

# Current Biology

## Arm Coordination in Octopus Crawling Involves Unique Motor Control Strategies

### Highlights

- Octopuses use unique strategies to coordinate their arms in crawling
- They can crawl in any direction relative to the facing (body) direction
- Arms create pushing thrust by simple shortening and then elongating movements
- Arm coordination in octopus crawling lacks any obvious rhythmical pattern

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### In Brief

Levy et al. show that octopuses use non-rhythmical arm coordination for crawling in any direction, while at the same time independently controlling their body orientation. They are able to do so because they decide in a moment-to-moment fashion which of the eight arms to recruit for pushing the body with simple shortening and then elongating movements.



# Arm Coordination in Octopus Crawling Involves Unique Motor Control Strategies

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## SUMMARY

To cope with the exceptional computational complexity that is involved in the control of its hyper-redundant arms [1], the octopus has adopted unique motor control strategies in which the central brain activates rather autonomous motor programs in the elaborated peripheral nervous system of the arms [2, 3]. How octopuses coordinate their eight long and flexible arms in locomotion is still unknown. Here, we present the first detailed kinematic analysis of octopus arm coordination in crawling. The results are surprising in several respects: (1) despite its bilaterally symmetrical body, the octopus can crawl in any direction relative to its body orientation; (2) body and crawling orientation are monotonically and independently controlled; and (3) contrasting known animal locomotion, octopus crawling lacks any apparent rhythmical patterns in limb coordination, suggesting a unique non-rhythmical output of the octopus central controller. We show that this uncommon maneuverability is derived from the radial symmetry of the arms around the body and the simple pushing-by-elongation mechanism by which the arms create the crawling thrust. These two together enable a mechanism whereby the central controller chooses in a moment-to-moment fashion which arms to recruit for pushing the body in an instantaneous direction. Our findings suggest that the soft molluscan body has affected in an embodied way [4, 5] the emergence of the adaptive motor behavior of the octopus.

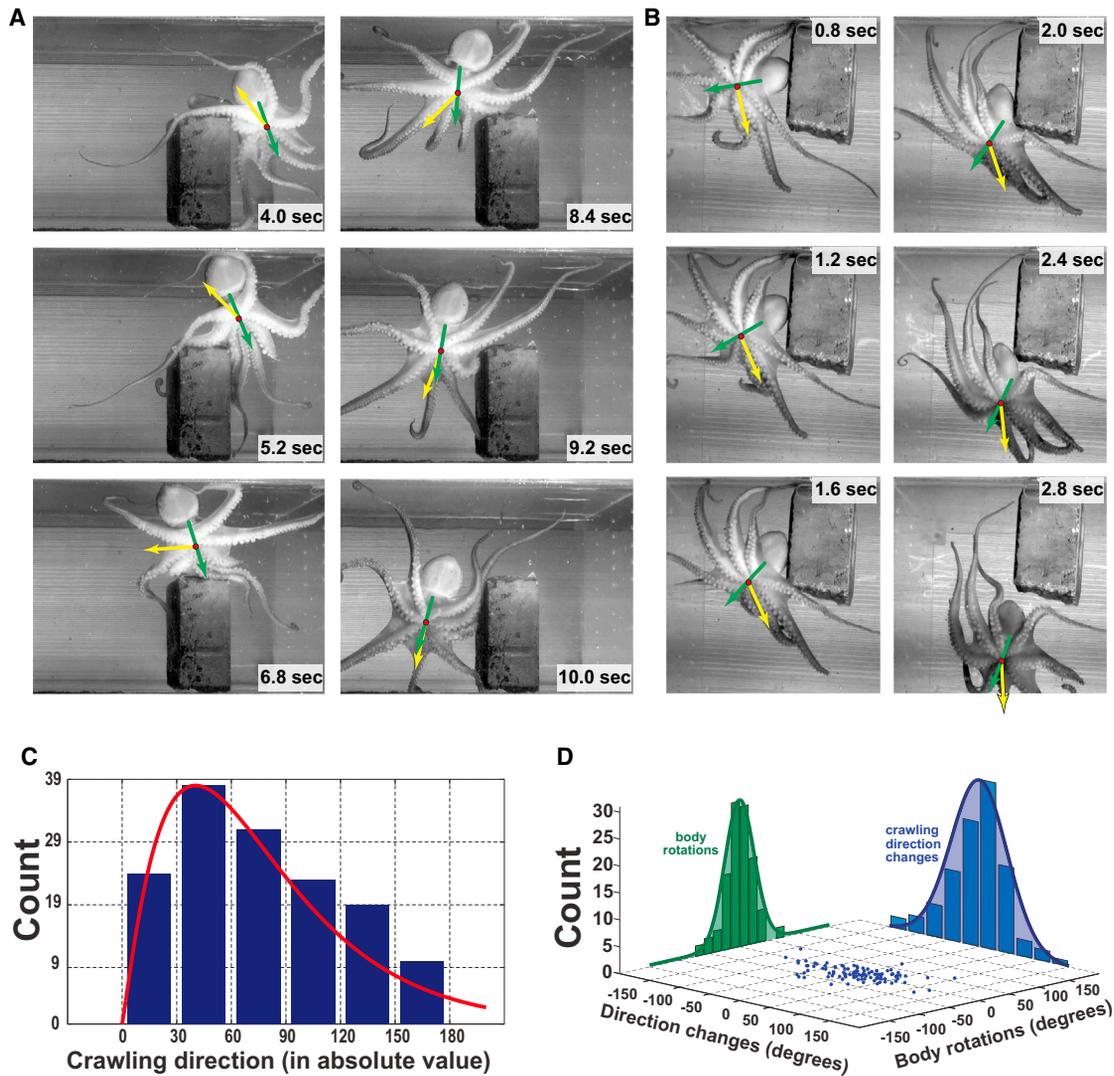
## RESULTS

*Octopus vulgaris*, a member of the bilaterian clade, has a bilaterally symmetrical body plan [6]. Its two eyes and optic lobes are set on the sides of the head, and they are connected to the central brain, which is situated inside a cartilaginous capsule in the center of the head. The mouth of the octopus has a fixed position relative to the brain and thus, also to the head and eye sockets.

As in all modern cephalopods (Coleoidea), the arms emerge close to the mouth in a fixed position and orientation around it (see Figure S1B). The arms can be seen as having a bilaterally symmetrical organization (four on each side) but also as having radial symmetry, as they emerge in a circle around the mouth with a 45° angle between adjacent arms. The morphology of the head [7] prevents its rotation relative to the arms, causing body orientation and facing direction to be the same. The octopus thus differs from animals that have a flexible neck allowing separation between the head and body orientation systems. Therefore, we used the line running between the bases of the four left arms (L1–L4) and the four right arms (R1–R4) as an accurate measurement of the octopus's body and head orientation (the mantle lies on the rear side, Figure S1B; see Supplemental Experimental Procedures). We used positive and negative ranges of 0° to ±180° to describe, respectively, crawling into the right or left hemi-plane relative to the longitudinal axis of the body (see inset in Figure 3). All experiments were carried out according to the regulations of the Hebrew University of Jerusalem (see Supplemental Experimental Procedures for details).

Data from 145 non-consecutive, and thus independent, pairs of video frames showed that octopuses virtually crawled in all directions relative to their body direction with a mean value of approximately zero and a very large variance (mean ± SD was  $-4.8^\circ \pm 88.3^\circ$ ). Negative and positive crawling direction values (to the left or right hemi-plane, respectively) were symmetrically distributed, as the median value was almost precisely zero, and the two-sample Kolmogorov-Smirnov test was also unable to reject the hypothesis of symmetrical distribution ( $p \approx 0.4$ ). The direction was not normally distributed around zero (Lilliefors test,  $p < 0.01$ ), but the absolute value of crawling direction (i.e., between 0° and 180°; Figure 1C) was a skewed  $\Gamma$  (gamma) distribution around a mode value of about 45° (Kolmogorov-Smirnov test  $k \approx 2.13$  and  $\theta \approx 35.68$ ,  $p > 0.2$ ; red line in Figure 1C). This shows that despite the very large variation in crawling direction, overall octopuses preferred crawling in an average direction of ±45° relative to their body orientation.

During crawling, octopuses could monotonically change their crawling direction while maintaining a fixed body orientation (Figure 1A; Movie S1) and vice versa (Figure 1B; Movie S2), suggesting that these two parameters are controlled independently. To test this, we collected data from 100 non-consecutive video frames, and body rotations and changes in crawling direction



**Figure 1. Octopuses Crawl in All Directions Relative to Body Direction**

(A and B) Six time frames from two crawling sequences. Green arrows mark body direction; yellow arrows give the crawling direction.

(C) Histogram showing the absolute values of crawling direction from 145 pairs of time frames with the fitted  $\Gamma$  (gamma) distribution (red line).

(D) Histograms of body rotations (green) and changes in crawling direction (blue) from 100 time frames with the fitted normal distributions. Changes in body direction as a function of changes in crawling direction are shown on the XY plane (blue dots).

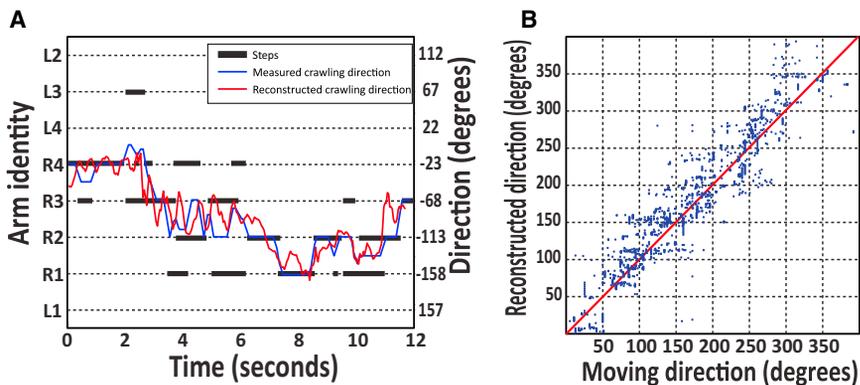
See also [Movies S1](#) and [S2](#).

were calculated over 2.8-s periods. Both parameters were found to be normally distributed around approximately zero (Lilliefors test,  $p > 0.2$  for both; [Figure 1D](#)). However, Pearson's linear correlation test showed no correlation between them ( $\rho \approx 0.12$ ,  $p \approx 0.23$ ), confirming their independence. Body direction (and therefore also facing direction) appeared more stable than crawling direction with respect to the external world ([Figure 1D](#); SD with 95% confidence intervals was  $21.39^\circ$ – $28.30^\circ$  for rotations and  $40.87^\circ$ – $50.08^\circ$  for direction changes).

The biomechanics of crawling is based on stereotypical arm shortening and then elongating movements. This stereotypical arm behavior that pushes the body (described in detail in the [Supplemental Experimental Procedures](#)) involves shortening of a proximal arm segment, followed by a group of suckers

anchoring to the substrate, and then elongation of the proximal segment, thereby generating the pushing thrust to move the body. This movement resembles locomotion patterns in other flexible worm-like animals [8, 9], including other mollusks [9–11]. The independent control of body rotation was achieved by one of two control strategies, both based on the fact that the angle between the base of each arm and the body remained constant, and both are described qualitatively in the [Supplemental Experimental Procedures](#).

We next wished to understand the mechanism enabling the octopus to change its crawling direction smoothly. If arms do indeed push the body mainly by elongation, and if arms pushing simultaneously apply equal forces, then it should be possible to calculate the direction of crawling using the geometrical fact that



**Figure 2. Arms Push the Body Only by Elongating and Apply Equal Pushing Forces when Working Together**

(A) Stepping record of a  $\sim 12$ -s movement. Arm identities are given on the left and their fixed pushing direction on the right. The measured (blue) and predicted (red) crawling directions in body orientation coordinates are superimposed. (B) Reconstructed crawling direction (y axis) and measured crawling direction (x axis) taken from 1,636 time frames (Pearson linear correlation test values:  $\rho \approx 0.94$ ,  $p < 0.001$ ). See also [Figure S2](#).

each arm has a fixed pushing direction, which is dictated by its position on the body (see inset in [Figures 3](#) and [S1B](#)). Thus, the predicted crawling direction was calculated as the simple (weightless) vectorial summation of the pushing arms. [Figure 2A](#) shows the stepping record of a continuous crawl of about 12 s, with the time intervals during which each arm actively participated in the pushing. The identity of each arm is given on the left axis, and its predefined pushing direction is also shown in the same graph (right axis). The superposition of the predicted (red) and measured (blue) crawling direction shows the high level of precision of this reconstructed crawling direction. This confirmed our assumption that the arms push only by elongating and arms that push together apply equal forces. The direction of crawling is therefore determined simply by the identity of the pushing arms. The highly significant correlation ([Figure 2B](#)) between the reconstructed and the measured crawling direction from 1,636 time frames (Pearson's linear correlation test,  $\rho \approx 0.94$ ,  $p < 0.001$ ) conclusively supports our hypothesis.

[Figure 3A](#) demonstrates that octopuses generally prefer to use some arms over others in crawling (the test for significance of these preferences is detailed in [Supplemental Experimental Procedures](#)). More specifically, octopuses showed preference for pushing with the four hind arms and a rather small but significant preference for using the third arm over the fourth on each side. Measuring the frequency of using specific pairs of arms ([Figure 3B](#) and statistical analysis in [Supplemental Experimental Procedures](#)) also revealed a general preference for using specific pairs of arms, particularly for pushing with the third arm together with the fourth arm on the same side of the body or the second arm on one side together with the fourth arm on the other side. Both types of coupling arm pairs fit the distribution of crawling direction around  $\pm 45^\circ$  ([Figure 1C](#)), providing additional and independent support for the idea that the identity of the active arms is what determines the crawling direction. This idea is further supported by the finding that L4 + R4 activation, which would result in forward crawling, was less significant than the combinations that would result in the preferred  $\pm 45^\circ$  crawling direction ([Figure 3](#), and see statistical analysis in [Supplemental Experimental Procedures](#)).

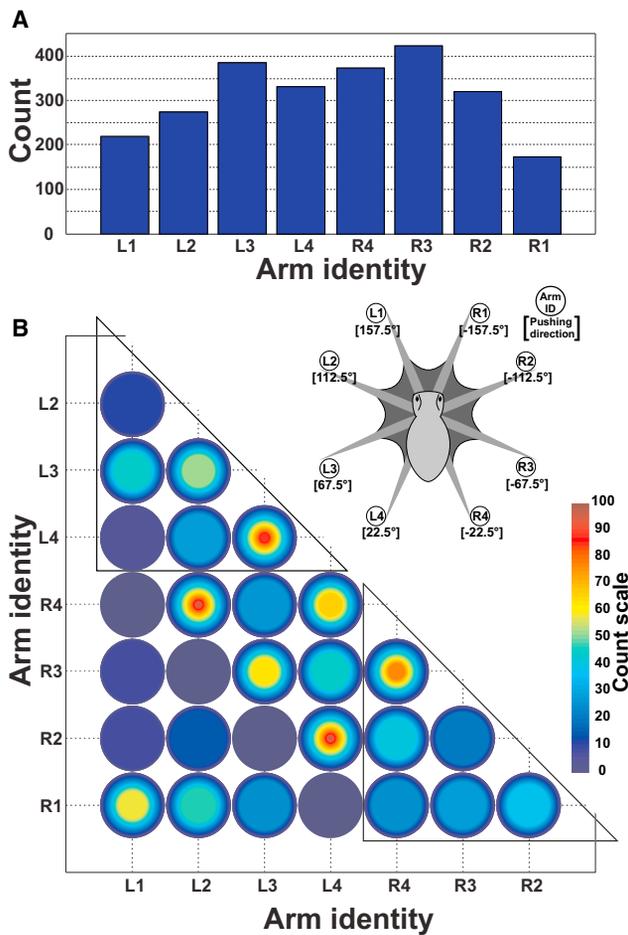
We next analyzed the pattern of arm recruitment in crawling. Inspection of octopus stepping records like those in [Figures 2A](#) and [4A1–4A4](#) suggested that although the arms may have some independent rhythmical repetitive patterns (e.g., traces of arms L2, L3, and R4 in [Figure 4A1](#) and arms L4 and R3 in [Fig-](#)

[ure 4A3](#)), the coordination between the arms lacked any obvious rhythmical pattern. This lack of a clear rhythmical pattern is especially highlighted when compared with examples of the stepping records of locomotion in other animals, such as walking in stick insects and in *Drosophila* ([Figures S3A2](#) and [S3A1](#), based on [12] and [13], respectively). Intrinsic rhythmical repetitive patterns of locomotion can be easily detected in the records of the insect stepping movements. This contrasts sharply to the four examples of stepping records of the octopus crawling movements in [Figures 4A1–4A4](#), which show what seems to be “erratic,” unorganized stepping.

To look for possible hidden rhythmicities in arm coordination in octopus crawling, we analyzed the instantaneous crawling velocity (i.e., mouth velocity) (superimposed on the stepping records in [Figures 4A1–4A4](#), blue) and used fast Fourier transform (FFT) to extract power spectra of the frequencies from each of these velocity profiles ([Figures 4B1–4B4](#)). No dominant frequencies could be found in any of the velocity profiles; the FFT analysis showed several dominant frequencies that merely reflected the frequencies related to the time of the entire movement (or one-half or one-third of it). No clear pattern was found in arm recruitment even when octopuses crawled on a straight path (e.g., [Figures 4A1](#), [4A2](#), [4B1](#), and [4B2](#)), suggesting that the erratic order is not associated with the changing of crawling direction. Applying a similar FFT technique to the velocity profiles of the walking stick insect and *Drosophila* extracted a single clear and dominant frequency for each ([Figure S3](#)). This confirmed both that in each of these species, a single dominant frequency is present in its velocity profile and that it could be extracted by FFT.

In further searching for an organized temporal pattern in octopus crawling, we collected the step durations from 12 continuous movements and normalized them to the average velocity of the movement. Then we examined the output sequence using the extended distribution free version of the Wald-Wolfowitz runs test [14], described in [15] (details about this test are given in [Supplemental Experimental Procedures](#)). The sequence was found to be random (number of runs: 48  $z = -1.0348$ ,  $p = 0.3008$ ). Applying the same procedure to the data from the *Drosophila* and stick insect showed lack of randomness in their stepping (see [Supplemental Experimental Procedures](#)).

Therefore, failure of the FFT to extract dominant frequencies from octopus crawling records together with the randomness of step duration suggest that arm coordination in octopus crawling may involve mechanisms that are different from the



**Figure 3. Distribution of Arm Usage during Crawling**

(A) Histogram showing the distribution of arm usage in pushing (2,506 time frames). Arm identity is given below each bar.

(B) Graphical pseudo-3D (truncated cone from above) depiction of the distribution of pairs of arms used together in pushing (980 time frames). The frequency color scale is given on the right (from blue up to red). The upper left triangle marks pairs of arms from the left side of the body, the lower right triangle marks pairs of arms from the right side of the body, and the remainders are pairs where one arm is from the right side and the other is from the left side of the body. Note that the pairs used most frequently together give a crawling direction of  $45^\circ$ .

The inset identifies the arms and gives their pushing direction relative to the body.

See also Figure S1.

conventional central pattern generator (CPG)-driven rhythmicities involved in locomotion of other animals [16–18]. The runs test rejected the hypothesis of randomness in the spatial pattern of multiple arm recruitment during octopus crawling, showing that not all aspects in the crawling are random, as would be expected since the animal succeeds in crawling in a non-random (desired) direction after all.

## DISCUSSION

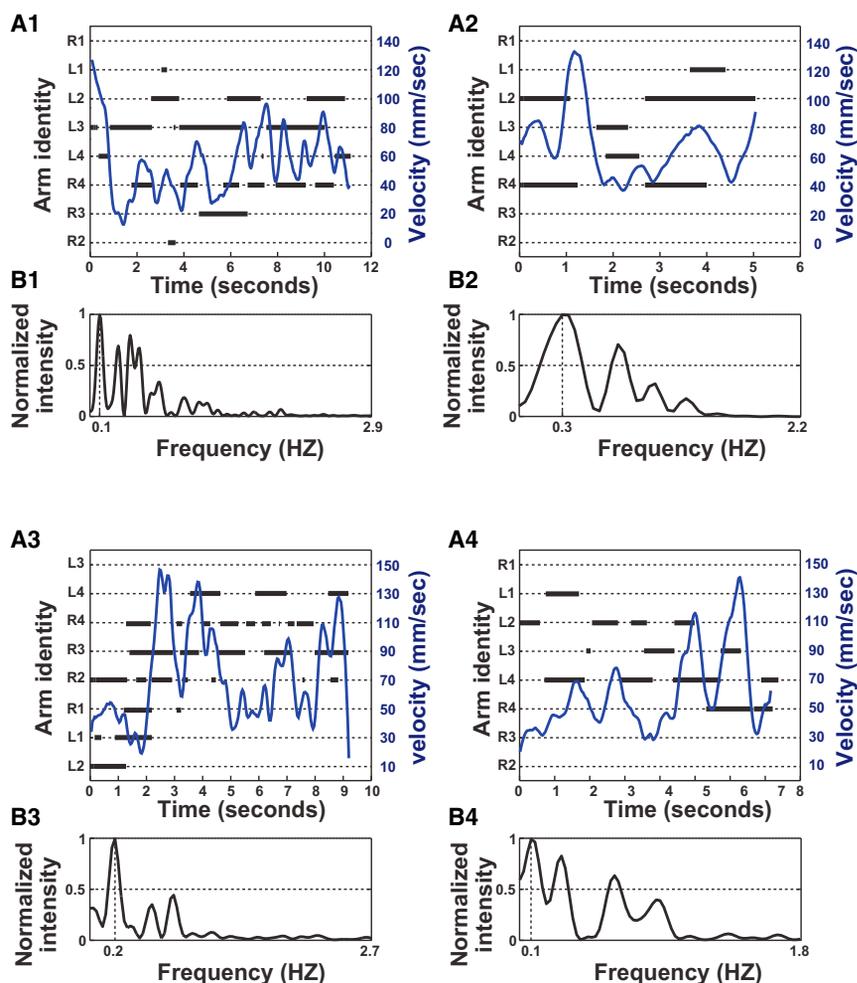
The flexible body and arms of the octopus are bilaterally symmetrical, but the arms are also distributed with a fixed radial sym-

metry around the mouth. Radially organized animals (e.g., adult starfish and brittle stars) can crawl in any direction relative to their body orientation [19, 20]. The radial distribution of the arms provides the octopus with the same physical ability. Yet, what we have found here shows that unlike the brittle star and like other animals with bilateral body organization, the octopus still coordinates crawling direction with its body orientation in order to control the direction of its sensing and feeding apparatuses relative to the environment.

Several aspects of octopus vision and body plan may explain why the preferred average crawling direction is  $\pm 45^\circ$  relative to its body orientation (Figure 1C). The octopus eye lacks a fovea centralis, having instead a central horizontal strip which may emphasize vision along the horizontal axis of each eye [21]. Therefore, despite the absence of head rotations and only limited eye movements relative to the body [7, 21, 22], the horizontal field of vision of each eye covers roughly  $180^\circ$  with virtually zero intersection. We speculate that octopuses prefer not to crawl forward or backward ( $0^\circ$  or  $180^\circ$ , respectively) relative to the body direction because this would place the target at the border line of the visual fields of the two eyes. The preferred average crawling direction of the octopus ( $\pm 45^\circ$ ) fits the generalization that most animals with bilateral symmetry move in the direction (not necessarily parallel to body orientation) in which the sensory systems can function effectively [6]. However, in the octopus, the deviation around this preferred direction of locomotion is very large. As explained above, this may be due to the fact that the field of vision is largely independent of body orientation. This relaxes the tight relationship between vision and the direction of locomotion, enabling the octopus to change its body orientation (Figure 1D) and still follow a target.

The stereotypical pushing-by-elongation mechanism simplifies the control of crawling because as in goal-directed arm movements, it can be generated by a simple peripheral motor program, thus freeing the central control from the complex task of directly controlling arm behavior [4, 23]. Elongation in muscular-hydrostatic structures like the octopus arm [24, 25] may be achieved by a rather simple command of a global simultaneous activation of the transverse muscles relative to the longitudinal muscles ([26] and S. Hanassy, A. Botvinnik, T.F., and B.H., unpublished data). This type of motor program fits the special distribution of control between the  $\sim 170$  million neurons in the central brain (together with the optic lobes), and the  $\sim 330$  million neurons in the elaborate and rather autonomous peripheral nervous systems of the arms [4, 5]. For example, the octopus reaching movement has only three adjustable degrees of freedom (df) [1] and can be generated in amputated arms [2], suggesting that central commands are necessary only to activate and scale peripheral motor programs (i.e., motor primitives [2, 27]). It is conceivable that the pushing by elongation is also a motor primitive generated by a predefined motor program that is embedded in the peripheral nervous system of the arms.

The fact that all recruited arms generate similar thrust forces further simplifies the control because the ratio between the forces doesn't need to be considered. This allows a feedforward type of crawling control, where the controlled variable is simply which arms to recruit. Such a simplification has already been demonstrated in the octopus reaching movement, where arms that are extended together have similar velocity profiles,



**Figure 4. Lack of Stepping Pattern in Octopus Crawling**

(A1–A4) Examples of stepping records from different crawling octopuses. Each horizontal dashed line represents one arm (arm identity on the left), with accentuated parts indicating when this arm actively participated in the movement. The instantaneous mouth velocity is superimposed in blue (with respect to the right axis).

(B1–B4) The normalized frequency spectrum extracted from the velocity in the panel above it (shown in A1–A4, respectively) by the fast Fourier transform (FFT). Note the absence of any characteristic frequency peak.

See also Figure S3.

In summary, we believe that our findings provide a striking demonstration of the emergence of special control mechanisms well embodied within the unique morphology and flexibility of the octopus. This is because our results suggest that the special maneuverability of the octopus in crawling emerges from the radially symmetrical distribution of the eight arms around the body and the stereotypical arm pushing movements used for creating the thrust in crawling. These two properties enable the reduction of the complexity involved in the control of motion in a hyper-redundant body to only few controlled variables—the arms identity. Our results also support the embodied-organization concept of adaptive behaviors (in the

suggesting they are controlled together by a single central motor command [1].

Can the morphology and the biomechanics explain the unusual arm coordination in crawling? It is widely accepted that locomotion patterns, both in vertebrates and invertebrates, are driven by dedicated neural circuits that function as CPGs, which generate a repetitive rhythmical pattern of motor output [16, 17, 28–31]. The fact that we could not find any rhythmical temporal pattern in arm recruitment in octopus crawling raises the intriguing possibility that contrasting locomotion in other animals, the central control of octopus crawling generates a complex temporal pattern that is hard to detect (at least with our techniques) or perhaps does not exist at all. We suggest that a *central command generator* of crawling exists in the motor centers of the octopus brain and directly commands what appears to be ad hoc or moment-to-moment recruitment of octopus arms for instantaneously controlling the direction of crawling, similar to the generation of saccadic eye movements by the superior colliculus [32–34]. The analogy between saccadic eye movements and moment-to-moment control of octopus crawling raises the possibility that the octopus uses body motions like “body saccades” (that were shown to exist in other animals [35]), which result in a controlled motion of the visual image on the octopus retina, a stage that is likely to be important for the processing of visual information [36].

general sense, not only in octopuses) [4, 5, 37], as they show the marvelously reciprocal interaction between the control system, the physical properties of the body, and the morphology, an interaction that leads to an evolutionary successful adaptation of the emerging behavior to the ecological niche.

#### SUPPLEMENTAL INFORMATION

Supplemental Information includes Supplemental Experimental Procedures, three figures, one table, and two movies and can be found with this article online at <http://dx.doi.org/10.1016/j.cub.2015.02.064>.

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