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14. ABSTRACT

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RPPR Final Report
as of 25-Jan-2023

Agency Code: 21XD

Proposal Number: 68276ME

Agreement Number: W911NF-16-1-0074

INVESTIGATOR(S):

Name: Eva Adnan Kanso
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Phone Number: 2138215788
Principal: Y

Organization: **University of Southern California**
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Country: USA
DUNS Number: 072933393
EIN: 951642394

Report Date: 30-Sep-2022
Date Received: 18-Jan-2023
Final Report for Period Beginning 01-May-2016 and Ending 30-Jun-2022
Title: Section II, A, 1.3.2: Active and passive actuation of bio-inspired locomotory systems
Begin Performance Period: 01-May-2016
End Performance Period: 30-Jun-2022
Report Term: 0-Other
Submitted By: Eva Kanso
Email: kanso@usc.edu
Phone: (213) 821-5788
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STEM Degrees: 2 **STEM Participants:** 7

Major Goals: The topic of this research project is to examine bio-inspired actuation strategies for efficient and versatile locomotion in three model systems: slow viscosity-driven systems, inertial underwater systems with undulatory swimming, and airborne flying and gliding systems. The specific objectives are to (1) develop quantitative measures of maneuverability in each of these model systems, and (2) devise a novel mathematical framework that incorporates combinations of active and passive shape actuation in these models of bio-inspired locomotion.

Accomplishments: In 2022, our activities focused on wrapping up major results under this grant and sending them for publication.

We submitted 9 research manuscript: two are published, one is in-press, and six are under review. We also have 10 research manuscripts in preparation. See attached document for a complete list of research activities in the Kanso Bio-inspired Motion Lab over the past year.

Over the course of this grant, we developed key understanding of the roles of (i) mechanosensing, (ii) mechanical coupling, and (iii) active and passive actuation in the control of locomotion and behavior. In the last year of this grant, we focused on applying these key insights to cooperative transport and collective behavior both at the microscopic and collective levels.

At the microscopic scale, we studied the role of the fluid medium in the emergent coordination, wave propagation, and wave stability in ciliary carpets. We identified minimal requirements for the emergence of stable collective coordination and fluid pumping by (infinitely) many individually-beating cilia. Our framework opens up the prospect to evaluate and design ciliated tissues that break symmetry and pump fluids in biological and engineered systems. This work was published in PNAS in November 2022, and picked up by half-a-dozen news outlets so far.

At the macroscopic scale, we studied the role of the fluid medium in the emergent formation, spatial patterns, stability, and energy savings in finite groups of flapping swimmers. Schooling fish interact, in addition to socially, physically through the fluid medium. Cooperative versus selfish group dynamics are often associated with social interactions, whereas flow interactions are thought to enable individuals to derive energetic benefits when swimming in groups. Here, using a hierarchy of fluid-structure interactions (FSI) models, we corroborated previous findings that mechanical coupling via the fluid medium only, with no sensorimotor feedback, can create physical conditions that allow oscillating swimmers to self-organize into stable, energy saving formations. We further showed, and provided a mechanistic explanation for, the existence of a universal relationship where, in these stable formations, the separation distance between pairs of swimmers varies linearly with the flapping phase. Importantly, we demonstrated that flow interactions lead to the emergence of dynamic and versatile formations of various spatial patterns, ranging from cooperative ``phalanx" patterns that favor fair distribution of energy savings among group members to greedy ``inline" patterns where few members get maximal benefit, leaving trailing swimmers with diminished opportunities for maintaining group coherence and gaining energetic benefits. These findings emphasize the role of the physical environment in the emergence of cooperative versus competitive group dynamics and the ability of the group to fluidly transition between these states. This work is currently in preparation for submission to Nature Physics.

Both systems, carpets of microscopic cilia and groups of macroscopic swimmers, share common features. They both belong to a larger class of problems that the community refers to as "Kuramoto oscillators." But neither system is a classic Kuramoto oscillator, per se. The nonlinearities that arise in each case (cilia versus swimmers) are specific, but a general theory that encompasses these forms of "mechanical communication" or mechanical coupling, and guide us as to how to exploit such coupling in engineering behavior and function is not out of reach. Intriguingly, the mechanical coupling in the flapping swimmers example are non-reciprocal, which opens up a great venue for theoretical exploration in future grants.

Training Opportunities: This project offered opportunities for post-doctoral and graduates student training, including training in conducting scientific research, writing research manuscript, giving scientific talks, and mentoring others.

Kanso is committed to promoting a diverse student population in her lab.

Results Dissemination: This work was disseminated in scientific publications, conference presentations, invited seminars, and other formal and informal venues. See attached documents for a complete list of talks and manuscripts.

Honors and Awards: Kanso was elected Fellow of the American Physical Society, Division of Fluid Dynamics. in 2022.

Protocol Activity Status:

Technology Transfer: One international patent application is under review.

PARTICIPANTS:

Participant Type: Postdoctoral (scholar, fellow or other postdoctoral position)
Participant: Basile Radisson
Person Months Worked: 2.00 **Funding Support:**
Project Contribution:
National Academy Member: N

Participant Type: Graduate Student (research assistant)
Participant: Feng Ling
Person Months Worked: 1.00 **Funding Support:**
Project Contribution:
National Academy Member: N

Participant Type: Graduate Student (research assistant)
Participant: Sina Heydari
Person Months Worked: 1.00 **Funding Support:**
Project Contribution:
National Academy Member: N

Participant Type: Graduate Student (research assistant)
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Person Months Worked: 1.00 **Funding Support:**
Project Contribution:
National Academy Member: N

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Participant: Yusheng Jiao
Person Months Worked: 1.00 **Funding Support:**
Project Contribution:
National Academy Member: N

Participant Type: Graduate Student (research assistant)
Participant: Haotian Hang
Person Months Worked: 1.00 **Funding Support:**
Project Contribution:
National Academy Member: N

Participant Type: Graduate Student (research assistant)
Participant: Morgan Jones
Person Months Worked: 1.00 **Funding Support:**
Project Contribution:
National Academy Member: N

Participant Type: Graduate Student (research assistant)
Participant: Chenchen Huang
Person Months Worked: 1.00 **Funding Support:**
Project Contribution:
National Academy Member: N

ARTICLES:

Publication Type: Journal Article Peer Reviewed: Y **Publication Status:** 1-Published
Journal: Experimental Brain Research
Publication Identifier Type: ISSN Publication Identifier: 1432-1106
Volume: 235 Issue: 4 First Page #: 1139
Date Submitted: 9/20/17 12:00AM Date Published: 2/4/17 6:08PM
Publication Location:
Article Title: Cortical activity predicts good variation in human motor output
Authors: Sarine Babikian, Eva Kanso and Jason Kutch
Keywords: EEG, motor cortex, goal-equivalent variability, finger
Abstract: Human movement patterns have been shown to be particularly variable if many combinations of activity in different muscles all achieve the same task goal (i.e., are goal-equivalent). The nervous system appears to automatically vary its output among goal-equivalent combinations of muscle activity to minimize muscle fatigue or distribute tissue loading, but the neural mechanism of this “good” variation is unknown. Here we use a bimanual finger task, electroencephalography (EEG), and machine learning to determine if cortical signals can predict goal-equivalent variation in finger force output. 18 healthy participants applied left and right index finger forces to repeatedly perform a task that involved matching a total (sum of right and left) finger force.
Distribution Statement: 3-Distribution authorized to U.S. Government Agencies and their contractors
Acknowledged Federal Support: **Y**

Publication Type: Journal Article Peer Reviewed: Y **Publication Status:** 1-Published
Journal: Journal of Fluid Mechanics
Publication Identifier Type: Publication Identifier:
Volume: Issue: First Page #:
Date Submitted: 8/30/18 12:00AM Date Published:
Publication Location:
Article Title: Bistability in the synchronization of actuated microfilaments
Authors: Hanliang Guo, Lisa Fauci, Michael Shelley and Eva Kanso
Keywords: Flagella and cilia, synchronization, hydrodynamic interactions
Abstract: Cilia and flagella are essential building blocks for biological fluid transport and locomotion at the micron scale. They often beat in synchrony and may transition between different synchronization modes in the same cell type. Here, we investigate the behavior of elastic microfilaments, protruding from a surface and driven at their base by a configuration-dependent torque. We consider full hydrodynamic interactions among and within filaments and no slip at the surface. Isolated filaments exhibit periodic deformations, with increasing waviness and frequency as the magnitude of the driving torque increases. Two nearby but independently-driven filaments synchronize their beating in-phase or anti-phase. This synchrony arises autonomously via the interplay between hydrodynamic coupling and filament elasticity. Importantly, in-phase and anti-phase synchronization modes are bistable and co-exist for a range of driving torques and separation distances.
Distribution Statement: 3-Distribution authorized to U.S. Government Agencies and their contractors
Acknowledged Federal Support: **Y**

Publication Type: Journal Article Peer Reviewed: Y **Publication Status:** 1-Published
Journal: Journal of Fluid Mechanics
Publication Identifier Type: Publication Identifier:
Volume: Issue: First Page #:
Date Submitted: 8/30/18 12:00AM Date Published:
Publication Location:
Article Title: Bistability in the rotational motion of rigid and flexible wings
Authors: Yangyang Huang, Leif Ristroph, Mitul Luhar and Eva Kanso
Keywords: Flying, aerodynamics, vortex-sheet model, quasi-steady force model
Abstract: We explore the rotational stability of hovering flight. Our model is motivated by an experimental pyramid-shaped object and a computational wedge-shaped analog hovering passively in oscillating airflows. Both systems were previously shown to maintain rotational balance during free flight. Here, we attach the wedge-shaped flyer at its apex, allowing it to rotate freely akin to a pendulum. We find that the flyer exhibits stable concave-down and concave-up behavior. Importantly, the down and up configurations are bistable and co-exist for a range of background flow properties. We explain the aerodynamic origin of this bistability and compare it to the inertia-induced stability of an inverted pendulum oscillating at its base.We then allow the flyer to flap passively by introducing a rotational spring at its apex. For stiff springs, flexibility diminishes upward stability but as stiffness decreases, a new transition to upward stability is induced by flapping.
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Publication Type: Journal Article Peer Reviewed: Y **Publication Status:** 1-Published
Journal: Bioinspiration & Biomimetics
Publication Identifier Type: DOI Publication Identifier: 10.1088/1748-3190/aaa787
Volume: 13 Issue: 2 First Page #: 025003
Date Submitted: 8/30/18 12:00AM Date Published: 2/1/18 8:00AM
Publication Location:
Article Title: Classifying vortex wakes using neural networks
Authors: Brendan Colvert, Mohamad Alsalman, Eva Kanso
Keywords: sensing, swimming, unsteady flows
Abstract: Unsteady flows contain information about the objects creating them. Aquatic organisms offer intriguing paradigms for extracting flow information using local sensory measurements. In contrast, classical methods for flow analysis require global knowledge of the flow field. Here, we train neural networks to classify flow patterns using local vorticity measurements. Specifically, we consider vortex wakes behind an oscillating airfoil and we evaluate the accuracy of the network in distinguishing between three wake types, 2S, 2P+2S and 2P+4S. The network uncovers the salient features of each wake type.
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Publication Type: Journal Article Peer Reviewed: Y **Publication Status:** 1-Published
Journal: Physical Review Letters
Publication Identifier Type: DOI Publication Identifier: 10.1103/PhysRevLett.120.198101
Volume: 120 Issue: 19 First Page #:
Date Submitted: 8/30/18 12:00AM Date Published: 5/1/18 12:00AM
Publication Location:
Article Title: Model of Collective Fish Behavior with Hydrodynamic Interactions
Authors: Audrey Filella, François Nadal, Clément Sire, Eva Kanso, Christophe Eloy
Keywords: collective behavior, fish schooling
Abstract: Fish schooling is often modeled with self-propelled particles subject to phenomenological behavioral rules. Although fish are known to sense and exploit flow features, these models usually neglect hydrodynamics. Here, we propose a novel model that couples behavioral rules with far-field hydrodynamic interactions. We show that (1) a new “collective turning” phase emerges, (2) on average, individuals swim faster thanks to the fluid, and (3) the flow enhances behavioral noise. The results of this model suggest that hydrodynamic effects should be considered to fully understand the collective dynamics of fish.
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Publication Type: Journal Article Peer Reviewed: Y **Publication Status:** 1-Published
Journal: Journal of The Royal Society Interface
Publication Identifier Type: DOI Publication Identifier: 10.1098/rsif.2020.0352
Volume: 17 Issue: 168 First Page #: 20200352
Date Submitted: 9/15/20 12:00AM Date Published: 7/1/20 2:00PM
Publication Location: England
Article Title: Enhanced flight performance in non-uniformly flexible wings
Authors: Lionel Vincent, Min Zheng, John H. Costello, Eva Kanso
Keywords: aerodynamics, tumbling wings, heterogeneous wing design
Abstract: The flexibility of biological propulsors such as wings and fins is believed to contribute to the higher performance of flying and swimming animals compared with their engineered peers. Flexibility seems to follow a universal design rule that induces bending patterns at about one-third from the distal tip of the propul- sor's span. However, the aerodynamic mechanisms that shaped this convergent design and the potential improvement in performance are not well understood. Here, we analyse the effect of heterogeneous flexibility on the flight performance (range and descent angle) of passively tumbling wings. Using experiments, numerical simulations, and scaling analysis, we demonstrate that spanwise tip flexibility that follows this empirical rule leads to improved flight performance. Improvement in flight range seems to be related to flutter-induced drag reduction. This mechanism is independent of the wing's auto-rotation and represents a more general trait of wings with non-uniform tip.
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Publication Type: Journal Article Peer Reviewed: Y **Publication Status:** 1-Published
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Publication Identifier Type: DOI Publication Identifier: 10.1017/jfm.2020.88
Volume: 889 Issue: First Page #:
Date Submitted: 9/15/20 12:00AM Date Published: 2/1/20 8:00AM
Publication Location:
Article Title: Shape optimization of tumbling wings
Authors: Lionel Vincent, Yucen Liu, Eva Kanso
Keywords: swimming/flying, low-dimensional models
Abstract: The flexibility of biological propulsors such as wings and fins is believed to contribute to the higher performance of flying and swimming animals compared with their engineered peers. Flexibility seems to follow a universal design rule that induces bending patterns at about one-third from the distal tip of the propul- sor's span. However, the aerodynamic mechanisms that shaped this convergent design and the potential improvement in performance are not well understood. Here, we analyse the effect of heterogeneous flexibility on the flight performance (range and descent angle) of passively tumbling wings. Using experiments, numerical simulations, and scaling analysis, we demonstrate that spanwise tip flexibility that follows this empirical rule leads to improved flight performance. Improvement in flight range seems to be related to flutter-induced drag reduction. This mechanism is independent of the wing's auto-rotation and represents a more general trait of wings with non-uniform tip.
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Publication Type: Journal Article Peer Reviewed: Y **Publication Status:** 1-Published
Journal: Philosophical Transactions of the Royal Society B: Biological Sciences
Publication Identifier Type: DOI Publication Identifier: 10.1098/rstb.2019.0157
Volume: 375 Issue: 1792 First Page #: 20190157
Date Submitted: 9/15/20 12:00AM Date Published: 12/1/19 8:00AM
Publication Location:
Article Title: Cilia oscillations
Authors: Yi Man, Feng Ling, Eva Kanso
Keywords: axoneme, molecular motors, microfilament deformation
Abstract: Cilia, or eukaryotic flagella, are microscopic active filaments expressed on the surface of many eukaryotic cells, from single-celled protozoa to mammalian epithelial surfaces. Cilia are characterized by a highly conserved and intricate internal structure in which molecular motors exert forces on microtubule doublets causing cilia oscillations. The spatial and temporal regulations of this molecular machinery are not well understood. Several theories suggest that geometric feedback control from cilium deformations to molecular activity is needed. Here, we implement a recent sliding control model, where the unbinding of molecular motors is dictated by the sliding motion between microtubule doublets. We investigate the waveforms exhibited by the model cilium, as well as the associated molecular motor dynamics, for hinged and clamped boundary conditions. Hinged filaments exhibit base- to-tip oscillations while clamped filaments exhibit both base-to-tip and tip-to-base oscillations.
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Publication Type: Journal Article Peer Reviewed: Y **Publication Status:** 1-Published
Journal: Proceedings of the National Academy of Sciences
Publication Identifier Type: DOI Publication Identifier: 10.1073/pnas.2018193118
Volume: 118 Issue: 29 First Page #:
Date Submitted: 11/8/21 12:00AM Date Published: 7/1/21 7:00AM
Publication Location:
Article Title: Teamwork in the viscous oceanic microscale
Authors: Eva A. Kanso, Rubens M. Lopes, J. Rudi Strickler, John O. Dabiri, John H. Costello
Keywords: phytoplankton / nutrient limitation / symbiosis / diffusion limitation / cell size
Abstract: Nutrient acquisition is crucial for oceanic microbes, and competitive solutions to solve this challenge have evolved among a range of unicellular protists. However, solitary solutions are not the only approach found in natural populations. A diverse array of oceanic protists form temporary or even long-lasting attachments to other protists and marine aggregates. Do these planktonic consortia provide benefits to their members? Here, we use empirical and modeling approaches to evaluate whether the relationship between a large centric diatom, Coscinodiscus wailesii, and a ciliate epibiont, Pseudovorticella coscinodisci, provides nutrient flux benefits to the host diatom. We find that fluid flows generated by ciliary beating can increase nutrient flux to a diatom cell surface four to 10 times that of a still cell without ciliate epibionts. This cosmopolitan species of diatom does not form consortia in all environments but frequently joins such consortia in nutrient-depleted waters. Our res
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Volume: 6 Issue: 5 First Page #:
Date Submitted: 11/8/21 12:00AM Date Published: 5/1/21 2:00PM
Publication Location:
Article Title: Learning to swim in potential flow
Authors: Yusheng Jiao, Feng Ling, Sina Heydari, Nicolas Heess, Josh Merel, Eva Kanso
Keywords: Learning, swimming, biological fluid dynamics
Abstract: Fish schools are ubiquitous in marine life. Although flow interactions are thought to be beneficial for schooling, their exact effects on the speed, energetics and stability of the group remain elusive. Recent numerical simulations and experimental models suggest that flow interactions stabilize in-tandem formations of flapping foils. Here, we employ a minimal vortex sheet model that captures salient features of the flow interactions among flapping swimmers, and we study the free swimming of a pair of in-line swimmers driven with identical heaving or pitching motions. We find that, independent of the flapping mode, heaving or pitching, the follower passively stabilizes at discrete locations in the wake of the leader, consistent with the heaving foil experiments, but pitching swimmers exhibit tighter and more cohesive formations. Further, in comparison to swimming alone, pitching motions increase the energetic efficiency of the group while heaving motions result in a slight increase...
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Publication Type: Journal Article Peer Reviewed: Y **Publication Status:** 1-Published
Journal: Journal of Fluid Mechanics
Publication Identifier Type: DOI Publication Identifier: 10.1017/jfm.2021.551
Volume: 922 Issue: First Page #:
Date Submitted: 11/8/21 12:00AM Date Published: 7/1/21 7:00AM
Publication Location:
Article Title: School cohesion, speed and efficiency are modulated by the swimmers flapping motion
Authors: Sina Heydari, Eva Kanso
Keywords: Biological Fluid Dynamics: Swimming/flying Nonlinear Dynamical Systems: Low-dimensional models Wakes/Jets: Wakes
Abstract: Fish schools are ubiquitous in marine life. Although flow interactions are thought to be beneficial for schooling, their exact effects on the speed, energetics and stability of the group remain elusive. Recent numerical simulations and experimental models suggest that flow interactions stabilize in-tandem formations of flapping foils. Here, we employ a minimal vortex sheet model that captures salient features of the flow interactions among flapping swimmers, and we study the free swimming of a pair of in-line swimmers driven with identical heaving or pitching motions. We find that, independent of the flapping mode, heaving or pitching, the follower passively stabilizes at discrete locations in the wake of the leader, consistent with the heaving foil experiments, but pitching swimmers exhibit tighter and more cohesive formations. Further, in comparison to swimming alone, pitching motions increase the energetic efficiency of the group while heaving motions result in a slight increase...
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Publication Type: Journal Article Peer Reviewed: Y **Publication Status:** 1-Published
Journal: Journal of The Royal Society Interface
Publication Identifier Type: DOI Publication Identifier: 10.1098/rsif.2020.0660
Volume: 18 Issue: 174 First Page #: 20200660
Date Submitted: 11/8/21 12:00AM Date Published: 1/2/21 12:00AM
Publication Location:
Article Title: Intracellular coupling modulates biflagellar synchrony
Authors: Hanliang Guo, Yi Man, Kirsty Y. Wan, Eva Kanso
Keywords: flagella / elastic filaments / mechanical coupling / coordination modes
Abstract: Nutrient acquisition is crucial for oceanic microbes, and competitive solutions to solve this challenge have evolved among a range of unicellular protists. However, solitary solutions are not the only approach found in natural populations. A diverse array of oceanic protists form temporary or even long-lasting attachments to other protists and marine aggregates. Do these planktonic consortia provide benefits to their members? Here, we use empirical and modeling approaches to evaluate whether the relationship between a large centric diatom, Coscinodiscus wailesii, and a ciliate epibiont, Pseudovorticella coscinodisci, provides nutrient flux benefits to the host diatom. We find that fluid flows generated by ciliary beating can increase nutrient flux to a diatom cell surface four to 10 times that of a still cell without ciliate epibionts. This cosmopolitan species of diatom does not form consortia in all environments but frequently joins such consortia in nutrient-depleted waters. Our res
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Publication Type: Journal Article Peer Reviewed: Y **Publication Status:** 1-Published
Journal: Proceedings of the National Academy of Sciences
Publication Identifier Type: DOI Publication Identifier: 10.1073/pnas.2214413119
Volume: 119 Issue: 45 First Page #:
Date Submitted: 1/18/23 12:00AM Date Published: 11/1/22 7:00AM
Publication Location:
Article Title: Spontaneous phase coordination and fluid pumping in model ciliary carpets
Authors: Anup V. Kanale, Feng Ling, Hanliang Guo, Sebastian Fürthauer, Eva Kanso
Keywords: CILIA, COORDINATION, PUMPING, HYDRODYNAMIC INTERACTIONS
Abstract: Ciliated tissues, such as in the mammalian lungs, brains, and reproductive tracts, are specialized to pump fluid. They generate flows by the collective activity of hundreds of thousands of individual cilia that beat in a striking metachronal wave pattern. Despite progress in analyzing cilia coordination, a general theory that links coordination and fluid pumping in the limit of large arrays of cilia remains lacking. Here, we conduct in silico experiments with thousands of hydrodynamically interacting cilia, and we develop a continuum theory in the limit of infinitely many independently beating cilia by combining tools from active matter and classical Stokes flow. We find, in both simulations and theory, that isotropic and synchronized ciliary states are unstable. Traveling waves emerge regardless of initial conditions, but the characteristics of the wave and net flows depend on cilia and tissue properties. That is, metachronal phase coordination is a stable global attractor in large ci
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Acknowledged Federal Support: **Y**

Partners

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I certify that the information in the report is complete and accurate:
Signature: Eva Kanso
Signature Date: 1/18/23   6:22PM

ABSTRACT

This document outlines the major research dissemination activities (manuscripts and talks) as well as provides a short synopses of major research findings for 2022.

SERVICE

I am currently a Program Director in the Engineering Directorate at the National Science Foundation via an Intergovernmental Personnel Act (IPA) Assignment.
Appointment start date: August 30, 2021. Appointment expected end date: August 28, 2023.

My work at NSF includes: running panels, processing awards and declines, reviewing annual reports, and working to increase diversity of review panelists. Additionally, I served on two job search committees and I serve on several working groups for defining and shaping interdisciplinary research initiative within and across directorate boundaries.

HONORS and AWARDS

I was elected Fellow of the American Physical Society, Division of Fluid Dynamics. Announced at the APS-DFD meeting in Indianapolis in November 2022.

Together with a team of co-PIs, I received a mini-MURI ONR grant entitled: **Hydrodynamics, Sensing, & Control in the Coordinated Swimming of Fish & Fish-inspired Vehicles** in July 2022**.**

JOURNAL PUBLICATIONS 2022-2023

Published or in Press

1. Kanale A.V., F. Ling, H. Guo, S. Fürthauer, E. Kanso, **Spontaneous phase coordination in model ciliary carpets,** PNAS, 2022, https://doi.org/10.1073/pnas.2214413119
   Picked up in 10 news outlets: https://pnas.altmetric.com/details/134900740/news

2. Gundlach K., J.C. Nawroth, E. Kanso, F. Nasrin, E. G. Ruby, M. McFall-Ngai, **Ciliated epithelia as key elements in the recruitment of bacterial partners into a host-animal symbiosis**, Frontiers in Cell and Developmental Biology, vol 10, 2022, https://doi.org/10.3389/fcell.2022.974213

3. Jiao Y., B. Colvert, Y. Man, M.H. McHenry, E. Kanso, **Evaluating Evasion Strategies in Zebrafish Larvae**, PNAS, accepted, in press, 2023.

Submitted

4. Nawroth J.C., F. Ling, T. Essock-Burns, D. Stein, M. McFall-Ngai, K. Katija, M. Shelley, E. Kanso, **Flow Physics Explains Morphological Diversity of Ciliated Ducts** submitted to Nature Physics in January 2023.

5. Costello J.H., S.P. Colin, B.J. Gemmell, J.O. Dabiri, E.A. Kanso, **A fundamental propulsive mechanism employed by swimmers and flyers throughout the animal kingdom**, submitted to Journal of Experimental Biology in December 2022.

6. Lin Y.L., S. N. Smith, E. Kanso, A. N. Septer, C.H. Rycroft. **A subcellular biochemical model for T6SS dynamics reveals winning competitive strategies**, PNAS Nexus, under review.

7. J.C. Nawroth, C. Giez, A. Klimovich, E.A. Kanso, T.C.G. Bosch**, Spontaneous body wall contractions shape and stabilize the symbiotic microbiota,** eLife, under review.

8. Radisson B., E. Kanso, **Elastic snap-through instabilities are governed by geometric symmetries**, Physical Review Letters (PRL), under review.

9. Radisson B., E. Kanso, **Dynamic behavior of elastic strips near shape transition**, Physical Review E (PRE), under review

Manuscripts in preparation

10. Ellers O., S. Heydari, K.-I. Ellers, T. Po, A. Johnson, E. Kanso, M.J. McHenry, **Soft skeletons transmit force with variable gearing**, in preparation.

11. F. Ling, Y. Man, E. Kanso, **Controlling flagellar wave directions via forward-aft molecular motor asymmetry**, in preparation.

12. Heydari S., J. Merel, M.J. McHenry, E. Kanso, **Resolving optimal mechanosensory cues in cooperative transport using deep reinforcement learning**, in preparation.

13. Heydari S., H. Hang, E. Kanso, **Flow-coupled swimmers self-organize into spatial patterns that favor cooperative or selfish energy savings**, in preparation.

14. Huang C., E. Kanso, **Spontaneous phase transitions in hydrodynamically-coupled fish schools,** in preparation.

15. Hang H., S. Heydari, Y. Jiao, E. Kanso, **Minimal sensoricontrol strategies for following hydrodynamic trails**, in preparation.

16. Huang C., E. Kanso, **Evaluating flow sensing in fish rheotaxis**, in preparation.

17. Jiao Y., F. Ling, S. Heydari, N. Heess, J. Merel, E. Kanso, **Reinforcement learning for optimal animal and robotic locomotion: a tutorial**, in preparation.

18. Jiao Y., E. Kanso, **Learning to exploit unsteady flows using egocentric sensory cues**, in preparation.

19. Liu J., Y. Man, J.H. Costello, E. Kanso, **Optimal feeding rates of sessile and motile ciliates are asymptotically equivalent**, in preparation

Published in 2021

1. Byron M.L., D.W. Murphy K. Katija, A.P. Hoover, J. Daniels, K. Garayev, D. Takagi, E. Kanso, B. J. Gemmell, M. Ruszczyk, and others, **Metachronal motion across scales: current challenges and future directions**, Integrative and comparative biology, 61(5): 1674—1688, 2021.

2. E. Kanso, R.M. Lopes, J.R. Strickler, J.O. Dabiri, and J.H. Costello, **Teamwork in the viscous oceanic microscale**, PNAS, 118 (29), e2018193118, 2021.
   Featured in Science Daily and SciTechDaily
   Featured in Nature Reviews Microbiology, **Ciliate symbionts create the flow**

3. Heydari S. and E. Kanso, **School cohesion, speed, and efficiency are modulated by the swimmers flapping motion**, Journal of Fluid Mechanics, 992, A7, 2021.

4. Jiao Y., F. Ling, Heydari S., N. Heess, J. Merel, and E. Kanso [2021], **Learning to swim in potential flow**, Phys. Rev. Fluids 6, 050505, 2021.

5. Guo H., Y. Man, K.Y. Wan, and E. Kanso [2021], **Intracellular coupling modulates biflagellar synchrony**, Journal of Royal Society Interface, 18:174, 20200660, 2021.

6. Ling F. and E. Kanso, **Octopus-inspired arm movement**, In D. Paley & N. Wereley(Eds.) Bioinspired Sensing, Actuation, and Control in Underwater Soft Robotic Systems, Springer, 2021.

PATENT

- **Provisional Patent: USC Invention 2022-071 / Disclosure 2022-0072 "Rational Design of Microfluidic Pumps incorporating Actively Beating Ciliated Surfaces and Methods of Use"** Eva Kanso (30%), Janna Nawroth (30%), Feng Ling (25%), Margaret McFall-Ngai (5%), Kakani Katija (5%), Michael Shelley (5%). **International Patent Application under review.**

INVITED TALKS 2022

1. **Cilia Powered Pumps**, Invited Symposium Talk, S6: Large-Scale Biological Phenomena Arising From Small-Scale Biophysical Processes, Society of Integrative and Comparative Biology (SICB 2023), January 2023.
2. **Cilia Powered Flows,** Mechanical Engineering: Fluid Mechanics Seminar, Stanford University, November 2022.
3. **Cilia Powered Pumps,** Galcit: Fluid Mechanics Seminar, Caltech University, May 2022.
4. **Cilia Coordination**, invited to focus session "Self organization in active filament systems" at the 2022 APS March meeting in Chicago, March 2022. (Due to family circumstances, I asked my PhD student Feng Ling to give the talk in my place).

INVITED TALKS 2021

5. **Cilia-Powered Flows**, Invited Talk, American Physical Society, Division of Fluid Dynamics (APS-DFD) meeting, November 21, 2021.
6. **The Sea Star Bounce**, Interdisciplinary Seminar Series on Biolocomotion, October 6, 2021.
7. **Spontaneous Ciliary Waves**, Biophysics and Physical Biology (BPPB) Seminar, August 6, 2021.
8. **Ciliated Tissues: from form to function**, Biophysics and Physical Biology (BPPB) Turorial, August 6, 2021.
9. **Coordination and Symmetry-Breaking in Cilia and Flagella**, 20 Years of Regularized Stokeslets: Cilia, Flagella, and Microswimmers - Part I of IIRIMS. SIAM Annual Meeting, July 22, 2021.
10. **Waves in Ciliary Carpets**, Seminar at LadHyX Ecole Polytechnique, Palaiseau, France, July 8, 2021.
11. **The biophysics of cilia and flagella**, PSL Soft and Living Matter Days, Paris, France, July 6, 2021.
12. **Emergent Waves in Ciliary Carpets**, Invited talk, Minisymposium: Mathematics of Microswimming, Multiscale Modeling in Physiology and Biophysics, Society of Mathematical Biology, June 17, 2021.
13. **Multi-synchrony in Ciliary Systems**, Invited talk, Biofluid Symposium, Kyoto, Japan, June 21-24, 2021.
14. **One Fish, Two Fish**, Seminar at PMMH, Ecole Supérieure de Physique et de Chimie Industrielles (ESPCI), Paris, France, June 25, 2021.
15. **Emergent Waves in Ciliary Carpets**, Informal talk at PMMH, Ecole Supérieure de Physique et de Chimie Industrielles (ESPCI), Paris, France, June 16, 2021.
16. **One Fish, Two Fish**, Seminar at Institut de Recherche sur les Phénomènes Hors Equilibre (IRPHE), Marseille, France, June 18, 2021.
17. **One Fish, Two Fish**, University of Washington's Data-Driven Methods in Science and Engineering seminar, May 28, 2021.

18. **Cilia Coordination**, Invited Talk, Society of Integrative and Comparative Biology Conference, January 2021.
19. **Teamwork within and across organisms**, Tweetorial, DBIO (link) August 18, 2021.

ONR REVIEW MEETINGS 2022

- **Bioinspired sensory and control principles for underwater multi- vehicle coordination,** (N00014-19-1-2035), ONR Bioinspired Autonomous Systems Review, PD Tom McKenna, June 1-3, 2022.
- **Mini-MURI Kick-off meeting: Hydrodynamics, Sensing, & Control in the Coordinated Swimming of Fish & Fish-inspired Vehicles**, (Mini-MURI award N00014-22-1-2655), PDs: Bob Brizzolara, Tom McKenna, Marc Steinberg. September 29, 2022

KANSO LAB PRESENTATIONS

- 1 invited symposium talk at the SICB meeting in Austin in January 2023, and 2 contributed talks.
- 5 contributed talks and 1 poster presentation at the APS DFD meeting that was held in Indianapolis in November 2022.
- 7 contributed talks and 1 poster presentation at the APS DFD meeting that was held in Phoenix in November 2021.
- 3 talks at the APS March meeting in Chicago in March 2022.
- 6 contributed talks to the Southern California Fluid Symposium to be held at San Diego State University on April 11, 2022.
- 2 talks at the SICB conference in January 2022.
- Seminar at the Frontiers in Bio-inspired Soft Robotics, 2 seminars at the Remote Colloquium on Vortex Flows (ReCoVor), seminar at Microsoft Autonomous Systems Research Reading Series
- 1 PhD student (Sina Heydari) attended and presented at the **Junior Scientist Workshop on Theoretical Neuroscience, Janelia Research Campus** in November 2022.
- 1 PhD student (Yusheng Jiao) attended and presented at the **Frontiers in Applied & Computational Mathematics Conference** at New Jersey Institute of Technology in May 2022.
- See details of these talks in the attached document entitled **Kanso Lab Presentations**

MAJOR RESEARCH ACCOMPLISHMENTS

Over the course of this grant, we developed key understanding of the roles of (i) mechanosensing, (ii) mechanical coupling, and (iii) active and passive actuation in the control of locomotion and behavior. In the last year of this grant, we focused on applying these key insights to cooperative transport and collective behavior both at the microscopic and collective levels.

At the microscopic scale, we studied the role of the fluid medium in the emergent coordination, wave propagation, and wave stability in ciliary carpets. We identified minimal requirements for the emergence of stable collective coordination and fluid pumping by (infinitely) many individually-beating cilia. Our framework opens up the prospect to evaluate and design ciliated tissues that break symmetry and pump fluids in biological and engineered systems. This work was published in PNAS in November 2022, and was picked up by half-a-dozen news outlets so far.

At the macroscopic scale, we studied the role of the fluid medium in the emergent formation, spatial patterns, stability, and energy savings in finite groups of flapping swimmers. Schooling fish interact, in addition to socially, physically through the fluid medium. Cooperative versus selfish group dynamics are often associated with social interactions, whereas flow interactions are thought to enable individuals to derive energetic benefits when swimming in groups. Here, using a hierarchy of fluid-structure interactions (FSI) models, we corroborated previous findings that mechanical coupling via the fluid medium only, with no sensorimotor feedback, can create physical conditions that allow oscillating swimmers to self-organize into stable, energy saving formations. We further showed, and provided a mechanistic explanation for, the existence of a universal relationship where, in these stable formations, the separation distance between pairs of swimmers varies linearly with the flapping phase. Importantly, we demonstrated that flow interactions lead to the emergence of dynamic and versatile formations of various spatial patterns, ranging from cooperative ``phalanx" patterns that favor fair distribution of energy savings among group members to greedy ``inline" patterns where few members get maximal benefit, leaving trailing swimmers with diminished opportunities for maintaining group coherence and gaining energetic benefits. These findings emphasize the role of the physical environment in the emergence of cooperative versus competitive group dynamics and the ability of the group to fluidly transition between these states. This work is currently in preparation for submission to Nature Physics.

Both systems, carpets of microscopic cilia and groups of macroscopic swimmers, share common features. They both belong to a larger class of problems that the community refers to as "Kuramoto oscillators." But neither system is a classic Kuramoto oscillator, per se. The nonlinearities that arise in each case (cilia versus swimmers) are specific, but a general theory that encompasses these forms of "mechanical communication" or mechanical coupling, and guide us as to how to exploit such coupling in engineering behavior and function is not out of reach. Intriguingly, the mechanical coupling in the flapping swimmers example are non-reciprocal, which opens up a great venue for theoretical exploration in future grants.al exploration in future grants.