ANIMAL ROBOTS

Robots mediating interactions between animals for interspecies collective behaviors

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Self-organized collective behavior has been analyzed in diverse types of gregarious animals. Such collective intelligence emerges from the synergy between individuals, which behave at their own time and spatial scales and without global rules. Recently, robots have been developed to collaborate with animal groups in the pursuit of better understanding their decision-making processes. These biohybrid systems make cooperative relationships between artificial systems and animals possible, which can yield new capabilities in the resulting mixed group. However, robots are currently tailor-made to successfully engage with one animal species at a time. This limits the possibilities of introducing distinct species-dependent perceptual capabilities and types of behaviors in the same system. Here, we show that robots socially integrated into animal groups of honeybees and zebrafish, each one located in a different city, allowing these two species to interact. This interspecific information transfer is demonstrated by collective decisions that emerge between the two autonomous robotic systems and the two animal groups. The robots enable this biohybrid system to function at any distance and operates in water and air with multiple sensorimotor properties across species barriers and ecosystems. These results demonstrate the feasibility of generating and controlling behavioral patterns in biohybrid groups of multiple species. Such interspecies connections between diverse robotic systems and animal species may open the door for new forms of artificial collective intelligence, where the unrivaled perceptual capabilities of the animals and their brains can be used to enhance autonomous decision-making, which could find applications in selective "rewiring" of ecosystems.

INTRODUCTION

Robotics has become a valuable tool in the study of animal behavior. For instance, robots have been introduced into groups of animals by building them to emit certain cues that are used by the animals within individual-level interactions. These robots can be simple observers (*1*) or sample the biodiversity (*2*). Moreover, they can act on certain animal behaviors, to modulate, for instance, the movements of cattle (*3*); to investigate factors involved in mate choice (*4*); or to simulate predator-prey interactions (*5*). Several studies have involved biohybrid systems composed of groups of robots and animals, where the artificial devices were working in a closed loop according to the change of behavior of the animals and thus autonomously interacted with them (*6*–*16*). This approach is possible when the designed robots are capable of socially integrating into groups of animals by mimicking some of the signals used during social interactions (*6*). These closed robot-animal interaction loops can provide access to richer dynamics as compared with preprogrammed or human-operated robot approaches and can be used to test hypotheses about the way animals interact and how self-organized collective behavior can emerge from these local interactions (*17*–*19*), such as identifying behaviors in which a small fraction of agents can change group-level behaviors (*6*). These systems also represent a novel kind of biohybrid information and communication technologies system because the animals can enrich the capabilities of the machines, and vice versa (*20*). However, studies involving biohybrid systems have only focused on the interaction between one particular group of animal species and one particular group of specifically designed robotic systems. The coupling of several biohybrid systems that would allow the study of how collective decision-making can arise at a larger scale, among multiple individuals of different species, with their own sensing and acting properties, has not been explored to the best of our knowledge.

Honeybees (*Apis mellifera* L.) and zebrafish (*Danio rerio* L.) are two animals of great interest for the scientific community. Honeybee colonies as superorganisms show various self-organized collective behaviors driven by feedbacks that amplify and stabilize the actions leading to optimal collective decisions at the colony level (e.g., nest site selection or forager recruitment) that are crucial for the survival of the colony (*21*, *22*).

The zebrafish is a model organism in genetics and neurophysiology (*23*, *24*); thus, its behavior is well studied. In addition, the zebrafish is a social species, forming shoals both in nature and in laboratory conditions (*25*). It is a common animal model for studying the link between individual variability and collective behaviors (*26*). Although the dynamics of interactions differ between honeybees and zebrafish—as well as many other factors, such as their environments and the mechanisms used in local interactions—both honeybees and zebrafish exhibit decision-making at the collective level, opening the possibility to facilitate some form of indirect exchange of information between groups of the two animals.

Here, we introduce a methodology to create interaction links at a collective level between animal species. In particular, we showcase this by selecting two animal species that would not directly interact in nature, i.e., zebrafish and honeybees. By exploiting selected mechanisms in gregarious animals, we designed robotic agents to integrate themselves into these two animal groups and to participate in the self-organized collective choices in binary choice systems (*6*). Using these two biohybrid systems, we established a long-distance communication channel between two types of robotic agents to create an interaction link between two animal groups of different species and to translate the

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information between the two biohybrid systems. These robotic agents allowed these two biohybrid systems to share their collective decision-making, which enabled the emergence of a global consensus. We observed how the collective decision from one species was transferred to another via information exchanged between the robots.

RESULTS

The robotic design approach we followed for animal-robot interaction was based on the methodology to create mixed groups of robots and animals to study self-organized collective behaviors (*20*). First, the robot presence was accepted by the animal group such that the usual animal behavior was not modified; second, the active behavior of the robots modulated the animal behavior in a parsimonious way. This means that the robotic agents had to be designed to be socially accepted and capable of reaching consensus with the animal groups. Such biohybrid groups have similar properties to the animal ones but can also enhance collective behavior by sharing properties between the animals and the robots (*6*). Because self-organized collective behaviors are frequently amplification phenomena, a small number of robotic agents can be enough to influence the whole group (*6*, *27*, *28*).

The system we developed is shown in Fig. 1. For each species, we created the simplest and smallest set of robotic agents that could either autonomously reproduce some of the signals used by animals during their social interactions or emit physical cues that are present in the animals' natural environment and to which the animals will react in a predictable way. On the side of honeybees, these robots produced heat (*12*), which is an attractive cue for young honeybees because they rely on a specific thermal environment in the brood nest area (*29*). On the fish side, a lure with the same size and shape ratio as zebrafish moved in the water by reproducing the same motion patterns (i.e., trajectories, speeds, and accelerations) as the fish (*30*). It was also previously demonstrated (*12*, *15*) that the animals responded to the stimuli created by these two robotic devices in the same way that they responded to their conspecifics and that the robotic agents and the animals could reach consensus (see text S2). For sensing purposes, the bee-robots were equipped with proximity sensors to estimate the density of bees close to each robot. In the fish-robot system, a camera continuously filmed the aquarium from above, and a blob detector was used to determine the position of each agent (fish and robots). This sensory information could be used either to close the interaction loop between robots and animals (*12*, *14*, *15*, *31*) or to transmit information from one species to another. On both sides, there was a binary collective choice for the animal groups, which is a common setup for studying self-organization in animal groups (*32*). The honeybees had to choose around which of the two bee-robots they aggregated. The fish were constrained inside a ring, and they had the choice to move in the clockwise (CW) or counterclockwise (CCW) direction.

The experimental setups for fish and bees were located in two different cities. The fish setup was located at École Polytechnique Fédérale de Lausanne, Lausanne, Switzerland, and the bee setup was located at the University of Graz, Graz, Austria. Therefore, these experiments tested not only the possibility of connecting two different animal species but also the ability to perform these complex tasks through a long-distance link (the two universities are separated by a distance of approximately 680 km).

We performed three sets of experiments, each with different connectivity between the biohybrid systems (Fig. 2). Our main goal was to connect the two biohybrid systems in a closed loop, such that (i) each animal group contributed to the overall system dynamics and collaborated with the other group and (ii) a consensus decision emerged from the system (Fig. 2D). To examine the interactions in more detail, we also tested two further settings, where only one biohybrid system had a closed-loop interaction and shared information with the other system (Fig. 2, B and C). As noted above, each biohybrid system was faced with a collective binary choice: left or right side of the arena for bees and CW or CCW swimming direction for fish. In each biohybrid system, the robots stimulated the animals and received sensory information about the animals (see text S1).

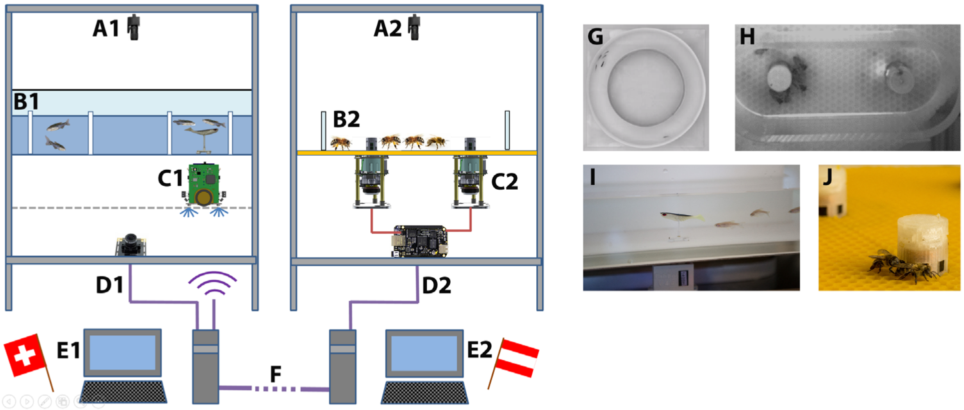

Fig. 1. Automated setup for interspecies experiments composed of two animal species (zebrafish and honeybees) and two artificial devices (fish- and bee-robots). The two setups are composed of a metallic frame, with a camera (**A1** and **A2**) to capture the arenas in high definition. The fish arena (**B1**) includes a tank filled with water and a circular corridor (**G**). This space constrains the zebrafish and lure, presenting a binary choice: The mixed group can move either CW or CCW (G and **I**). Underneath the tank (**C1**), a wheeled mobile robot moved, which also moved its lure via magnetic coupling. The honeybees were contained within a silicon oil–coated Plexiglas arena (**B2**) with two bee-robots, forming a binary choice: The honeybees decided to aggregate around one of these bee-robots (**H**). The "head" of each immobile robot incorporated six IR sensors (**J**). The main bodies were mounted below the arena floor (**C2**) and included a Peltier element to modulate the local temperature inside the arena. The two setups were interfaced (**D1** and **D2**) with computers (**E1** and **E2**) on which programs controlled the robots in a closed loop. The fish setup (in Lausanne, Switzerland) was connected virtually (**F**) to the bee setup (in Graz, Austria)

In experiment 1 (B → F), the bee biohybrid system exhibited self-contained decision-making dynamics and also transmitted signals to the fish biohybrid system, which operated in an open-loop mode. In experiment 2 (B ← F), the fish biohybrid system governed the overall dynamics through coupling the fish swimming direction to the fish-robot swimming direction and transmitting this direction signal to the bee-robots operating in an open-loop mode. In experiment 3 (B ⇌ F), both biohybrid systems were connected in a single closed loop: The sensed fish direction was used to determine the bee-robot temperatures, and the sensed bee densities were used to determine the fish-robot swimming direction. In this experiment, each animal species

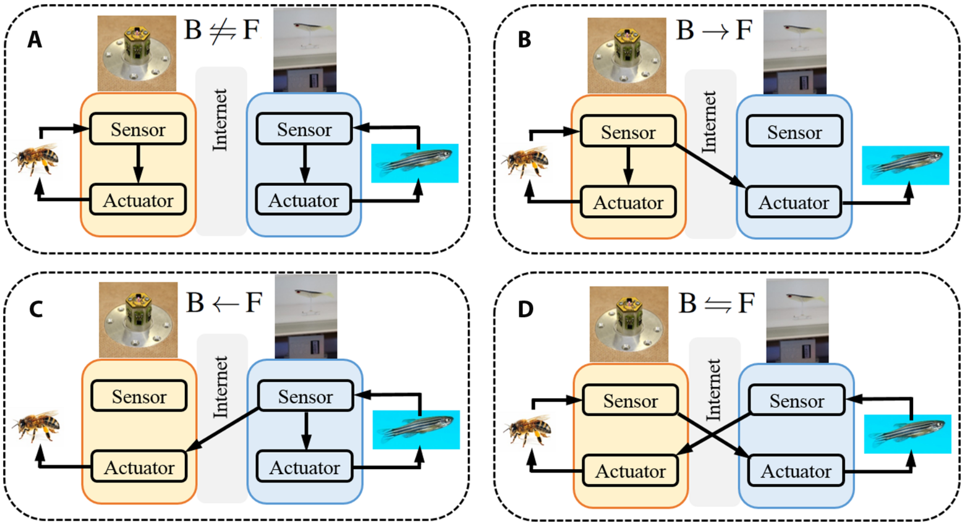

Fig. 2. The four conditions implemented to test connectivity between bee and fish experimental setups. (**A**) Control condition, where the robots interacted with the animals in a closed loop but did not exchange information between the setups. (**B**) Condition $B \rightarrow F$, where the fish-robot behavior was modulated according to what was sensed by the bee-robot, which interacted in a closed loop with the honeybees in a self-contained decision-making dynamics. (**C**) Condition $B \leftarrow F$, where the bee-robot behavior was modulated according to what was sensed by the fish-robot, which was interacting in a closed loop with the zebrafish in a self-contained decision-making dynamics. (**D**) Condition $B \rightleftharpoons F$, where the bee-robot behavior was modulated according to what was sensed by the fish-robot and the fish-robot behavior was modulated according to what was sensed by the bee-robots. The setup established a long-distance closed-loop interaction between the two biohybrid systems, which could share their collective decision-making to allow the emergence of a global consensus.

had to select from two identical choices with their respective robots, and the robots were sharing this information to allow the emergence of a global consensus in the system. To provide a control condition, we produced a surrogate dataset that used bee-side results and fish-side results where these systems acted without influence from the other ($B \not\rightleftharpoons F$).

Figure 3A shows a time series for selected runs of each condition. For the case of $B \rightarrow F$, where the bees influenced the collective decisions of fish, we observed that the bees took ~6 min to make a collective decision by aggregating closer to the right bee-robot. When the right bee-robot started to detect that the majority of bees was located around it, this information was transmitted to the fish-robot, which started to rotate more in the CW direction. After some time, we observed a bias of the fish collective decisions that were influenced by the fish-robot rotating more in the CW direction (see movie S1).

In the presented run of $B \leftarrow F$, the fish were continuously changing swimming direction, which resulted in the measure fluctuating around 50%. This behavior influenced the fish-robot to also switch swimming direction, and this information was transmitted to the bee system. For example, when the fish were mostly swimming in the CCW direction, the left bee-robot heated more than the right bee-robot, which influenced the bees to aggregate more around the left bee-robot. Because of the way fish were continuously switching swimming direction, the side with bee majority also oscillated (see movie S2).

Last, we also show a run of $B \rightleftharpoons F$. In the first half of the experiment, the two species did not succeed in deciding. This was probably mainly due to the fish, which were swimming in each direction around half of the time during this period. However, after 20 min, the two systems stabilized, and the two animal groups made a collective decision together (see movie S3). More broadly across the experiments, bees made strong decisions frequently in $B \rightarrow F$, as we have observed in previous work (*33*); the ability to reach and maintain aggregations was disrupted by the influence of the fish in $B \rightleftharpoons F$ and even more so in $B \leftarrow F$ (see text S5).

To evaluate the coordination between the animal species, we sampled the measurements of collective behavior at each second and then averaged the results over each minute.

For each run, we computed a collective decision coefficient Q_{BF} that is given by

$$Q_{\mathrm{BF}} = 100 \times \sum_{t}^{T} \frac{\left|C_t^{\mathrm{B}} - C_t^{\mathrm{F}}\right|}{T} \qquad (1)$$

where C_t^{B} and C_t^{F} are the collective decisions of bees (bee density in one of the two halves of the arena) and fish (swimming direction, CW or CCW), respectively, at a given time t, and T is the total duration of the experiment.

Figure 3B shows the distribution of collective decision coefficient Q_{BF} for all experiments. We found that the four distributions differ statistically (Kruskal-Wallis, $P < 0.05$), and a post hoc analysis using Tukey's honest significant difference criterion shows that the mean ranks of the distribution of conditions $B \rightarrow F$, $B \leftarrow F$, and $B \rightleftharpoons F$ significantly differ from condition $B \not\rightleftharpoons F$, whereas conditions $B \rightarrow F$, $B \leftarrow F$, and $B \rightleftharpoons F$ have no significantly different distributions. It seems that $B \leftarrow F$ and $B \rightleftharpoons F$ obtained a higher score than $B \rightarrow F$, because the fish were less influenced by the fish-robot in $B \rightarrow F$ than the bees by the bee-robot in $B \leftarrow F$ and $B \rightleftharpoons F$, as observed in (*12*) and (*14*). Overall, this shows that we succeeded in designing a system in which two animal species were capable of collectively interacting through the robotic devices.

To investigate information exchange between the two animal groups, we measured the transfer entropy (*34*) in each direction (see Fig. 4 and text S4). The transfer entropy measured between bees and fish indicates that the driving species in $B \rightarrow F$ and $B \leftarrow F$ transferred information to the other species and that there was no significant transfer in the reverse direction, as expected. Furthermore, in $B \rightleftharpoons F$, information was exchanged in both directions, although the exchange from bees to fish appeared to be stronger. Conversely, no significant transfer was measured in the control condition, $B \not\rightleftharpoons F$, where the two biohybrid systems were not connected electronically. A comparison of the distribution of local transfer entropy (TE) values between experimental conditions reveals a significant difference between the $\mathrm{TE}_{B \Rightarrow F}$ for the cases where the bee-fish link was present ($B \rightarrow F$ and $B \rightleftharpoons F$) and where it was not ($B \leftarrow F$), but that there is no significant difference between the distributions for $B \rightarrow F$ and $B \rightleftharpoons F$ (Mann-Whitney U test with Bonferroni correction, $P < 0.05$). Similarly, for the $\mathrm{TE}_{F \Rightarrow B}$ distributions, $B \rightarrow F$ differs from $B \leftarrow F$ and $B \rightleftharpoons F$, but $B \leftarrow F$ and $B \rightleftharpoons F$ do not differ significantly (see text S5 and fig. S3).

The evidence from this analysis of transfer entropy shows that the actions of one species were informative in predicting the future states of the other species, when the robot-robot link is active. Note that

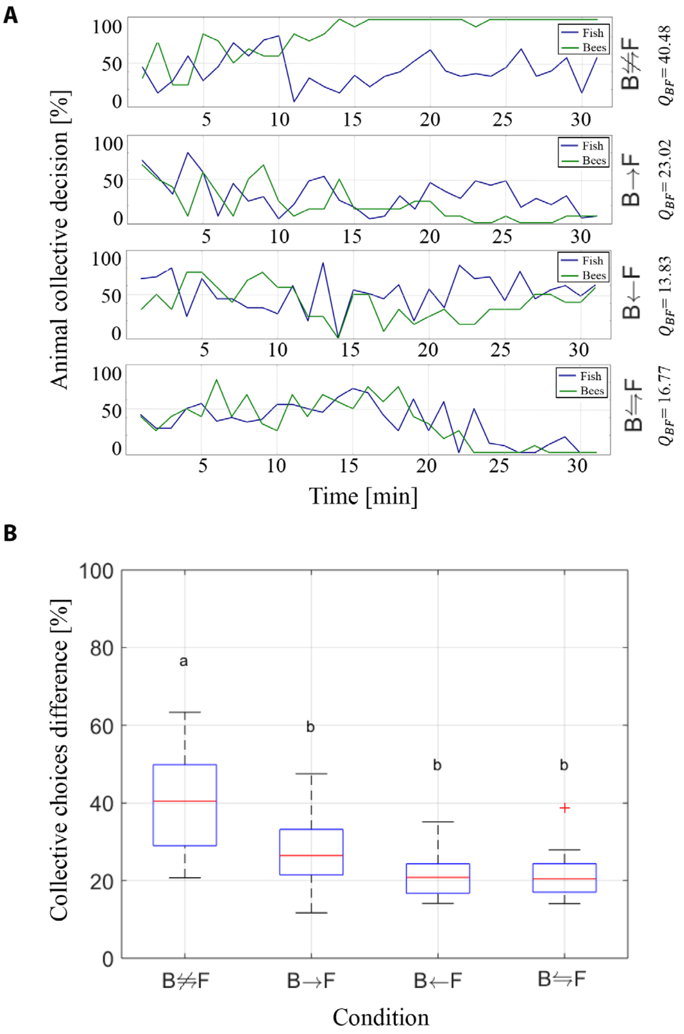

Fig. 3. Coordinated collective decision-making. (**A**) Time series of collective decisions in each species (bees and fish) for selected runs of each condition. The fish choose their rotation direction (% CW), and the bees choose their resting place (% right side). (**B**) Collective decision difference coefficient Q_{BF} for all runs of each condition, reflecting closely correlated behavior across the two animal species. With bidirectional link, $B \rightleftharpoons F$, the low Q_{BF} values indicate a highly coordinated system. The four distributions differ statistically (Kruskal-Wallis, $P < 0.05$), and a post hoc analysis using Tukey's honest significant difference criterion shows that the mean ranks of the distribution of conditions $B \rightarrow F$, $B \leftarrow F$, and $B \rightleftharpoons F$ significantly differ from condition $B \not\rightleftharpoons F$, whereas conditions $B \rightarrow F$, $B \leftarrow F$, and $B \rightleftharpoons F$ do not have significantly different distributions.

this technique infers relationships from observational data and thus can report significant relationships between pairs of variables that "appear to be causally linked" (*35*) where there is not a direct causal relationship, such as when a third, unobserved variable causes changes in both the observed variables. However, a comparison between the various experimental conditions that used different robot-robot links supports the conclusion that the collective behavior of fish was the underlying cause of the transfer entropy between fish and bees.

DISCUSSION

We developed an autonomous robotic system capable of coordinating the collective behavior of two animal species using socially integrated robots. The designed system involves a group of zebrafish and a group of honeybees located in two different cities connected through the internet. This system is thus scalable because any biohybrid system in any location at any distance with a data connection can remotely connect to such an interspecies network, thus enabling the behaviors of distant animals to be coordinated. Moreover, the systems that we have designed support a larger number of robotic agents to interact with either group of animals (*12*, *14*). However, in this study, we took a parsimonious approach (*20*) that strives to use the smallest number of robots and animals necessary to demonstrate the interspecies interactions. Each experiment lasted 32 min and showed that the two species could reach consensus for several minutes or longer periods, and further studies could be designed to test these effects over longer time scales.

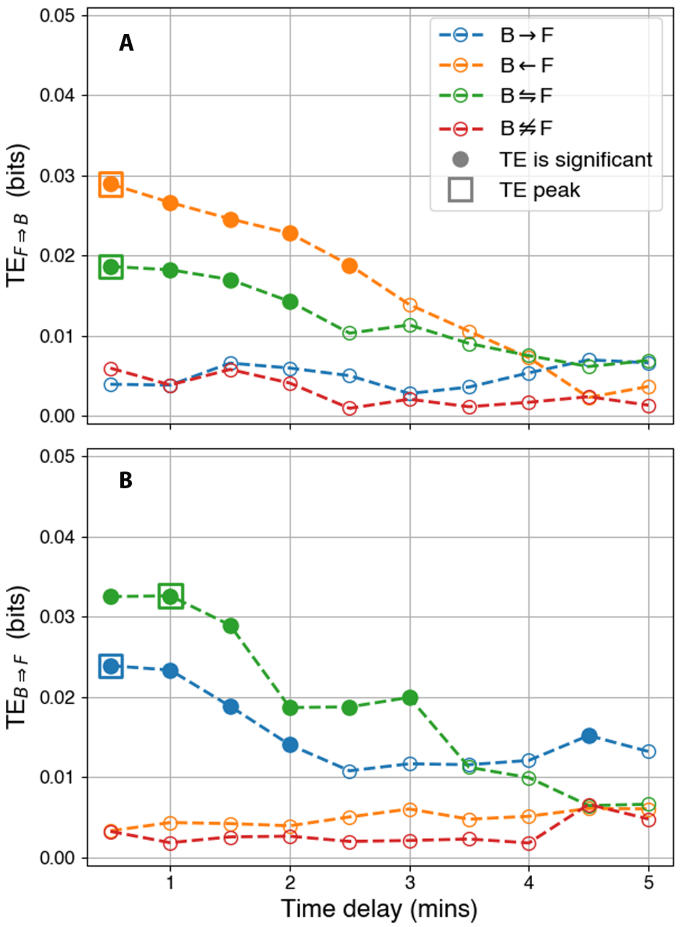

Fig. 4. Measurements of transfer entropy (TE), a directional information-theoretic measure that can indicate dependencies between actors in a complex system. We measured (**A**) $TE_{F \Rightarrow B}$, from fish to bees, and (**B**) $TE_{B \Rightarrow F}$, from bees to fish. When the two biohybrid systems were connected, we found substantial TE in at least one direction. The solid markers indicate statistical significance (Mann-Whitney *U* test with Bonferroni correction, $P < 0.05$). Specifically, in $B \rightarrow F$, we have only information flowing from bee-robots to fish-robots, and this is reflected in high $TE_{B \Rightarrow F}$ only. Conversely, in $B \leftarrow F$, we only have high $TE_{F \Rightarrow B}$. The condition $B \rightleftharpoons F$ shows significant bidirectional information exchange between the animals.

We demonstrated the interaction between the two animal groups by analyzing the statistical coherence of the collective decisions of the two species. This coherence was quantified by the transfer entropy between them for three different scenarios: The bees influence the collective decisions of the fish, the fish influence the collective decisions of the bees, and mutual influence between the two species. We also showed that, when the two biohybrid systems were not connected, no information could flow and the distribution of the collective decision difference was significantly different from the three other conditions where the two systems were connected. It shows that, using the interspecies link that we designed, animal groups that do not collectively interact in nature can reach a consensus.

The presented system shows that it is possible to mediate the interactions between animal species. Here, we performed these experiments in laboratories, but one can envisage being able to insert such artificial agents within the groups of animals in the wild. This approach may also be generalized to other living species, such as plants (*36*), fungi, or even microorganisms, to allow systems to interact even at different scales. It would then be possible, on the one hand, to exploit the unrivaled sensory properties of the living systems, their behaviors and their ease to move in the wild, and, on the other hand, to influence their choices and to add physical properties like telecommunication and other capacities. This approach may also enable the study of information flow in ecosystems and natural phenomena, such as cascade effects or other effects that might be responsible for the collapse of ecosystems (*37*), and identify solutions to repair broken links in these ecosystems.

Various studies have been done on how information is transmitted within a group of animals of the same species (*35*, *38*, *39*). The system we developed allows the study of the information transfer between agents whose properties fundamentally differ (communication channel and movement dynamics), aiming toward a better understanding of how biohybrid and multispecies systems are capable of exchanging information. One can also envision future applications in which the robotic systems would be able to learn and to adapt their behavior to animal species. Elsewhere, we have already begun to explore these possibilities in the two individual biohybrid systems (*40*, *41*) based on methodology for continuous real-time adaptation of multilevel behavioral models by evolutionary algorithms. We envision robotic systems that can discover by themselves new properties of biohybrid artificial intelligence toward synthetic transitions (*42*) and organic computing devices (*43*), where robots could passively evolve among animals.

MATERIALS AND METHODS

Animals

The experiments performed with honeybees (*A. mellifera*) were conducted with freshly emerged bees, aged from 1 to 24 hours. Bees this age are not yet able to actively produce heat (*44*) or to fly. To provide bees of this specific age for the experiments, we removed brood combs with sealed pupae from colonies and hatched them in incubators at a relative humidity of 60% and a temperature of 35°C. Every morning, all bees that had hatched overnight were brushed off the combs and kept in ventilated plastic boxes on heating plates set to 35°C. The bees were provided with honey ad libitum. All bees were reintroduced into the hives at the end of the day. Each individual was only tested once in an experiment, and individuals with visible damage, i.e., missing or mutilated extremities (legs, antennae, and wings) or attached varroa mites, were not used in experiments. The experiment with honeybees was performed in Graz, Austria; for such experimentation with invertebrates, no restrictions to experimentation apply, and no specific ethical board approval of experiments is required.

On the zebrafish side, the experiments performed in this study were conducted under the authorization number 2778 delivered by the Department of Consumer and Veterinary Affairs of the Canton de Vaud (Switzerland) after approval by the state ethical board for animal experiments. The fish were bred following the guidance of Reed and Jennings (*45*), and that was imposed by our state and institution.

For the experiments, we used 100 wild-type zebrafish *D. rerio* with short fins. These zebrafish were acquired from a pet shop (Qualipet, Crissier, Switzerland) and were stored in two 60-liter housing aquariums. The average total length of our zebrafish was ~4 cm. The water temperature of the housing aquarium was 26°C. The fish were fed twice a day with commercial food using a food distributor. The housing aquarium environment was enriched with plastic plants, cladophoras, gravel, rocks, and aquatic snails. Each individual was only tested once per day, but the same fish could have been tested for several runs presented in this study.

Robotic bee arena

The bee experimental setup is shown in Fig. 1 (A2 to E2). The bees were placed on a horizontal surface covered by a sheet of pressed beeswax, which was placed above an acrylic glass floor. The floor had 6.0-cm holes cut for the thermal control surface of the robotic devices. Holes (2.0 cm) were cut in the wax for the robot heads to protrude, where the infrared (IR) sensors to detect the bees were sited (Fig. 1J) (*12*). A Plexiglas stadium-shaped wall with a length of 16.5 cm, a width of 6.0 cm, and a height of 5 cm was placed over two robots, forming an arena with 91 cm^2 for the bees to move within (Fig. 1H). The robots were separated by 9.0 cm from center to center. The entire setup was in a darkened room without windows at Karl-Franzens University in Graz, Austria.

The robots were specifically designed to interact with juvenile honeybees and could generate stimuli with several modalities that the bees are sensitive to, including heat and vibrations. Because the bee-robot was programmable by a computer and could carry out a complex series of actions automatically using sensors and actuators, we considered it as a robot, although it is a stationary device. The robots were also equipped with IR and temperature sensors (*12*). Beaglebone single-board computers managed the robots, including executing the user-level controller, which, in turn, depended on the low-level actuator regulation and sensor readings through an application programming interface. These simple computers provided data logging and communication with other robot controllers and the host PC, which was connected by the internet to the fish biohybrid system PC host.

The arena was filmed using a Basler ac2040-25gmNIR camera sensitive to IR light. The camera was mounted at 123 cm above the arena and, at full resolution of 2040 pixels by 2040 pixels, captured a 100 cm–by–100 cm region. The relevant part of the arena was cropped from the entire frame for each experiment (Fig. 1H). The arena was surrounded by white sheets to provide a cleanly lit environment, and three IR light-emitting diode (LED) devices (each device comprised 48 LEDs with peak wavelength at 940 nm and consumed 7.2 W) were placed above the setup to provide IR light for the camera.

Robotic fish arena

The fish experimental setup is presented in Fig. 1 (A1 to E1) (*46*). It consisted of an aluminum structure that supported an aquarium (100 cm by 100 cm by 25 cm) made of glass. The bottom surface of the aquarium was covered with white Teflon sheets to avoid the reflection of light on the glass and to have a smooth surface for the motion of the module moving inside the aquarium (Fig. 1I). The tank was filled with water up to a level of 6 cm, and the temperature was set to 26°C. The whole setup was confined behind white sheets to isolate the experiments from the rest of the room and to ensure consistent luminosity. Three 110-W fluorescent lamps were placed around the setup and oriented toward the white sheets to provide indirect daylight-level lighting of the tank.

Underneath the tank, a wheeled mobile robot moved on a fixed support. The robot transmitted two-dimensional motion to a fish-lure module that moved inside the tank using magnets and was able to achieve the required speeds and accelerations to reproduce the fish displacements underwater (*30*). The wheeled mobile robot was continuously powered using brushes that acquire power from two conductive plates and was controlled via a wireless Bluetooth link. The fish lure was the part that was visible to the fish (Fig. 1I) and with which the fish interacted. The lure had dimensions close to those of the zebrafish, and its tail beat when it moved at a constant speed. We have shown in previous studies that this robot can be socially accepted and participate in the zebrafish collective behaviors (*14*, *15*).

To constrain the zebrafish movements, we placed inside the tank an arena composed of an outer circular wall and an inner circular wall, forming a circular corridor (Fig. 1G). This is a common setup to study the collective behavior of fish (*14*, *39*, *47*–*49*) and offers a binary choice for the fish because they can move either in a CW or a CCW direction, which was used to evaluate the effect of the robots on the collective decisions of the fish (*14*). The dimensions of the corridor were as follows: an external diameter of 58 cm, an internal diameter of 38 cm, and a corridor width of 10 cm.

Long-distance communication

To demonstrate the applicability and potential impact of the interspecies link, we purposefully chose two species that do not interact in nature (zebrafish in the water and honeybees on land). Thus, the two species never have direct physical contact in their natural habitats. To stress this point even further, we separated them by a substantial physical distance. This raised additional challenges, like time delays and network traffic. Solving those challenges demonstrates the general applicability of our system. This also shows that the system is scalable, because we could connect two biohybrid systems located at any distance, as soon as they can be connected to the internet.

To enable the coordination and collective choice experiments across the two spatially separated species, we designed an interspecies communication protocol. The protocol was built on ZeroMQ (*50*) and Google's Protocol Buffers package (https://developers.google.com/protocol-buffers/) and supported sending aggregation information from the bee-robot to the fish-robot, as well as sending swimming direction information in the other direction, from the fish setup to the bee-robot controller. The message format is listed in Table 1.

Experimental procedure

The experiments with zebrafish took place at the École Polytechnique Fédérale de Lausanne, Lausanne, Switzerland, and the experiments with honeybees took place at the University of Graz, Graz, Austria, between 21 July and 16 August 2017. Each interaction experiment with the recording of data lasted 32 min. We predetermined a fixed starting time for each experiment to be synchronized between Graz and Lausanne. For both biohybrid setups, we established an experiment procedure that was used for each experiment.

Table 1. The messages exchanged in the interspecies communication protocol. The ⟨ and ⟩ symbols imply a variable value in the protocol.

Direction	Target	Sender name	Data format
Fish→bees	Bee-robot ID	Fish-robot	fish-⟨direction⟩
Bees→fish	Fish-robot	Bee-robot ID	bee-⟨density⟩

In total, we performed 25 runs of B → F, 21 runs of B ← F, 26 runs of $B \rightleftharpoons F$, and 21 runs of $B \not\rightleftharpoons F$. However, several runs had to be removed from the analysis, either due to a problem during the experiment, such as a honeybee escaping from the arena, or due to a technical problem during the data acquisition, such as failure of video recording or logging of robot data. Therefore, the analysis in this study took into account 22 runs of B → F, 19 runs of B ← F, 23 runs of $B \rightleftharpoons F$, and 19 runs of $B \not\rightleftharpoons F$. The details concerning the replicates that had to be excluded can be found in the Supplementary Materials, in the folder containing the experimental data.

On the bee side, we performed each experiment with groups of 12 honeybees in the stadium-shaped arena around two bee-robots as described above. This group size was determined in preliminary experiments to best facilitate the density-dependent collective thermotaxis of the honeybees without leading to crowding effects [for density dependency, see also (*29*)].

The ambient temperature of the experimentation room was 27°C during experiments. Air conditioning was only used between experiments to regulate the room temperature and to minimize disturbances during experiments. Before each experimental run, the wax floor in the arena was replaced to remove any chemical cues for the bees. Both robots were initially set to a temperature of 28°C before starting the experiment. After starting the recording and initializing the robot controller, we calibrated the IR sensors. As soon as the calibration phase was over, 12 randomly chosen bees were transferred into the arena. In contrast to the fish, no acclimatization time was needed, and the experiment started synchronized with the fish side. After the experiment, the data were stored for analysis, and the bees were removed from the arena.

On the fish side, we performed the experiments using groups composed of six agents: one fish-robot and five zebrafish. This was determined in preliminary experiments to obtain a strong observed effect of the robotic agent on the animals, as well as homogeneity of the overall mixed group (*14*).

The water in the experimental tank was maintained at the same temperature (26°C) and water quality as the water of the housing aquarium to minimize the effect of the water transition on the zebrafish. In the morning of an experiment session, zebrafish were selected at random from their housing aquarium and were maintained inside a transfer tank next to the experimental tank during the experiment. Then, five zebrafish were selected among the entire group with a hand net from the transfer tank and transferred into the experimental tank. We let them acclimatize for 10 min inside the experimental tank before starting an experiment because we have observed that, for the first 5 to 10 min, the behavior of the zebrafish was not the same compared with the behavior during the rest of the experiment, probably due to the stress during transfer and acclimatization to the new environment (*14*). After each experiment, the fish were placed in a second transfer tank near the experimental setup, so that they could not be reused for further experiments during the same day. After the experiment session, all the fish were put back into their housing aquarium.

Data analysis

We quantified the bees over the course of each experiment in two primary ways: the bees' locations and the rates of motion. The first is particularly challenging due to the level of occlusion and interference from robot IR sensors in the films recorded with an IR-sensitive camera. Accordingly, this was performed by hand, using a tool that was developed to provide guidance as to where the bees are located; its suggestions are then manually corrected where necessary. We annotated an average of 100 frames per experiment (112 in B → F, 107 in B ← F, and 96 in B ⇌ F). Given how labor intensive this task is, it is not feasible to label at a rate that made motion estimates derivable from the same data. However, optical flow can be computed automatically and provides us an approximation of motion in the bee group, without the need for individual identities.

On the fish side, the high-resolution (1024 pixels by 1024 pixels) videos created were processed using the open-source software idTracker (*51*) to retrieve the individual trajectory of each agent separately. idTracker allows the reliable identification of six agents in a 32-min high-definition video. There were no false positives and no propagation of identification errors, and fish were identified correctly in 95% of the time steps on average. The agents' positions estimated using idTracker were used to compute multiple values such as individual direction of swimming, linear speed, interindividual distances, and number of switches of direction.

The analysis described above produced a time series of group behavior for each species in each replicate (Fig. 3A). We used these time series in further steps of analysis to better characterize the whole system. This includes transfer entropy measures from information theory, differences in collective choices, and correlations between the animals and robots and between the animal species (see texts S2 to S5).

SUPPLEMENTARY MATERIALS

robotics.sciencemag.org/cgi/content/full/4/28/eaau7897/DC1
Text S1. Robot controllers
Text S2. Correlation between robotic agents and animals
Text S3. Optical flow as a measure of motion in the bee arena
Text S4. Application of transfer entropy analysis
Text S5. Modulation of animal collective behavior
Text S6. Links to the software
Fig. S1. Correlation between the animals and the robots in each biohybrid system.
Fig. S2. Time series of the moments of the optical flow distribution, extracted from films of the bee arena.
Fig. S3. Statistical comparison of the transfer entropy distributions, using a Mann-Whitney *U* test.
Table S1. Parameters of interaction network.
Movie S1. Example of an experiment of condition B → F.
Movie S2. Example of an experiment of condition B ← F.
Movie S3. Example of an experiment of condition B ⇌ F.
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Robots mediating interactions between animals for interspecies collective behaviors

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