



SYMPOSIUM

Metachronal Motion across Scales: Current Challenges and Future Directions

Margaret L. Byron,^{1,*} David W. Murphy ,[†] Kakani Katija,[‡] Alexander P. Hoover ,[§] Joost Daniels ,[‡] Kuvvat Garayev,[†] Daisuke Takagi,[¶] Eva Kanso,^{||} Bradford J. Gemmell,^{|||} Melissa Ruszczyk^{**} and Arvind Santhanakrishnan ,^{††}

¹Department of Mechanical Engineering, Penn State University, 201 Old Main, University Park, PA 16801, USA;

[†]Department of Mechanical Engineering, University of South Florida, 4202 E. Fowler Avenue, Tampa, FL 33620, USA;

[‡]Monterey Bay Aquarium Research Institute, 7700 Sandholdt Road, Moss Landing, CA 95039, USA; [§]Department of

Mathematics, University of Akron, 302 E Buchtel Avenue, Akron, OH 44325, USA; [¶]Department of Mathematics,

University of Hawaii at Manoa, 2500 Campus Road, Honolulu, HI 96822, USA; ^{||}Department of Mechanical and

Aerospace Engineering, University of Southern California, University Park, Los Angeles, CA 90007, USA; ^{|||}Department

of Integrative Biology, University of South Florida, 4202 E. Fowler Avenue, Tampa, FL 33620, USA; ^{**}Ocean Science and

Engineering, Georgia Institute of Technology, 310 Ferst Drive, Atlanta, GA 30332, USA; ^{††}School of Mechanical and

Aerospace Engineering, Oklahoma State University, 201 General Academic Building, Stillwater, OK 74078, USA

From the symposium “Metachronal coordination of multiple appendages for swimming and pumping” presented at the virtual annual meeting of the Society for Integrative and Comparative Biology, January 3–7, 2021.

¹E-mail: mbyron@psu.edu

Synopsis Metachronal motion is used across a wide range of organisms for a diverse set of functions. However, despite its ubiquity, analysis of this behavior has been difficult to generalize across systems. Here we provide an overview of known commonalities and differences between systems that use metachrony to generate fluid flow. We also discuss strategies for standardizing terminology and defining future investigative directions that are analogous to other established subfields of biomechanics. Finally, we outline key challenges that are common to many metachronal systems, opportunities that have arisen due to the advent of new technology (both experimental and computational), and next steps for community development and collaboration across the nascent network of metachronal researchers.

Introduction: what is metachronal motion?

Metachrony refers to a motion that is not synchronous (meaning “occurring at the same time”); it is a specific subcategory of asynchrony (meaning the opposite). Metachrony implies a sequence of similar events which occur in sequential order. Biologically, metachronal motion occurs when a series of (usually morphologically similar) appendages sequentially perform a cyclic, repeated motion at a fixed phase lag from one another. This creates a “metachronal wave,” whose frequency and wavelength are governed by the spacing of the appendages and the phase lag between them. Each appendage, as it moves, drags the surrounding fluid along with it.

Advance Access publication 28 May 2021

© The Author(s) 2021. Published by Oxford University Press on behalf of the Society for Integrative and Comparative Biology.
All rights reserved. For permissions please email: journals.permissions@oup.com.

Together, the sequentially coordinated appendages can generate fluid flows that are categorically different than those that would be created by a single appendage, or by the same group of appendages moving synchronously. Indeed, in some contexts, synchronous motion cannot create fluid flow at all, but metachronal motion can (Takagi 2015). Metachronally coordinated appendages can also produce a steadier, more efficient flow than the same appendages using synchronous coordination (Ford et al. 2019).

Metachronal motion is used across a staggering spectrum of species and scales, from microns to centimeters (e.g., Fig. 1). Because of this great functional and morphological diversity, there has been little



SYMPOSIUM

Metachronal Motion across Scales: Current Challenges and Future Directions

Margaret L. Byron,^{1,*} David W. Murphy ,[†] Kakani Katija,[‡] Alexander P. Hoover ,[§] Joost Daniels ,[‡] Kuvvat Garayev,[†] Daisuke Takagi,[¶] Eva Kanso,^{||} Bradford J. Gemmell,^{|||} Melissa Ruszczyk^{**} and Arvind Santhanakrishnan ,^{††}

¹Department of Mechanical Engineering, Penn State University, 201 Old Main, University Park, PA 16801, USA;

[†]Department of Mechanical Engineering, University of South Florida, 4202 E. Fowler Avenue, Tampa, FL 33620, USA;

[‡]Monterey Bay Aquarium Research Institute, 7700 Sandholdt Road, Moss Landing, CA 95039, USA; [§]Department of

Mathematics, University of Akron, 302 E Buchtel Avenue, Akron, OH 44325, USA; [¶]Department of Mathematics,

University of Hawaii at Manoa, 2500 Campus Road, Honolulu, HI 96822, USA; ^{||}Department of Mechanical and

Aerospace Engineering, University of Southern California, University Park, Los Angeles, CA 90007, USA; ^{|||}Department

of Integrative Biology, University of South Florida, 4202 E. Fowler Avenue, Tampa, FL 33620, USA; ^{**}Ocean Science and

Engineering, Georgia Institute of Technology, 310 Ferst Drive, Atlanta, GA 30332, USA; ^{††}School of Mechanical and

Aerospace Engineering, Oklahoma State University, 201 General Academic Building, Stillwater, OK 74078, USA

From the symposium “Metachronal coordination of multiple appendages for swimming and pumping” presented at the virtual annual meeting of the Society for Integrative and Comparative Biology, January 3–7, 2021.

¹E-mail: mbyron@psu.edu

Synopsis Metachronal motion is used across a wide range of organisms for a diverse set of functions. However, despite its ubiquity, analysis of this behavior has been difficult to generalize across systems. Here we provide an overview of known commonalities and differences between systems that use metachrony to generate fluid flow. We also discuss strategies for standardizing terminology and defining future investigative directions that are analogous to other established subfields of biomechanics. Finally, we outline key challenges that are common to many metachronal systems, opportunities that have arisen due to the advent of new technology (both experimental and computational), and next steps for community development and collaboration across the nascent network of metachronal researchers.

Introduction: what is metachronal motion?

Metachrony refers to a motion that is not synchronous (meaning “occurring at the same time”); it is a specific subcategory of asynchrony (meaning the opposite). Metachrony implies a sequence of similar events which occur in sequential order. Biologically, metachronal motion occurs when a series of (usually morphologically similar) appendages sequentially perform a cyclic, repeated motion at a fixed phase lag from one another. This creates a “metachronal wave,” whose frequency and wavelength are governed by the spacing of the appendages and the phase lag between them. Each appendage, as it moves, drags the surrounding fluid along with it.

Advance Access publication 28 May 2021

© The Author(s) 2021. Published by Oxford University Press on behalf of the Society for Integrative and Comparative Biology.
All rights reserved. For permissions please email: journals.permissions@oup.com.

Together, the sequentially coordinated appendages can generate fluid flows that are categorically different than those that would be created by a single appendage, or by the same group of appendages moving synchronously. Indeed, in some contexts, synchronous motion cannot create fluid flow at all, but metachronal motion can (Takagi 2015). Metachronally coordinated appendages can also produce a steadier, more efficient flow than the same appendages using synchronous coordination (Ford et al. 2019).

Metachronal motion is used across a staggering spectrum of species and scales, from microns to centimeters (e.g., Fig. 1). Because of this great functional and morphological diversity, there has been little



SYMPOSIUM

Metachronal Motion across Scales: Current Challenges and Future Directions

Margaret L. Byron,^{1,*} David W. Murphy ,[†] Kakani Katija,[‡] Alexander P. Hoover ,[§] Joost Daniels ,[‡] Kuvvat Garayev,[†] Daisuke Takagi,[¶] Eva Kanso,^{||} Bradford J. Gemmell,^{|||} Melissa Ruszczyk^{**} and Arvind Santhanakrishnan ,^{††}

¹Department of Mechanical Engineering, Penn State University, 201 Old Main, University Park, PA 16801, USA;

[†]Department of Mechanical Engineering, University of South Florida, 4202 E. Fowler Avenue, Tampa, FL 33620, USA;

[‡]Monterey Bay Aquarium Research Institute, 7700 Sandholdt Road, Moss Landing, CA 95039, USA; [§]Department of

Mathematics, University of Akron, 302 E Buchtel Avenue, Akron, OH 44325, USA; [¶]Department of Mathematics,

University of Hawaii at Manoa, 2500 Campus Road, Honolulu, HI 96822, USA; ^{||}Department of Mechanical and

Aerospace Engineering, University of Southern California, University Park, Los Angeles, CA 90007, USA; ^{|||}Department

of Integrative Biology, University of South Florida, 4202 E. Fowler Avenue, Tampa, FL 33620, USA; ^{**}Ocean Science and

Engineering, Georgia Institute of Technology, 310 Ferst Drive, Atlanta, GA 30332, USA; ^{††}School of Mechanical and

Aerospace Engineering, Oklahoma State University, 201 General Academic Building, Stillwater, OK 74078, USA

From the symposium “Metachronal coordination of multiple appendages for swimming and pumping” presented at the virtual annual meeting of the Society for Integrative and Comparative Biology, January 3–7, 2021.

¹E-mail: mbyron@psu.edu

Synopsis Metachronal motion is used across a wide range of organisms for a diverse set of functions. However, despite its ubiquity, analysis of this behavior has been difficult to generalize across systems. Here we provide an overview of known commonalities and differences between systems that use metachrony to generate fluid flow. We also discuss strategies for standardizing terminology and defining future investigative directions that are analogous to other established subfields of biomechanics. Finally, we outline key challenges that are common to many metachronal systems, opportunities that have arisen due to the advent of new technology (both experimental and computational), and next steps for community development and collaboration across the nascent network of metachronal researchers.

Introduction: what is metachronal motion?

Metachrony refers to a motion that is not synchronous (meaning “occurring at the same time”); it is a specific subcategory of asynchrony (meaning the opposite). Metachrony implies a sequence of similar events which occur in sequential order. Biologically, metachronal motion occurs when a series of (usually morphologically similar) appendages sequentially perform a cyclic, repeated motion at a fixed phase lag from one another. This creates a “metachronal wave,” whose frequency and wavelength are governed by the spacing of the appendages and the phase lag between them. Each appendage, as it moves, drags the surrounding fluid along with it.

Advance Access publication 28 May 2021

© The Author(s) 2021. Published by Oxford University Press on behalf of the Society for Integrative and Comparative Biology.
All rights reserved. For permissions please email: journals.permissions@oup.com.

Together, the sequentially coordinated appendages can generate fluid flows that are categorically different than those that would be created by a single appendage, or by the same group of appendages moving synchronously. Indeed, in some contexts, synchronous motion cannot create fluid flow at all, but metachronal motion can (Takagi 2015). Metachronally coordinated appendages can also produce a steadier, more efficient flow than the same appendages using synchronous coordination (Ford et al. 2019).

Metachronal motion is used across a staggering spectrum of species and scales, from microns to centimeters (e.g., Fig. 1). Because of this great functional and morphological diversity, there has been little



SYMPOSIUM

Metachronal Motion across Scales: Current Challenges and Future Directions

Margaret L. Byron,^{1,*} David W. Murphy ,[†] Kakani Katija,[‡] Alexander P. Hoover ,[§] Joost Daniels ,[‡] Kuvvat Garayev,[†] Daisuke Takagi,[¶] Eva Kanso,^{||} Bradford J. Gemmell,^{|||} Melissa Ruszczyk^{**} and Arvind Santhanakrishnan ,^{††}

¹Department of Mechanical Engineering, Penn State University, 201 Old Main, University Park, PA 16801, USA;

[†]Department of Mechanical Engineering, University of South Florida, 4202 E. Fowler Avenue, Tampa, FL 33620, USA;

[‡]Monterey Bay Aquarium Research Institute, 7700 Sandholdt Road, Moss Landing, CA 95039, USA; [§]Department of

Mathematics, University of Akron, 302 E Buchtel Avenue, Akron, OH 44325, USA; [¶]Department of Mathematics,

University of Hawaii at Manoa, 2500 Campus Road, Honolulu, HI 96822, USA; ^{||}Department of Mechanical and

Aerospace Engineering, University of Southern California, University Park, Los Angeles, CA 90007, USA; ^{|||}Department

of Integrative Biology, University of South Florida, 4202 E. Fowler Avenue, Tampa, FL 33620, USA; ^{**}Ocean Science and

Engineering, Georgia Institute of Technology, 310 Ferst Drive, Atlanta, GA 30332, USA; ^{††}School of Mechanical and

Aerospace Engineering, Oklahoma State University, 201 General Academic Building, Stillwater, OK 74078, USA

From the symposium “Metachronal coordination of multiple appendages for swimming and pumping” presented at the virtual annual meeting of the Society for Integrative and Comparative Biology, January 3–7, 2021.

¹E-mail: mbyron@psu.edu

Synopsis Metachronal motion is used across a wide range of organisms for a diverse set of functions. However, despite its ubiquity, analysis of this behavior has been difficult to generalize across systems. Here we provide an overview of known commonalities and differences between systems that use metachrony to generate fluid flow. We also discuss strategies for standardizing terminology and defining future investigative directions that are analogous to other established subfields of biomechanics. Finally, we outline key challenges that are common to many metachronal systems, opportunities that have arisen due to the advent of new technology (both experimental and computational), and next steps for community development and collaboration across the nascent network of metachronal researchers.

Introduction: what is metachronal motion?

Metachrony refers to a motion that is not synchronous (meaning “occurring at the same time”); it is a specific subcategory of asynchrony (meaning the opposite). Metachrony implies a sequence of similar events which occur in sequential order. Biologically, metachronal motion occurs when a series of (usually morphologically similar) appendages sequentially perform a cyclic, repeated motion at a fixed phase lag from one another. This creates a “metachronal wave,” whose frequency and wavelength are governed by the spacing of the appendages and the phase lag between them. Each appendage, as it moves, drags the surrounding fluid along with it.

Advance Access publication 28 May 2021

© The Author(s) 2021. Published by Oxford University Press on behalf of the Society for Integrative and Comparative Biology.
All rights reserved. For permissions please email: journals.permissions@oup.com.

Together, the sequentially coordinated appendages can generate fluid flows that are categorically different than those that would be created by a single appendage, or by the same group of appendages moving synchronously. Indeed, in some contexts, synchronous motion cannot create fluid flow at all, but metachronal motion can (Takagi 2015). Metachronally coordinated appendages can also produce a steadier, more efficient flow than the same appendages using synchronous coordination (Ford et al. 2019).

Metachronal motion is used across a staggering spectrum of species and scales, from microns to centimeters (e.g., Fig. 1). Because of this great functional and morphological diversity, there has been little



SYMPOSIUM

Metachronal Motion across Scales: Current Challenges and Future Directions

Margaret L. Byron,^{1,*} David W. Murphy ,[†] Kakani Katija,[‡] Alexander P. Hoover ,[§] Joost Daniels ,[‡] Kuvvat Garayev,[†] Daisuke Takagi,[¶] Eva Kanso,^{||} Bradford J. Gemmell,^{|||} Melissa Ruszczyk^{**} and Arvind Santhanakrishnan ,^{††}

¹Department of Mechanical Engineering, Penn State University, 201 Old Main, University Park, PA 16801, USA;

[†]Department of Mechanical Engineering, University of South Florida, 4202 E. Fowler Avenue, Tampa, FL 33620, USA;

[‡]Monterey Bay Aquarium Research Institute, 7700 Sandholdt Road, Moss Landing, CA 95039, USA; [§]Department of

Mathematics, University of Akron, 302 E Buchtel Avenue, Akron, OH 44325, USA; [¶]Department of Mathematics,

University of Hawaii at Manoa, 2500 Campus Road, Honolulu, HI 96822, USA; ^{||}Department of Mechanical and

Aerospace Engineering, University of Southern California, University Park, Los Angeles, CA 90007, USA; ^{|||}Department

of Integrative Biology, University of South Florida, 4202 E. Fowler Avenue, Tampa, FL 33620, USA; ^{**}Ocean Science and

Engineering, Georgia Institute of Technology, 310 Ferst Drive, Atlanta, GA 30332, USA; ^{††}School of Mechanical and

Aerospace Engineering, Oklahoma State University, 201 General Academic Building, Stillwater, OK 74078, USA

From the symposium “Metachronal coordination of multiple appendages for swimming and pumping” presented at the virtual annual meeting of the Society for Integrative and Comparative Biology, January 3–7, 2021.

¹E-mail: mbyron@psu.edu

Synopsis Metachronal motion is used across a wide range of organisms for a diverse set of functions. However, despite its ubiquity, analysis of this behavior has been difficult to generalize across systems. Here we provide an overview of known commonalities and differences between systems that use metachrony to generate fluid flow. We also discuss strategies for standardizing terminology and defining future investigative directions that are analogous to other established subfields of biomechanics. Finally, we outline key challenges that are common to many metachronal systems, opportunities that have arisen due to the advent of new technology (both experimental and computational), and next steps for community development and collaboration across the nascent network of metachronal researchers.

Introduction: what is metachronal motion?

Metachrony refers to a motion that is not synchronous (meaning “occurring at the same time”); it is a specific subcategory of asynchrony (meaning the opposite). Metachrony implies a sequence of similar events which occur in sequential order. Biologically, metachronal motion occurs when a series of (usually morphologically similar) appendages sequentially perform a cyclic, repeated motion at a fixed phase lag from one another. This creates a “metachronal wave,” whose frequency and wavelength are governed by the spacing of the appendages and the phase lag between them. Each appendage, as it moves, drags the surrounding fluid along with it.

Advance Access publication 28 May 2021

© The Author(s) 2021. Published by Oxford University Press on behalf of the Society for Integrative and Comparative Biology.
All rights reserved. For permissions please email: journals.permissions@oup.com.

Together, the sequentially coordinated appendages can generate fluid flows that are categorically different than those that would be created by a single appendage, or by the same group of appendages moving synchronously. Indeed, in some contexts, synchronous motion cannot create fluid flow at all, but metachronal motion can (Takagi 2015). Metachronally coordinated appendages can also produce a steadier, more efficient flow than the same appendages using synchronous coordination (Ford et al. 2019).

Metachronal motion is used across a staggering spectrum of species and scales, from microns to centimeters (e.g., Fig. 1). Because of this great functional and morphological diversity, there has been little



SYMPOSIUM

Metachronal Motion across Scales: Current Challenges and Future Directions

Margaret L. Byron,^{1,*} David W. Murphy ,[†] Kakani Katija,[‡] Alexander P. Hoover ,[§] Joost Daniels ,[‡] Kuvvat Garayev,[†] Daisuke Takagi,[¶] Eva Kanso,^{||} Bradford J. Gemmell,^{|||} Melissa Ruszczyk^{**} and Arvind Santhanakrishnan ,^{††}

¹Department of Mechanical Engineering, Penn State University, 201 Old Main, University Park, PA 16801, USA;

[†]Department of Mechanical Engineering, University of South Florida, 4202 E. Fowler Avenue, Tampa, FL 33620, USA;

[‡]Monterey Bay Aquarium Research Institute, 7700 Sandholdt Road, Moss Landing, CA 95039, USA; [§]Department of

Mathematics, University of Akron, 302 E Buchtel Avenue, Akron, OH 44325, USA; [¶]Department of Mathematics,

University of Hawaii at Manoa, 2500 Campus Road, Honolulu, HI 96822, USA; ^{||}Department of Mechanical and

Aerospace Engineering, University of Southern California, University Park, Los Angeles, CA 90007, USA; ^{|||}Department

of Integrative Biology, University of South Florida, 4202 E. Fowler Avenue, Tampa, FL 33620, USA; ^{**}Ocean Science and

Engineering, Georgia Institute of Technology, 310 Ferst Drive, Atlanta, GA 30332, USA; ^{††}School of Mechanical and

Aerospace Engineering, Oklahoma State University, 201 General Academic Building, Stillwater, OK 74078, USA

From the symposium “Metachronal coordination of multiple appendages for swimming and pumping” presented at the virtual annual meeting of the Society for Integrative and Comparative Biology, January 3–7, 2021.

¹E-mail: mbyron@psu.edu

Synopsis Metachronal motion is used across a wide range of organisms for a diverse set of functions. However, despite its ubiquity, analysis of this behavior has been difficult to generalize across systems. Here we provide an overview of known commonalities and differences between systems that use metachrony to generate fluid flow. We also discuss strategies for standardizing terminology and defining future investigative directions that are analogous to other established subfields of biomechanics. Finally, we outline key challenges that are common to many metachronal systems, opportunities that have arisen due to the advent of new technology (both experimental and computational), and next steps for community development and collaboration across the nascent network of metachronal researchers.

Introduction: what is metachronal motion?

Metachrony refers to a motion that is not synchronous (meaning “occurring at the same time”); it is a specific subcategory of asynchrony (meaning the opposite). Metachrony implies a sequence of similar events which occur in sequential order. Biologically, metachronal motion occurs when a series of (usually morphologically similar) appendages sequentially perform a cyclic, repeated motion at a fixed phase lag from one another. This creates a “metachronal wave,” whose frequency and wavelength are governed by the spacing of the appendages and the phase lag between them. Each appendage, as it moves, drags the surrounding fluid along with it.

Advance Access publication 28 May 2021

© The Author(s) 2021. Published by Oxford University Press on behalf of the Society for Integrative and Comparative Biology.
All rights reserved. For permissions please email: journals.permissions@oup.com.

Together, the sequentially coordinated appendages can generate fluid flows that are categorically different than those that would be created by a single appendage, or by the same group of appendages moving synchronously. Indeed, in some contexts, synchronous motion cannot create fluid flow at all, but metachronal motion can (Takagi 2015). Metachronally coordinated appendages can also produce a steadier, more efficient flow than the same appendages using synchronous coordination (Ford et al. 2019).

Metachronal motion is used across a staggering spectrum of species and scales, from microns to centimeters (e.g., Fig. 1). Because of this great functional and morphological diversity, there has been little



SYMPOSIUM

Metachronal Motion across Scales: Current Challenges and Future Directions

Margaret L. Byron,^{1,*} David W. Murphy ,[†] Kakani Katija,[‡] Alexander P. Hoover ,[§] Joost Daniels ,[‡] Kuvvat Garayev,[†] Daisuke Takagi,[¶] Eva Kanso,^{||} Bradford J. Gemmell,^{|||} Melissa Ruszczyk^{**} and Arvind Santhanakrishnan ,^{††}

¹Department of Mechanical Engineering, Penn State University, 201 Old Main, University Park, PA 16801, USA;

[†]Department of Mechanical Engineering, University of South Florida, 4202 E. Fowler Avenue, Tampa, FL 33620, USA;

[‡]Monterey Bay Aquarium Research Institute, 7700 Sandholdt Road, Moss Landing, CA 95039, USA; [§]Department of

Mathematics, University of Akron, 302 E Buchtel Avenue, Akron, OH 44325, USA; [¶]Department of Mathematics,

University of Hawaii at Manoa, 2500 Campus Road, Honolulu, HI 96822, USA; ^{||}Department of Mechanical and

Aerospace Engineering, University of Southern California, University Park, Los Angeles, CA 90007, USA; ^{|||}Department

of Integrative Biology, University of South Florida, 4202 E. Fowler Avenue, Tampa, FL 33620, USA; ^{**}Ocean Science and

Engineering, Georgia Institute of Technology, 310 Ferst Drive, Atlanta, GA 30332, USA; ^{††}School of Mechanical and

Aerospace Engineering, Oklahoma State University, 201 General Academic Building, Stillwater, OK 74078, USA

From the symposium “Metachronal coordination of multiple appendages for swimming and pumping” presented at the virtual annual meeting of the Society for Integrative and Comparative Biology, January 3–7, 2021.

¹E-mail: mbyron@psu.edu

Synopsis Metachronal motion is used across a wide range of organisms for a diverse set of functions. However, despite its ubiquity, analysis of this behavior has been difficult to generalize across systems. Here we provide an overview of known commonalities and differences between systems that use metachrony to generate fluid flow. We also discuss strategies for standardizing terminology and defining future investigative directions that are analogous to other established subfields of biomechanics. Finally, we outline key challenges that are common to many metachronal systems, opportunities that have arisen due to the advent of new technology (both experimental and computational), and next steps for community development and collaboration across the nascent network of metachronal researchers.

Introduction: what is metachronal motion?

Metachrony refers to a motion that is not synchronous (meaning “occurring at the same time”); it is a specific subcategory of asynchrony (meaning the opposite). Metachrony implies a sequence of similar events which occur in sequential order. Biologically, metachronal motion occurs when a series of (usually morphologically similar) appendages sequentially perform a cyclic, repeated motion at a fixed phase lag from one another. This creates a “metachronal wave,” whose frequency and wavelength are governed by the spacing of the appendages and the phase lag between them. Each appendage, as it moves, drags the surrounding fluid along with it.

Advance Access publication 28 May 2021

© The Author(s) 2021. Published by Oxford University Press on behalf of the Society for Integrative and Comparative Biology.
All rights reserved. For permissions please email: journals.permissions@oup.com.

Together, the sequentially coordinated appendages can generate fluid flows that are categorically different than those that would be created by a single appendage, or by the same group of appendages moving synchronously. Indeed, in some contexts, synchronous motion cannot create fluid flow at all, but metachronal motion can (Takagi 2015). Metachronally coordinated appendages can also produce a steadier, more efficient flow than the same appendages using synchronous coordination (Ford et al. 2019).

Metachronal motion is used across a staggering spectrum of species and scales, from microns to centimeters (e.g., Fig. 1). Because of this great functional and morphological diversity, there has been little



SYMPOSIUM

Metachronal Motion across Scales: Current Challenges and Future Directions

Margaret L. Byron,^{1,*} David W. Murphy ,[†] Kakani Katija,[‡] Alexander P. Hoover ,[§] Joost Daniels ,[‡] Kuvvat Garayev,[†] Daisuke Takagi,[¶] Eva Kanso,^{||} Bradford J. Gemmell,^{|||} Melissa Ruszczyk^{**} and Arvind Santhanakrishnan ,^{††}

¹Department of Mechanical Engineering, Penn State University, 201 Old Main, University Park, PA 16801, USA;

[†]Department of Mechanical Engineering, University of South Florida, 4202 E. Fowler Avenue, Tampa, FL 33620, USA;

[‡]Monterey Bay Aquarium Research Institute, 7700 Sandholdt Road, Moss Landing, CA 95039, USA; [§]Department of

Mathematics, University of Akron, 302 E Buchtel Avenue, Akron, OH 44325, USA; [¶]Department of Mathematics,

University of Hawaii at Manoa, 2500 Campus Road, Honolulu, HI 96822, USA; ^{||}Department of Mechanical and

Aerospace Engineering, University of Southern California, University Park, Los Angeles, CA 90007, USA; ^{|||}Department

of Integrative Biology, University of South Florida, 4202 E. Fowler Avenue, Tampa, FL 33620, USA; ^{**}Ocean Science and

Engineering, Georgia Institute of Technology, 310 Ferst Drive, Atlanta, GA 30332, USA; ^{††}School of Mechanical and

Aerospace Engineering, Oklahoma State University, 201 General Academic Building, Stillwater, OK 74078, USA

From the symposium “Metachronal coordination of multiple appendages for swimming and pumping” presented at the virtual annual meeting of the Society for Integrative and Comparative Biology, January 3–7, 2021.

¹E-mail: mbyron@psu.edu

Synopsis Metachronal motion is used across a wide range of organisms for a diverse set of functions. However, despite its ubiquity, analysis of this behavior has been difficult to generalize across systems. Here we provide an overview of known commonalities and differences between systems that use metachrony to generate fluid flow. We also discuss strategies for standardizing terminology and defining future investigative directions that are analogous to other established subfields of biomechanics. Finally, we outline key challenges that are common to many metachronal systems, opportunities that have arisen due to the advent of new technology (both experimental and computational), and next steps for community development and collaboration across the nascent network of metachronal researchers.

Introduction: what is metachronal motion?

Metachrony refers to a motion that is not synchronous (meaning “occurring at the same time”); it is a specific subcategory of asynchrony (meaning the opposite). Metachrony implies a sequence of similar events which occur in sequential order. Biologically, metachronal motion occurs when a series of (usually morphologically similar) appendages sequentially perform a cyclic, repeated motion at a fixed phase lag from one another. This creates a “metachronal wave,” whose frequency and wavelength are governed by the spacing of the appendages and the phase lag between them. Each appendage, as it moves, drags the surrounding fluid along with it.

Advance Access publication 28 May 2021

© The Author(s) 2021. Published by Oxford University Press on behalf of the Society for Integrative and Comparative Biology.
All rights reserved. For permissions please email: journals.permissions@oup.com.

Together, the sequentially coordinated appendages can generate fluid flows that are categorically different than those that would be created by a single appendage, or by the same group of appendages moving synchronously. Indeed, in some contexts, synchronous motion cannot create fluid flow at all, but metachronal motion can (Takagi 2015). Metachronally coordinated appendages can also produce a steadier, more efficient flow than the same appendages using synchronous coordination (Ford et al. 2019).

Metachronal motion is used across a staggering spectrum of species and scales, from microns to centimeters (e.g., Fig. 1). Because of this great functional and morphological diversity, there has been little



SYMPOSIUM

Metachronal Motion across Scales: Current Challenges and Future Directions

Margaret L. Byron,^{1,*} David W. Murphy ,[†] Kakani Katija,[‡] Alexander P. Hoover ,[§] Joost Daniels ,[‡] Kuvvat Garayev,[†] Daisuke Takagi,[¶] Eva Kanso,^{||} Bradford J. Gemmell,^{|||} Melissa Ruszczyk^{**} and Arvind Santhanakrishnan ,^{††}

¹Department of Mechanical Engineering, Penn State University, 201 Old Main, University Park, PA 16801, USA;

[†]Department of Mechanical Engineering, University of South Florida, 4202 E. Fowler Avenue, Tampa, FL 33620, USA;

[‡]Monterey Bay Aquarium Research Institute, 7700 Sandholdt Road, Moss Landing, CA 95039, USA; [§]Department of

Mathematics, University of Akron, 302 E Buchtel Avenue, Akron, OH 44325, USA; [¶]Department of Mathematics,

University of Hawaii at Manoa, 2500 Campus Road, Honolulu, HI 96822, USA; ^{||}Department of Mechanical and

Aerospace Engineering, University of Southern California, University Park, Los Angeles, CA 90007, USA; ^{|||}Department

of Integrative Biology, University of South Florida, 4202 E. Fowler Avenue, Tampa, FL 33620, USA; ^{**}Ocean Science and

Engineering, Georgia Institute of Technology, 310 Ferst Drive, Atlanta, GA 30332, USA; ^{††}School of Mechanical and

Aerospace Engineering, Oklahoma State University, 201 General Academic Building, Stillwater, OK 74078, USA

From the symposium “Metachronal coordination of multiple appendages for swimming and pumping” presented at the virtual annual meeting of the Society for Integrative and Comparative Biology, January 3–7, 2021.

¹E-mail: mbyron@psu.edu

Synopsis Metachronal motion is used across a wide range of organisms for a diverse set of functions. However, despite its ubiquity, analysis of this behavior has been difficult to generalize across systems. Here we provide an overview of known commonalities and differences between systems that use metachrony to generate fluid flow. We also discuss strategies for standardizing terminology and defining future investigative directions that are analogous to other established subfields of biomechanics. Finally, we outline key challenges that are common to many metachronal systems, opportunities that have arisen due to the advent of new technology (both experimental and computational), and next steps for community development and collaboration across the nascent network of metachronal researchers.

Introduction: what is metachronal motion?

Metachrony refers to a motion that is not synchronous (meaning “occurring at the same time”); it is a specific subcategory of asynchrony (meaning the opposite). Metachrony implies a sequence of similar events which occur in sequential order. Biologically, metachronal motion occurs when a series of (usually morphologically similar) appendages sequentially perform a cyclic, repeated motion at a fixed phase lag from one another. This creates a “metachronal wave,” whose frequency and wavelength are governed by the spacing of the appendages and the phase lag between them. Each appendage, as it moves, drags the surrounding fluid along with it.

Advance Access publication 28 May 2021

© The Author(s) 2021. Published by Oxford University Press on behalf of the Society for Integrative and Comparative Biology.
All rights reserved. For permissions please email: journals.permissions@oup.com.

Together, the sequentially coordinated appendages can generate fluid flows that are categorically different than those that would be created by a single appendage, or by the same group of appendages moving synchronously. Indeed, in some contexts, synchronous motion cannot create fluid flow at all, but metachronal motion can (Takagi 2015). Metachronally coordinated appendages can also produce a steadier, more efficient flow than the same appendages using synchronous coordination (Ford et al. 2019).

Metachronal motion is used across a staggering spectrum of species and scales, from microns to centimeters (e.g., Fig. 1). Because of this great functional and morphological diversity, there has been little



SYMPOSIUM

Metachronal Motion across Scales: Current Challenges and Future Directions

Margaret L. Byron,^{1,*} David W. Murphy ,[†] Kakani Katija,[‡] Alexander P. Hoover ,[§] Joost Daniels ,[‡] Kuvvat Garayev,[†] Daisuke Takagi,[¶] Eva Kanso,^{||} Bradford J. Gemmell,^{|||} Melissa Ruszczyk^{**} and Arvind Santhanakrishnan ,^{††}

¹Department of Mechanical Engineering, Penn State University, 201 Old Main, University Park, PA 16801, USA;

[†]Department of Mechanical Engineering, University of South Florida, 4202 E. Fowler Avenue, Tampa, FL 33620, USA;

[‡]Monterey Bay Aquarium Research Institute, 7700 Sandholdt Road, Moss Landing, CA 95039, USA; [§]Department of

Mathematics, University of Akron, 302 E Buchtel Avenue, Akron, OH 44325, USA; [¶]Department of Mathematics,

University of Hawaii at Manoa, 2500 Campus Road, Honolulu, HI 96822, USA; ^{||}Department of Mechanical and

Aerospace Engineering, University of Southern California, University Park, Los Angeles, CA 90007, USA; ^{|||}Department

of Integrative Biology, University of South Florida, 4202 E. Fowler Avenue, Tampa, FL 33620, USA; ^{**}Ocean Science and

Engineering, Georgia Institute of Technology, 310 Ferst Drive, Atlanta, GA 30332, USA; ^{††}School of Mechanical and

Aerospace Engineering, Oklahoma State University, 201 General Academic Building, Stillwater, OK 74078, USA

From the symposium “Metachronal coordination of multiple appendages for swimming and pumping” presented at the virtual annual meeting of the Society for Integrative and Comparative Biology, January 3–7, 2021.

¹E-mail: mbyron@psu.edu

Synopsis Metachronal motion is used across a wide range of organisms for a diverse set of functions. However, despite its ubiquity, analysis of this behavior has been difficult to generalize across systems. Here we provide an overview of known commonalities and differences between systems that use metachrony to generate fluid flow. We also discuss strategies for standardizing terminology and defining future investigative directions that are analogous to other established subfields of biomechanics. Finally, we outline key challenges that are common to many metachronal systems, opportunities that have arisen due to the advent of new technology (both experimental and computational), and next steps for community development and collaboration across the nascent network of metachronal researchers.

Introduction: what is metachronal motion?

Metachrony refers to a motion that is not synchronous (meaning “occurring at the same time”); it is a specific subcategory of asynchrony (meaning the opposite). Metachrony implies a sequence of similar events which occur in sequential order. Biologically, metachronal motion occurs when a series of (usually morphologically similar) appendages sequentially perform a cyclic, repeated motion at a fixed phase lag from one another. This creates a “metachronal wave,” whose frequency and wavelength are governed by the spacing of the appendages and the phase lag between them. Each appendage, as it moves, drags the surrounding fluid along with it.

Advance Access publication 28 May 2021

© The Author(s) 2021. Published by Oxford University Press on behalf of the Society for Integrative and Comparative Biology.
All rights reserved. For permissions please email: journals.permissions@oup.com.

Together, the sequentially coordinated appendages can generate fluid flows that are categorically different than those that would be created by a single appendage, or by the same group of appendages moving synchronously. Indeed, in some contexts, synchronous motion cannot create fluid flow at all, but metachronal motion can (Takagi 2015). Metachronally coordinated appendages can also produce a steadier, more efficient flow than the same appendages using synchronous coordination (Ford et al. 2019).

Metachronal motion is used across a staggering spectrum of species and scales, from microns to centimeters (e.g., Fig. 1). Because of this great functional and morphological diversity, there has been little



SYMPOSIUM

Metachronal Motion across Scales: Current Challenges and Future Directions

Margaret L. Byron,^{1,*} David W. Murphy ,[†] Kakani Katija,[‡] Alexander P. Hoover ,[§] Joost Daniels ,[‡] Kuvvat Garayev,[†] Daisuke Takagi,[¶] Eva Kanso,^{||} Bradford J. Gemmell,^{|||} Melissa Ruszczyk^{**} and Arvind Santhanakrishnan ,^{††}

¹Department of Mechanical Engineering, Penn State University, 201 Old Main, University Park, PA 16801, USA;

[†]Department of Mechanical Engineering, University of South Florida, 4202 E. Fowler Avenue, Tampa, FL 33620, USA;

[‡]Monterey Bay Aquarium Research Institute, 7700 Sandholdt Road, Moss Landing, CA 95039, USA; [§]Department of

Mathematics, University of Akron, 302 E Buchtel Avenue, Akron, OH 44325, USA; [¶]Department of Mathematics,

University of Hawaii at Manoa, 2500 Campus Road, Honolulu, HI 96822, USA; ^{||}Department of Mechanical and

Aerospace Engineering, University of Southern California, University Park, Los Angeles, CA 90007, USA; ^{|||}Department

of Integrative Biology, University of South Florida, 4202 E. Fowler Avenue, Tampa, FL 33620, USA; ^{**}Ocean Science and

Engineering, Georgia Institute of Technology, 310 Ferst Drive, Atlanta, GA 30332, USA; ^{††}School of Mechanical and

Aerospace Engineering, Oklahoma State University, 201 General Academic Building, Stillwater, OK 74078, USA

From the symposium “Metachronal coordination of multiple appendages for swimming and pumping” presented at the virtual annual meeting of the Society for Integrative and Comparative Biology, January 3–7, 2021.

¹E-mail: mbyron@psu.edu

Synopsis Metachronal motion is used across a wide range of organisms for a diverse set of functions. However, despite its ubiquity, analysis of this behavior has been difficult to generalize across systems. Here we provide an overview of known commonalities and differences between systems that use metachrony to generate fluid flow. We also discuss strategies for standardizing terminology and defining future investigative directions that are analogous to other established subfields of biomechanics. Finally, we outline key challenges that are common to many metachronal systems, opportunities that have arisen due to the advent of new technology (both experimental and computational), and next steps for community development and collaboration across the nascent network of metachronal researchers.

Introduction: what is metachronal motion?

Metachrony refers to a motion that is not synchronous (meaning “occurring at the same time”); it is a specific subcategory of asynchrony (meaning the opposite). Metachrony implies a sequence of similar events which occur in sequential order. Biologically, metachronal motion occurs when a series of (usually morphologically similar) appendages sequentially perform a cyclic, repeated motion at a fixed phase lag from one another. This creates a “metachronal wave,” whose frequency and wavelength are governed by the spacing of the appendages and the phase lag between them. Each appendage, as it moves, drags the surrounding fluid along with it.

Advance Access publication 28 May 2021

© The Author(s) 2021. Published by Oxford University Press on behalf of the Society for Integrative and Comparative Biology.
All rights reserved. For permissions please email: journals.permissions@oup.com.

Together, the sequentially coordinated appendages can generate fluid flows that are categorically different than those that would be created by a single appendage, or by the same group of appendages moving synchronously. Indeed, in some contexts, synchronous motion cannot create fluid flow at all, but metachronal motion can (Takagi 2015). Metachronally coordinated appendages can also produce a steadier, more efficient flow than the same appendages using synchronous coordination (Ford et al. 2019).

Metachronal motion is used across a staggering spectrum of species and scales, from microns to centimeters (e.g., Fig. 1). Because of this great functional and morphological diversity, there has been little



SYMPOSIUM

Metachronal Motion across Scales: Current Challenges and Future Directions

Margaret L. Byron,^{1,*} David W. Murphy ,[†] Kakani Katija,[‡] Alexander P. Hoover ,[§] Joost Daniels ,[‡] Kuvvat Garayev,[†] Daisuke Takagi,[¶] Eva Kanso,^{||} Bradford J. Gemmell,^{|||} Melissa Ruszczyk^{**} and Arvind Santhanakrishnan ,^{††}

¹Department of Mechanical Engineering, Penn State University, 201 Old Main, University Park, PA 16801, USA;

[†]Department of Mechanical Engineering, University of South Florida, 4202 E. Fowler Avenue, Tampa, FL 33620, USA;

[‡]Monterey Bay Aquarium Research Institute, 7700 Sandholdt Road, Moss Landing, CA 95039, USA; [§]Department of

Mathematics, University of Akron, 302 E Buchtel Avenue, Akron, OH 44325, USA; [¶]Department of Mathematics,

University of Hawaii at Manoa, 2500 Campus Road, Honolulu, HI 96822, USA; ^{||}Department of Mechanical and

Aerospace Engineering, University of Southern California, University Park, Los Angeles, CA 90007, USA; ^{|||}Department

of Integrative Biology, University of South Florida, 4202 E. Fowler Avenue, Tampa, FL 33620, USA; ^{**}Ocean Science and

Engineering, Georgia Institute of Technology, 310 Ferst Drive, Atlanta, GA 30332, USA; ^{††}School of Mechanical and

Aerospace Engineering, Oklahoma State University, 201 General Academic Building, Stillwater, OK 74078, USA

From the symposium “Metachronal coordination of multiple appendages for swimming and pumping” presented at the virtual annual meeting of the Society for Integrative and Comparative Biology, January 3–7, 2021.

¹E-mail: mbyron@psu.edu

Synopsis Metachronal motion is used across a wide range of organisms for a diverse set of functions. However, despite its ubiquity, analysis of this behavior has been difficult to generalize across systems. Here we provide an overview of known commonalities and differences between systems that use metachrony to generate fluid flow. We also discuss strategies for standardizing terminology and defining future investigative directions that are analogous to other established subfields of biomechanics. Finally, we outline key challenges that are common to many metachronal systems, opportunities that have arisen due to the advent of new technology (both experimental and computational), and next steps for community development and collaboration across the nascent network of metachronal researchers.

Introduction: what is metachronal motion?

Metachrony refers to a motion that is not synchronous (meaning “occurring at the same time”); it is a specific subcategory of asynchrony (meaning the opposite). Metachrony implies a sequence of similar events which occur in sequential order. Biologically, metachronal motion occurs when a series of (usually morphologically similar) appendages sequentially perform a cyclic, repeated motion at a fixed phase lag from one another. This creates a “metachronal wave,” whose frequency and wavelength are governed by the spacing of the appendages and the phase lag between them. Each appendage, as it moves, drags the surrounding fluid along with it.

Advance Access publication 28 May 2021

© The Author(s) 2021. Published by Oxford University Press on behalf of the Society for Integrative and Comparative Biology.
All rights reserved. For permissions please email: journals.permissions@oup.com.

Together, the sequentially coordinated appendages can generate fluid flows that are categorically different than those that would be created by a single appendage, or by the same group of appendages moving synchronously. Indeed, in some contexts, synchronous motion cannot create fluid flow at all, but metachronal motion can (Takagi 2015). Metachronally coordinated appendages can also produce a steadier, more efficient flow than the same appendages using synchronous coordination (Ford et al. 2019).

Metachronal motion is used across a staggering spectrum of species and scales, from microns to centimeters (e.g., Fig. 1). Because of this great functional and morphological diversity, there has been little



SYMPOSIUM

Metachronal Motion across Scales: Current Challenges and Future Directions

Margaret L. Byron,^{1,*} David W. Murphy ,[†] Kakani Katija,[‡] Alexander P. Hoover ,[§] Joost Daniels ,[‡] Kuvvat Garayev,[†] Daisuke Takagi,[¶] Eva Kanso,^{||} Bradford J. Gemmell,^{|||} Melissa Ruszczyk^{**} and Arvind Santhanakrishnan ,^{††}

¹Department of Mechanical Engineering, Penn State University, 201 Old Main, University Park, PA 16801, USA;

[†]Department of Mechanical Engineering, University of South Florida, 4202 E. Fowler Avenue, Tampa, FL 33620, USA;

[‡]Monterey Bay Aquarium Research Institute, 7700 Sandholdt Road, Moss Landing, CA 95039, USA; [§]Department of

Mathematics, University of Akron, 302 E Buchtel Avenue, Akron, OH 44325, USA; [¶]Department of Mathematics,

University of Hawaii at Manoa, 2500 Campus Road, Honolulu, HI 96822, USA; ^{||}Department of Mechanical and

Aerospace Engineering, University of Southern California, University Park, Los Angeles, CA 90007, USA; ^{|||}Department

of Integrative Biology, University of South Florida, 4202 E. Fowler Avenue, Tampa, FL 33620, USA; ^{**}Ocean Science and

Engineering, Georgia Institute of Technology, 310 Ferst Drive, Atlanta, GA 30332, USA; ^{††}School of Mechanical and

Aerospace Engineering, Oklahoma State University, 201 General Academic Building, Stillwater, OK 74078, USA

From the symposium “Metachronal coordination of multiple appendages for swimming and pumping” presented at the virtual annual meeting of the Society for Integrative and Comparative Biology, January 3–7, 2021.

¹E-mail: mbyron@psu.edu

Synopsis Metachronal motion is used across a wide range of organisms for a diverse set of functions. However, despite its ubiquity, analysis of this behavior has been difficult to generalize across systems. Here we provide an overview of known commonalities and differences between systems that use metachrony to generate fluid flow. We also discuss strategies for standardizing terminology and defining future investigative directions that are analogous to other established subfields of biomechanics. Finally, we outline key challenges that are common to many metachronal systems, opportunities that have arisen due to the advent of new technology (both experimental and computational), and next steps for community development and collaboration across the nascent network of metachronal researchers.

Introduction: what is metachronal motion?

Metachrony refers to a motion that is not synchronous (meaning “occurring at the same time”); it is a specific subcategory of asynchrony (meaning the opposite). Metachrony implies a sequence of similar events which occur in sequential order. Biologically, metachronal motion occurs when a series of (usually morphologically similar) appendages sequentially perform a cyclic, repeated motion at a fixed phase lag from one another. This creates a “metachronal wave,” whose frequency and wavelength are governed by the spacing of the appendages and the phase lag between them. Each appendage, as it moves, drags the surrounding fluid along with it.

Advance Access publication 28 May 2021

© The Author(s) 2021. Published by Oxford University Press on behalf of the Society for Integrative and Comparative Biology.
All rights reserved. For permissions please email: journals.permissions@oup.com.

Together, the sequentially coordinated appendages can generate fluid flows that are categorically different than those that would be created by a single appendage, or by the same group of appendages moving synchronously. Indeed, in some contexts, synchronous motion cannot create fluid flow at all, but metachronal motion can (Takagi 2015). Metachronally coordinated appendages can also produce a steadier, more efficient flow than the same appendages using synchronous coordination (Ford et al. 2019).

Metachronal motion is used across a staggering spectrum of species and scales, from microns to centimeters (e.g., Fig. 1). Because of this great functional and morphological diversity, there has been little



SYMPOSIUM

Metachronal Motion across Scales: Current Challenges and Future Directions

Margaret L. Byron,^{1,*} David W. Murphy ,[†] Kakani Katija,[‡] Alexander P. Hoover ,[§] Joost Daniels ,[‡] Kuvvat Garayev,[†] Daisuke Takagi,[¶] Eva Kanso,^{||} Bradford J. Gemmell,^{|||} Melissa Ruszczyk^{**} and Arvind Santhanakrishnan ,^{††}

¹Department of Mechanical Engineering, Penn State University, 201 Old Main, University Park, PA 16801, USA;

[†]Department of Mechanical Engineering, University of South Florida, 4202 E. Fowler Avenue, Tampa, FL 33620, USA;

[‡]Monterey Bay Aquarium Research Institute, 7700 Sandholdt Road, Moss Landing, CA 95039, USA; [§]Department of

Mathematics, University of Akron, 302 E Buchtel Avenue, Akron, OH 44325, USA; [¶]Department of Mathematics,

University of Hawaii at Manoa, 2500 Campus Road, Honolulu, HI 96822, USA; ^{||}Department of Mechanical and

Aerospace Engineering, University of Southern California, University Park, Los Angeles, CA 90007, USA; ^{|||}Department

of Integrative Biology, University of South Florida, 4202 E. Fowler Avenue, Tampa, FL 33620, USA; ^{**}Ocean Science and

Engineering, Georgia Institute of Technology, 310 Ferst Drive, Atlanta, GA 30332, USA; ^{††}School of Mechanical and

Aerospace Engineering, Oklahoma State University, 201 General Academic Building, Stillwater, OK 74078, USA

From the symposium “Metachronal coordination of multiple appendages for swimming and pumping” presented at the virtual annual meeting of the Society for Integrative and Comparative Biology, January 3–7, 2021.

¹E-mail: mbyron@psu.edu

Synopsis Metachronal motion is used across a wide range of organisms for a diverse set of functions. However, despite its ubiquity, analysis of this behavior has been difficult to generalize across systems. Here we provide an overview of known commonalities and differences between systems that use metachrony to generate fluid flow. We also discuss strategies for standardizing terminology and defining future investigative directions that are analogous to other established subfields of biomechanics. Finally, we outline key challenges that are common to many metachronal systems, opportunities that have arisen due to the advent of new technology (both experimental and computational), and next steps for community development and collaboration across the nascent network of metachronal researchers.

Introduction: what is metachronal motion?

Metachrony refers to a motion that is not synchronous (meaning “occurring at the same time”); it is a specific subcategory of asynchrony (meaning the opposite). Metachrony implies a sequence of similar events which occur in sequential order. Biologically, metachronal motion occurs when a series of (usually morphologically similar) appendages sequentially perform a cyclic, repeated motion at a fixed phase lag from one another. This creates a “metachronal wave,” whose frequency and wavelength are governed by the spacing of the appendages and the phase lag between them. Each appendage, as it moves, drags the surrounding fluid along with it.

Advance Access publication 28 May 2021

© The Author(s) 2021. Published by Oxford University Press on behalf of the Society for Integrative and Comparative Biology.
All rights reserved. For permissions please email: journals.permissions@oup.com.

Together, the sequentially coordinated appendages can generate fluid flows that are categorically different than those that would be created by a single appendage, or by the same group of appendages moving synchronously. Indeed, in some contexts, synchronous motion cannot create fluid flow at all, but metachronal motion can (Takagi 2015). Metachronally coordinated appendages can also produce a steadier, more efficient flow than the same appendages using synchronous coordination (Ford et al. 2019).

Metachronal motion is used across a staggering spectrum of species and scales, from microns to centimeters (e.g., Fig. 1). Because of this great functional and morphological diversity, there has been little



SYMPOSIUM

Metachronal Motion across Scales: Current Challenges and Future Directions

Margaret L. Byron,^{1,*} David W. Murphy ,[†] Kakani Katija,[‡] Alexander P. Hoover ,[§] Joost Daniels ,[‡] Kuvvat Garayev,[†] Daisuke Takagi,[¶] Eva Kanso,^{||} Bradford J. Gemmell,^{|||} Melissa Ruszczyk^{**} and Arvind Santhanakrishnan ,^{††}

¹Department of Mechanical Engineering, Penn State University, 201 Old Main, University Park, PA 16801, USA;

[†]Department of Mechanical Engineering, University of South Florida, 4202 E. Fowler Avenue, Tampa, FL 33620, USA;

[‡]Monterey Bay Aquarium Research Institute, 7700 Sandholdt Road, Moss Landing, CA 95039, USA; [§]Department of

Mathematics, University of Akron, 302 E Buchtel Avenue, Akron, OH 44325, USA; [¶]Department of Mathematics,

University of Hawaii at Manoa, 2500 Campus Road, Honolulu, HI 96822, USA; ^{||}Department of Mechanical and

Aerospace Engineering, University of Southern California, University Park, Los Angeles, CA 90007, USA; ^{|||}Department

of Integrative Biology, University of South Florida, 4202 E. Fowler Avenue, Tampa, FL 33620, USA; ^{**}Ocean Science and

Engineering, Georgia Institute of Technology, 310 Ferst Drive, Atlanta, GA 30332, USA; ^{††}School of Mechanical and

Aerospace Engineering, Oklahoma State University, 201 General Academic Building, Stillwater, OK 74078, USA

From the symposium “Metachronal coordination of multiple appendages for swimming and pumping” presented at the virtual annual meeting of the Society for Integrative and Comparative Biology, January 3–7, 2021.

¹E-mail: mbyron@psu.edu

Synopsis Metachronal motion is used across a wide range of organisms for a diverse set of functions. However, despite its ubiquity, analysis of this behavior has been difficult to generalize across systems. Here we provide an overview of known commonalities and differences between systems that use metachrony to generate fluid flow. We also discuss strategies for standardizing terminology and defining future investigative directions that are analogous to other established subfields of biomechanics. Finally, we outline key challenges that are common to many metachronal systems, opportunities that have arisen due to the advent of new technology (both experimental and computational), and next steps for community development and collaboration across the nascent network of metachronal researchers.

Introduction: what is metachronal motion?

Metachrony refers to a motion that is not synchronous (meaning “occurring at the same time”); it is a specific subcategory of asynchrony (meaning the opposite). Metachrony implies a sequence of similar events which occur in sequential order. Biologically, metachronal motion occurs when a series of (usually morphologically similar) appendages sequentially perform a cyclic, repeated motion at a fixed phase lag from one another. This creates a “metachronal wave,” whose frequency and wavelength are governed by the spacing of the appendages and the phase lag between them. Each appendage, as it moves, drags the surrounding fluid along with it.

Advance Access publication 28 May 2021

© The Author(s) 2021. Published by Oxford University Press on behalf of the Society for Integrative and Comparative Biology.
All rights reserved. For permissions please email: journals.permissions@oup.com.

Together, the sequentially coordinated appendages can generate fluid flows that are categorically different than those that would be created by a single appendage, or by the same group of appendages moving synchronously. Indeed, in some contexts, synchronous motion cannot create fluid flow at all, but metachronal motion can (Takagi 2015). Metachronally coordinated appendages can also produce a steadier, more efficient flow than the same appendages using synchronous coordination (Ford et al. 2019).

Metachronal motion is used across a staggering spectrum of species and scales, from microns to centimeters (e.g., Fig. 1). Because of this great functional and morphological diversity, there has been little