to describe shimmering behaviour previously and in this paper do not represent colony- or nest-specific traits, but can be considered as representative for the behaviour of A. dorsata generally.

Dummy wasp stimulation of bees. For eliciting shimmering waves, colonies were stimulated with a dummy wasp fixed to a cable car device [7–9,13] at the sun-exposed side of the nests. A dummy with white, yellow and black stripes was made of Styrofoam (LxWxH: 40×15×15 mm) and suspended from a thin thread. Close to the mouth zone, the dummy was swung horizontally at an angle of 90° perpendicularly to the nest. The movement of the dummy was computer-controlled at variable velocities (0.1–0.5 m/s) and directions (towards and away from the nest). For more intense stimulation the dummy was connected to a 1.5 m long stick and moved manually (see Movie S1).

Characterization of shimmering

Identification of agents. In a giant honeybee nest, the colony members are arranged on both sides of the central comb in several layers, whereby several functional regions can be discerned, such as the mouth zone [10], the attachment zone, the rim zone and the quiescent zone [6–9,11–13]. Shimmering behaviour is mainly seen in surface bees in the quiescent zone [7–9,12]; Movies S1, S2, S3, S4, S5, S6), flipping their abdomens upwards at an angle of up to 120°. In each frame, such agents were identified individually by stereoscopic imaging [7,9] using the coordinates of their thoraces, measured as x- (horizontal directions), y- (vertical directions) and z- (directions towards and away from the comb) positions at resolutions of fractions of a millimetre. More than 600 agents were continuously tracked in successive frames throughout multiple shimmering processes. A total of over 50 episodes of 2 min duration, each comprising 2 waves, were recorded and analysed under defined stimulation protocols [7,9].
Definition of spreading directions. The bee curtain of giant honeybee nests displays a polar topology where the individual bees are arranged with their heads upwards and their abdomens downwards [7,9; Fig. 1]. Four key directions of wave spreading were defined (dir wave ∈ [L, R]), namely two horizontal directions (from Left to Right [L, R] and from Right to Left [R, L]), whereby Left and Right refer to the recorded image, and two vertical directions (from Top to Bottom [T, B] and from Bottom to Top [B, T]).

Assessment of motion strength. The image-analysis software Image-pro plus (Media Cybernetics) was used to measure the parameter $M_{xy}$ [7,9] that quantifies the motion of an individual agent bee. $M_{xy}$ refers to the luminance changes ($\Delta\text{lum}=\text{lum}[f]-\text{lum}[f_{-1}]$) in a 60 × 60 px zone around the thorax of the selected agent bee and was assessed in differential images (e.g., Fig. 1B, C1; [6-9,12-13,15]) by pixel-wise substractions of data from one frame $[f_{-1}]$ to the consecutive one $[f]$ at intervals of $\Delta f_{t}=|f_{-1}-f|$ = 16.67 ms (fps = 60 Hz). The value $M_{xy}$ includes mainly positional changes in horizontal (x-) and vertical (y-) directions, as well as movements of head, abdomen and extremities, such as legs, antennae or wings. Bees can move actively during shimming [9-14], flickering [12-13] or locomotion (i.e., moving around on the nest surface or penetrating into or emerging from the subsurface layers of the nest). Bees can also be shifted passively when affected by the movements of their immediate neighbours [7]. Values for quiescent conditions were $M_{xy}=0.3 \times 10^6\text{px per }\Delta f_{t}$, and for massive shimming activity they were $M_{xy}=1.10 \times 10^6\text{px per }\Delta f_{t}$. Values for $M_{xy}$ were normalised as $\text{rel}M_{xy}$ relative to the maxima in each recording [7,9], because they depend on conditions of video recording such as reduction filtering and segmentation.

Determination of time zero. When the wave front arrived at an agent bee, weak deflections in $\text{rel}M_{xy}$ values of the agent bee were assessed [7,9] even before she started to flip her abdomen (Fig. 2). Such small motions of an agent bee were caused by the shimming-active neighbours. During abdominal flipping, the $\text{rel}M_{xy}$ value sharply rises and peaks within 40 ms. In addition, the arrival of the wave can be traced by this parameter some frames before the sharp rise of $\text{rel}M_{xy}$ detected by the trigger algorithm at the time $t_{th}$ when the motion strength exceeded the threshold value according to $t_{th}=t[f_{th}]$ and $t_0=t[f_{th}-1]$.

For each shimming incident (Figs. 2,3A) the following parameters were assessed: (a) the start time zero ($t_{0}$) was defined one frame before the sharp rise of $\text{rel}M_{xy}$ detected by the trigger algorithm at the time $t_{th}$ when the motion strength exceeded the threshold value according to $t_{th}=t[f_{th}]$ and $t_0=t[f_{th}-1]$.

(b) The motion strength of the shimming incident of a selected agent was defined by the maximal $\text{rel}M_{xy}$ value measured within 10 frames after $t_{0}$. These strength values were graded in eight steps proportional to the $\text{rel}M_{xy}$ values (with motion strength categories $c_{M_{xy}} \in \{1...8\}$). Hereby, the assignment of $c_{M_{xy}}=1$ was particularly important, as this minimum level of active shimming motion of a selected agent bee had to be clearly distinguished from unambiguous (passive) sub-threshold motions (cf. Fig. 2A2). Only active, supra-threshold movements with $c_{M_{xy}} \geq 1$ were considered. In contrast to the agent-related $\text{rel}M_{xy}$ values the pseudo colours of differential images (Figs. 1–2,4–5) visualize the relative motion...
strength by the luminance differences pixel by pixel, scaled with \( \text{rel} M_{xy} \sim 0 \) on the rainbow palette.

**Focus bees and their neighbours.** The participation in shimmering greatly varies from agent to agent and ranges from passive motions (Fig. 2A2) caused by the approaching wave front to active participation with abdominal flipping at variable strengths (Fig. 3A). To support the automated evaluation and sorting of the various types of shimmering incidents, the concept of the focus bee was introduced. For every focus bee, two sets of neighbour bees (nb) were defined, which were positioned in the near neighbourhood (40 mm; Fig. 1C2) and in the far neighbourhood (>40 mm, <100 mm). The numbers were distinguished according to whether these neighbour agents had participated in shimmering before \( N_{\text{pre}} \) the wave front arrived at the focus bee, or afterwards \( N_{\text{post}} \). Thus, an agent bee was treated either as a focus bee, or as a neighbour bee.

In the in-depth study, focus-bee or neighbour-bee status was assigned to agents regarding all four main wave directions \( \text{dir}_{WAV} = R_{L}L \): \( N_{\text{fb}} = 2,823; N_{\text{nb}} = 138,190 \) [for >40 mm, <100 mm]/29,248
First, the *Nnb* wave before the focus bee for a given bee of an incident comparison, the thick grey line fl 01 gives the shows the scale for the relative motion strength (see Fig. 2). For better 4 (for distance measures, see Fig. 1B). The pseudo colour bar in panel 3 relative count of selected frames (ff 01–22), comparable to Figs. 1, 2 and right corners (1–6) show the panel count, small numbers give the

waves in the direction *Nfb* of all four data sets.

The time point $t_{fb}$ of a shimmering incident of a focus bee was used to define the potential trigger neighbour bee for a given shimmering incident (Fig. 3) by considering two criteria: First, the trigger neighbour must have already participated in the same wave before the focus bee; however, this participation was only considered if this neighbour was active within the time window of 88 ms ($\sim 5$ ff) prior to $t_{fb}$. Second, the agent defined as trigger neighbour had to be positioned closest of all other candidates to the focus bee and in her near neighbourhood. This criterion excluded those bees from analysis that flipped their abdomen outside the near

Figure 4. Propagation of a shimmering wave across the nest surface (survey view). This example refers to a wave that spread from left to right (dirWAV $= \{\text{L,R}\}$) in the image. Capital letters in the right corners (1–6) show the panel count; small numbers give the

Figure 5. Propagation of a shimmering wave across the nest surface (detail view). The same wave is shown as in Fig. 3 but zoomed (for distance measures, see Fig. 1C).Continuous sequence of frames as pseudo coloured differential images and inverted video images; numbers (01–14) indicate the relative frame counts (fps = 60 Hz with interframe intervals of 16.67 ms). Scale below panel f 07 shows the relative motion strength (see Fig. 2). Red dots indicate the selected focus bee (the same as in Fig. 4) that started to flip her abdomen at f 02, acting as a generator bee for the subsequent daughter wave. One of her neighbours (marked with a yellow arrow) was passively shifted in f 05 and started the abdominal flip in f 06. The resulting daughter wave merged with the *parental* wave at f 10. The red curves on the left side of the images are shown for comparison with the initial position of the *parental* wave front as indicated in f 01.

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![Image 58x406 to 297x730](image1)

![Image 315x408 to 553x730](image2)

neighbourhood (in many cases such bees generated daughter waves; Figs. 1–2, 4–5). The trigger direction of a focus bee ($z_{TRIG}^{fb}$) was defined by the angle of the direction of her trigger neighbour, measured from the position of the focus bee, categorized according to the eight sectors of neighbourhood ($dirNH \in \{1..8\}$; Fig. 1C2) in which the trigger neighbour was positioned.

Relative time scales of focus bees and their neighbours. The time courses of the shimmering incidents of selected neighbour bees were synchronized to the time $t_{fb}$. This synchronization conjoined the movements of focus bees and her triggering neighbours with the positional ($x,y,z$) parameters and the $\text{rel} M_{xy}$ values. This enabled sorting and pooling of identified focus bees and their neighbours, collected at different locations and times according to main wave directions ($dirWAV \in \{1..4\}$), motion strengths ($c_{MN} \in \{1..8\}$), and trigger directions ($dirTRIG \in \{1..8\}$) for further statistical analysis.
Benchmarking of bucket-bridging. Bucket bridging was characterised for manually selected agents by the assessment of the information transfer between two neighbouring bees (Fig. 2A), and over a chain of adjacent agents (Fig. 2B). The thorax-to-thorax distances were calculated in mm. A motion detection method was used that utilized differential images (see above) considering the following criteria [9]: (a) Chains of agent pairs were selected (Fig. 2), in which emitter bees (which flipped their abdomen first) could clearly be distinguished from receiver bees (which followed the action of the emitter bee) throughout a continuous and linear sequence of actions. (b) Emitters and receivers participated in the same chain (see Introduction and [9]). (c) Bees were excluded from data assessment if they did not show any interaction, if they were activated synchronously (instead of sequentially, i.e. they did not participate in the same chain) and if they showed abdominal flipping with a delay larger than 167 ms (=10 ff). (d) In differential images, the temporal information transfer was estimated using the abdominal flipping of the emitter and the receiver bee. The time t0 was determined by weighting $M_{sy}$ values in deciles whereby $relM_{sy} = 0.0$ indicated quiescence of the focus bee ($\Delta lum<5$), and $relM_{sy} = 1.0$ defined a fully lifted abdomen. The first and last frames ($f1,f_{last}$) with traces of motions of individual agents were weighted accordingly ($relM_{sy}[f1]$, $relM_{sy}[f_{last}]$) to estimate the start and end points of information transfer ($t_{start}$, $t_{end}$) by bucket bridging. This measure retraced the start point of abdominal flipping by retrograde extrapolation (Equation 2a) on the basis of the weighting value $relM_{sy}[f1]$. Similarly, the abdominal flipping of the last bee in a chain was calculated by determining the last frame ($f_{last}$) with motion activity by prograde extrapolation (Equation 2b):

$$t_{start} = t[f1] - (\Delta t_f \times relM_{sy}[f1])$$

(2a)

$$t_{end} = t[f_{last}] + (1 - relM_{sy}[f_{last}] \times \Delta t_f)$$

(2b)

Ethics Statement

The research expedition to Chitwan, Nepal, entitled “Study on the behaviour of the giant honeybees: Observations and recording of behaviours at the nesting site” was supported by the Rector of the Centre for International Relations of the Tribhuvan University (Kathmandu, Nepal).

Results

Bucket-bridging

An example of bucket bridging is shown in differential images in Fig. 2A1–4 (ff 74–79 corresponding to 100 ms). The emitter bee showed maximum activity in f 76. The silhouette of the receiver bee was already visible in f 76, when it was slightly moved passively by the advancing wave front. In f 77, the shape of the right forewing of the receiver bee appeared, indicating active participation in shimering. In f 79 her abdomen started to be lifted actively, followed by a massive motion of the whole body accompanied by a beat of both wings.

An individual abdominal flipping typically lasts 67.16±0.97 ms (mean ± SE; n = 174 abdominal flips; Figs. 2, 3A, 4; [14]). The manually evaluated shimering waves (n = 47) showed that information transfer between adjacent shimering-active neighbours (positioned at distances $d_{bb} = 15.94\pm0.66$ mm, where bb stands for bucket bridging) was completed within $\Delta t_{bb} = 39.16\pm2.84$ ms (Fig. 2A1–4), corresponding to a velocity of $v_{bb} = 0.5085\pm0.0413$ m/s. However, with $v_{bb} = 0.317\pm0.0145$ m/s the speed was lower when assessed over a short chain of agents (Fig. 2B, $n_{bb} = 2.60\pm0.17$ bees; $d_{bb} = 43.32\pm1.98$ mm; $\Delta t_{bb} = 107.90\pm5.30$ ms; n = 40 shimmering waves). We then used this speed value ($v_{bb}$ = 0.317 for nest B) as a benchmark for characterizing the bucket-bridging process. For comparison, similar speed values were found for nests A and C (nest A: $v_{bb} = 0.2461\pm0.0193$ m/s, n = 28 shimmering waves; nest C: $v_{bb} = 0.3598\pm0.0263$ m/s, n = 26).

Saltatoric processes

Saltatoric wave propagation involves bees that are more than 80 mm away from the approaching wave front, and lift their abdomens typically 30–50 ms earlier than other participants in their own near neighbourhood. These bees generate daughter waves and are termed generator agents. In Figs. 4, 5 (compare Movies S1, S2, S3), one of these generator agents is marked by a red point on the thorax. During the abdominal lifting of this agent (ff 02–06, Fig. 5), the parental wave (pw) moved from left to right in the image. Using the position of the wave front in two subsequent frames the velocity of the parental wave was found to be $v_{pw} = 0.239$ m/s, which is in the same order of magnitude as calculated for bucket bridging in the same nest (Fig. 2A).

In f 09 of Fig. 4 the daughter wave is visible as a small circular batch, and in f 12 this daughter wave started to merge with the parental wave. The frontline of the parental wave “jumped” from the left to the right side of the daughter wave (from f 10, immediately before the daughter wave merged with the parental wave, to f 11, just after merging) within 16.67 ms or even less. The frontline of the merged waves advanced over a distance of 160 mm, which corresponds to an acceleration of the shimering velocity ($v_{sh}$) to a value of at least 0.960 m/s by saltatoric information transfer. This is roughly three times faster than bucket-bridging alone.

Fig. 5 demonstrates the saltatoric information transfer in more detail for the same focus bee. This bee started abdominal flipping in f 02, and one of her neighbours joined 70 ms later (marked by a yellow arrow, first visible in ff 04–05). Subsequently, other neighbours followed, producing a daughter wave. The parental wave on the left side of the image continued to spread to the right, while the daughter wave spread into all directions by bucket bridging. Finally, 170 ms after the start of abdominal flipping of the generator bee (in f 10), the daughter wave merged on its left side with the parental wave, while the frontline of the merged waves “jumped” to the right side of the former daughter wave.

Propagation velocity of shimmering waves

A shimmering wave lasts up to 800 ms (Fig. 3B) and includes the ascending phase of 200–300 ms, in which the number of synchronously shimmering surface bees increases to the maximum, the climax phase, when a maximum number of agents were simultaneously active (lasting approximately 200 ms), and the descending phase (300–400 ms), in which the number of synchronously shimmering surface bees decreases ([6,12] and Fig. 3B). When measured from the start to the end of a wave by the detection of the positions of the wave fronts in differential images (Figs. 1–2,4–5), $v_{sh}$ was calculated to be 0.367±0.020 m/s (n = 10 waves, see Movies S1, S2, S3), similarly slow as for bucket bridging. Alternatively, when measured during the climax phase, $v_{sh}$ was 0.514±0.019 m/s, significantly (P<0.01, Student’s t-test) faster than the benchmark value for bucket bridging ($v_{bb}$ = 0.325 m/s). The $v_{sh}$ value for the climax phase was calculated for the wave direction $dir_{wAV} = \theta_{R,L}$ regarding nest B by selecting pairs of agents that
were positioned horizontally (at an angle of $\alpha_{WAV} = 7.95 \pm 5.40^\circ$; $n = 41$ waves; definition of angle of wave direction in Fig. 1C2) at a distance of $112.90 \pm 4.08$ mm between those emitters and receivers that were subsequently affected by the same wave fronts within ten frames or more ($226.06 \pm 8.21$ ms) in a straight line (cf. Fig. 2B).

This $v_{th}$ value of $0.514 \pm 0.019$ was taken as a benchmark value for the mixed propagation mode (bucket bridging and saltatoric processing). Hence, $v_{th}$ during the climax phase is faster than during the start or the end phases, likely due to the higher probability of the occurrence of saltatoric events.

**Communication statuses of agents**

The contributions of individual agents to the spreading of shimmering waves, i.e. to bucket bridging or saltatoric propagation were assessed by automated techniques using the algorithms described below. The “communication status” of a focus bee was characterized spatially and temporally by considering her neighbours in the near neighbourhood as a reference region ($<40$ mm, see schematic in Fig. 6), and the pre-stroke and post-stroke intervals of $\pm 167$ ms ($\pm 10$ ff) as a reference time window, whereby the abdomen flipping commenced at the time $t_0$. Shimmering waves were assessed regarding four wave directions (Table S1, [7]), and for in-depth analysis of communication status the wave direction

![Communication statuses of agents](image)

Figure 6. Definition of three communication statuses of surface bees (shown for the wave direction $dir_{WAV} = L/R$). Sketches of activity plots for distinguishing the statuses (I,II,III) of focus bees. (A1–3) Focus bees are marked by red full rectangles at $t_0$; abscissa, time in frames (fps = 60 Hz) in relation to $[t_0/2]$ when the focus bee started her flipping; ordinate, distance of neighbours from the focus bee in mm; grey thin horizontal lines symbolize the quiescent state of the sample agents; small full rectangles with numbers mark the onset of their abdominal flips; orange coding refers to positions of the neighbours within the near neighbourhood ($<40$ mm) with flipping activities within the critical time window of $\pm 10$ ff; black coding refers to complimentary attributes ($>40$ mm; $>\pm 10$ ff). Thick horizontal lines (black, orange, red) symbolize that abdomen flipping is still going on. (B1–3) The panels Pre $t_0$ and Post $t_0$ display the near neighbourhood of a focus bee which is marked black when quiescent and marked red when she flips her abdomen. The numbers and colour codes of shimmering-active neighbours are the same as in the panels $A_{1,2,3}$; arrows of the central panels (regarding the time $t_0$) explain the directions of information transfer: status I (bucket-bridging) agents in the pre-stroke (Pre $t_0$) phase receive mechanical information (full orange arrows) predominantly from the side where the wave came, in the post-$[t_0/2]$-stroke (Post $t_0$) phase information is transmitted predominantly to the side where the wave is spreading (open red arrows); status II (chain-tail) agents receive and emit mechanical information but fail to recruit other neighbours as transmitters; status III (generator) agents utilize predominantly visual information from the threatening cues, but not from shimmering-active agents in their near neighbourhood. They are leaders in emitting mechanical information and generate parental or daughter waves.

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Three communication statuses (I–III) of focus bees were distinguished. Status I agents are driven by shimmering-active neighbours in the pre-stroke phase, positioned at their ipsi-directional side (from where the wave came), passing information on to their contra-directional side (to where the wave is continuing) in the post-stroke phase (Fig. 6A1,B1). This strategy of propagating information conforms to bucket-bridging [7,9], and these bees are termed bucket-bridging agents. They comprised the majority of surface bees and were represented by 54.33% of agents at a reference window of ±2 ff (whereby ‘−2 ff’ defines the time window in the pre-stroke phase and ‘+2 ff’ the time window in the post-stroke phase). The number of bucket-bridging agents increased (Fig. 7A1–2,B1) with the reference time window (±10 ff) up to a value of 74.98±2.83%. This increase was due to the definition of status II agents (Fig. 6A2,B2; see below), which may turn into bucket-bridging agents with increasing length of the reference window (Fig. 7). The neighbours of the bucket-bridging agents were similarly large in number in the pre-stroke and post-stroke phases (Fig. 7C1, Table S2: Nnb [at −10 ff] = 7.56±0.90; Fig. 7C2: Nnb [at +10 ff] = 6.06±1.16) corresponding to 47.16% of all shimmering-active neighbours evaluated in the pre-stroke phase and to 41.01% of neighbours in the post-stroke phase.

In Fig. 8A, these bucket-bridging agents were sorted into two classes based on the number of shimmering-active neighbours in the pre-stroke and post-stroke phases (class 1 : fb [Nnb [pre] < Nnb [post]]; class 2 : fb [Nnb [pre] > Nnb [post]]). Hereby, the maximal numbers of neighbours found for focus bees were similar for both phases (max Nnb [pre] = 24; max Nnb [post] = 26) and both classes showed similar percentages (class 1: 50.27%; class 2: 49.73%; P = 0.1925, χ² (test) with a polynomial distribution, when sorted in steps of 0.1 parts of the ratio Qnb = Nnb [pre] / Nnb [post]; Table S1). This data symmetry applies to all phases of a shimmering wave (ascending, climax or descending phase; Fig. 3B and [6]). Furthermore, the selected wave direction ddir WAV = −1 R L (red symbols in Fig. 8) was found to be representative of all four wave directions investigated (black symbols in Fig. 8), which shows that shimmering is invariant regarding the direction of wave propagation (cf. [9]).

Status II agents flip their abdomens triggered by their shimmering neighbours, (Fig. 6A2,B2), but thereafter their new neighbourhood becomes quiescent. These bees terminate the information transfer in their chains and are, henceforth termed chain-tail agents. The relative numbers of chain-tail agents increased from rel Nb = 9.20±0.94% (at −10 ff, corresponding to 166.67 ms, where rel N stands for relative number in per cent) to rel Nb = 28.46±3.14% (at −2 ff=33.33 ms; Fig. 7B2) and had Nb = 7.28±0.57 shimmering-active neighbours at −10 ff (Fig. 7C3, Table S1).

In contrast to chain-tail agents, Status III agents (Fig. 6A3,B3) are not triggered by their neighbours [<40 mm] in a reference time window in the pre-stroke phase of −10 ff but flip their abdomens before their neighbours do so. They generate parent or daughter waves (as demonstrated in Figs. 1,4–5 and Movies S1, S2, S3, S4, S5, S6) and are termed generator agents. In contrast to status-I and II agents, generator agents occurred at numbers which were roughly independent of the length of the post-stroke phase (at +3 ff=50 ms: rel Nb = 17.65±2.69%; at +10 ff: rel Nb = 15.82±2.61%; Fig. 7B4, Table S1) and activated Nb = 6.36±0.45 neighbours at +10 ff (Fig. 7C4; Table S1), which corresponds to rel Nb = 6.75% of the shimmering-active neighbours of all surface bees.

In Fig. 3B,C chain-tail and generator agents were sorted according to the number of shimmering-active neighbours in the pre-stroke (−10 ff) and post-stroke (+10 ff) phases. These data distributions allow discerning agents with less than five shimmering-active neighbours (subgroup 1), and those agents with more than five active neighbours (subgroup 2). In both agent types, subgroup 1 was larger, while subgroup 2 converged to zero with increasing
numbers of active neighbours (Table S1). Hence, only few shimmering-active neighbours (<5) suffice to trigger both agent types.

Acceleration of shimmering by saltatoric propagation

The propagation of shimmering is based on complex synchronous and cascaded recruitment of surface bees, and was simplified in a mathematical model (see lookup tables in Fig. 9) that considers both the bucket bridging and the saltatoric propagation mode under climax conditions. This model allows to assess the impact of both processes on the $v_{sh}$ of the compound wave considering three parameters (where bb stands for bucket bridging and sp for the saltatoric propagation): (a) $v_{sh}$, this is the $v_{sh}$ under solely bucket-bridging conditions (Fig. 9A), where $v_{sh}$ was varied in the model from 0.10 to 0.45 m/s (the benchmark value is 0.317 m/s, see above); (b) $v_{sp}$, this is the $v_{sh}$ characterised by the saltatoric propagation, which was set to $v_{sp} = 0.800$ m/s (Fig. 9A–C); this velocity was slightly below the value of $v_{sh} = 0.960$ m/s that was found for a single saltatoric jolt of the wave front in the example in Fig. 4 (note that $v_{sp}$ is only of theoretical relevance because a real shimmering wave never spreads saltatorically alone and that bucket bridging is the dominant propagation mode of shimmering); (c) the distance $d_{E - R}$ between the emitters and the receivers (E–R) in a chain of bucket-bridging agents; according to the conditions in the nest $d_{E - R}$ was varied from 20 to 45 mm (Fig. 9C,D). These three parameters were used to describe two wave properties that result from the combination of bucket-bridging and saltatoric propagation: First, the factor $k_{bb}$ (Equations 3a,b) by which shimmering is speeded up by the saltatoric process (Fig. 9A,B).

$$v_{sh} = v_{bb} \times k_{bb} + v_{sp} \times k_{sp}$$ (3a)

with the weighting factors in %: $k_{sp} = 1.100$ and $k_{bb} = 100 - k_{sp}$.

For the above benchmark values under climax conditions ($v_{sh} = 0.514$ m/s; $v_{bb} = 0.317$ m/s) the impact of the saltatoric component ($v_{sp} = 0.800$ m/s) was $k_{sp} = 41.5\%$ for $v_{sh}$ (Equation 3b) and the complementary $58.5\%$ for $k_{bb}$ (Fig. 9B). Second, $I_{dec}$ was considered, the time interval within which an agent “decides” whether or not to participate in shimmering (Fig. 9C; conforming with $I_{dec} = d_{E - R} / v_{sh}$).

The values of $I_{dec}$ calculated for the distance of $d_{E - R} = 25$ mm (which is characteristic for the side-to-side distance between bees at the surface of the bee curtain) ranged from 78.86 ms for mere bucket-bridging ($v_{sh} = 0.317$ m/s) to 48.33 ms (Fig. 9C) for the combination of bucket bridging and saltatoric propagation Fig. 9A ($I_{dec} = 41.5\%$; $v_{sp} = 0.8$ m/s).

Directional control in shimmering

Theoretically, the simplest way of wave propagation is by spreading energy along a straight line by directed and non-stochastic processes. In shimmering, information is transferred by bucket bridging and saltatoric propagation: First, the factor $k_{bb}$ (Equations 3a,b) by which shimmering is speeded up by the saltatoric process (Fig. 9A,B). $k_{bb} = (v_{sh} - (v_{bb} \times k_{bb})) / v_{sp}$ (3b)
PEAK and SINK concepts. The directed-trigger hypothesis [7, 9] predicts for every focus bee that their shimmering-active neighbours are distributed in angular sectors ($\theta_{Nh}$) of the near neighbourhood according to Equation 4.

$$P_{Nh} [\theta_{Nh}] = \text{rel} N_{ab} \times \sin^2(\theta_{Nh})$$

where $P_{Nh}$ is the probability of the occurrence of shimmering-active neighbours ($\text{rel} N_{ab}$) of a focus bee at the respective angle $\theta_{Nh}$ (for definition, see Fig. 10A).

The directed-trigger hypothesis postulates that in the pre-stroke phase of a shimmering incident the most shimmering-active neighbours ($\text{rel} N_{ab}$) of focus bees are at the ipsi-directional side (where the wave is propagating from; see red arrows in Fig. 10A), and the least neighbours are present at the contra-directional side (where the wave is propagating to). For the pre-stroke phase, this hypothetical distribution of neighbours is described by Equations 5a, b and displayed in Fig. 10C1, E1, where blue curves show the maximal rates of shimmering neighbours $\text{rel} N_{ab}$ at the ipsi-directional side defined by $\theta_{Nh} \equiv \theta_{WAV} = 0^\circ$ (under $\text{dir}_{WAV} = / R, L$). The distribution pattern shown in these curves is referred to as PEAK distribution pattern.

$$\text{PEAK}_{\text{min}} P_{Nh} = P_{Nh} [\theta_{Nh} \equiv 180^\circ]$$

In the post-stroke phase, the hypothetical distribution of shimmering-active neighbours conforms to the SINK distribution pattern, with a maximum occurrence of $\text{rel} N_{ab}$ at the contra-directional side and a minimum occurrence of $\text{rel} N_{ab}$ at the ipsi-directional side for $\theta_{ab} \equiv \theta_{WAV} = 0^\circ$ (see Equations 6a, b; green curves in Fig. 10 D1, F1).

$$\text{SINK}_{\text{min}} P_{Nh} = P_{Nh} [\theta_{Nh} \equiv 0^\circ]$$
Matching the empirical data with the hypothetical PEAK and SINK patterns

The empirical \(r_{\text{rel}}N_{\text{nb}}\) data were plotted against \(\alpha_{\text{Nh}}\) and the resulting distributions compared with the hypothetical PEAK and SINK distribution patterns. \(r_{\text{rel}}N_{\text{nb}}\) data of all three agent types (bucket, chain-tail and generator agents) were tested for correspondence with the hypothetical PEAK and SINK distribution patterns by cross-correlation according to Equation 7.

\[
P_{\text{Nh}}[\alpha_{\text{Nh}} + \beta] = r_{\text{rel}}N_{\text{nb}} \times \sin^2(\alpha_{\text{Nh}} + \beta)
\]

Here, the neighbourhood angle \(\alpha_{\text{Nh}}\) (for definition, see Figs. 1C, 10A) was altered by the deviation angle \(\beta\) in steps of 45° (with \(-180° \leq \beta \leq +180°\)) to identify the best match between the empirical data (displayed by full circles and vertical lines) and the PEAK and SINK curves. The hypothetical PEAK and SINK curves were calculated using the empirical differences between \(r_{\min}N_{\text{nb}}\) and \(r_{\max}N_{\text{nb}}\) values for each agent type as reference (the normalized forms are indicated as \(\{P_{\text{Nh}}\}\)). The sums of the square differences between the \(r_{\text{rel}}N_{\text{nb}}\) values with the \(\{P_{\text{Nh}}\}\) values were calculated for every angular step of neighbourhood \([\alpha_{\text{Nh}} + \beta]\) of the focus bees. The total deviation \(\text{DEV}\) over the total range of neighbourhood \((\text{dir}_{\text{Nh}} \in [1, 8])\) between the empirical values \(r_{\text{rel}}N_{\text{nb}}\) and the normalized PEAK and SINK values were determined by Equations 8a,b.

\[
\text{PEAK DEV} = \sqrt{\sum_1^6 \{r_{\text{rel}}N_{\text{nb}} - P_{\text{Nh}}[\alpha_{\text{Nh}} + \text{PEAK}\beta]\}^2}
\]

\[
\text{SINK DEV} = \sqrt{\sum_1^6 \{r_{\text{rel}}N_{\text{nb}} - P_{\text{Nh}}[\alpha_{\text{Nh}} + \text{SINK}\beta]\}^2}
\]

with \(\text{PEAK}\beta = 180°\) and \(\text{SINK}\beta = 0°\).

Their reciprocal values constitute the goodness of the fit \(\text{PEAK}\ G\) and \(\text{SINK}\ G\) (Equations 9a,b) which can be tested using the \(\chi^2\)-test.

\[
\text{PEAK} G = G[\alpha_{\text{Nh}} + \text{PEAK}\beta] = 1/\text{PEAK DEV}
\]

\[
\text{SINK} G = G[\alpha_{\text{Nh}} + \text{SINK}\beta] = 1/\text{SINK DEV}
\]

Furthermore, the probabilities \(\text{PEAK} P_m\) and \(\text{SINK} P_m\) for the match between the empirical data and the hypothetical PEAK and SINK distribution patterns was calculated according to Equations 10a,b, explaining the coincidence of the agents’ directional properties with the directed-trigger hypothesis.

\[
\text{PEAK} P_m = 1 - \text{PEAK DEV}
\]

\[
\text{SINK} P_m = 1 - \text{SINK DEV}
\]
The angular positions \((\alpha_{Nh} + \beta_i)\), at which the DEV values exhibit a minimum (Fig. 10C2–F2), represent the maximal goodness \((\text{max} G)\) of the fit (Fig. 10C1–F1). The resulting angular mismatch (MM) between the empirical data and the hypothetical PEAK and SINK distribution patterns was estimated by Equation 11, defined as the absolute deviation between the angle \(\alpha_{Nh}\) (the angle with the minimum value of PEAK or SINK patterns, see Fig. 10C1–F1), and \(\beta_{Nh}\) (the angle with the maximum goodness of the fit, see Fig. 10C2–F2).

\[
\Theta_{MM} = |\alpha_{Nh} - \beta_{Nh}|
\]  

Finally, the level \(E_{dirWAV}\) by which the different agent types contributed to the propagation of the main wave direction was estimated according to Equation 12.

\[
E_{dirWAV} = \text{rel} N_{nb} \times \frac{\text{max} - \text{min} \Delta N_{nb}}{\text{max} - \text{min} \Delta N_{nb} \times P_{m} \times f_r}
\]

where \(\text{rel} N_{nb}\) is the occurrence of shimmering-active neighbours of a focus bee in her near neighbourhood; \(\text{max} - \text{min} \Delta N_{nb}\) is the percentage of active neighbours in defined \(\alpha_{Nh}\) angles between maximal and minimal occurrences of \(\text{rel} N_{nb}\); \(P_{m}\) is the probability for the match between the empirical data and the hypothetical PEAK or SINK distribution patterns (Equations 10a,b); \(f_R\) is the reinforcement factor with \(f_R = +1\) when the main wave direction is reinforced and \(f_R = -1\) when the main wave direction is restrained.

**Matching bucket-bridging agents.** The bucket-bridging agents conformed to the directed-trigger hypothesis under pre-stroke and post-stroke conditions (Fig. 10C1–D1) in different ways: the shimmering-active neighbours in the pre-stroke phase matched the PEAK distribution pattern four times more likely...
\( \text{PEAK } P_G = 0.0061, \ \chi^2\text{-test} \) than the SINK distribution pattern (Fig. 10 C1–2; Table S2; \( \text{PEAK } DEV = 5.39\%; \text{SINK } DEV = 19.28\%; \text{PEAK } G = 18.54; \text{SINK } G = 5.19; \text{PEAK } \Theta_{MM} = 0\%) \) and the factors calculated from equation 8 were \( \text{ref } N_{hab} = 0.4716; \text{max} - \text{min } \Delta N_{hab} = 0.3697; \text{PEAK } P_m = 0.9461; f_R = +1 \). Conversely, in the post-stroke phase the shimmering-active neighbours matched the SINK distribution pattern rather than the PEAK distribution pattern (Fig. 10 D1–2, Table S2; \( \text{PEAK } DEV = 19.20\%; \text{SINK } DEV = 25.77; \text{PEAK } G = 21.87; \text{SINK } G = 4.57\%; \text{PEAK } P_m = 0.0014, \chi^2\text{-test}; \text{SINK } \Theta_{MM} = 0\%) \). The factors calculated from equation 8 were \( \text{ref } N_{hab} = 4.1011; \text{max} - \text{min } \Delta N_{hab} = 0.4073; \text{SINK } P_m = 0.9543; f_R = +1 \). The total estimate of the influence of bucket-bridging agents to contribute to the wave propagation in the main shimmering direction was 32.44%, by adding up the \( E_{BRL} \) value in the pre-stroke phase (16.50%) and that in the post-stroke phase (15.94%); Fig. 11B, Table S2).

**Matching chain-tail agents.** The angular distribution of shimmering-active neighbours of the chain-tail agents agreed stronger with the SINK than the PEAK distribution pattern \( \text{PEAK } DEV = 9.23\%; \text{SINK } DEV = 20.04\%; \text{PEAK } G = 10.83; \text{SINK } G = 4.99; \text{PEAK } P_D = 0.0459, \text{PEAK } P_G = 0.1421, \chi^2\text{-test}; \text{Fig. 10 E1–2, Table S3}, \) showing a small mismatch with the PEAK-pattern (Fig. 10E, \( \text{PEAK } \Theta_{MM} = 45^\circ, \text{SINK } \Theta_{MM} = 0\%) \). This result shows that chain-tail agents can be identified by their match with the PEAK distribution pattern in the pre-stroke phase, and as they are the last agents in a chain they are the components that terminate the chain. Their contribution to shimmering \( \left( E_{BRL} = -2.20\% \right) \) can be considered as constraining the wave propagation, which is noted by the negative value of \( f_R \) \( \text{ref } N_{hab} = 0.0556; \text{max} - \text{min } \Delta N_{hab} = 0.4781; \text{PEAK } P_m = 0.9077; f_R = -1; \text{Fig. 11B, Table S3} \).

**Matching generator agents.** In their post-stroke phase, generator agents activate their neighbours. Their distribution pattern agreed twofold more with the SINK than the PEAK pattern \( \text{SINK } DEV = 8.79\%; \text{PEAK } DEV = 15.61\%; \text{PEAK } G = 6.40; \text{Table S4}, \) although this difference was not significant \( \text{PEAK } P_D = 0.1669, \text{SINK } P_D = 0.2390, \chi^2\text{-test}. \) There was a small mismatch with the SINK pattern \( \text{SINK } \Theta_{MM} = 45^\circ; \text{pre } \Theta_{MM} = 180^\circ; \text{post } \Theta_{MM} = 135^\circ \). This result shows that shimmering-active bees [7,9] to join the wave. This result shows that shimmering-active bees [7,9] to join the wave.

\[ \text{Discussion} \]

**Applying swarm models to giant honeybees**

Shimmering in giant honeybees [1–9,11–14] is an intricate communication behaviour based on swarm intelligence [18–20] with emergent [20–23] social waves. The term swarm [24–26] is used for the ability of aggregations of similar morphological units to self-organize [19–22], form patterns, store information, and reach collective decisions [26–28]. Swarms display fluidity and uniformity in response, which emerge in dynamic behavioural patterns, such as in fish schools [26–28], in the fast ephemeral rolling patterns of starlings flocks [in particular under predation by falcons or gulls [24,29]], in the huddles of emperor penguins [30] or in groups of moving mammals [28,31]. The simplest mathematical model of an animal swarm defines individual agents with a Lagrangian approach [24,31–32], which have a gradient of repulsion and alignment around them following three rules: (a) move in the same direction as your neighbours, (b) remain close to your neighbours, and (c) avoid collisions with your neighbours. However, shimmering in giant honeybees does not match this swarm model: shimmering-active bees do not change their relative position in the bee curtain, and they move only parts of their body (Movies S1, S2, S3; [12]), although with the potential to generate directed moving patterns.

**Goals of social waves**

Social waves are hallmarks of animal aggregations. Besides giant honeybees, which display shimmering waves in response to wasps, birds and mammals [4–6,12], social waves have also been described for avian flocks [24,29,37,40–45], for the huddles of Emperor penguins [30], and for aggregations of humans in football stadiums [15]. A main question concerning social waves is whether they are advantageous for the aggregation, having received evolutionary function and conveying fitness benefits, or alternatively, whether they are simply a mere epiphenomenon of reactivity [43]. In the following, this question is discussed comparing the ephemeral rolling patterns in starlings and the shimmering waves in giant honeybees.

**Waves in starling flocks.** Starlings form flocks especially before they roost, to effectively maintain cohesion of the group, strongly supporting survival [37,41–42]. Under predation they...
display spectacular ephemeral rolling patterns. Individual starlings may be kept informed in the flock about the progress and the state of such an ongoing “wave” by continuous inspection from the momentary vantage point. In reality, this information is restricted to a topological group of 6–7 neighbours [37]. Although an individual starling has some room to modify its decision to participate in the concerted flight manoeuvre, it cannot decline to conjointly move together with its neighbours. This constraint is less due to the potential danger of being eaten by the predator [29] but more due to the danger of collision [37, 41–42]. These rolling patterns display trains of pulses of optical density that propagate across the flock and are produced within the swarm body, mostly without affecting the swarm surface. The authors explain [29] that such pulses are formed in proximity to the bird of prey, mostly laterally, and are propagated typically away from it. These patterns may lead to confusion [6, 46] of the predator and encounter dilution [47] but the cause for their evolution is only poorly understood.

**Shimmering waves.** The goals of shimmering [5–13] in giant honeybees differ from the rolling waves of starling flocks [29, 37, 41–42] in the following ways: Shimmering waves are produced by stationary agents (Movies S1, S2, S3, S4, S5, S6). Most of the colony members, including those in subsurface layers or at the opposite comb side, continually receive information about the shimmering status mechanocentrally [7–9, 12]. Surface bees also release Nasonov pheromone [30], motivating others to participate in the wave. Shimmering giant honeybees may or may not join the wave, and if they join, they can determine when to start their contribution and at which strength [7, 9]. Both, starlings and giant honeybees have the potential to respond rapidly to changing visual cues, and in both cases directivity seems to be strongly controlled.

In giant honeybees, the directivity of bucket bridging was described previously [8]. In the present work, we show that the majority of shimmering-active bees (63.13%) do not contribute to the wave-propagation in the main direction (Fig. 11B3). Of the other 36.82% of the shimmering-active bees which contribute to the directional control, 90.09% are bucket-bridging agents, 5.90% are chain-tail agents and 5.99% are generator agents (Table S2, S3, S4). **Generator agents** are less affected by the oncoming wave than the other two agent types (Fig. 7Bb, 10F), contributing less, and fuzzily, to wave direction control. This fuzziness of generator agents is important, because it enables rapid changes in wave direction in response to rapidly moving cues (cf. [39]).

**Why do giant honeybees speed up shimmering waves?**

Taken together, the aspects discussed above appear to contribute to the confusion and repulsion of predators [6, 12, 39], but they cannot explain why saltatoric propagation has evolved. Three possible explanations for this conundrum are discussed below: saltatoric propagation could reinforce (a) the recruitment of shimmering agents, (b) the repelling effect on preying wasps by directed visual patterns and (c) the bottom-up attention in vertebrate predators.

**Saltatoric propagation reinforces recruitment.** More agents are recruited when shimmering is accelerated above the “base” speed of bucket bridging \(v_{\text{BP}} = 0.317 m/s\) by saltatoric propagation \(v_{\text{BP}} = 0.517 m/s\) than during bucket bridging alone (Figs. 1–2, 3–4, 9). This increased recruitment is due to the generation of daughter waves, causing rapid, exponential growth of the visual pattern with a concomitantly greater repelling effect, which likely benefits the giant honeybee colony. This explanation is in agreement with previous findings [6] that more bees contribute to shimmering the faster and the nearer to the bee nest a preying wasp flies.

**Saltatoric propagation increases the repelling effect on preying wasps by directed visual patterns.** Giant honeybees have the capability to align the direction of their shimmering waves with the flight path of a preying wasp [6, 39]. In this prey-predator interaction both, the bees and the wasp emit signals and both respond to stimuli of their counterparts, whereby the honeybees can change the direction of their shimmering waves faster than the wasps can turn [39]. This asymmetry between bee and wasp is based upon the greater speed of wave propagation and the fuzziness in directional control by saltatoric propagation.

**Saltatoric propagation may reinforce bottom-up attention in vertebrates.** Giant honeybees display shimmering in response to wasps, but also to birds and mammals that approach the nest within distances of about 3 m (own observations). Shimmering produces repetitively moving circular areas, typically with a diameter of 20 cm or more. Mammals and birds may perceive these patterns as supernormal cues that represent moving, head-like structures [48], outwitting their perceptual systems. Such cues may release a startle response [48–49] in vertebrates based on bottom up (BU) attention [50–53]. Bottom up attention depends upon the properties of a sensory stimulus to capture full attention, such as a bright spot of colour, an area of sharp contrast, or a rapidly moving pattern, such as typically involved in shimmering [1–13].

In higher vertebrates, the retinal fovea is the main sensory interface for attention retrieval [50–51]. When a shimmering wave is imaged by the fovea under covert conditions (with fixated eyes), BU attention is likely stronger the greater the image of the shimmering wave is, until the image fully covers the fovea. The fovea receptors are most densely packed in the central 1–2°, and the maximal trace length of a moving object that crosses a central projection at the main acuity region of the fovea is less than 10° [50–51]. The trace length of a shimmering wave on a vertebrate fovea in the 200 ms of the ascending phase (Fig. 3B, [6]) will cover an angle of 1°, provided that circular patterns of 20 cm or more are produced and viewed from a distance of 1 m from the nest. In the climax phase of a shimmering wave (Fig. 3B), when the patterns move at a speed of \(v_{\text{BP}} = 0.514 m/s\) (Fig. 9A) they will be viewed with a foveal path length of 8.15”, whereas mere bucket-bridging propagation \(v_{\text{BP}} = 0.325 m/s\) will affect only a path length of 5.400”.

**Summary and Conclusions**

Characteristics and benchmark data of two propagation mechanisms (Fig. 11A) of shimmering, bucket bridging and the saltatoric processes were investigated. Combining both mechanisms speeds up the shimmering waves from 0.317 m/s (bucket bridging only) to 0.517 m/s, which shows that the saltatoric component, also associated with the generation of daughter waves, increases the overall propagation speed of shimmering by 40%. Three categories of shimmering-active surface bees were identified regarding their communication status: the bucket-bridging, chain-tail and generator agents. These agents comprise a characteristic proportion (Fig. 11B1) and a characteristic recruitment status with respect to their neighbours (Fig. 11B2), and they contribute differently to the directivity of the main shimmering wave (Fig. 11B3). Summarizing, the wave-like shimmering process in giant honeybees displays adaptive complexity, particularly regarding the generation and propagation of information, and is an impressive example of swarm intelligence [19–21]. Shimmering conforms to rules of bucket-bridging such as linearity, continuity and graduality [9] and involves an additional saltatoric strategy to speed
up signal transmission, but also to provide a high level of fuzziness (Fig. 11B3) which may enable giant honeybee colonies to respond to rapidly changing threats [39].

Supporting Information

Glossary S1: List of important terms, definitions and abbreviations used in this paper.

Movie S1: In this episode two successive waves were generated by a dummy wasp that was moved from left to right (in the image). The episode started at f1, but the playback session refers only to f1 550–650 (corresponding to 1,700 ms). The dummy wasp was moved 20 cm in front of the nest (shown at the left bottom corner of the image). The part of the nest displayed in the film corresponded to the area marked by the four yellow spots in Fig. 1A and comprised about 1,250 bees of the surface layer; the thorax of the focus bee selected for this film was marked in red. Left panel: black-and-white images, inverted to enhance the contrast of the abdomen; right panel: the same view but displayed as differential image with the motion strength in pseudo colours (with relative motion strength scaled from red = 0.0 to blue = 1.0; see rainbow scale on the right bottom side). Original recording speed: fps = 60 Hz; playback speed: fps = 60 Hz.

Movie S2: The same episode as in Movie S1, but zoomed for about 60 bees; original recording speed: fps = 60 Hz; playback speed: fps = 60 Hz.

Movie S3: The same episode as in Movie S1, playback speed: fps = 25 Hz (slow motion factor: 0.42 of original speed).

Movie S4: The same episode as in Movie S2, but with a playback speed of fps = 25 Hz as in Movie S3.

Movie S5: The same episode as in Movie S1, but with a playback speed of fps = 6 Hz (slow motion factor: 0.10 of original speed).

Movie S6: The same episode as in Movie S2, but with a playback speed of fps = 6 Hz as in Movie S3.

Table S1: Accessory table to the Fig. 7 B–C, Fig. 8 A–C and Fig. 10 B with details of the regression functions regarding individual bees on the surface of the experimental giant honeybee nest B identified as status I–III agents (for definition, see text); tw, time window in [s] at fps = 60 Hz, all, four main directions of the spreading of the shimmering waves as selected in the paper: /R,L, /L,R, /T,B, /B,T; with R,L,T,B as right, left, top, bottom; abscissa and ordinate, the parameters used in the respective Figures/panels; coefficients of regressions (polynomials, exponential functions) are not detailed here; number of cases gives the number of focus bees or neighbour bees as evaluated in the data sets; goodness of fit ($R^2$) regards the regression functions of mean values.

Table S2: Survey of the data associated to Figs. 7, 10 concerning agents of the bucket-bridging (Status I) type; experimental nest B (see Methods); a, significant differences ($P_{D.EV}<0.01$, $X^2$ test) within groups. The hypothetical distributions are normalized denotations of PEAK and SINK distribution patterns (see Results).

Table S3: Survey of the data associated to Figs. 7, 10 concerning agents of the chain-tail (Status II) type; experimental nest B (see Methods); a non-significant differences ($P_{D.EV}=0.1669$, $X^2$ test) within groups; na, not available data; the hypothetical distributions are normalized denotations of PEAK and SINK distribution patterns (see Results).

Table S4: Survey of the data associated to Figs. 7, 10, concerning agents of the generator (Status III) type; experimental nest B (see Methods); a non-significant differences ($P_{D.EV}=0.1669$, $X^2$ test) within groups; na, not available data; the hypothetical distributions are normalized denotations of PEAK and SINK distribution patterns (see Results).

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Author Contributions

Conceived and designed the experiments: GK TH FW. Performed the experiments: FW TH MM GK. Analyzed the data: GK FW TH SW MM. Contributed reagents/materials/analysis tools: GK FW TH SW MM. Wrote the paper: GK IK.

References

1. Roepke W (1930) Beobachtungen an indischen Honigbienen, insbesondere an Apis dorsata. Meded LandbHoogesch Wageningen, 34: 1–28.
2. Butler CG (1936) The world of the honeybee. London.
3. Lindauer M (1956) Über die Verständigung bei indischen Bienen. Z Vergl Physiol 38: 521–537.
4. Seeley TD, Seeley RH, Aratanakul P (1982) Colony defense strategies of the honeybees in Thailand. Ecological monographs 52: 43–63.
5. Kastberger G (1999) The magic trees of Assam – Documentary film about the biology of the giant honeybee Apis dorsata. National Geographic, ZDF, ORF & epo-film, Wien.
6. Kastberger G, Schmelzer E, Kranmer I (2008) Social waves in Giant honeybees (Apis dorsata). PLoS ONE, 3(9): e3141. doi:10.1371/journal.pone.0003141.
7. Kastberger G, Weihmann F, Hoetzl T (2013) Stereoscopic motion analysis in densely packed clusters: 3D analysis of the shimmering behaviour in Giant honey bees. Frontiers in Zoology, 8: 3. doi:10.1186/1742-9994-8-3.
8. Kastberger G, Weihmann F, Hoetzl T (2013) Social waves in giant honeybees (Apis dorsata) elicit nest vibrations. Naturwissenschaften 100: 595–609. doi:10.1007/s00114-013-1056-z.
9. Kastberger G, Weihmann F, Hoetzl T, Weiss SE, Maurer M (2012): How to Join a Wave: Decision-Making Processes in Shimmering Behavior of Giant Honeybees (Apis dorsata). PLoS ONE, 7(5): e36736. doi:10.1371/journal.pone.0036736.
10. Morse RA, Laigo FM (1969) Apis dorsata in the Philippines. Philipp Assoc Ent 1: 1–96.
11. Schmelzer E, Kastberger G (2009) “Special agents” trigger social waves in Giant honeybees (Apis dorsata). Naturwissenschaften, 96:1431–1441.
12. Kastberger G, Weihmann F, Hoetzl T (2011) Self-Assembly Processes in Honeybees: The Phenomenon of Shimmering. In: Honeybees of Asia, Hepburn R, Rackoff S (eds), Chapter 18. ISBN: 978-3-642-16421-7 (Print) 978-3-642-16422-4 (Online).
13. Weihmann F, Hoetzl T, Kastberger G (2012) Training for defence? From stochastic traits to synchrony in Giant honeybees (Apis dorsata). Insects, 3(3): 789–820. doi:10.3390/insects3030789.
14. Woyke J, Wilde J, Wilde M (2008) Comparison of Defense Body Movements of Apis laboriosa, Apis dorsata dorsata and Apis dorsata brevicula Honey Bees. J Insect Behav 21:481–494.
15. Farkas ID, Helbing D, Vicsek T (2002) Social behaviour: Mexican waves in an excitable medium. Nature, 419:131–132. doi:10.1038/419131a.
16. Phillips OM (1977) The dynamics of the upper ocean. Cambridge University Press, USA.
17. Holtsjægeren, LH (2007) Waves in oceanic and coastal waters. Cambridge: Cambridge University Press.
18. Camazine S, Deneubourg JL, Franks NR, Sneyd J, Theraulaz G, et al. (2003) Self-organization in biological systems. Princeton University Press, Princeton.
19. Beni G, Wang J (1989) Swarm Intelligence in Cellular Robotic Systems. Proceed NATO Advanced Workshop on Robots and Biological Systems, Tuscany, Italy.
20. Bonabeau E, Dorigo M, Theraulaz G (1999) Swarm Intelligence: From Natural to Artificial Systems. Oxford University Press, Inc. New York, NY, USA, ISBN 0-19-513159-2.
21. Kauffman S (1993) The Origins of Order: Self-Organization and Selection in Evolution. Oxford University Press, ISBN 0-19-507951-5.
22. Goodwin B (2001) How the Leopard Changed Its Spots. The Evolution of Complexity. Princeton University Press.
23. Johnson SR: Emergence (2001) The Connected Lives of Ants, Brains, Cities, and Software. Scribner's, ISBN 0-684-86876-8.
24. Hildenbrandt H, Carere C, Hemelrijk CK (2010) Self-organized aerial displays of thousands of starlings: a model. Behav Ecol 21, 1349–1359. doi:10.1093/beheco/arq149.
25. Reynolds CW (1987) Flocks, herds and schools. A distributed behavioral model. Computer Graphics 21 (4): 25–34. doi:10.1145/37401.37406. ISBN 0-89791-227-6.
26. Parrish JK, Viscido SV (2005) Traffic rules of fish schools: a review of agent-based approaches. In: Self-Organization and the Evolution of Social Behaviour, Hemelrijk CK (ed). Cambridge University Press.
27. Gerlotti F, Bertrand S, Bez N, Gutiérrez M (2006) Waves of agitation inside anchovy schools observed with multibeam sonar: a way to transmit information in response to predation. ICES Journal of Marine Science 63: 1405–1417.
28. Couzin ID, Krause J (2003) Self-organization and collective behaviour in vertebrates. Advances in the Study of Behavior 32 :1–75.
29. Procasini A, Orlandi A, Cavagna A, Giardina I, Zoratto F, et al. (2011) Propagating waves in starling, Sturnus vulgaris, flocks under predation. Animal Behaviour 82:759–765.
30. Zitterbart DP, Wienecke B, Butler JP, Fabry B (2011) Coordinated Movements Prevent Jamming in an Emperor Penguin Huddle. PLoS ONE, 6(6): e20260.
31. Couzin ID, Krause J, Franks NR, Levin SA (2005) Effective leadership and decision-making in animal groups on the move. Nature 433:513–516.
32. Virmmani S, Adrian EC, Imhof K, Mukherjee S (1989) Implementation of a Lagrangian relaxation based unit commitment problem. IEEE Trans Power Syst 4(3): 373–380.
33. An G, Mi Q, Dutta-Moscato J, Vodovotz Y (2009) Agent-based models in translational systems biology. Systems Biology and Medicine 1 : 159–171; doi:10.1002/sbmt.43.
34. Grasse P (1959) La reconstruction du nid et les coordinations inter-individuelles chez Bellicositermes natalensis et Cubitermes sp. La theorie de la stigmergie: Essai d’interpretation du comportement des termes constructeurs. Insectes Sociaux 6:41–80.
35. Mason Z (2002) Programming with Stigmergy: Using Swarms for Construction. In: Artificial Life VIII, Stellmach, Abbas, Bedau (eds), MIT Press 371–374.
36. Small P (2003) Stigmergic systems. http://www.stigmeircsystems.com/stig_v1/stigrefs/article1.html?540817.
37. Ballerini M, Cabibbo N, Candelier R, Cavagna A, Cisbani E, et al. (2008) Interaction ruling animal collective behavior depends on topological rather than metric distance: Evidence from a field study. PNAS105:1232–1237.
38. Kaushberge G, Rapotin G, Biais W, Winder O (1998) Evidence of Nasonov scenting in colony defence of the Giant honeybee Apis dorsata. Ethology 104: 27–37.
39. Kaushberge G, Weihmann F, Zierler M, Hoetel T (2013) Wasps Giant honeybees (Apis dorsata) mob wasps away from the nest by directed visual patterns. Naturwissenschaften, submitted.
40. Potts WK (1984) The choro-line hypothesis of manoeuvre coordination in avian flocks. Nature 309: 344–345.
41. Ballerini M, Cabibbo N, Candelier R, Cavagna A, Cisbani E, et al. (2011) Empirical investigation of starling flocks: a benchmark study in collective animal behaviour. Animal Behaviour 76:201–215.
42. Creasey D (2011) Starling waves help flocks flummox falcons. Nature News Blog, http://blogs.nature.com/news/2011/08/starling_waves_help_flocks_fox.html
43. Parrish JK, Edelstein-Keshet L (1999) Complexity, Pattern, and Evolutionary Trade-Offs in Animal Aggregation. Science, 284: 99–101.
44. Winter D: Winter Starlings on Omloop. http://www.youtube.com/watch?v=6-XF-g0CzK6, uploaded 21.02.2007.
45. Hoffmann T (2011) Sprceuwenspaktkeul Hoograven Utrecht http://www. youtube.com/watch?feature = player_detailpage&v = sEFRAj9WNE, uploaded 03.03.2011.
46. Downer J (2012) Peregrine Falcon Hunts Starlings in Rome: http://www. youtube.com/watch?feature = player_detailpage&v = _tEFRAI9WSE, uploaded 11.01.2012.
47. Landee L, Terborgh J (1986) Oddity and the `confusion effect' in predation. Animal Behaviour 34, 1372–1380.
48. Hamilton WD (1971) Geometry for the selfish herd. J Theor Biology 31, 295–311.
49. Alcock J (2005) Animal Behaviour. Sinauer Associates Inc, Massachusetts, Eighth edition 2005.
50. Zupanc GKH (2010) Behavioral Neurobiology: An Integrative Approach. Foreword by Theodore H. Bullock. Second Edition. ISBN 978-0-19-920830-2. Oxford University Press.
51. Itti L, Gold C, Koch C (2001) Visual Attention and Target Detection in Cluttered Natural Scenes. Optical Engineering 40(9):1784–1793.
52. Droll JA (2011) Think Fast! The Velocity of Visual Attention in Vehicle Clutter.耶 Honda Research Institute, submitted.
53. Balci Z, 1 (1999) Gorillas in our midst: Sustained in attentional blindness for dynamic events. Perception 28:1059–1074.
54. Olson PL (1996) Forensic aspects of driver perception and response. Tucson, AZ: Lawyers & Judges Publishing Company, Inc.