



# A syntactic analysis of a complex motor action: the octopus arm ‘slap’

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## Abstract

The analysis of a natural motor action is always difficult, especially when different motor programs are combined within the same interaction with the environment. We analyzed the behavior of an octopus, *Abdopus* sp., filmed in tidal pools in Okinawa, Japan, which used the kinematic primitives of rotation and translation of its hydrostatic arms, and combined these kinematic behaviors serially and in parallel to ‘slap’ at fish in the wild. In total, 19 slaps were analyzed. The kinematics of arm movement were measured in both external and animal-centered reference frames, while the octopus was slapping at the fish. By combining these primitives, the octopus is able to maintain flexibility while controlling only a few degrees of freedom, a concept we term ‘flexible rigidity’. This slapping action supports Flash and Hochner’s *embodied organization* view of motor behavior, as well as their idea that motor primitives can combine syntactically to form a complex action. The octopus’s ability to use sensory feedback from the position of a moving fish target, along with the feed-forward motor primitives, allows for the building of complex actions at dynamic equilibrium with the environment. Over all, these findings lead to a more realistic view of how a complex behavior allows an animal to coordinate with its environment.

**Keywords** Octopus · Muscular hydrostat · Motor control · *Abdopus*

## Introduction

An animal interacting with its environment has what Latash (2012) called *the bliss of motor abundance*, a multitude of strategies that it can choose from to achieve its goals (Bernstein 1967). An animal with rigid bodies meeting at joints, for instance, can choose from an abundance of combinations of joint angles and torques. This abundance is not a problem of choice for the animal (Gelfand and Tsetlin 1966), as is sometimes thought, since it is at the root of an

animal’s ability to accomplish complex tasks in environments imposing many constraints (Gera et al. 2010). Indeed, Newell (1986) and Hu and Newell (2011) proposed that the motor system’s selection from the multitude of strategies is based on the simultaneous satisfaction of weighted constraints originating in the organism, environment, and task. How satisfaction of these simultaneous constraints is accomplished is perhaps the central problem of motor control. Two suggestions for how this constraint satisfaction problem is solved by animals are: (1) the use and repeated reuse of flexible organizations or synergies of muscles in a variety of actions, usually called *coordinative structures* (Turvey 1990) or *motor primitives* (Flash and Hochner 2005; Latash 2020); (2) methods for combining these motor primitives hierarchically, or *syntactically*, to accomplish complex actions (Turvey 1977; Gallistel 1980; Flash and Hochner 2005). Therefore, the constraint satisfaction process encompassing the organism, environment, and task is computationally analogous to how language combines primitives like sounds into words or words into sentences (Gallistel 1980; Flash and Hochner 2005).

The nature of the primitives and how they combine is especially interesting for muscular hydrostats, as their abundance of strategies is at an even higher level than that for

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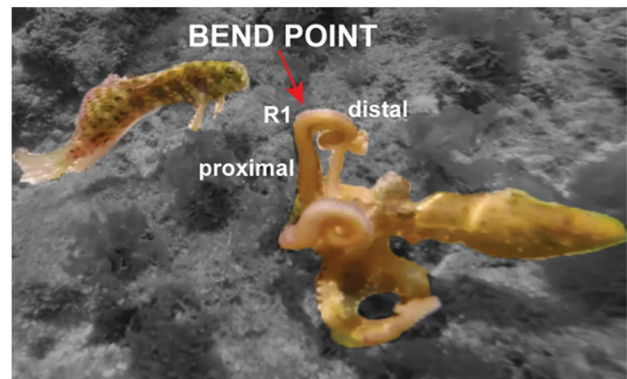
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rigid-bodied animals since there are no fixed joints (Kier and Smith 1985). Octopus arms, for instance, have “exceptional flexibility”, with a three-dimensional array of muscles that can extend, contract, bend, and twist different amounts anywhere along their length (Kennedy et al. 2020). This has therefore become an important system for understanding motor control (Yekutieli et al. 2005a, b; Neshet et al. 2020; Kennedy et al. 2020; Mather and Alupay 2016). It began with detailed descriptions of stereotyped motor programs of the arm associated with simple tasks, specifically ‘reaching’ towards and ‘fetching’ from a stationary goal (Gutfreund et al. 1996, 1998; Sumbre et al. 2001, 2005). Recent studies have found more complexity and plasticity in the arm motor system, combining multiple motor primitives in a stationary task (Hanassy et al. 2015), modulability of the primitives through feedback (Levy and Hochner 2017; Gutnick et al. 2020), and adaption to the constraints of a novel environmental situation (Richter et al. 2015). This complexity and plasticity allow the octopus to maneuver through the abundance of choices (Latash 2012), when octopuses interact in a dynamic environment (Mather 1992; Mather and Anderson 1999; Kuba et al. 2006).

Still, little is known about how they control arm movement in these complex situations, or more theoretically, what the primitives really are, if any, and how they are syntactically (Flash and Hochner 2005) combined. To investigate these problems, we were able to evaluate in *Abdopus* sp. a behavior first described by Mather (1992) in *Octopus vulgaris*, and more recently, Sampaio et al. (2020) in field observations of *Octopus cyanea*, which they call ‘punching’. Functionally, the slapping action is also related to cuttlefish tentacle strikes (Messenger 1968), which were once thought stereotyped but have now been shown to be tuned through feedback (Wu et al. 2020). Our aim is to describe this complex interaction and to discuss its implications for motor control. The slap behavior, which we will evaluate in this study, is defined as the movement from when the point of highest curvature on an arm (henceforth referred to as the bend point) first travels from a proximally oriented bend to when the bend is most distal prior to retraction (Fig. 1). We will argue for two basic primitives, which we will call rotation and translation, which can be used separately (Fig. 2A, B), or, as we will show, can combine on two separate arms or even one arm action (Hanassy et al. 2015). These primitives, which we will argue are flexible and modulable by the task, have been extensively investigated for the achievement of other tasks such as reaching and fetching in simple situations in laboratory studies (Gutfreund et al. 1996, 1998; Sumbre et al. 2006; Hanassy et al. 2015; Levy et al. 2015), and is here extended to complex action in field situations. In reaching, there is arm extension toward an object by (1) propagating a bend down the arm without changing its length (Yekutieli et al. 2005a, b), or by (2) elongating the arm, thus increasing the length (Hanassy et al. 2015). Since this motor primitive is



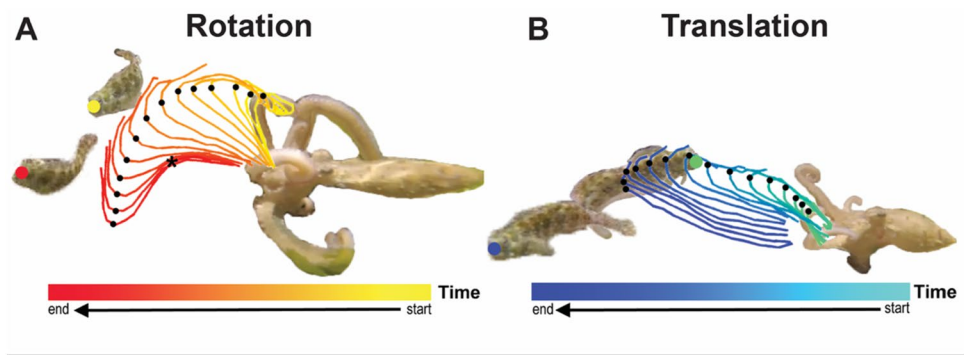
**Fig. 1** Octopus and fish, with arm curled and bend point is marked, before it moves. See Also Video 1, Frame 1 (Supplementary Information)

more general than the reaching task, and is also used in slapping, we call it *translation*, here. This is because the bend point travels quasi-linearly (Flash and Sejnowski 2001). In fetching an object, the octopus stiffens and rotates arm segments, fixed in length, along three pseudo-joints (distal, medial, and proximal) (Sumbre et al. 2006). We will call this primitive *rotation*, since the bend point curves in space. The concepts of rotation and translation would seem to apply only to animals whose motion depends anatomically on rigid bodies, which can translate and rotate, and not be applicable to an animal like an octopus whose arms are extremely flexible (Kier 2016). However, Kier and Smith (1985) and Kier (2012) have shown that the *biomechanical* concept of leverage, which used to be thought of as requiring rigid motion is applicable to animals lacking permanently rigid parts, and we believe that, in addition, the *kinematic* notions of rotation and translation also apply to the motor control of soft-bodied animals as primitives. These primitives can then be used in multiple *tasks* like reaching, fetching, and slapping, each requiring modulation of the primitives to meet the specific constraints imposed by the task. Based on Newell’s (1986) multiple constraint satisfaction framework for abundance utilization, our work, therefore, presupposes a distinction between the (1) organism-centered primitives of rotation and translation, (2) tasks such as reaching, fetching, and slapping, and (3) environmental constraints like being stable with respect to the environment. The in situ interaction of the octopus and fish we describe in this work is an illustration of how these aspects of animal action come together.

## Methods

**Field work** From June to July 2014, field observations in Okinawa, Japan consisted of following the octopus *Abdopus* sp., which appears different from the well-known *Abdopus*

**Fig. 2** Two basic motor primitives of motion Rotation and Translation, previously studied in the tasks of fetching and reaching, respectively



*aculeatus* (Huffard 2006). Video observations from six researchers with GoPro® Hero3 cameras were recorded at one location, Tropical Beach in Ginowan facing the East China Sea. The habitat consists of a rocky plateau scattered with algae and many holes that create tidal pools known to contain a high density of octopuses. Observations were made between the mid-tides at the low part of the tidal cycle. Each researcher followed an individual octopus for as long as possible before the octopus retreated into the dead coral substrate. The initial position where each individual octopus was found was marked using a yellow tag (later collected) during each observation day and became a reliable tag for finding an individual, possibly the same octopus, on subsequent days. However, individuals were never interfered with physically, formally marked or identified. This species was fairly active during periods of low tide, with its long arms and display patterns characteristic of the *Abdopus* genus making it easy to find. Although the total number of individuals that were observed is difficult to determine without individual tags, as a group the researchers followed between four to sixteen individuals per day. One individual was recorded interacting with a blenny fish (*Salaria* sp.) using the arm ‘slap’ behavior described by Mather (1992). The slaps described were from one continuous session, and no further observations of this behavior were made. Arms were described as Left (L) 1, 2, 3, 4 and Right (R) 1, 2, 3, 4, starting from the anterior midline. All arms were intact except R2, a partially regenerating arm about half the length of other arms. During this interaction, a total of 28 instances of ‘slaps’ was observed. Nineteen of those slaps were used for detailed analysis as they were minimally covered by obstructions in the environment (e.g., fish, algae, overlapping arms, coral structures) or affected by recording conditions (e.g., stability of the camera, focus, view out of frame). Due to the nature of field studies, we were limited in sample size, but rich in detailed information regarding interactions between the animal and its surroundings.

*Video analysis: videos of slaps are included in Supplementary Information* Clips were recorded at 48 frames per second. Each of the individual 19 ‘slap’ examples was

manually tracked using MATLAB®. Each instance could not be considered independent from another as they all occurred in the same individual in a short time frame. In the next section, we do describe each slap as a complex action, with the understanding that all of them compose an even more complex action. We number the slaps from 1 to 19, however, in 4 instances, multiple active arms are acting simultaneously, designated as grouped. Specifically, Slaps 3–5 are parts of one event, where 3 different arms (details described later), move towards the fish. The same is true of Slaps 6–7, 8–9, and 10–11. Manual tracking was necessary for this data-rich video set to account for individual slap differences that automated tracking cannot detect with a heterogeneous background. Distinguishable points (i.e. specific holes and algal patches) in the environment were manually tracked and used to transform the video into standardized, comparable images for measurements, following Yekutieli et al. (2005a, b), to overcome field video recording conditions. The midline of each arm slap was tracked manually. Annotated videos are provided in Supplementary Information. Points on the octopus (eyes, mantle tip, and bend point on the arm) and the fish (nose, mid-body, and tail) were also manually tracked for each frame to determine their relationship in each action. Using these tracked points, we measured the following features for each slap: duration, the number for each actively slapping arm, where on the arm the bend point starts (proximal base, mid-arm, or distal tip), whether the slap is initiated with a curled distal tip, proximal translation, rotation, and change in total length of the arm. The trajectory of the bend point was tracked for every frame to characterize the different slap motor programs. Methods for calculating measurements are described below.

*Measure of octopus-fish dynamics* Fish positions were measured as a function of angle with relation to the position of the octopus arm. This angle was used to test if it was a predictor of what motor program the octopus used for each slap. The angle between three key points, the arm’s bend point, the base of the arm, and the nose of the fish was determined for the first frame of each slap. To measure the degree of rotation and translation used in the motor program

for each slap, the ratio between the changing angle of the proximal arm and its changing length from the start to end of the slope was calculated.

**Measure of arm rotation and translation** Rotation in the proximal segment was measured over time by taking the angular change between the proximal segment (straight-line segment from arm base to bend point) at the start of the slap and the proximal segment at each time point. We also estimated a line of binocular vision going through the midpoint between the eyes and mantle (Video 1, red). To determine whether what we measured as rotation was rotation of the whole arm or the whole animal, we also measured the angular change of the arm with respect to this binocular vision line, to have a reference for arm rotation in terms of animal rotation. Translation was measured as the change in distance between the bend point and the base of the arm over time. To classify whether a slap was primarily a translation or a rotation, we followed the following steps: (1) the trajectory of the bend point was determined; (2) the area of a polygon formed by the bend point trajectory was determined and normalized by the perimeter of the polygon; (3) a threshold was determined by the authors separating low normalized-area trajectories as translations and high normalized-area trajectories as rotations. The rationale behind this classification is that a translation linear trajectory spans very little area, whereas in a rotation trajectory, there is a great deal of direction change and hence a large area is spanned.

**Analysis of multiple arm slaps** In the nine instances of grouped slaps, the following were measured for each group: arm number, start, and ending frame, duration of each slap based on the frame number, lag time (time between the start of the first slap and start of the subsequent slap), time overlap (how much of the slap duration overlapped between every two or three arms), and fish reaction time (how long after the start of each slap did the fish move away).

A ‘slap’ was defined as the movement from when the point of highest curvature on an arm (henceforth referred to as the bend point) first travels from a posteriorly oriented bend to when the bend is most distal prior to retraction (Fig. 1). The slap ended with the arm extended, bend point at or near the tip of the arm. These slaps were rapid, averaging  $378 \text{ ms} \pm 130 \text{ ms}$ , and performed by the nearest arm to the fish, usually one of the anterior arms. Several measurements were obtained including extension and changing angle of the arm during slap and angle of the arm with respect to

the position of the fish. Table 1 provides information about which arms were involved in each of the slaps, including their roles. Table 2 provides basic quantitative information about each of the slaps.

## Results

In terms of coordination, arms have three possible tasks in a slap (Table 1). The first is participating in active slapping (‘A’). The second is stabilizing (‘S’) by maintaining contact with the ground, arms in crevices or holding on to the substrate. The third is preparing (‘P’) for future slaps by keeping arms bent and splayed, medial portions held upright with the distal tips curled (Mather and Alupay 2016). These are not mutually exclusive. Although the arms were equipotential in performing all three tasks, preferential arm use was observed (Chi-square goodness of fit test  $p$ -value = 0.0001,  $n = 19$ ). 79% of the arms actively used for slapping were anterior (R1, L1). Posterior arms were used for stabilizing, and arms surrounding active arms were prepared for future slaps. This task division in anterior and posterior arms has been observed in other tasks (Mather 1998; Byrne et al. 2006a, b) such as anterior use in more reaching and exploring and posterior arm use for locomotion, like walking (Byrne et al. 2006a, b) especially bipedally in *A. aculeatus* (Huffard 2006). During grouped arm slaps, the nearest neighboring arm closest to the fish was usually recruited (Video 3–5, Supplementary Information). The exception was slapping with R1 with no recruitment of R2, a regenerating arm (Lange 1920) about half the length of the other ones. Instead, we observed recruitment of R3 (10% of 19 trials) after initial slaps with R1. Direct recruitment is possible through the circumoral commissure which surrounds the mouth and connects the brachial ganglia that control each individual arm or from central commands (Byrne et al. 2006a, b; Gutnick et al. 2020; Kuuspalu et al. 2022).

As mentioned in the Methods section, we classified slaps into translations and rotations based on the area the slap trajectory spans. Figure 3 shows the bend point trajectories of the slaps. The trajectories were all aligned so that they start at the same point. In translation, the bend point travels semi-linearly through the arm away from the animal, whereas, in rotation, there is a crosswise movement of the whole arm through an arc. Examination of the trajectories,

**Table 1** Characterization of each slap based on the role of each arm. ‘S’ represents a stabilizing arm, ‘P’ represents a preparing arm, and ‘A’ represents the active arm in slap

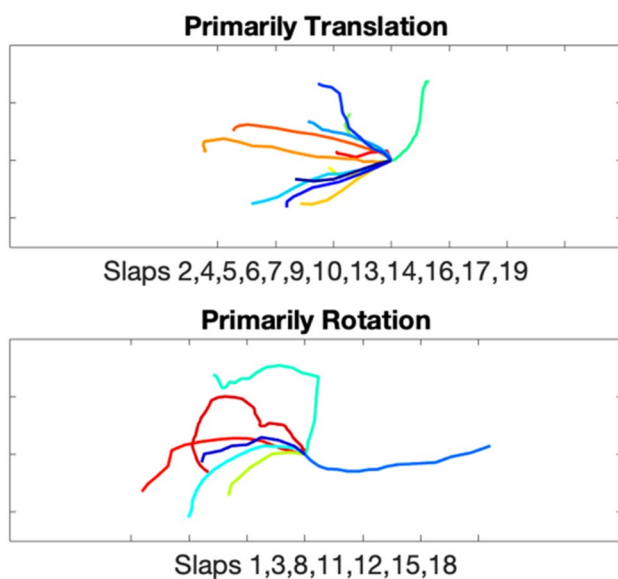
Slap	L4	L3	L2	L1	R1	R2	R3	R4
1	S	P	P	P	S	N/A	A	S

‘N/A’ for arm R2 represents not applicable because the regenerating arm was not used

**Table 2** Summary characteristics of all 19 analyzed slaps including duration of each slap in milliseconds, the arm number (R1–R4, L1–L4), where the bend originates along the arm (base, middle), whether the tip of the arm is curled, and measurements of extension (in cm) in the proximal segment (base to bend point), rotation (in degrees), the change in distance between the total length of the arm after the tip is fully curled and the total length of the arm at the end of the slap

Slap	Duration (ms)	Arm Number	Bend Origin	Curled Tip	Proximal Extension (cm)	Proximal Rotation (degrees)	$\Delta$ Total Length (cm)
1	729	R3	Mid	Yes	0.4	92	-0.1
2	229	R1	Mid	No	1.0	77	0.3
3	375	R1	Mid (curl)	Yes	2.0	63	1.2
4	292	L1	Mid/base	Yes	2.8	21	2.0
5	542	L2	Base	No	3.2	20	1.5
<sup>a</sup> 6	312	L1	Mid (curl)	Yes	2.2	46	1.3
7	354	L2	Base	No	1.3	17	0.1
8	208	R1	Mid (curl)	Yes	0.4	90	0.05
9	396	L1	Base	Yes	1.1	37	-0.5
10	396	R1	Base	No	1.5	28	1.1
11	542	R3	Mid/base	No	2.3	90	0.9
12	438	R1	Mid (curl)	Yes	0.8	102	0.1
<sup>a</sup> 13	479	L1	Mid (curl)	Yes	2.5	74	1.4
14	250	R1	Mid (curl)	Yes	1.4	41	0.04
15	417	R1	Base	No	3.6	23	4.7
16	375	R1	Mid	Yes	2.1	57	1.0
<sup>a</sup> 17	229	L1	Mid	Yes	2.3	24	1.2
18	375	R1	Mid	Yes	1.0	82	0.2
19	208	L1	Mid	Yes	1.7	92	1.1

<sup>a</sup>Slap examples where the fish does not move locations during the duration of the slap. The arm number given is for the arm we believe is most crucial in repelling the fish

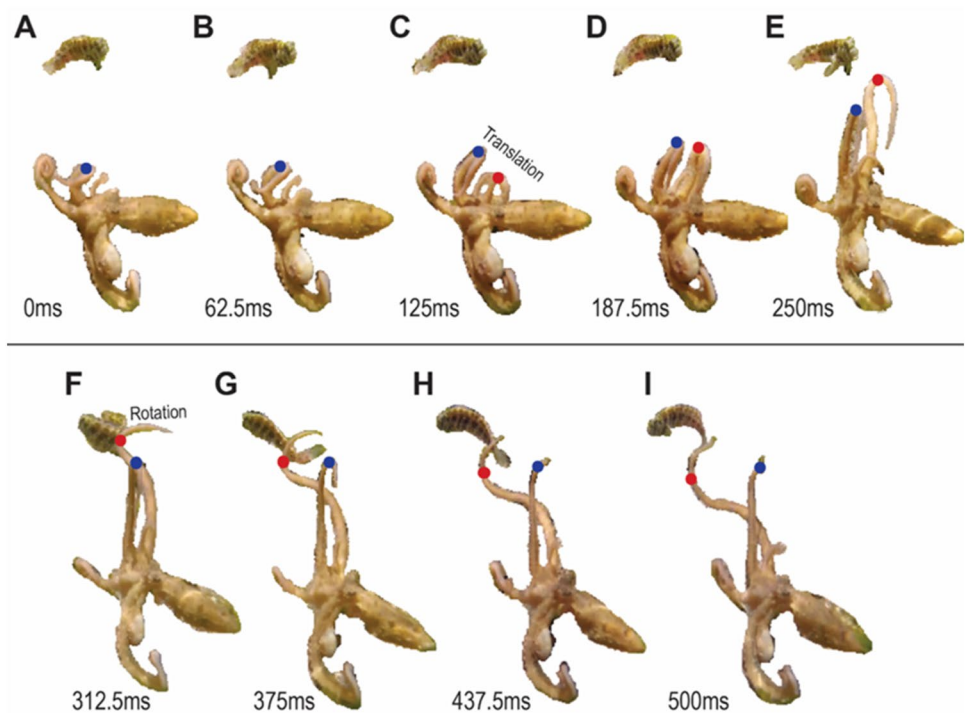


**Fig. 3** Classification of slaps into translations and rotations. The slaps are color coded from 1 (dark red) to 19 (dark blue)

though, shows that the slaps are almost never exclusively translations or rotations. Rotations usually start with translation, and sometimes the translation of the bend point continues as the arm rotates, as discussed later. Also, at the very end of translations, there is often a quick swing towards

the fish, as can be seen in the hooks at the end of several translations and videos in Supplementary Information. An ecologically significant aspect of slap behavior is that slaps can co-occur in different arms at the same time. Gutfreund et al. (1996) found instances of two arms reaching towards a target to be synchronous (moving together) or consecutive (moving one after another), performing the same motor pattern regardless of timing. We observed three instances of two arms (Slaps 6–7, 8–9, 10–11) and one instance of three arms slapping (Slaps 3–5). Unlike in Gutfreund et al. (1996), the motor patterns of each reaching arm were not always the same. Figure 4 shows Slaps 10 and 11, where one arm (blue bend point) performs a translation motor primitive, while the other arm performs a rotation (red bend point). In translation, the bend point travels along the arm almost in a straight line, while in a rotation, the bend point forms a joint around two stiffened portions, and the entire arm waves (Sumbre et al. 2006). These primitives are, as mentioned, also observed in reaching and fetching. Both involve prior stiffening (henceforth referred to as ‘rigidification’) of the proximal arm segment by co-contracting different muscles at different orientations (Kier and Stella 2007; Kier 2016). This effectively makes the segment act like a rigid body that can reposition (in rotation) or makes the end point of the straight segment move towards the fish (in translation). The ability to make and combine components that involve rigid bodies provides a means for reducing the number of

**Fig. 4** Slaps 10,11, with simultaneous translation and rotation on 2 arms. See Video 10 and 11 (Supplementary Information)

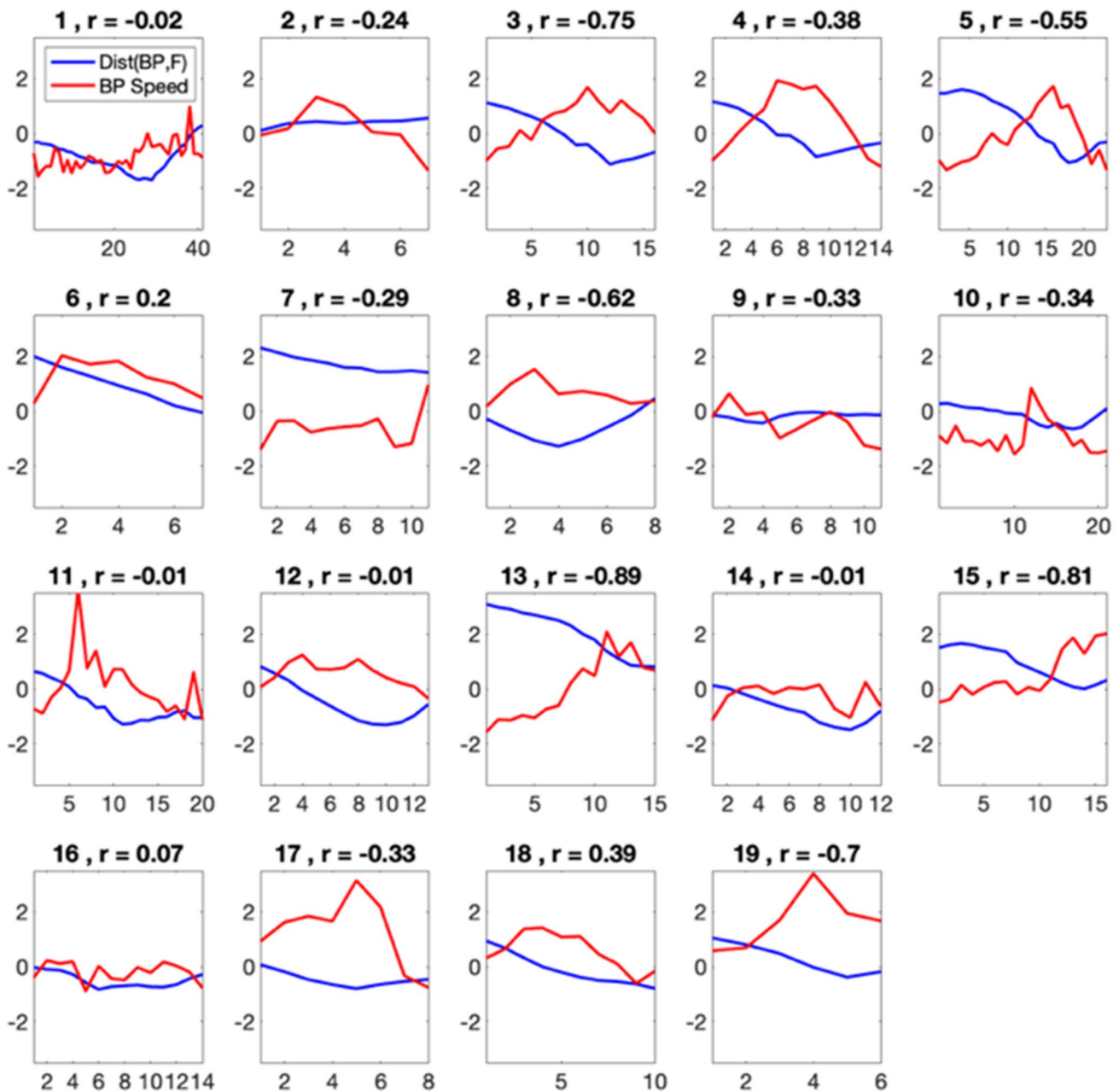


variables the octopus controls while still maintaining high flexibility by varying components over time (See Video 3). The octopus uses this ‘flexible rigidity’ to produce diverse motor programs in response to a complex situation. We see here that these two actions can be used simultaneously on different arms, combined, in parallel, to achieve the act of repelling the fish. This observation supports the idea that motor primitives, like linguistic objects such as speech segments and words, can combine together to form complex actions (Gallistel 1980; Flash and Hochner 2005).

Translation and rotation are not only composed in parallel as in Slaps 10–11, but also in combination on the same arm. Video 1 (Supplementary Information) and Fig. 7a show Slap 1, where the bend point first translates through the arm, but at about the middle of the action, the arm starts to rotate or swing towards the fish. But interestingly, the bend point still keeps translating through the rest of the arm, while it is also rotating. The translation of the bend point along the arm and towards the fish and the simultaneous rotation of the arm as a whole both serve to repel the fish. We take the superposition of the translation and rotation to be an additional syntactic combinatorial possibility in the syntax of the slap, as well as pointing to the extraordinary flexibility of the basic action repertoire of the octopus arms. We would like to note that the rotation we are discussing is a rotation of the arm, not of the whole animal, and this can be seen in Video 1. Besides the arm, we have also plotted the binocular line which we pass through the midpoint between the eyes and the mantle (of course this is difficult given the flexibility of

the mantle, but visual inspection gives us confidence that this binocular line is a good representation of the general orientation of the animal). The orientation of the animal changes slightly during Slap 1, but the arm rotates far more, providing evidence that the rotation we discuss is true of the arm, not the whole animal. Additional evidence for this point is in the rotation in Slap 10, where the animal does change its orientation towards the right during the slap, but the arm is rotating to the right.

Two perspectives need to be considered in analyzing the slap, the internal reference of the octopus itself and the external view of the fish which sees translation of the bend point and rotation of the proximal arm as it gets closer. Unlike in previous work with a stationary goal (Gutfreund et al. 1996, 1998), the fish target is constantly changing its position and direction in space. The octopus arm trajectory depends on the fish’s position. This is to be expected based on Hochner’s *embodied organization* framework. Using the external task-based external reference frame (Saltzman and Kelso 1986), Fig. 5 shows the distance between the bend point and the center of the fish as a function of time for each slap (blue), as well as the speed of the bend point as it travels. Each time series was standardized with respect to all others of its type, so that both kinds of signals can be placed onto the same plot. It should be kept in mind, of course, that distances and speeds projected onto 2D video from 1 camera are not an accurate measure of distances and angles in 3D space, but based on our visual examination of the video and the traces in the panels of Fig. 5, we believe



**Fig. 5** Distance between the bend point (BP) and the center of the fish (F) (blue), and the speed of the bend point, both as a function of time

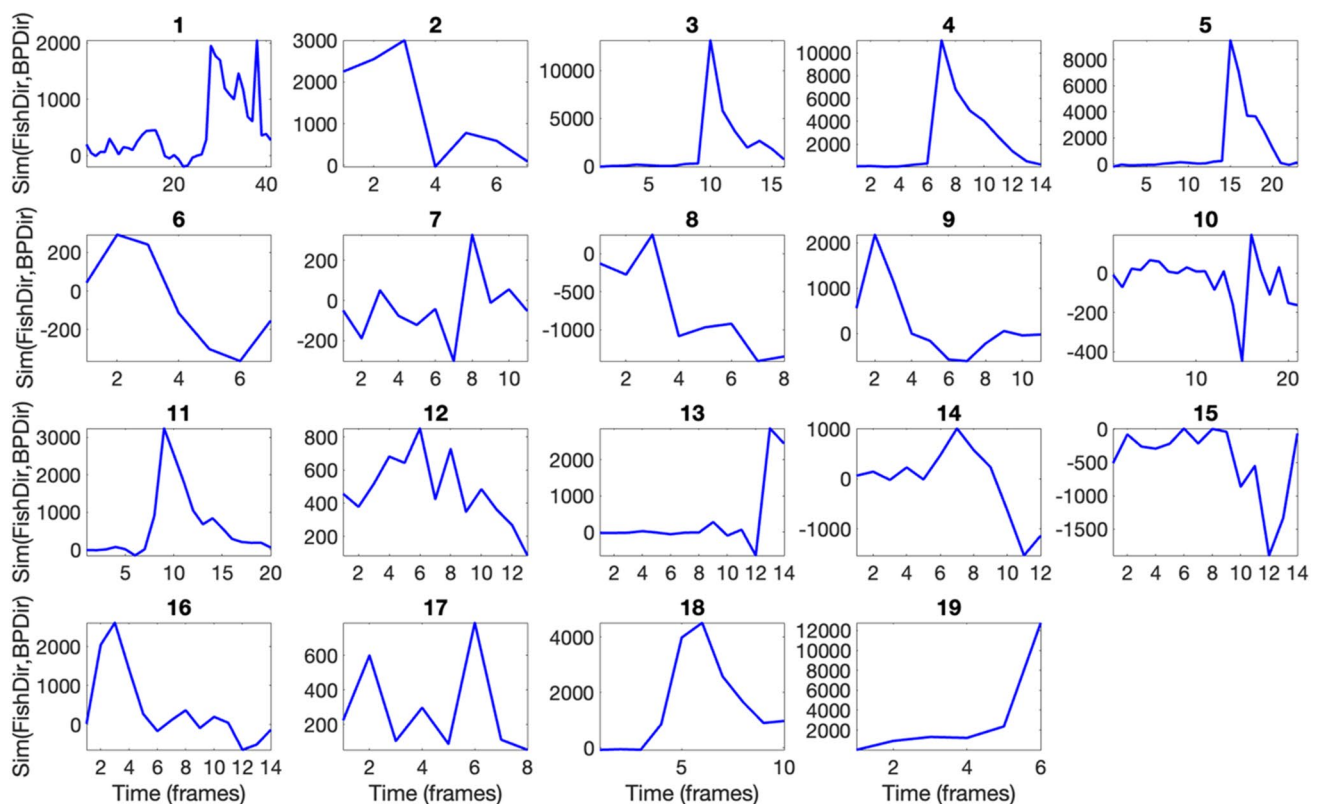
that the traces are good indicators of the change in the relationship between arms and the fish. The objective of the octopus is to get the fish away from itself. In most slaps, the distance between the bend point and the fish decreases. As the bend point approaches the fish, the latter moves away, increasing the distance between the bend point and the fish again. In a few slaps, e.g., Slap 2, the fish moves at about the same rate as the bend point, maintaining the same distance. In some of the slaps (e.g., Slap 5), the tangential speed profile of the bend point is somewhat similar to the profiles shown for reaching in Gutfreund et al. (1996) and Hanassy

et al. (2015), where the peak velocity is reached late in the movement. However, in other slaps (e.g., Slap 8), the peak velocity is achieved much earlier. We believe that since the octopus is trying to repel the fish, as opposed to catching it as in the reaching movements of the octopus described in Gutfreund et al. (1996), the movement gets faster and faster the closer the fish is to the bend point. We calculated the Pearson correlation coefficient between the bend point-fish distance and the speed and found that in 11 of the 19 slaps, there was a correlation  $r$  of  $-0.3$  or lower, suggesting that speed increased the closer the bend point is to the fish, the

target of the slap. The tendency for the peak velocity to be near the point of lowest distance, whether that point occurs early or late in the slap suggests, we believe, that the reaching motor primitive in its use for slapping is quite flexible, not fixed. In the slaps where there is actual contact, the high velocity as the fish approached the bend point suggests that those slaps are force-based, perhaps similar to the punch described by Sampaio et al. (2020)'s Video 3 at 00:19, where velocity seems to be maximal at contact.

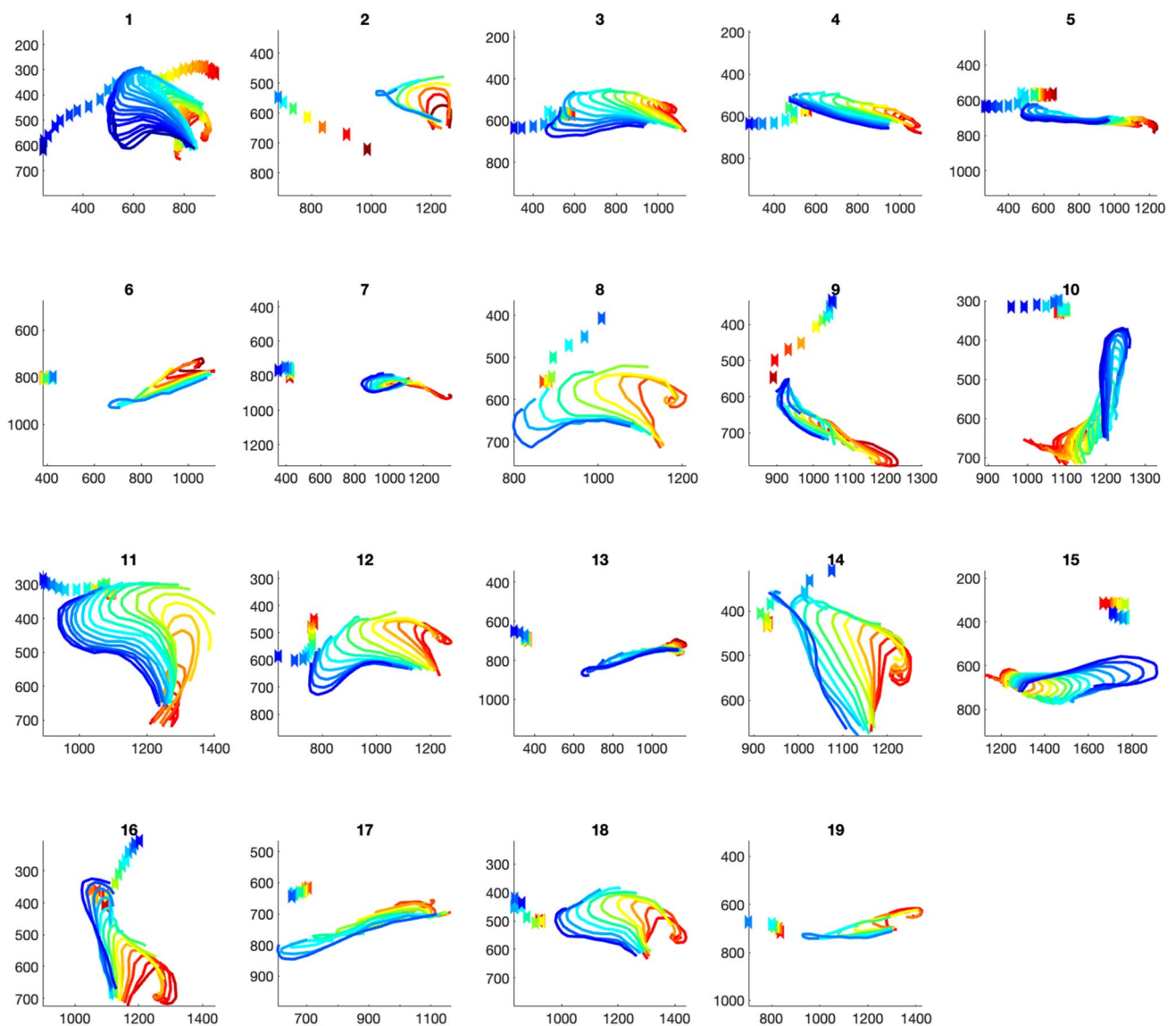
A more abstract way of seeing the dynamic animal environment is by measuring the degree to which the octopus is able to push the fish away through slapping. To do so, we determined two vectors at each frame: (1) the direction vector of the bend point; (2) the direction vector of the nose of the fish. We took their inner product to determine the degree to which the two vectors point in the same direction via the similarity of the vectors. Figure 6 shows these data. Slap 1, for instance, starts with translation, with the bend point traveling along the arm with basically no relation to the direction of motion of the fish—it is simply a motion towards the fish, not following the fish. But at point 23, the bend point is at a place in the arm where it can be used to push away the fish, and the arm, now stiffened, is moved by a joint proximal to the animal to rotate the arm in the direction of the fish, as can be seen in

the sharp increase in the similarity of directions of motion of the bend point and the fish. This can be seen in Fig. 7, where we have provided all frames for each slap color-coded from start (red) to end (blue). In other Slaps, such as 3 and 4, there is a translation of the end-point towards the fish, but not following the fish, followed by a place at which the slap occurs, and there is a bit of rotation towards the fish. We believe that this figure adds to the evidence for the visual guidance of action by the octopus (Gutnick et al. 2011; Levy et al. 2015), since the octopus is able to change motor primitives when it needs to based on where the fish is. And it also indicates that Slaps can contain the two motor primitives produced together, to accomplish the complete goal of getting the fish away from itself. Figure 3 showed parallel combinations of motor primitives, whereas Figs. 6 and 7 show, also, sequential combinations. This furthers the evidence for the syntax of action hypothesis, due to the series and parallel organization of actions, and it is exactly this organization that is evidence for the *embodied* organization (Hochner 2012), since the dynamical environment imposes different constraints in time leading to a shift in motor primitive. Further evidence for simultaneously behaving arms and slaps of the type we have described from carefully controlled laboratory experiments are of course necessary before these



**Fig. 6** Similarity in direction of motion of the bend point (BPDir) and the center of the fish (FishDir)





**Fig. 7** Arm positions (curves) and fish center positions (crosses) as a function of time, indicated by color: red for start and blue for end

observations can be accepted, since distances and directions as in Figs. 5 and 6 are only indicators of true distance and direction.

## Discussion

This movement analysis of the slapping action, related to actions mentioned by Mather (1992), and Sampaio et al. (2020), provides evidence for the flexibility of a syntax of action-embodied organization approach to motor control (Flash and Hochner 2005; Hochner 2012). The combination of the primitives reminds us of a long tradition in motor control in which actions are conceived of as syntactic hierarchies of sub-actions (Sherrington 1947; Turvey 1977;

Gallistel 1980; Flash and Hochner 2005). We do not claim that we thoroughly understand the syntax of the slap, but we have evidence of some basic principles of syntactic combination: (1) parallel combination of translation and rotation on two different arms as in Slaps 10 (translation) and 11 (rotation), as well as Slap 3 (rotation) and Slaps 4 and 5 (translation); (2) parallel combination of several translations as in Slaps 4–5; (2) simultaneous activation of translation and rotation as in Slap 1 and to different degrees in most other slaps. For the reaching task, Gutfreund et al. (1996) also observed instances of synchronous and asynchronous translation as in Principle 2, and Hanassy et al. (2015) observed simultaneous activations of the two primitives as in Principle 3, suggesting that these syntactic principles are applicable in different tasks. It remains to be seen whether

additional combinatory principles are necessary, for instance for the crawling task (Levy et al. 2015), or whether the principles above can be generalized to encompass even more tasks. We hope that future work would clarify how the muscles implement the complex superposition of translation and rotation on the same arm, based on what has already been demonstrated of how muscles realize reaching (Gutfreund et al. 1998) and fetching (Sumbre et al. 2006).

The relation between what we have termed a “slap” (Mather 1992) and what Sampaio et al. (2020) call a “punch” is unclear at this time, since no kinematic analyses of the “punch” were available. We hope that future work on interactions between octopus and other animals will help us understand the relationship between the two actions if they are indeed different. Regarding the similarity of slaps to the reaching behavior, the bend point’s trajectory and speed do not seem to be rigidly specified for the slap, but are very much informed by the motion of the fish, necessitating flexibility in the motor primitives used. Analysis of the speed profiles of the slaps shows that there is some similarity to the speed profiles of the reaching motor primitive (Gutfreund et al. 1996; Hanassy et al. 2015). However, the slap does not seem to be a simple instance of a reaching movement, since the point at which peak velocity is achieved seems less rigid in the slap than reaching a static target, being informed by the distance between the fish and the bend point. We speculate that there is a “programmable” motor primitive (Schaal and Sternad 1998) involved for different tasks such as reaching and slapping, but the kinematic properties of this primitive adapt to dynamic environments. This supports the embodied organization concept, where actions are flexible (Newell 1986; Neshet et al. 2020).

Feedback, the presence of building movement blocks, and the syntactic organization of these blocks are all aspects of motor control that help an animal select from an abundance of options (Bernstein 1967; Gelfand and Tsetlin 1966; Gallistel 1980; Flash and Hochner 2005). The strategies for multiple constraint satisfaction (Newell 1986) which we have described in the slapping action have interesting parallels in the tasks of swallowing and speech production by the human tongue, as would be expected from their similar muscular hydrostatic structure (Kier and Smith 1985). Specifically, both use hierarchical flexible, yet rigid-like strategies. When the tongue produces different vowels and consonants of a language, every point of it moves continuously. But if tongue movement is measured through its contribution to the change in the cross-sectional area of the vocal tract (the relevant variable for vowel and consonant differentiation), that contribution is measured as a rotation, or ‘pivoting,’ where a great deal of change in the cross-sectional area occurs at the task locations, and no change occurs at some intermediate point of the pivot (Iskarous 2005; Iskarous et al.

2010). It was suggested (Iskarous 2005) that the reason a thoroughly flexible muscular hydrostat like the tongue should execute what may seem like a rigid body motion is that the complexity of controlling this highly flexible medium is reduced by coupling the many degrees of freedom to produce quasi rigid motions that vary spatially and temporally. Rigid motions have very few degrees of freedom, solving the motor control problem of minimizing the degrees of freedom by linking units of movement into rigid-like motor primitives. In the tongue’s achievement of the swallowing task, a different rigid primitive is invoked, where a point of highest curvature translates downward on a bolus moving it downward (Iskarous 2019). Iskarous (2005) pointed out a strategy in speech production called *arching* where translation and rotation primitives can be combined. Therefore, even though octopus arms and mammalian tongues are in animals which shared a last common ancestor about 540 million years ago, they seem to use similar rigid primitives and combinatorics of these primitives in tasks which show *flexible rigidity*: Rotation in fetching, primarily rotational slaps, and speech pivoting; Translation in reaching, primarily translational slaps, and swallowing. We believe that these similarities can serve as a bridge between the study of the two systems, which can be of benefit to understanding both.

We believe that kinematic description of octopus behavior in the wild can combine with understanding based on careful laboratory work, which is of course indispensable, despite obvious limitations on exact quantification from such data. In the wild descriptions provide settings for laboratory environments to provide more realistic situations in which to investigate behavior in ecologically valid conditions. There is a great deal of ethological description of animal behavior in the wild (Mather and Alupay 2016). But we believe that a better bridge can be built between ethological description and careful laboratory work if the kinematic description of behavior is provided in graphical form, as this serves to extend verbal description to suggest designs and measures for quantitative laboratory research.

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manuscript, and JM and KI contributed revisions. KI acquired funding and administered the project.

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## Declarations

**Conflict of interest** The authors have not disclosed any competing interests.

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