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研究課題名（和文）Minimal Physical Model of Crawling and Dividing Cells

研究課題名（英文）Minimal Physical Model of Crawling and Dividing Cells

研究代表者
ＭＯＬＩＮＡ　ＪＯＨＮ（Molina, John）

京都大学・工学研究科・助教

研究者番号：２０７２７５８１

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研究成果の概要（和文）：本研究の目的は、這い回る細胞が環境からのシグナルにどのように応答するかを明らかにすることである。まず、変形可能な形状、推進力、基質への接着を考慮した詳細な細胞モデルを用いて周期的に伸長する基質上での細胞特異的な再配向を研究した。その結果、伸長・圧縮時のあらゆる非対称性を利用して、伸長に対して平行・垂直に細胞を整列させることができることを見出した。実験結果と同様に、この応答は周波数に強く依存する。第二に、最小限の物理モデルを用いて、這い回り、分裂する細胞の集団運動を研究した。その結果、形状、運動性、分裂と結合する局所的な力学的相互作用が、実験で見られる大規模な集団運動を説明できることを見出した。

研究成果の学術的意義や社会的意義
We have developed physical models that can be used to understand the way in which interactions with the environment determine the behavior of crawling and dividing cells. Our models help explain how external stretching can reorient cells, and how local interactions can give rise to ordered motion.

研究成果の概要（英文）：In purpose of this study is to clarify how crawling cells respond to signals from their environment. First, a detailed cell model, which accounts for the deformable shape, the propulsion and the adhesions to the substrate, was used to study the cell-specific reorientation on cyclically-stretched substrates. We found that any asymmetry during extension/compression can be used to align the cells parallel/perpendicular to the stretching. As observed experimentally, this response depends strongly on the frequency. Second, a minimal physical model was used to study the collective motion of crawling and dividing cells. We found that local mechanical interactions, which couple to the shape, motility, and division, can explain the large-scale collective motion seen experimentally.

研究分野：Computational Soft Matter Physics

キーワード：Crawling Cells　Dividing Cells　Mechanosenstitivity　Contact Inhibition

１．研究開始当初の背景

The dynamics of Eukaryotic cells (e.g., animal, plant and fungal cells), is crucial to understand basic biology and develop treatment for many diseases. Here, particular focus is given to substrate-based crawling, due to its biological significance, and the ease with which experiments can be performed. These motile cells migrate using a basic three-step crawling procedure that has been well known for almost 50 years ([1] Abercrombie M., Proc. R. Soc. Lond. B **207**, 129, 1980). First, actin filaments polymerize at the front of the cell, pushing against the cell membrane and creating forward protrusions. Second, focal adhesions are formed at the front, creating anchor points for the actin filament network to transfer the forces to the substrate. Third, myosin motors contract the actin-network, releasing the adhesions at the back and moving the cell forward. While the basics of single-cell motion are understood, the way in which cells react to signals from their environment, and thus regulate their biological functions, is still largely unknown. At the single-cell level, these signals can affect everything from the shape, motion, and cell division, as well as the differentiation of stem cells. This last example has many applications, as demonstrated by recent experiments, in which the pore sizes on honeycomb lattice scaffolds are tuned to drive stem-cell differentiation into bone or muscle cells ([2] Kawano et al., Biomater. Sci. **2**, 52,2014). At the tissue level, the response to external signals will affect the collective motion present in embryo development, wound healing, and cancer invasion.

Understanding such complex dynamical phenomena is an incredibly challenging task, given that they lie at the intersection of physics, chemistry, and biology. However, it has been recognized that many aspects of cell motion can be understood from a purely physical/mechanical standpoint, allowing us to sidestep the bio-chemical pathways at the origin of a specific cellular response. First, we have an intrinsic coupling between the cell shape and its motility, owing to the fact that the actin-network that provides structural support is also heavily involved in the propulsion. Second, the focal adhesions provide a mechanical link between the actin network and the substrate, allowing for the transfer of forces and the ability to sense the mechanical properties of its environment and respond accordingly (i.e, mechanosensitivity). Furthermore, when considering multi-cellular environments, the cell-cell interactions, can also be understood in terms of cell-cell contacts (i.e., mechanically). Thus, there has been dramatic progress in developing cell-level phenomenological models, which account for the cell-shape, propulsion, and substrate adhesions, among others, from a purely physical point of view ([3]Ziebert and Aranson, Npj Comput. Mater.**2**, 1609, 2016). These models have started to provide clues for understanding how cells move, and how they interact with and respond to their environment, but many questions remain unanswered.

A salient example of such an open question is the dynamical response of crawling cells on cyclically stretched substrates, which show a frequency dependent cell-specific reorientation ([4] Okimura et al., Cell Adh.Migr.**106**, 16 2014). Here a distinction is made between slow-crawling (e.g., fibroblasts) and fast-crawling (e.g., Dictyostelium) cells. The former typically possess stress fibers (thick actin bundles), while the later typically do not. Under cyclic stretching slow-crawling cells will usually reorient with their stress fibers perpendicular to the direction of stretching. In the case of fast-crawling cells, Okimura et al. reported a preference of the cells to crawl perpendicular to the stretching. Crucially, no ordering of the actin-network was observed. This cell-specific response is not clearly understood. While several theories have been developed to explain such behaviour, they tend to focuse on slow-crawling cells, where motility and reorientation can be decoupled. For fast-crawling cells, this decoupling is not suitable, and it is necessary to consider how the sub-cellular elements (e.g., actin network, focal adhesion) respond to the stretching as a whole.

２．研究の目的

The purpose of this study is to clarify how crawling and dividing cells respond to

signals from their environment. In particular, we want to understand how the internal cellular processes and the cell dynamics can couple to external signals to give rise to the large-scale behaviours observed experimentally. This includes the reorientation of cells on cyclically stretched substrates, as well as the collective cell migration responsible for wound closure and tissue development. Fort this, we focus on two main themes: developing cell-specific models of crawling/dividing cells and studying the dynamics of cells in various biologically relevant environments.

３．研究の方法

The purpose of this study is to elucidate how cells respond to signals from their environment, in particular mechanical signals, in order to pursue their biological functions. For this, we consider the dynamics of cells in a variety of distinct biologically motivated situations: (A) cells crawling over cyclically stretched substrates, (B) through complex environments, and (C) proliferating (crawling and dividing) over planar substrates. To accomplish this, we have developed two minimal physical models capable of describing the mechano-sensitive response of (A-C), and proceeded to implement them numerically. For (A-B) we have used (1) a detailed cell-level model, which incorporates the relevant sub-cellular processes (variable cell shape, actin propulsion, adhesions, etc.), whereas for (C) we have used (2) a minimal physical model that coarse-grains the intra-cellular degrees of freedom to allow for large-scale simulations. Finally, in an effort to bridge between these two levels of description, we have investigated the use of (3) Machine Learning techniques to learn “macroscopic” constitutive equations from more detailed “microscopic” models.

(1) Detailed cell-level model of crawling cells

We have further developed a cell-level phase field model of fast-crawling cells, originally introduced to describe crawling over rigid substrates[3], in order to study the crawling dynamics over cyclically stretched substrates, as well as crawling through complex environments (e.g., through micro-pillar assays). The model accounts for the dynamics of the cell membrane, the actomyosin based propulsion, the membrane-tension feedback on the polymerization, the bending rigidity, and the focal adhesion dynamics with the (deformable) substrate. Thus, even though we are using a phenomenological model, it is possible to incorporate the basic physical mechanisms responsible for the mechanosensitive response of crawling cells. In particular, for crawling over cyclically stretched substrates, we have focused on the stability of the focal adhesions to explain the reorientation behaviour. This is accomplished by introducing an adhesion detachment rate that depends on the rate of deformation (i.e., how fast the cell is being compressed and/or extended), and is motivated by theoretical predictions for the instability of adhesion bonds at high frequencies ([5]Zhong et al., Cell. Mol. Bioeng. **4**, 442, 2011). For cells crawling through complex/crowded environments we have incorporated an additional force feedback on the actin-polymerization rate coming from the forces exerted by the walls, which must balance with the forces due to the filament and membrane tension. This can be understood with a Brownian ratchet model, and results in a polymerization rate that decays exponentially with the forces on the filaments.

(2) Minimal model of crawling and dividing cells

To study the dynamics at large-scales, we have developed a minimal physical model, in which cells are represented by two particles/disks connected by a finitely-extensible spring. An active propulsion force is added to the front disk (representing the protrusions driven by the actin polymerization), while the friction with the substrate is set to act on both disks (representing the effect of adhesions). To account for contact inhibition of locomotion (CIL), which describes the manner in which cells stop moving or change direction upon contact with other cells, the active force was considered proportional to the separation between the disks. In this way, contact with external bodies will change the relative orientation and separation of the two disks, and can naturally give rise to rich collision dynamics (i.e., CIL).

Furthermore, to account for the Contact Inhibition of Proliferation (CIP), which describes the reduction in proliferation as the cell density increases, the model was extended to include the life-cycle of the cell. We consider two states: crawling or dividing. During division the active force is added to both the front/back disks, such that the cell stops moving as it attempts to increase its size. If the size is large enough to accommodate two cells at the end of the cycle, the original mother cell is

replaced with two new daughter cells. Otherwise, in cases where the environment is too crowded, cell division is unsuccessful (resulting in CIP).

(3) Machine-Learning of constitutive relations

In order to connect the (micro) cell-level and (macro) tissue-level descriptions, we have developed a framework to learn constitutive equations. However, given the complexity of studying cellular tissues (e.g., variable density, active stresses) we have used polymer melts as a benchmark. In common with other Soft Matter systems, they exhibit a hierarchy of length- and time-scales and a non-trivial response to external perturbations. Thanks to their industrial importance, they have been extensively studied, with many theoretical models available to test our learning method. We have used Gaussian Process regression to learn the constitutive equation for the stress from training data generated from microscopic polymer simulations at fixed-strain rates.

４．研究成果

To study (A) the mechanosensitive response of cells to cyclically stretched substrates, which is one of the preferred experimental methods for probing the cell, we developed a phase field model that could incorporate the large amplitude deformations used in experiments (~30%). A program implementing this model was developed and extensively tested by reproducing the results on fixed viscoelastic substrates[3]. To model the frequency-dependent stability of focal adhesions[5], we use a detachment rate that can respond to compression $d^{(-)}$, extension $d^{(+)}$, or both $d^{(\pm)}$. Thus, if the rate of compression/extension/stretching is above a given threshold, the adhesions will break $d = 1$, otherwise they are undisturbed $d = 0$. Using model parameters for fast-crawling cells, we explore the reorientation response over a wide range of frequencies ω and initial orientations θ (Fig. 1). We observed a complete realignment, in either the parallel or perpendicular direction, at most ω; this shows the crucial role played by the focal adhesions. The perpendicular reorientation was pronounced for cells responding to extension, whereas a response to compression seemed to favor parallel reorientation. In any case, at large-enough frequencies, all cells aligned parallel to the stretching (similar to passively advected cells, with $d = 0$). Thus, we predict that an asymmetry in the adhesion dynamics during stretching, whether inherent to the cell or the stretching protocol, can be used to selectively align the cells. Furthermore, we find that the frequency dependent reorientation depends on the sub-cellular process being probed. In cases where the adhesion dynamics dominate, this reorientation is explained by the anisotropic role of the driving force, which can stabilize/destabilize the actin polarization in either parallel/perpendicular directions.

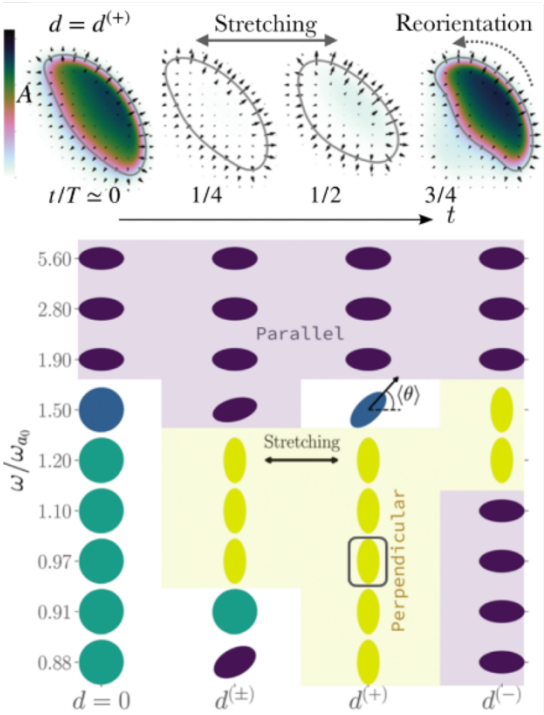

Fig. 1. Cell reorientation under cyclic stretching. (top) Simulation snapshots of cell boundary (solid line), actin polarization field (arrow), and adhesions (color map). (bottom) Phase-diagram for average reorientation response as a function of stretching frequency and cell detachment rate. Adapted from Molina & Yamamoto, Soft Matter **15**, 683, 2019.

Further studies using this detailed model have been performed for (B) cells crawling through complex environments, here consisting of periodic arrays of pillars. To account for the cell/obstacle interactions, we have extended the model to (i) prevent adhesions over the pilar surface, as well as (ii) add the obstacle contribution to the force-feedback on the actin polymerization rate (i.e., polymerization perpendicular to an obstacle should decrease as the force exerted by the obstacle increases). We studied the dynamics of various cell types as they navigated rectangular and hexagonal arrays of pillars. We found a strong dependence on the cell type and the geometry of the

environment (Fig. 2), e.g., soft cells with strong propulsion are better at navigating through the maze. This opens the door to designing custom arrays for cell-sorting and testing.

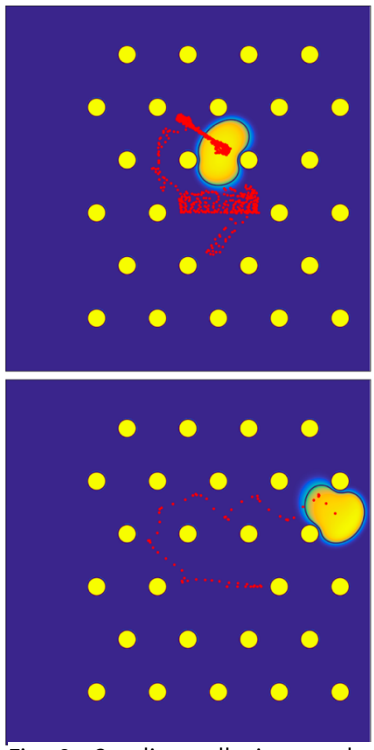

Fig. 2. Crawling cells in complex environments. (top) Soft cell with weak propulsion, (bottom) soft cell with strong propulsion. Adapted from Y. Kobayashi, Kyoto Univ., 2020.

To investigate (C), the dynamics of crawling and dividing cells, we have replaced (1) the detailed phase-field model used for (A-B), with (2) the simplified mechanical model representing cells as active dumbbells. To understand the role of CIL, we first performed simulations of non-proliferating cells. Our results are in good qualitative agreement with experiments. This includes the velocity decrease with density, as well as the velocity distributions. Notably, when the CIL mechanism is turned off (when using a constant motility force), the correspondence with experiments is lost. Furthermore, we find that collective motion depends strongly on the cell shape (Fig. 3a-c). Cells with larger fronts $r = \sigma_b/\sigma_f < 1$ show ordered collective motion, whereas cells with smaller fronts $r > 1$ result in immobile clusters. Counterintuitively, we see that CIL actually enhances the alignment, even though it does not directly provide an aligning mechanism. This is a direct consequence of the collision dynamics and the propulsion mechanism. We have observed backward-travelling density and velocity waves, i.e., traffic jams, which have also been reported experimentally. These results highlight the role that CIL plays in determining the collective properties of migrating cell colonies. This active-dumbbell model was also refined by explicitly considering the extension and contraction stages of the crawling motion (through the repeated attachment/detachment of the front and back disks). Our results show that the shape oscillations inherent to this crawling provide a purely mechanical signal to locally synchronize and enhance their global motion (to avoid traffic jams). Previously it was thought that this could only be achieved through bio-chemical signaling or cell-cell adhesions. Finally, we have also used this minimal model to study the CIP in growing cell colonies (Fig. 3d-e). As reported experimentally, we find two distinct regimes: early-time exponential growth (determined by the proliferation rate) and late-time sub-exponential growth (determined by single cell velocity). The crossover between the two regimes is determined by the onset of CIP.

Finally, we note that we have successfully learned the constitutive relation of polymeric flows with memory from microscopic stress/strain data. We used a Gaussian Process regression technique to infer the constitutive relation for the polymer stress, from fixed strain-rate microscopic polymer simulations. Crucially, no assumptions are made regarding the form of the constitutive relation. We tested our method on non-interacting Hookean dumbbells, for which the exact constitutive equation is known, but recent work on entangled polymer melts has shown the versatility of this approach to more complex systems. In conclusion, we have developed minimal physical models to understand how cells respond to external signals to modulate their biological functions. However, more work is required before we can provide quantitative predictions with experiments (improved models, multi-scale descriptions, etc.).

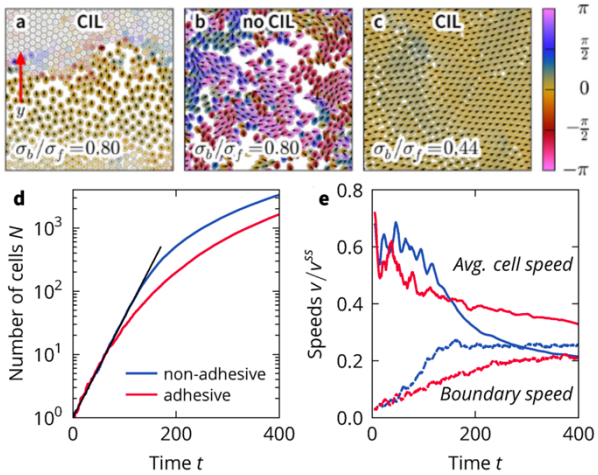

Fig.3. (a-c) Simulation snapshots of motile colonies showing traffic jams, disordered motion, and ordered motion, as a function of motility type and size asymmetry σ_b/σ_f. (d-e) Number of cells and average speed of dividing cell colonies as a function of time, for both adhesive and non-adhesive cells. Adapted from Schnyder et al., Sci. Rep. **7**, 5163 (2017) and Sci. Rep. **10**, 6713 (2020).

５．主な発表論文等

〔雑誌論文〕　計15件（うち査読付論文　13件／うち国際共著　3件／うちオープンアクセス　6件）

１．著者名 Seryo Naoki、Sato Takeshi、Molina John J.、Taniguchi Takashi	４．巻 2
２．論文標題 Learning the constitutive relation of polymeric flows with memory	５．発行年 2020年
３．雑誌名 Physical Review Research	６．最初と最後の頁 33107
掲載論文のDOI（デジタルオブジェクト識別子） 10.1103/PhysRevResearch.2.033107	査読の有無 有
オープンアクセス オープンアクセスとしている（また、その予定である）	国際共著 －

１．著者名 Fadda Federico、Molina John Jairo、Yamamoto Ryoichi	４．巻 101
２．論文標題 Dynamics of a chiral swimmer sedimenting on a flat plate	５．発行年 2020年
３．雑誌名 Physical Review E	６．最初と最後の頁 52608
掲載論文のDOI（デジタルオブジェクト識別子） 10.1103/PhysRevE.101.052608	査読の有無 有
オープンアクセス オープンアクセスではない、又はオープンアクセスが困難	国際共著 －

１．著者名 Seryo Naoki、Molina John J.、Taniguchi Takashi	４．巻 49
２．論文標題 Select Applications of Bayesian Data Analysis and Machine Learning to Flow Problems	５．発行年 2021年
３．雑誌名 Nihon Reoroji Gakkaishi	６．最初と最後の頁 97～113
掲載論文のDOI（デジタルオブジェクト識別子） 10.1678/rheology.49.97	査読の有無 有
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１．著者名 Campo Matteo、Schnyder Simon K.、Molina John J.、Speck Thomas、Yamamoto Ryoichi	４．巻 15
２．論文標題 Spontaneous spatiotemporal ordering of shape oscillations enhances cell migration	５．発行年 2019年
３．雑誌名 Soft Matter	６．最初と最後の頁 4939～4946
掲載論文のDOI（デジタルオブジェクト識別子） 10.1039/C9SM00526A	査読の有無 有
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1．著者名 Schnyder Simon K., Molina John J., Yamamoto Ryoichi	4．巻 10
2．論文標題 Control of cell colony growth by contact inhibition	5．発行年 2020年
3．雑誌名 Scientific Reports	6．最初と最後の頁 6713~6713
掲載論文のDOI（デジタルオブジェクト識別子） 10.1038/s41598-020-62913-z	査読の有無 有
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1．著者名 Molina John J.、Yamamoto Ryoichi	4．巻 15
2．論文標題 Modeling the mechanosensitivity of fast-crawling cells on cyclically stretched substrates	5．発行年 2019年
3．雑誌名 Soft Matter	6．最初と最後の頁 683～698
掲載論文のDOI（デジタルオブジェクト識別子） 10.1039/C8SM01903G	査読の有無 有
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1．著者名 Shih Chunyu、Molina John J.、Yamamoto Ryoichi	4．巻 14
2．論文標題 Field-induced dipolar attraction between like-charged colloids	5．発行年 2018年
3．雑誌名 Soft Matter	6．最初と最後の頁 4520～4529
掲載論文のDOI（デジタルオブジェクト識別子） 10.1039/C8SM00395E	査読の有無 有
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1．著者名 YAMAMOTO Ryoichi、MOLINA John J.、SCHNYDER Simon K.	4．巻 17
2．論文標題 Modeling of Cells which Migrate and Proliferate on a Substrate	5．発行年 2018年
3．雑誌名 Journal of Computer Chemistry, Japan	6．最初と最後の頁 14～19
掲載論文のDOI（デジタルオブジェクト識別子） 10.2477/jccj.2018-0003	査読の有無 無
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1．著者名 Oyama Norihiro、Molina John Jairo、Yamamoto Ryoichi	4．巻 40
2．論文標題 Do hydrodynamically assisted binary collisions lead to orientational ordering of microswimmers?	5．発行年 2017年
3．雑誌名 The European Physical Journal E	6．最初と最後の頁 95 (1-8)
掲載論文のDOI（デジタルオブジェクト識別子） 10.1140/epje/i2017-11586-4	査読の有無 有
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1．著者名 Oyama Norihiro、Teshigawara Kosuke、Molina John Jairo、Yamamoto Ryoichi、Taniguchi Takashi	4．巻 97
2．論文標題 Reynolds-number-dependent dynamical transitions on hydrodynamic synchronization modes of externally driven colloids	5．発行年 2018年
3．雑誌名 Physical Review E	6．最初と最後の頁 032611 (1-12)
掲載論文のDOI（デジタルオブジェクト識別子） 10.1103/PhysRevE.97.032611	査読の有無 有
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1．著者名 Schnyder Simon K.、Molina John J.、Tanaka Yuki、Yamamoto Ryoichi	4．巻 7
2．論文標題 Collective motion of cells crawling on a substrate: roles of cell shape and contact inhibition	5．発行年 2017年
3．雑誌名 Scientific Reports	6．最初と最後の頁 5163 (1-14)
掲載論文のDOI（デジタルオブジェクト識別子） 10.1038/s41598-017-05321-0	査読の有無 有
オープンアクセス オープンアクセスとしている（また、その予定である）	国際共著 －

〔学会発表〕　計50件（うち招待講演　10件／うち国際学会　32件）

1．発表者名 Miyamoto Souta (*), Molina John J. Taniguchi Takashi
2．発表標題 Application of machine-learned constitutive relations for well-entangled polymer melt flows
3．学会等名 American Physical Society (APS) March Meeting 2022 (online)（国際学会）
4．発表年 2022年

１．発表者名
Molina John J. (*), Miyamoto Souta, Taniguchi Takashi

２．発表標題
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３．学会等名
2021 International Chemical Congress of Pacific Basin Societies (Pacifichem 2021) (online)（国際学会）

４．発表年
2021年

１．発表者名
Molina John J. (*), Taniguchi Takashi

２．発表標題
Gaussian Processes for Machine Learning of Fluid Flows

３．学会等名
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４．発表年
2021年

１．発表者名
Molina John J. (*), Taniguchi Takashi

２．発表標題
A Machine Learning approach to flow problems

３．学会等名
69th Annual Meeting of the Society of Rheology, Japan (online)

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2021年

１．発表者名
Miyamoto Souta (*), Molina John J., Taniguchi Takashi

２．発表標題
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３．学会等名
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４．発表年
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１．発表者名
Molina John J. (*)

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４．発表年
2021年

１．発表者名
Seryo Naoki、Sato Takeshi、Taniguchi Takashi、Molina John J. (*)

２．発表標題
Learning the Constitutive Relation of Polymeric Flows with Memory

３．学会等名
American Physical Society (APS) March Meeting 2021 (online)（国際学会）

４．発表年
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１．発表者名
Molina John J. (*)、Seryo Naoki、Sato Takeshi、Taniguchi Takashi

２．発表標題
Learning the Constitutive Relation of Polymer Flows with Memory: from Micro-Scale Dynamics to Macro-Scale Flow

３．学会等名
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４．発表年
2021年

１．発表者名
Seryo Naoki、Taniguchi Takashi、 Molina John J. (*)

２．発表標題
Learning the Constitutive Relation of Non-Newtonian Fluids from Microscopic Dynamics

３．学会等名
18th International Congress on Rheology (online)（国際学会）

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〔図書〕　計0件

〔産業財産権〕

〔その他〕

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６．研究組織

	氏名 （ローマ字氏名） （研究者番号）	所属研究機関・部局・職 （機関番号）	備考
研究協力者	山本　量一 (Yamamoto Ryoichi) (10263401)		
研究協力者	谷口　貴志 (Taniguchi Takashi)		
研究協力者	シュニーダー　サイモン　カスパー (Schnyder Simon Kaspar)		

７．科研費を使用して開催した国際研究集会

〔国際研究集会〕　計0件

８．本研究に関連して実施した国際共同研究の実施状況

共同研究相手国	相手方研究機関