Stereotypical reaching movements of the octopus involve both bend propagation and arm elongation

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Abstract

The bend propagation involved in the stereotypical reaching movement of the octopus arm has been extensively studied. While these studies have analyzed the kinematics of bend propagation along the arm during its extension, possible length changes have been ignored. Here, the elongation profiles of the reaching movements of Octopus vulgaris were assessed using three-dimensional reconstructions. The analysis revealed that, in addition to bend propagation, arm extension movements involve elongation of the proximal part of the arm, i.e., the section from the base of the arm to the propagating bend. The elongations are quite substantial and highly variable, ranging from an average strain along the arm of $-0.12$ (i.e. shortening) up to $1.8$ at the end of the movement ($0.57 \pm 0.41$, $n = 64$ movements, four animals). Less variability was discovered in an additional set of experiments on reaching movements ($0.64 \pm 0.28$, $n = 30$ movements, two animals), where target and octopus positions were kept more stationary. Visual observation and subsequent kinematic analysis suggest that the reaching movements can be broadly segregated into two groups. The first group involves bend propagation beginning at the base of the arm and propagating towards the arm tip. In the second, the bend is formed or present more distally and reaching is achieved mainly by elongation and straightening of the segment proximal to the bend. Only in the second type of movements is elongation significantly positively correlated with the distance of the bend from the target. We suggest that reaching towards a target is generated by a combination of both propagation of a bend along the arm and arm elongation. These two motor primitives may be combined to create a broad spectrum of reaching movements. The dynamical model, which recapitulates the biomechanics of the octopus muscular hydrostatic arm, suggests that achieving the observed elongation requires an extremely low ratio of longitudinal to transverse muscle force ($<0.0016$ for an average strain along the arm of around $0.5$). This was not observed and moreover such extremely low value does not seem to be physiologically possible. Hence the assumptions made in applying the dynamic model to behaviors such as static arm stiffening that leads to arm extension through bend propagation and the patterns of activation used to simulate such behaviors should be modified to account for movements combining bend propagation and arm elongation.

Introduction

Octopuses and their relatives, squids and cuttlefish, belong to the group of modern Cephalopoda (Coleoidea), whose eight flexible arms are unique among mollusks (Hochner 2012). These constitute a highly redundant biomechanical structure which has virtually an infinite number of degrees of freedom (DOF). The adaptability, dexterity and maneuverability of octopus arms have attracted considerable attention from robotic engineers as source of inspiration for designing and constructing a new class of flexible robotic arms (Hochner 2012, Margheri et al 2012).
The octopus arm is a ‘muscular hydrostat’ (MH), belonging to a group of organs lacking skeletal support and almost entirely comprised of muscle cells. In such structures the muscle itself is responsible for both support and movement (like the tongues of many terrestrial vertebrates, the appendages of cephalopod mollusks and the elephant trunk (Kier and Kathleen 1985)). The most important biomechanical feature of the MH is that it maintains a constant volume, since muscle cells are composed primarily of an aqueous liquid, which is practically incompressible at physiological pressure (Kier and Kathleen 1985). In structures that maintain a constant volume, any change in one dimension causes a compensatory change in at least one other dimension. In the octopus arm, the typical MH structure consists of a densely packed three-dimensional (3D) arrangement of muscle fibers (transverse muscle fibers, longitudinal muscle fibers, helical or oblique muscle fibers) and connective tissue fibers surrounding a central axial nerve cord (figure 1;(Kier and Stella 2007, Feinstein et al 2011)).

Octopus movements (in the article we use the term ‘movement’ to describe a set of motions that are related to behavior like reaching movement and fetching movement) may be highly localized, as in searching movements, or may involve the entire length of the arm, for example in goal-directed movements like reaching (Gutfreund et al 1996) and fetching (Sumbre et al 2006). Therefore octopus arm movements provide an outstanding example of efficient movement control of a hyperredundant structure. Hyperredundancy makes the inverse kinematics a very complex process (Bizzi et al 1991, Flanders and Hermann 1992). Ignoring length changes, intensive analysis of the octopus’ reaching and fetching movements has shown that the octopus uses a stereotypical behavior. For example, stereotypical reaching is determined practically by three parameters, namely, pitch, yaw and the velocity of the bend point propagation (a point of maximal curvature along the arm), while in general the arm has an infinite number of DOF (Gutfreund et al 1996, 1998). This dramatically simplifies the motor control of a hyperredundant MH.

Previous work has shown that in the reaching movement a bend is formed somewhere along the arm and is then propagated toward the tip. In this stereotypical behavior the bend in the arm serves as the controlled end-effector (similar to our hand). This point has the highest curvature along the arm and therefore could be easily detected (Gutfreund et al 1996, Gutfreund et al 2006). Similar bend propagation is found in other behaviors involving arm extension, a term which was originally used in Gutfreund et al (2006) to describe a fundamental component in various behaviors of octopus, such as locomotion, searching, and reaching toward a target. In all of those cases, the arm is extended in what seems to be a stereotyped and robust pattern.

The kinematics of reaching movements were evaluated by measuring the trajectories of the maximal curvature of a propagating bend (bend point). The bend tends to move within a single plane in a simple, slightly curved path connecting the center of the animal’s body with the target location. This behavior is observed in spontaneous unconstrained movements and in goal-directed movements. Normalizing the velocity ($v(t)$) profiles and the time ($t$) according to the maximum velocity ($v_{\text{max}}$) and the distance ($d$) traveled by the bend revealed an invariant velocity profile of the bend point associated with the acceleration phase of the reaching. Here, the term ‘invariant’ refers to the shape of the velocity profile which looks similar in most of the reaching movements when the velocity is normalized with respect to duration and maximal velocity (see appendix A.1, Gutfreund et al 1996).

Arm extension comprises three phases, an initiation phase prior to extension, an invariant monotonically increasing extension phase and a third descending phase corresponding to the end of the movement (see figure 4; appendix A.1). These phases were interpreted as indicating the existence of an invariant motor program scaled for each movement (Gutfreund et al 1996). The inverse dynamics of reaching movement was studied by correlating the kinematic parameters with EMG recordings. This showed that the motor program for reaching has feed-forward characteristics (Gutfreund et al 1998, 2006, Sumbre 2004). Moreover, it was found that the motor program is embedded in the neuromuscular system of the
arm, since it is possible to induce extension movement in arms whose connection with the central brain has been severed (Sumbre et al 2001a, 2001b).

Because bend propagation along the arm is the main characteristic of arm extension, this feature was used as an end-point in defining reaching movements (for example, distinguishing between extension and sickle-like or opening movements where the bend does not propagate far along the arm; Sumbre et al 2001a, 2001b, Yekutieli et al 2005a, 2005b). A wave of muscle activation propagating along the arm to create stiffening that pushes the bend forward was suggested as a simple mechanism to explain arm extension. When this idea was tested in a dynamical model of the octopus arm, the natural behavior could be replicated (Yekutieli et al 2005a, 2005b).

For simplicity and because of biological plausibility, it was assumed that similar activation of all muscle groups of the arm causes stiffening without changing the arm shape (length/width) due to constant volume constraint (Yekutieli et al 2005a, 2005b, Matzner et al 2000, Feinstein et al 2011). However, arm length was not measured in these studies, preventing testing whether arm extension is also mediated by changing the arm length. When inserting an arm into a tube octopuses can elongate their arms 70% from rest length (Margheri et al 2011, Mazzolai et al 2013). Therefore, in the current study we developed and used a 3D reconstruction technique for analyzing the reaching movements of the Octopus vulgaris. This allowed measuring the kinematics of length changes involving arm extension movements together with the kinematics of the bend point. The results suggest that reaching movements are achieved through variable combinations of bend propagation and arm elongation. We attempted to correlate these two motions to more accurately define the mechanisms of arm extension.

Materials and methods

The experimental animals

Specimens of Octopus vulgaris were caught off the Mediterranean shore by local fishermen. The animals were maintained in 50 × 40 × 40 cm tanks containing artificial seawater. This was continuously circulated in a closed system through a biological filter of Orlon, gravel and coral dust and protein skimmer. Water temperature was held at 17–19 °C in a 12 h light/dark cycle. Four animals weighing 200, 200, 450 and 470 g were used for this study. The data of one of the animals (Octopus A, 470 g) was taken from a previous experiment (Sumbre 2004, unpublished data) carried out in the same experimental environment.

Prior to the video recording sessions, the animals were moved to a larger glass tank (80 × 80 × 60 cm) with a water temperature of 18 °C, except for Octopus S (200 g) which was recorded in the same smaller tank in which it was maintained. Video recordings began only after the animals were well acclimatized to the new tank after several days.

The behavioral task and video recordings

The task started when a target, a green disk of 2 cm diameter or a dummy crab, both with a small weight attached (figure 5, green circle), was lowered into the water. The target was moved slightly to attract the octopus’ attention. The octopus either extended one or more arms or swam towards the target. Every few trials the animal was rewarded with a piece of shrimp meat, not attached to the target, as in Pavlovian classical conditioning.

Two digital video DV cameras (Panasonic AG-DVC30E camcorder) recorded the octopus arm movements. The cameras viewed the subject from the same aquarium face but with an angle of 50–60° between the principal rays, as suggested by Yekutieli et al (2007). Shutter speed of both cameras was set to 1/120. The PAL S-VHS video system was used, allowing a temporal resolution of 20 ms between adjacent images. To achieve this resolution, we used the PAL video system at 25 frames/s with image resolution of 720 × 576. Each frame is composed of two interlaced fields (half images that are composed either of the odd horizontal lines or the even horizontal lines). After retrieving the two fields, each was interpolated into a full-sized frame, achieving time resolution of 50 images/s. The data were later downloaded to a standard PC computer using Adobe Premier (1.5) software and a FireWire connection (IEEE 1394).

Trials in which the octopus extended its arm/s toward the target were termed 'successful trials', regardless of whether it actually touched the target. Successive video images of successful trials were captured from both cameras, digitized with the Adobe Premiere environment and saved on hard disk.

The computer environment for 3D reconstruction and analysis of octopus arm movements

A dedicated computer program was developed to manage and instantly create a database of movement reconstructions and analysis results from movements captured on video files. Using this system, 64 of 71 reaching movements were successfully reconstructed. This computer program, developed using Matlab (version 7.1), implements the previously developed methods for reconstruction of the 3D backbone curves of octopus arms in motion described in detail in Yekutieli et al (2007) with some further improvements. We now briefly describe the process of reconstruction and consider several main issues.

Similarly to Yekutieli et al (2007) the system we developed takes the following steps to achieve reconstruction

- camera synchronization
camera calibration

- movement recording using two cameras in a stereo configuration
- for each video frame, the method involves:
  1. manual (by eye) tracking of a marked starting point along the arm instead of automatic registration as described in figure 3.6 in Yekutieli et al (2007).
  2. Manual tracking of the contour of the arms from base to tip in the two views.
  3. Automatic extraction of the two-dimensional (2D) midline (the backbone) of each contour.
  4. Temporal and spatial spline smoothing of the results separately for each view point (a new feature added here).
  5. Matching the two 2D midlines using epipolar geometry.
  6. 3D reconstruction.
  8. Temporal and spatial spline smoothing of the 3D reconstructed results (a new feature added here).

After camera synchronization the times for both viewpoints were synchronized. In the second step of the algorithm, the direct linear transformation matrices representing the model for the camera’s projection from 3D space onto 2D images were calculated separately for each camera. This was achieved using the markings (by eye) and the predetermined calibration model in the calibration process described below.

We used the same simple pinhole camera model commonly used in computer vision for perspective projection as described in Yekutieli et al (2007). Each camera had 11 parameters defining its position and orientation, as well as optical characteristics, such as focal length, x−y ratio, and image center.

The following notation is used throughout. Using homogeneous coordinates, a 3D point \( q \) is represented by \((x, y, z, 1)^T\) and a 2D point \( p \) by \((x, y, 1)^T\). A 2D line satisfying the equation \( ax + by + c = 0 \) is described by the vector that includes its parameters \((a, b, c)^T\). A 3D point \( q \) is projected onto a 2D point \( p \) on the image plane by the projection equation

\[
p = Mq.
\]

The camera projection matrix \( M \) is a 3 × 4 matrix defined up to a scale factor. The elements of \( M \) are the 11 parameters of the pinhole camera model.

Calibration is the process of determining these 11 parameters for each camera. First, both cameras recorded a 3D object with known geometry—the calibration cube. This object must have at least six points that are clearly visible and detectable at the two views. Then, the 2D position of each of these points was marked in each view by eye. A least-square procedure estimated the camera parameters so that the viewed 2D points fitted the known 3D geometry (Abdel-Aziz and Karara 1971, Cipolla and Giblin 2000). The calibration frame was that used by Yekutieli et al (2007). Marking was manual with subpixel precision using a dedicated graphical user interface (GUI). Before calibration, the relative position of the center of each white dot should be known with submillimeter precision. These data for the calibration body were obtained from Yekutieli et al (2007). After calibration, it is possible to reconstruct the position of a 3D point from its projections using the direct linear transform (DLT) procedure (Yekutieli et al 2007). The space that the calibration frame occupies is referred to as the calibrated space and points outside this space have higher reconstruction errors. Therefore, to find the projection matrices of the two cameras images as described above, a calibration body was introduced and moved in the area where the behavior took place.

To reconstruct the movements, successive video frames of reaching movements were digitized and displayed in the system GUI. For each reaching movement the beginning of the movement was defined as the time at which the generated bend in the extended arm started to move in space, and the end was determined by the time the bend reached the target or the arm stopped moving.

To reconstruct the backbone curve (BBC) at each time frame, the contours of the arm were manually labeled and digitized and the 2D midlines were automatically extracted. Errors in length measurements are highly affected by errors in the alignment process between BBC indexes at different times. To reduce such errors we relied on a manual alignment of the first marking points. This could, for example, be a sucker close to the base of the arm or an obvious pattern, which could be seen clearly on the two views during the entire duration of the movement.

From the pair of 2D midlines, a 3D BBC was reconstructed using the DLT algorithm. During this process the cubic spline-smoothing method (CSS, appendix A.3) was separately applied to 2D and 3D reconstructed curves to reduce the spatial noise. In addition, temporal noise was smoothed by applying the CSS method to data points of matching indexes, assuming that the interval between two consecutive frames was short enough and therefore the local length change (i.e., the distance between two adjacent data points) between two frames pairs \( i \) and \( i + 1 \) was relatively small, \(~2\sim5\ mm\) (figure 2 gives an example of smoothing results applied to the 2D marked curves). For temporal smoothing, the reconstructed BBC were divided into 200 equal length segments separated by points and for each point an index was given which was used for applying the CSS method over time.

The reconstructed and smoothed 3D midlines were inspected by eye using the dedicated interface.
Figure 2. The spline smoothing method. (A)–(B) Example of smoothed single curves using the spline smoothing method on 2D marked curves for the left (A) and right view points (B). The original marking results are given by the black dotted curve, the red curve shows the results of applying spline smoothing to the dotted curve, the green line shows the curve after applying the smoothing method to all curves over time. (C)–(D) An example of consecutive midlines marked in a single movement. (E)–(F) Results of the spline smoothing method applied separately to each consecutive curve. Colors mark the data points from (C)–(D) that were smoothed together using the spline smoothing method (i.e., along the curves). (G)–(H) Results of the spline smoothing method applied to the curves over time. Colors mark the data points from (E)–(F) that were smoothed together using the spline smoothing method (i.e., over time), and the curves which the spline curves approximated. (A), (C), (E) and (G) show the left POV and (B), (D), (F) and (H) the right POV.
Movement sequences containing too many errors (more than 8% of unreconstructed frames or a time domain longer than three frames) were excluded from further analysis (seven movements). In the remaining movements with only short error sequences in data points or mistakes in reconstruction (not more then 8%), CSS was used to interpolate the erroneous section. To maintain uniform continuation of the curves, CSS was applied to the whole 3D sequence again after the interpolation.

The trajectory of the bend point position in space was reconstructed directly from the markings of the bend point by eye, in successive video frames, as two point of view (POV) pairs, in 2D using the DLT algorithm. These points were determined, by eye, as the point of intersection of the bend-point propagating trajectory (estimated from the points of maximal curvature in adjacent frames) and the reconstructed arm midline (figure 5(B)) and were marked manually, recorded and stored. While reaching movement could involve body motion toward the target, rotation of the body was negligible, therefore, to correct for whole body movements, the origin of the coordinate system was fixed at one of the animal’s eyes, which has a fixed position in the octopus body, and was marked manually with the mouse cursor. The coordinates of this points were also recorded.

Similar to the procedure used by (Gutfreund et al. 1996), these data were used for the analysis of the kinematic features of the bend point motion using the DLT algorithm. From this set of data the trajectory of the bend point relative to one of the eyes was then derived through vector subtraction of the eye 3D location coordinate’s vector from those of the bend point location coordinates’ vector. Thus, the trajectory of the bend-point in space was defined in a coordinate system relative to the animal’s body. The data were first smoothed by applying a CSS (see above and appendix A.3) to the reconstructed 3D points on the x-axis, y-axis and z-axis as a function of time. The tangential velocity of the bend point propagation in 3D was calculated from the derivatives of the smoothed

\[
\mathbf{q} = (x, y, z, 1)^T.
\]

We could thus measure the 3D trajectories of the bend point motion in space.

Finally, the positions of the suckers along the reconstructed midlines were estimated in four movements by projecting the 2D position of manually labeled suckers onto the 3D reconstructed midlines using the DLT method. This was achieved technically by intersecting the 3D line satisfying the linear equation \(ax + by + cz + d = 0\), described by the vector that includes its parameters \(\mathbf{r} = (a, b, c, d)^T\) which refers to the principle ray of the projection from 3D space to a 2D point \(\mathbf{p}\) marked on each sucker point, extracted from the DLT model and the 3D reconstructed midline backbone, i.e., by finding a point \(\mathbf{q}\) on the backbone which solved

\[
\mathbf{r}'\mathbf{q} = 0.
\]

We estimated \(\mathbf{q}\) by choosing the point on the backbone which minimized

\[
|\mathbf{r}'\mathbf{q}|.
\]

**Arm length and elongation velocity profiles**

The length of the arm was measured from the reconstructed 3D BBC. Each BBC was digitized into external \(x\ y\ z\) coordinates indexed from the base of the arm to the tip, ensuring that incremental indexes indicated adjacent points along the arm. Considering that, the length of the arm was calculated from the curves using:

\[
l_i = \text{length}(t) = \sum_i \|\mathbf{x}_i(i + 1) - \mathbf{x}_i(i)\|,
\]

where \(\mathbf{x}_i(i + 1)\) (i.e. bolded \(\mathbf{x}\)) describes a vector \((x, y, z)\) with values of the external coordinates of the indexed backbone point sequence at time \(t\) with index \(i\) along the BBC \((0 < i \leq n)\), where \(n\) is the number of points along the BBC, in which \(0\) denotes the first base point and \(n\) denotes the tip point. \(n = 200\) points and therefore there are 199 segments).

The elongation velocity was estimated using the discrete estimation of the length derivative with respect to time, denoted by:

\[
\text{ve}(t) = \frac{\Delta l_i}{\Delta t} = \frac{l_{i+1} - l_i}{0.02}.
\]

where \(l_{i+1}\) is the length of the arm at the next interval, \(\Delta t = 0.02\) s (the time resolution of the cameras) and \(t\) is a multiple of \(\Delta t\).

To measure the changes in length of the distal or proximal part of the arm at time interval \(t\), we first determined the bend location along the BBC by finding \(i_{\text{min}}\) which minimized the Euclidean distance between its BBC coordinates and the bend point coordinates at time interval \(t\):

\[
i_{\text{min}} = \arg \min_i \|\mathbf{b}_i - \mathbf{x}_i(i)\|, \tag{4}
\]

where \(\mathbf{b}_i\) is an \((x, y, z)\) external coordinate of the bend point at time \(t\) determined in the dedicated reconstruction procedure described above. Since the Euclidean distance between two adjacent BBC index points was small compared to the total length of the arm, the error using this method was negligible.

To acquire the elongation profile of the arm distal to the bend, the length of the distal part of the arm was measured with equation (3) using equation (4) to determine the first index point of the distal part. The same procedure acquired the elongation profile of the segment proximal to the bend.

The reconstruction and methods for measuring length were tested with different types of bent and flexible objects of lengths ranging from 5 to 50 cm. The reconstruction length errors in all reconstructions were negligible (below 4 mm and 0.75% of the length of the reconstructed object). Figure 3 shows...
an example of a dummy arm used to test the method for length measurement. The reconstructed length of the dummy, in this example, was 43.69 ± 0.45 (mean ± SD; \( n = 14 \)) and was significantly close (−0.31 cm) to its true length of 44 cm (\( p < 0.01 \); paired t-test; figure 3).

Appendix A.4 gives further information on the error in measurement of arm lengthening.

The envelope of the movement midlines
Creating the BBC envelope of the movement is a new graphical method we developed to describe a whole 3D movement pattern of an elongated organ in a single image. The trajectory, lengthening, velocity and other important kinematic parameters could be visualized using a variety of colors and the shapes created by the envelope. The envelope was created through a sampling function (Matlab’s grid data function), which took the midline backbone points as the sampled data point input and connected them to create a mesh or grid of heights. The 3D form thus created was defined as the envelope of the movement. The BBC were colored differently from the envelope and were plotted over the envelopes. The plot was created by Meshgrid (Matlab function, figure 5(A)).

T-test and paired t-test
We used Matlab’s function ‘t-test’ for hypothesis testing on single sample means to compare elongation and other kinematics measurement values in different times and conditions. Here the null hypothesis (mean is zero) was rejected if \( p < 0.05 \). A paired t-test compared different pairs of values when the sample group had several values per observation. The paired difference column of the two different value columns was applied as the input for the Matlab function. The rejection criteria were as described for the single t-test.

A computerized model of the octopus arm
To predict the patterns of muscle activation underlying arm elongation, simulations were carried out with minor modifications on a model of the octopus arm described in detail in (Yekutieli et al 2005a, 2005b). In that article several experiments and computational modeling were described in order to explain the relevance of that model for the simulations of an octopus arm and its musculature. Briefly, the model arm is divided into 20 segments, each segment being composed of four point masses connected by a single system containing a spring and a damper in parallel, representing the muscles (two longitudinal and one transverse; see figure 9 for several arm model drawings). Several forces act on the point masses. Gravity and buoyancy act vertically. Water drag forces act in opposition to movement. Two types of drag forces are considered—normal and the tangential drag. These forces, together with the masses and the acceleration, give rise to the equation of motion of the system. Accelerations were calculated from the forces and the masses. Then, numerical integrations were used to calculate the position of the masses based on their position in the previous time step. The inputs to the model were the initial form of the arm and the type of activation of the muscles. The results were the variations in time of the arm’s form.

In the simulations, similarly to Yekutieli et al (2005a, 2005b), input to the model (analogous to a neural command) was changed by changing the activation amplitude and the activation traveling time, keeping all other parameters fixed. The nonlinear muscle model was used. Activation signals were bell-shaped with peak velocity of 5 cm s\(^{-1}\) and a fixed duration of 1 s.

To produce the length changes here, instead of giving the same activation amplitude to both transversal and longitudinal muscle types as in Yekutieli et al (2005a, 2005b), the activation amplitude was modified differently for transverse and for longitudinal muscles.
to create different constant ratios between their activation amplitude values and to examine the arm elongation patterns generated due to these activations.

**Results**

**Arm elongation during natural reaching movements**

To determine whether reaching movements by *Octopus vulgaris* involve changes in arm length, a graph showing arm length during reaching was created for 64 reaching movements (figure 5(D) red curve, figures 6(A) and (B)). These graphs give the distribution of ‘elongation profiles’ and showed that most reaching movements were accompanied by arm elongation with an elongation average of 7.32 ± 4.34 cm (SD) (figure 6(D)). Average strain, along the arm, at the end of the movement (the average end strain: $\varepsilon = (l_{\text{end}} - l_0)/l_0$, where $l_{\text{end}}$ = end of movement arm length and $l_0$ = initial arm length) ranged from $-0.12$ (i.e., shortening) up to 1.8 with a mean of $0.57 \pm 0.41$ (SD%) (figure 6(E)). The average end strain value and end elongation difference ($l_{\text{end}} - l_0$; ‘elongation’ indicates net end elongation) were significantly positive ($p = 2 \times 10^{-16}$, $2 \times 10^{-20}$ respectively, paired t-test;
Figure 5. A reaching movement involving elongation and its elongation profile. (A) The envelope of the 3D backbone of an octopus reaching movement reconstructed from a sequence of images captured from two angles. From top to bottom, original movement, rotated 45° and 90° around the x-axis and 180° around the y-axis. (B) Snapshots from the right camera sequence. The red circle indicates the position of the bend point marking. (C) The midlines projected onto the plane of best fit of the reconstructed midlines (average distance of 0.65 cm per dot). (D) Blue dotted curve—elongation velocity of the arm during the movement. The arrows in (A), (C) and (D), mark the time of the first two minimum points of the elongation graph. Thick red curve—elongation profile. The arm extended from 10.5 to 16.5 cm during the movement (57% elongation relative to the initial length). Dotted green curve—bend propagation velocity profile—its bell-shape is typical for reaching movements. Solid cyan curve—distal shortening profile shows a decrease in the arm segment distal to the bend to almost zero, while the arm is still elongated, as shown by the red elongation curve.
Thus, arm length was modulated during reaching movement and both bend propagation and arm elongation determined the trajectories of the bend point in reaching movements. As reaching movements involve substantial arm elongation, reaching movement is not generated by a simple arm stiffening as previously suggested. That the elongation is highly variable (82%–180%) suggests that arm elongation is controlled independently of bend propagation.

In 43 of the 64 movements (67%), showed typical properties as reported for 70% of the movements in Gutfreund et al (1996, figure 4). These included stereotypical behavior of the tangential velocity of...
extension with an invariant second acceleration phase and a planar linear trajectory of bend propagation (figure 4(F)). The movements with a stereotypical arm extension like that shown in Gutfreund et al (1996) did not show a stereotypical elongation profile. No common shape was observed (figure 4(E)) with normalization of the bend propagation velocity profile as in Gutfreund et al (1996) (see introduction and figures 4(A)–(B)).

The origin of elongation along the arm
To test whether the arm elongated proximally or distally to the bend or, alternatively, whether arm elongation occurred all along the arm, the arm was divided into two segments, one distal to the bend and one proximal to the bend, and their lengths measured (see methods ‘arm length and elongation velocity profiles’ equation (4) for calculating $i_{\text{max}}$). Total arm elongation was then plotted against the length changes of the distal and proximal segments during 49 arm extension movements in which the proximal and distal segments could be tracked during the entire movement. The elongation was highly positively correlated with the length changes in the proximal part (figures 8(C)–(F); $p < 0.01$). Thus, both elongation and bend propagation appear to involve changes in the length of the proximal segment. Plotting the elongation of the distal segment versus total elongation gave a negative rather than a positive slope (data not shown), showing that the distal part was shortened rather than elongating, either due to the propagation of the bend or real shortening.

To refine our analysis we located the origins of lengthening by labeling specific suckers during several movements. Using our method, it was very difficult to track the suckers’ positions during the whole movement, since in many movements the suckers were temporarily hidden from the cameras’ view. We succeeded in reconstructing sucker positions completely only in four movements (figure 7).

In all these movements the distance between adjacent suckers close to the base increased during bend propagation, while the distance between distal suckers remained constant. Pairs of suckers from close to the middle of the arm to the tip preserved almost the same distance during the movement or exhibited only minor length changes. This supports the elongation occurring mostly in the proximal part of the reaching arm and that the strain is not uniform along the arm.

Contribution of elongation to bend extension
The total arm elongation during reaching was compared with the overall length of the bend trajectory. The mean length of the bend trajectory was 21.86 ± 8.73 cm while lengthening was 7.32 ± 4.34 cm (figures 6(D) and (F)) as mentioned above ($n = 64$; $p = 1 \times 10^{-13}$; paired t-test). Elongation accounted for 36.59 ± 22.96% (figure 6(G)) of the total distance traveled by the bend point, thus arm elongation plays a significant role in the reaching movement.

Further reaching movements ($n = 30$) were studied in two animals under more controlled conditions. Here the target and octopus were stationary and kept at predefined distances from each other. In these experiments arm extension also involved bend propagation and arm elongation. This observed elongation was quite substantial and highly variable.

Visual observation revealed a new type of reaching movements. Unlike the typical bend propagation in this movements behavior, the bend was formed closer to the tip of the arm, and reaching was achieved mainly by elongation and straightening of the segment proximal to the bend (data not shown). Moreover, in many observed movements in this work (e.g., figure 5), when the bend reached the tip it propagated further by elongation. Therefore, we segregated each movement into two periods of time: ‘Bend propagation’ and ‘Elongation’, making two groups of movements according to the position of the bend and the time of the peak velocity. The first group of movements lasted until the tangential velocity of bend propagation peaked and the second occurred from that peak until the end of the movement. Using a special GUI we observed that the second part of all movement (elongation) started when the bend was at the tip or at least very close to the tip (~75% of the arm length). We tested for a correlation between the bend position and the distance from the target in these two periods. In the ‘elongation’ group of movements the elongation was significantly positively correlated with the distance of the bend from the target ($\rho = 0.79$; $f$ test = 23.88; $p < 0.0001$; figure 8).

A model for muscle activation in reaching movements involving elongation
A biomechanical model was used to investigate what pattern of muscle activity can underlie arm elongation during reaching. This biomechanical model has been extensively used to study the extension movement but the possibility of elongation was not examined (see methods). Here the ratio of longitudinal to transverse muscle force was modified to simulate elongation. This activated the muscles during the extension and propelled the bend. Ten simulations of arm extension with constant ratios of longitudinal to transverse muscle force varying from 0.002 to 1 were generated (figures 9 and 10(A)). All results were independent of the segmentation process and were similar when either 20 or 40 segments were used in the simulation (figure 9; for further information see (Yekutieli et al 2005a, 2005b)).

In the simulations the model showed elongation only with muscle force ratios less than 0.5 (figure 10(D)). When the ratio was higher, the arm elongated until it reached a point, where it would have begun to shorten again, but its final length still would
have been longer than at the start of the movement. When the ratio was below 0.05, elongation velocity was always positive, elongating the arm in three steps (see arrows in figure 10(B)). In all cases, close to the end of the movement, the elongation reached a 'steady-state' (plateau), where the arm sustained its length. In some cases, when the ratio was low, a short, rapid elongation was created at the beginning of bend propagation, probably because of an instantaneous decline in arm stiffness. This elongated the arm without propagating any bend (figure 10(B) peak I). Then, a second and third peak of elongation velocity were created (figure 10(B) peak II–III). The second peak most likely represents the elongation during bend propagation, while the third probably occurred after the muscle activation wave approached the end of the arm and the bend no longer propagated. At the end of the movement, during this last peak, the distal portion of the arm was extended and straightened. The variability of the extension trajectories increased as the

Figure 7. Reconstruction and kinematic analysis of a Sucker’s location along the arm in a single movement. The upper panel shows a 3D plot of the distances (z-axis) between a pair of adjacent suckers along time ('frame no.') with their indexes indicated ('Sucker index'). The arm wireframe show the direction and location of the indexes. The bottom panel shows the results of reconstruction of the video frames (left images) of the reaching movement and their corresponding backbones (in red) and suckers (green triangles). Times and frame no. are shown near the tip of the backbones.
ratio of muscles activation decreased (figures 10(A)–(C)). This may indicate that arm stiffness is an important factor in shaping reaching, possibly because it determines the interaction with the passive external gravitational and drag forces.

Note that while the duration of the movement was fixed (1 s), the distance traveled by the bend was longer due to the elongation. Therefore, the peak velocity of bend point propagation increased with a decrease in the ratio of muscle force (figure 10(C)).

Figure 8. Elongation is significantly positively correlated with the distance of the bend from the target in the elongation type or second group of movements. Linear regression lines for the elongation of the arm during the first (A) and second (B) groups of movement (n = 30, from the current study). Only in the second group of movements did elongation data (second group) show a high correlation with the initial distance of the bend from the target at the beginning of that phase. (C)–(D) The relation between elongation of the proximal segment and total arm elongation during the second (C) and third (D) extension phase. (E)–(F) The relation between elongation of the distal segment and the total arm elongation during the second (E) and third (F) extension phase. The coefficient of correlation (r) and the p values of the F-test appear at the top left. The data presented in this figure imply that the reaching movement is composed of at least two kinds of active sub-movements.
**Discussion**

**Elongation in octopus arms**

Our results showed that typical octopus arm extension or reaching movements involve elongation of the proximal part of the arm in addition to bend propagation. The elongations were substantial and highly variable (average strain along the arm was $0.57 \pm 0.41$ in the first experiment and $0.64 \pm 0.28$ in the second experiment), ranging from an average strain of $-0.12$.
to 1.8 at the end of the movement. A 0.7 mean was reported when octopuses inserted their arms into a tube to grasp a bait (Margheri et al 2011, Mazzolai et al 2013).

The elongation of the arm derives only from the proximal part of the arm, as the distance between adjacent suckers increased only in the proximal part and total elongation was correlated with lengthening of the proximal part. Therefore, the decrease in the length of the distal segment can be used to monitor bend propagation along the arm. The bend propagation component can then be compared with the elongation component, which is given by the total changes in arm length. Further examination of the relation between these two components during the reaching movement should provide new insights on the motor control of reaching movement.

Our study suggests that the reaching movements can be broadly segregated into groups. Here we divided reaching movements into two groups on the basis of kinematic analysis. The first group involved bend propagation from the base of the arm towards the arm tip. In the second group, the bend was formed more distally and reaching was achieved mainly by elongation and straightening of the segment proximal to the bend. Further examination should determine the whole repertoire of reaching movements and explain the differences by kinematic analysis.

Gutfreund et al (1996) and Zullo et al (2009) suggested a connection between the distance from the target and the duration of the movement. Gutnick et al (2011) claimed that octopuses can combine peripheral information and visual arm location with visual cues to control the global direction of complex searching movements. Since, theoretically, elongation could be used to control the distance traveled by the bend, further analysis should clarify the involvement of elongation in distance control of the bend and explore if visual feedback is involved.

Studying reaching movements under more controlled conditions reduced the variability, suggesting that part of the variability here can be explained by the experimental paradigm. The high variability in these experiments can be seen as an outcome of octopus behavior in the less constrained conditions under which the reaching behavior was carried out.

The biomechanical mechanism underlying elongation in Octopus vulgaris typical reaching movement versus squid Loligo pealei tentacular strike

How can a non-specialized structure like the octopus arm elongate and how can the octopus elicit this lengthening? Kier and Stella (2007) suggested that, since the octopus arm tissue resists volume changes, any decrease in cross-sectional area must result in an increase in arm length. The decrease in cross-section and the consequent elongation can be highly localized, or it may occur along longer arm’s segment resulting in a robust arm elongation. The orientation and attachment of the transverse muscles indicate that their contraction would decrease the cross-sectional area of the arm, making it most likely that these muscles generate the force for elongation.

To understand how the biomechanics of the arm musculature can generate elongation during arm extension, it is most valuable to compare the performance in elongation in the octopus arm with elongation during the strike of the specialized stalk of the squid Loligo pealei (Kier and Van Leeuwen 1997). The octopus arm is a generalized MH structure evolved for manipulation. In contrast, the squid tentacle evolved specifically for rapid elongation during the strike movement when the squid catches its prey and is, thus, a remarkable example of specialization (Kier and Van Leeuwen 1997, Kier and Curtin 2002, Kier and Schachat 2007). It was surprising to discover that octopus arms can generate reaching movements with similar average strain values along the arm to those in the squid strike. Table 1 shows that the main difference lies in the speed of elongation.

Octopuses frequently use a typical arm extension movement in reaching to catch prey. A bend is created somewhere along the arm and aimed toward the target. It is then propelled toward the tip of the arm by a wave of muscle activation (Gutfreund
et al 1996, 1998). In the squid strike the tentacle stalk elongates rapidly toward the target through activation of the specialized transverse muscle mass, which squeezes and elongates the arm (Kier and Van Leeuwen 1997, Kier and Kathleen 1985).

Evolved from the same ancestral coleoid (Boltezky 1993, Naef 1921, 1923, Boltezky 1993, 1996), octopus and squid arms share some similarities in their muscular structure, such as the dimensions and organization of the longitudinal and transverse muscle fibers (Kier 1982, 1991, Kier and Curtin 2002). However, the squid’s specialized tentacle shows several differences in the arrangement and dimension of the myofilaments of the transverse muscles, resulting in its unique contractile properties (Kier 1996, Kier and Curtin 2002; table 2). The transverse muscle mass is larger in the squid than in the octopus, and the sarcomeres of the transverse muscles of the squid tentacle are shorter than those in the octopus and contain much shorter and thicker myofilaments. However, there is no major ultrastructural difference between the longitudinal fibers of the squid stalk and octopus arm.

The difference in extension performance of both animals, together with the differences in muscle structure and arrangement, emphasize the role of transverse musculature in elongation. Given their orientation and attachments, shortening of the transverse muscles decreases cross-sectional area and thus these muscles most likely generate the force for elongation (Kier and Stella 2007). However, the external and median oblique muscles may also generate some force for elongation (Kier and Stella 2007).

The constant volume constraint, preserves a condition in which any change in one dimension affect the other dimension, therefore, a change in the lengths affect the width. This biomechanical constraint creates a condition in which those muscles can function as antagonistic set of muscles (see introduction). For the matter of elongation the basic condition is that the transverse muscle will increase the relative forces in the transverse direction or that the longitudinal muscle will decrease the relative forces in longitudinal direction.

For example, in rest condition, the passive and active forces of the muscles are at equilibrium and this determines the rest or the steady-state shape of the arm. At this point, to actively change the length, the elongating force can be generated by actively increasing the relative force of the transversal muscles. This change in force balance, and the internal and external passive forces, determined the dynamics of elongation.

In octopus, the passive and active membrane properties of the transverse and longitudinal muscles fibers are similar as are their innervation and synaptic connections (Matzner et al 2000, Rokni and Hochner 2001, Feinstein et al 2011), but the transverse muscles mass is much smaller than the longitudinal mass (Kier and Stella 2007, Feinstein et al 2011). Thus, for elongation to occur, one would expect the transverse muscle to receive greater activation than the longitudinal musculature. This was substantiated by the simulations where a natural-like elongation was only generated when the ratio of the amplitude of longitudinal to transverse activation was smaller than one (<0.0016; figure 10(D)) what seems to be physiologically not realistic. However, this simulation result indicates that the assumption made when using the dynamical model that the longitudinal and transversal muscles generate similar forces, is not applicable for elongation movements. Therefore some modifications in the dynamic model might be needed to account for the behavior observed in movements combining bend propagation and arm elongation.

Alternatively, the muscles may be organized so that simultaneous and equal activation of the muscles results in unbalanced longitudinal versus transverse muscle forces and so causes elongation. The structural and electrical similarities of both muscle types make this less likely in the octopus.

### Table 1. Comparison between kinematics of Octopus vulgaris reaching movement and Loligo pealei strike.

<table>
<thead>
<tr>
<th></th>
<th>Octopus vulgaris ($n = 64$)</th>
<th>Loligo pealei ($n = 7$)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Duration of second extension phase/strike</td>
<td>0.15 – 1.36 ± 0.43 ± 0.32 (s)</td>
<td>0.020 – 0.040 ± 0.057</td>
</tr>
<tr>
<td>End average strain</td>
<td>0.57 ± 0.41</td>
<td>0.63 ± 0.14</td>
</tr>
<tr>
<td>Extension/strike peak velocity</td>
<td>16.11 – 68.64 cm s⁻¹ 30.76 ± 17.33 cm s⁻¹</td>
<td>175 – 250 cm s⁻¹</td>
</tr>
</tbody>
</table>

* Mean ± SD.

b Mean and SD were not reported nor could they be calculated from the reported data.

### Table 2. Comparison of features of the arm infrastructure in Octopus vulgaris and the stalk of Loligo pealei.

<table>
<thead>
<tr>
<th></th>
<th>Octopus vulgaris arm</th>
<th>Loligo pealei stalk</th>
</tr>
</thead>
<tbody>
<tr>
<td>Transverse/oblique muscle mass as a percentage of the intrinsic musculature</td>
<td>21% transverse + 17% oblique = 38%</td>
<td>60% transverse</td>
</tr>
<tr>
<td>Longitudinal muscle mass as a percentage of the intrinsic musculature</td>
<td>56%</td>
<td>&lt;40%</td>
</tr>
<tr>
<td>Transverse sarcomeres</td>
<td>Long</td>
<td>Short</td>
</tr>
<tr>
<td>Longitudinal sarcomeres</td>
<td>Long</td>
<td>Long</td>
</tr>
</tbody>
</table>
Acknowledgments

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Appendix

A.1. Normalization of tangential and elongation velocities

The tangential velocities were calculated from the time derivatives of the smoothed 3D position trajectory of the digitized bend point (relative to the eyes) (after Gutfreund et al 1996). The tangential velocities \( |\mathbf{v}(t)| \) of the bend and the movement duration \( (t) \) were then normalized to the peak velocity \( (v_{\text{max}}) \) and the distance traveled \( (d) \):

\[
\mathbf{v}_{\text{norm}}(t) = \frac{\mathbf{v}(t)}{v_{\text{max}}},
\]

\[
t_{\text{norm}}(t) = \frac{v_{\text{max}} (t - t_{\text{max}})}{d}.
\]

The distance traveled \( (d) \) was calculated from the first minimum to the maximum (at \( t_{\text{max}}) \) of the tangential velocity profile.

The elongation velocities were calculated from the time derivatives of the arm lengths during the movement. Similarly to the normalization process for tangential velocity described above, the arm elongation durations and velocities \( (\mathbf{v}e) \) were normalized by the peak elongation velocity \( (v_{\text{e, max}}) \) and elongation \( (\mathbf{e}) \) using:

\[
\mathbf{ve}_{\text{norm}}(t) = \frac{\mathbf{ve}(t)}{v_{\text{e, max}}},
\]

\[
t_{\text{norm}}(t) = \frac{v_{\text{e, max}} (t - t_{\text{max}})}{e},
\]

where \( \mathbf{ve}(t) \) is the elongation velocity. \( e \) was calculated using:

\[
e = l_{\text{max}} - l_{\text{min}},
\]

where \( l_{\text{min}} \) and \( l_{\text{max}} \) are arm lengths at the times of the first minimum and peak (at \( t_{\text{max}}) \) velocities, respectively. These were measured during the movement (i.e., \( t_{\text{max}}) \) always followed \( l_{\text{min}}) \).

A.2. The plane of best fit to the movement

To find the plane of best fit for a group of points \( \mathbf{p}_i = (x_i, y_i, z_i), 1 < i < n, n \gg 2 \), each point on that plane should satisfy \( ax_i + by_i + cz_i + d = 0 \), where \( i \) is a point index, \( a, b, c \) and \( d \) are the plane parameters (a normal to the plane), and \( x_i, y_i, z_i \) are the points’ external Cartesian coordinates.

In the plane of best fit for this set of points, these points minimize the value:

\[
\text{Error} = \sum_i (ax_i + by_i + cz_i + d)^2.
\]

Singular value decomposition (SVD) was applied to the variance matrix of all sampled points of the backbone’s sequence after subtracting the average value \( E(p) \) from each point, and the SVD results vector with the least Eigen value was taken. All these midline points were then projected onto this plane by finding the closest plane-point for each sampled backbone point.

The Se was defined as: \( \text{Se} = \text{Error}/n \)

A.3. Curve cubic spline-smoothing

We applied Matlab’s ‘cspaps’ cubic smoothing spline function to the data several times. This is a smoothing function which returns the \( pp \) form of a cubic smoothing spline \( f \) to the given discrete sequence of data points \( x_j = (x_j, y_j), \) with the value of \( f \) at the data site \( x_j \) approximating the data value \( y_j \), where \( 1 < j < n \) and \( n \) is the length of the sequence.

This smoothing spline \( f \) minimizes:

\[
J = \sum_{j=1}^n w_j \left( y_j - f(x_j) \right)^2 + (1 - p) \int_{\mathbb{R}} \lambda(t) \left( D^2 f(t) \right)^2 dt.
\]

Here, the integral was taken over the smallest interval containing all the \( x_j \) values. The smoothing spline was never used outside the basic interval. The default value for the weight \( w_j \) was 1. The default value for the piecewise constant weight function \( \lambda \) in the roughness measure was the constant function 1. Further, \( D^2 f \) denotes the second derivative of the function \( f \).

The smoothing parameter \( p \) determines the relative weight the user wishes to place on the contradictory demands of having \( f \) be smooth versus \( f \) being close to the data. Thus, the value for the smoothing parameter \( p \) was chosen depending on the given data set \( x \). For example, for \( p = 0, f \) is the straight line of fit to the data using the least-squares method, while, at the other extreme, \( p = 1 \) is the variational or ‘natural’ cubic spline interpolant. As \( p \) moves from 0 to 1, the smoothing spline changes from one extreme to the other. The interesting range for \( p \) is usually near \( 1/(1 + h^2/6), \) with \( h \) the average spacing of the data sites. Thus, the default value for \( p \) was chosen from this range. However, the default \( p \) value was not used here, because it was insufficient for discarding the noise. Unless mentioned otherwise, a uniform parameter value of 0.02 was used. This parameter, chosen by eye, was found sufficient to create curves which described the data in most cases.
A.4. Sources of error in the measurement of arm length during the reaching movement

A.4.1. Marking the arm contour. As described above, the 3D-reconstructions of the arm backbone was extracted from marking the arm contours in double view. Although the user was instructed to begin marking at the base of the arm, it was not always clear exactly where the arm originated. Marking was also more difficult, because the octopus could change colors and its arms sometimes crossed over each other. Those problems were independent of camera function and may distort the results, even though the visual conditions were ideal. Therefore, some of the variance in the average strain results may have been due to distortion through marking errors.

Some of the movement backbones could not be reconstructed due to epipolar parallelism. To avoid distortion of this kind, further cameras can be used. The reconstruction result could then consider the best data achieved from different camera combinations giving different 3D reconstruction results. It is likely that the best position for a further camera is above the other two.

A.4.2. Initial arm shortening. We found here that the average strain (defined as \( e = (l_{\text{end}} - l_0) / l_0 \), where \( l_{\text{end}} \) = end of movement arm length and \( l_0 = \) initial arm length) during the first phase of extension was lower than and significantly different from the average strain in the second and third phases (\( p < 0.001 \); data not shown). In some cases (16, ~25%) the average strain was negative in the first phase, indicating a shortening. It is still unclear whether this shortening is similar in all movements preserving a constant average strain value. However, it is reasonable that after an elongation, the arm may need to actively shorten before the next movement. Thus, variability in this initial average strain value can affect the results.

A.4.3. Bias toward lower values. It is also likely that the average strain measurement in the first phase may be inaccurate because the length measurements could not always be started from the actual initiation of the first phase. At the start of the first phase, the arm is usually in a resting position, lying buckled on the ground and thus hidden by its own curves and by other arms. Thus, it is likely that the first phase was truncated in our measurements, the analysis considering only part of it. In such cases, if the arm length increased during the first phase, as observed in 75% of the movements, the end average strain value would be biased towards lower values and therefore the accurate average strain value should have been even higher. Similarly, in the cases of shortening during the first phase (25% of cases) the end average strain values could be biased to higher values.

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