Octopus arm movements under constrained conditions. Adaptation, modification and plasticity of motor primitives

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ABSTRACT

The motor control of the eight highly flexible arms of the common octopus (*Octopus vulgaris*) has been the focus of several recent studies. Our study is the first to manage to introduce a physical constraint to an octopus arm and investigate the adaptability of stereotypical bend propagation in reaching movements and the pseudo-limb articulation during fetching. Subjects (n=6) were placed inside a transparent Perspex box with a hole at the center that allowed the insertion a single arm. Animals had to reach out through the hole toward a target, to retrieve a food reward and fetch it. All subjects successfully adjusted their movements to the constraint without an adaptation phase. During reaching tasks the animals showed two movement strategies: stereotypical bend propagation reachings, which were established at the hole of the Perspex box and variant waving-like movements that showed no bend propagations. During fetching movements, no complete pseudo-joint fetching was observed outside the box and subjects pulled their arms through the hole in a pull-in like movement. Our findings show that there is some flexibility in the octopus motor system to adapt to a novel situation. However, at the present it seems that these changes are more an effect of random choices between different alternative motor programs, without showing clear learning effects in the choosing between the alternatives. Interestingly animals showed the ability to either adapt the fetching movements to the physical constraint, or as alternative explanation, to switch the motor primitive fetching to a different motor primitive “arm pulling”.

INTRODUCTION

Octopuses represent an interesting model for the research of motor control in a soft-bodied animal due to their eight highly flexible arms and centralized nervous system. Recently octopuses have been a model for developing bio-inspired robots with highly flexible continuum appendages (Zheng et al., 2013; Pfeifer et al., 2014).

The lack of any skeletal structure (Feinstein et al., 2011) enables the animals to move their arms in any direction, they can bend, twist, elongate and shorten and
use virtually infinite degrees of freedom (DOF) (Kier and Smith, 1985). To reduce the complexity of arm control, the octopus uses motor primitives to perform stereotypical motor patterns. Motor primitives are loosely defined as the building blocks of a complex motion (Flash and Hochner, 2005), like an alphabet of elementary actions (Del Vecchio et al., 2003). Although the motor primitives themselves are considered invariant, they can be recombined dynamically to form complex movements (Moro et al., 2012).

Two discrete, stereotypical movements have been described in the octopus: *bend propagation reaching* and *pseudo-joint fetching*. During reaching toward a target, a bend propagates in a wave-like manner from the base of the arm toward the tip (Gutfreund et al., 1996). During these arm extension movements, motor neurons of the nerve cord activate the muscles in a wave-like manner and propagate the bend (Gutfreund et al., 1996; Gutfreund et al., 1998). This stereotypical movement can also be elicited by stimulation of the nerve cord in an *in vitro* preparation, which demonstrates that the respective motor program is embedded in the arm of the octopus (Sumbre et al., 2001).

To fetch an object to their mouth, animals form quasi-articulated limbs based on three dynamic joints (Sumbre et al., 2005). Here, two waves of muscle activation travel toward each other and set a pseudo-joint location at their point of collision (Sumbre et al., 2006). This emulates the situation in vertebrate arms with stiffened joints and enables the octopus to use precise point-to-point movements. Both reaching and fetching, are highly stereotypical and greatly reduce the number of DOFs and therefore the complexity of movement control.

One of the most important questions is about the limitations of the octopuses motor control system. To generate goal directed movements, both robustness and adaptivity are equally important. Strict feed-forward motor programs are a trade-off between reduction of complexity and flexibility. This trade-off could be compensated by higher-order motor centers, but little is known about such adaptations in the control system of the octopus.

The basal lobes, which are the higher motor centers in the octopus (Young, 1971; Wells, 1978), consist of about 2.5 million cells, but seem to lack somatotopical organization at this level (Zullo et al., 2009), which suggests reduced interconnections
of sensory and motor neurons. The large number of neurons in axial nerve cords of the arms on the other hand, may point toward an alternative control center for high level information processing: The peripheral nervous system contains about 350 million cells, comprising about two thirds of all neurons in the octopus. Most of the cells are located in axial nerve cords projecting from the brain to the arms (Budelmann et al., 1995). While a special division of labor between the central nervous system and the peripheral nervous system of the arms has been demonstrated before (Altman, 1971; Wells, 1978; Sumbre et al., 2001; Sumbre et al., 2005), lesion-studies suggest that at least in goal directed movements higher brain areas are necessary to control planning and execution of the motion, for example during fetching motions (Sumbre et al., 2006).

It is unknown to what extent reaching and fetching movements can be controlled to overcome a physical constraint. To investigate the flexibility and adaptability of the motor control system, we introduced a physical constraint to the arm and studied how it affects the previously described behaviors *bend propagation reaching* and *pseudo-joint fetching*. The limitation to the onset of the motor primitives forced the animals to adapt to the new situation. Animals were able to adapt to the constraint by dynamically generating feed-forward bend propagation reachings and stereotypical pull-in fetchings. These results show that octopuses have a flexible and dynamic motor control system, which adapts instantly to new situations.

### RESULTS

Six octopuses were put into a Perspex box and were required to reach toward a target and fetch the food reward by inserting their arm through a hole in the box. All animals were able to adapt to the physical constraint and used distinct strategies during the reaching (Figure 1A) and fetching tasks (Figure 1B). Overall, 286 successful reaching movements and 382 fetching movements were observed.

#### Reaching

During reaching tasks octopuses used motions that were classified into two strategies, a straight point-to-point reaching (please see supplemental movie clip...
“Reaching.mov”) and a seemingly undirected movement we termed waving-like
(please see supplemental movie clip “Waving.mov”). Straight reachings (n=148) are
linear point-to-point and goal directed bend propagation reachings as first described
by (Gutfreund et al., 1996), complemented by elongation of the arm. The octopus
positions the midsection of an arm over the hole of the Perspex wall and forms a loop
outside of the box (Figure 1A seconds 0.3 – 1). This loop initiates the new bend,
which will then travel toward the tip of the arm (see Figure 1A, seconds 1.4 – 2.4).
Next to loop-induced bend propagation movements, bend propagations were set up
freely outside the box in about 7% of all successful reachings. In these cases the arm
was put through the hole in a different manner (e.g. by stretching and pushing the tip
of the arm through the hole) and a bend was established outside the box without the
loop-building procedure at the hole.

In order to compare straight reaching motions in constrained situations to
unconstrained motions described by Gutfreund et al. (1996), the same analyzing and
normalization methods were used on ten random reaching movements, which
successfully hit the target. The normalized tangential velocity profiles of constrained
reaching movements showed typical invariant bell-shaped curves (Figure 2B) with
three corresponding phases, identical to reaching movements in an unconstrained
situation (Figure 2A). Phase I corresponds to the establishment of the bend and is the
most variable part of the movement. Phase II, the propagation of the bend along the
arm, corresponds to the steep velocity increase in the profile and is the most robust
part of the movement. The maximum and subsequent decrease of velocity in phase III
corresponds to a passive part of the movement in the vicinity of the object.

Waving-like movements (n=138) are seemingly undirected, explorative
movements outside the box with no bend propagation and random kinematic profiles
(Figure 3). In most cases the arm is put through the hole by using the loop-building
procedure similar to movements in the straight category.

The reaching strategies differed significantly in the duration until the object
was touched (Mann-Whitney $U= 312$, $N= 272$, $p< 0.001$, Figure 4), in which mean
duration for straight bend propagation reachings was short (2.4 ±1.3 sec) and longer
for waving-like motions (12.4 ±7.1 sec). While waving-like behavior was observed
more often than straight bend propagation reaching on average (N = 130 ±109 and 29 ±19), the success rate was higher for straight reachings (87% ±11.4) than for waving-like motions (27.7% ±29.8).

Since straight reachings were more successful, learning in the octopuses might mean a transfer of their strategy from a more undirected and waving-like movement to an efficient point-to-point reaching. To test if a shift in reaching strategies happened over time, strategy choices were compared between the beginning and the end of the experiments. Successful reaching motions were split into three trial bins for each animal and then compared between first and last bin (Figure 5). Two of six animals significantly changed the strategy in the last third of the experiment compared to the first; in the last third of the experiment Animal 5 increased the amount of waving-like motions ($\chi^2 (1) = 6.65$, N= 30, p= 0.01) and Animal 3 increased the amount of straight reachings ($\chi^2 (1) = 7.84$, N= 74, p= 0.005). The relative number of fails did not change over the course of the experiment ($\chi^2 (1) = 3.043$, N= 634, p= 0.081).

Fetching

All animals were able to pull the food reward through the hole in the Perspex wall and only a few trials were marked as fails (food dropped n= 24, general execution error n= 5). To test for differences in movement patterns, all movements were subjectively categorized into two categories, straight (please see supplemental movie clip “Fetching.mov”) or deflected (please see supplemental movie clip “Deflected.mov”) movements. Movements that showed a general immediacy and an overall straight and point-to-point shape were classified as straight movements and movements that could not clearly be classified as straight movements formed the deflected group. To differentiate the two categories in order to test if these movements are discrete, a sample of 60 successful fetching trials (ten per animal) were tested for general reliability of the classification into categories. First, the movements were reevaluated by subjective categorization of a second observer and then by a categorization based on 3D reconstruction of the movements’ trajectories and their tangential velocity profiles.
To test for inter-rater reliability of the subjective categorization, Krippendorff’s α (Hayes and Krippendorff, 2007) was calculated for two observers. The classification was accepted with an agreement of \( \alpha = 0.67 \) (95% CI, 0.443 to 0.851). The relatively vague criteria for classification justified the use of the minimum recommended α-values (Hayes and Krippendorff, 2007).

Movements with generally straight trajectories were categorized as straight (Figure 6A), as well as normalized tangential velocity profiles that showed stereotypic bell shaped curves (Figure 6B). Trajectories and tangential velocity profiles that were random and not stereotypical were categorized as deflected (Figure 6C and 6D). The three ratings per movement, based on subjective categorization, tangential velocity profiles and trajectories were tested for compliance and showed a general consent on their respective categorization (Krippendorff α = 0.71). Overall 281 trials were categorized as straight and 100 as deflected.

Mean fetching times also differed significantly between categories (Mann-Whitney \( U = 21.5, N= 381 \) \( p< 0.001 \)), with a mean duration of 2.7 ±1.66 sec for the straight category and 5.81 ±4.82 sec for the deflected category.

The distribution of the strategies during the first ten trials was not homogenous among the animals (Table 1). Four of the six animals showed straight fetching in the first trial and the general distribution of strategies was found to be random (One-sample Runs test, not significant; see Table 1).

To test if the animals changed their fetching strategies in the course of the entire experiment due to an adaptation to the constraint, all trials were divided into three trial bins for each animal and the respective movement categories were analyzed (Figure 7). The relative number of straight and deflected fetches did not change significantly from the first to the last third of the experiment (\( \chi^2 (1) = 1.748, N= 254 \) \( p= 0.1869 \)). Also the combined fetching time of all animals showed no significant improvement (\( U= 8752, N= 253 \) \( p= 0.191 \)), however, two individual animals significantly changed their mean fetching time in the course of the experiment: Animal 2 lowered the mean fetching time from 7.24 ±5.5 sec in the first third to 3.85 ±3.5 sec in the last third of the experiment (\( U= 69.5, N= 34, p= 0.009 \)) but Animal 5...
raised it from $1.71 \pm 0.75$ sec to $2.45 \pm 1.1$ sec ($U= 1015$, $N= 75$, $p= 0.001$). The two opposed changes in reaching time point toward individual, rather than general effects.

**DISCUSSION**

A very promising perspective to explain movement generation and to overcome the *motor equivalence problem* of increasing complexity with increasing DOF’s (Bernstein, 1967) is the modular approach. Movements result from the combination of a finite set of stable motor primitives (Bizzi et al., 2008) or a stereotypical co-activation of several muscles, called muscle synergies (d'Avella et al., 2003). Several studies showed the use of robust motor primitives during reaching (Gutfreund et al., 1996) and fetching movements (Sumbre et al., 2005) of unrestrained octopuses. However, there are no studies on the plasticity of movements and adaptivity of movement control. Our study is the first to manage to introduce a physical constraint to the octopus arm. This enabled us to gain new insights into the ability of the motor system to adapt and modify the motor primitives *bend-propagation reaching* and *pseudo-joint fetching*.

**Adaptation to constrains**

All animals adapted to the physical constraint and were able to reach and fetch through the hole in the Perspex wall. The animals showed flexibility in movement control by adapting to the constraint and using an appropriate movement to get to the food reward. In order to elucidate learning effects, movements of the reaching and fetching tasks were categorized into variant and invariant movements. Invariant movements had stereotypical kinematic profiles with straight trajectories and bell shaped tangential velocity profiles. Variant movements were described as waving-like reaching and deflected fetching and had no stereotypical trajectories, variable tangential velocity profiles and were longer in duration.

As there is no significant change in the amount of these movements over the course of the experiments, we assume that these movements are not transitional states during an adaptation period (Arce et al., 2009). Only one animal changed its behavior toward the more efficient straight reaching strategy, despite the higher success.
probability. Likewise, during fetching tasks animals did not entirely change to the faster pull-in movements. Interestingly, the relative number of fails, which presumably represented explorative movements without coincidental target hits, did not change over the course of the experiment per animal as well, which overall suggests an absence of learning effects (Sosnik et al., 2004) or an insufficient motivational state of the animal to trigger learning effects. The general absence of any clear learning effect in terms of improvement in performance or in terms of time taken to complete a task eludes toward an absence of the ability of octopus vulgaris to shape motor programs due to learning. Since these behaviors must then be innate, the variance in the strategies suggests that the animals switch between different movement strategies during the same condition. In general, the waving-like reaching and the variances in the fetching patterns showed that the octopus’ movement repertoire is probably not limited to a fixed set of movements. At least in the waving-like movements the high number of observations (N = 130 ±109) and low success rate (about 25%) compared to straight reachings (N = 29 ±19, about 85% success rate) might explain the movement as an explorative movement, in which the animal touched the target by accident.

**Stereotypical movements**

Movements of the reaching and fetchings tasks were categorized according to their kinematic profiles or movement patterns. Stereotypical movements were generally immediate and goal directed movements with straight trajectories.

During reaching tasks the animals used propagating bends that were either initiated by building up loops through the hole of the wall using approximately the midsection of the arm, or were freely initiated outside the box. These bend propagation movements showed linear trajectories and stereotypical invariant normalized tangential velocity profiles and were identical to movements in freely behaving animals (Gutfreund et al., 1996). The dynamic range of control over this robust feed-forward motor program has not been shown before in octopus: The animals were able to sequentially connect the motor primitive bend propagation reaching and the loop building at the hole of the wall or could even be initiated outside the box. Since loop building at the hole was also observed in most movements of the waving category, it should be seen as an independent movement from the bend propagation initiation. Our findings suggest the ability of the octopus to start the
motor primitive at any point along the arm and to subsequently hit the target. This is an important finding as it stands in contrast with previous hypothesis that the directional control of the reaching movement is determined by adjusting two DOF’s (yaw and pitch) at the base of the arm (Gutfreund et al., 1996).

Fetching movements categorized as straight consisted of a single linear motion. They were done with straight point-to-point pull-ins of the arms, with straight trajectories and bell shaped normalized tangential velocity profiles. These movements differ from fetching movements in freely behaving animals, as in our experiments no formation of stereotypical pseudo joints and quasi-articulated limbs could be observed. Interestingly, the kinematic profiles of straight fetching movements were very similar to the stereotypical bend propagation reaching movements in freely behaving animals, suggesting that these fetching movements are complete and uninterrupted movements. This suggests that this is either a modification of the existing motor primitive or an so far unknown new motor primitive – arm pulling.

Visual examination of all fetching movements showed a commonality between the two categories during fetching: In all trials the gripping shape of the arms seemed to be preserved and showed an S-shape, formed by the attachment of the food and an immediate second bend (see arrows in Figure 1B, 0.8 s). This has been described before (Sumbre et al., 2005; Sumbre et al., 2006) as “grasp of food item” and “distal joint”. It is unclear, however, if the grasping of the food item triggered pseudo-joint fetching, initiating for example the onset of medial and proximal joints, which might then have been masked or cancelled by a conflicting feedback signal triggered by the constrain on the arm. To clarify this possibility a further kinematic analysis would be required.

The neuromuscular control of the movement generation is unclear. It was hypothesized before, that the grip of the food item triggers two waves, which form pseudo-joints at the point of collision, creating dynamic joints along the arm with fixed ratios of inter-segment lengths (Sumbre et al., 2006). Although it is unclear if these joints were masked or cancelled by higher-order control mechanisms in the constraint situation, they did not interfere with the immediate switch to a straight pull-in movement in some animals (see Table 1). Unfortunately the proximal part and the base of the arm inside the box were not visible enough for a meaningful analysis of
the pull-in mechanism. The food items might have triggered the onset of a medial and
proximal bend at the very proximal part of the arm inside the box, which then were
dynamically altered by sensory information in terms of the length and stiffness of the
quasi-articulated structures.

Variant movements

Movements of each of the two stereotypical categories share similar motion
patterns and seem goal directed because of the stereotypical kinematic profiles.
However, the mechanisms underlying the movements in the variant category are
unclear. The variant movements of the reaching tasks, categorized as waving-like
movements, seemed to be fundamentally different from stereotypical bend
propagation movements. Waving-like movements had random kinematic profiles and
were seemingly undirected and the successful reaching to the target were lower than
the direct reaching thus less rewarding. The movement patterns of variant fetching
movements on the other hand differed only marginally from stereotypic point-to-point
fetching movements, although differences in the kinematic profiles and duration were
observed. The trajectories seemed to be random deviations from linear trajectories
and were thus labeled as deflected categories. A commonality of all fetching
movements seemed to be a pull-in motion pattern, controlled by the proximal segment
of the arm and by shortening the arm. In contrast to reaching movements the reward
gained by the two types of pulling were simialr.

Point-to-point pull-in fetchings with their stereotypical kinematic profiles, that
is, linear trajectories and the bell shaped normalized tangential velocity profiles, could
present another motor primitive, for situations, where an arm is pulled through a tight
opening. It is reasonable to assume that the pull-in movement itself was controlled by
more proximal parts of the arm, which were inside the box and unfortunately not
visible enough for a meaningful analysis. A common mechanism for pull-in fetchings
could explain why the movement showed both, robust and variant forms and still
seemed to have the same motion mechanics: While the proximal part of the arm
controls the pull-in, the distal part is passive. Movement speed or immediacy of the
pull-in changes the kinematic profile of the tip of the arm, which was the reference
point during the kinematic analysis (see methods section). The animal would then be
able to switch between activating a pull-in motor primitive and active control of the
distal part of the arm. This switch between robust motor primitives and flexible movements would be similar in principal to the dynamic linking of movement patterns during reaching movements in the constrained situation.

**Sensory feedback**

It has been discussed previously if octopuses are able to use sensory feedback to control their movements (Wells, 1978; Gutfreund et al., 2006) and Gutnick et al. (2011) presented evidence that animals use visual feedback from their arms during three-choice-maze experiments. In our findings tactile sensors might collect additional information on the arm. The restriction due to the hole should provide sensory information to recognize the restricted mobility of the arm and thus this information is used to generate appropriate movements to overcome the constraint. The lack of systematic change in strategy choices between the variant and stereotypical form of the respective movement implies that no trial-and-error learning phase occurred in the course of the experiment. In the fetching task most animals used point-to-point pull-in motions without an adaptation phase. In the reaching task the animals initiated the loop of the bend propagation at the hole, which suggests that they used sensory feedback to identify the dimension of the obstacle and the point at which the initiation of the feed-forward motor program bend propagation reaching was possible.

Since feedback-controlled movements are generally considered to be too slow for fast online correction (Kawato, 1999), we propose that the octopus uses sensory feedback to gather information about its environment and incorporate them in its feed-forward inverse model to compute adequate actions and trajectories. While no change in categories over the course of the experiment was recorded, which could have been an indication for trial-and-error learning, all animals explored the box and its opening extensively during the experiments.

**Résumé**

The results of this study suggest that the octopus higher motor control system is flexible and adapts to novel situations mainly by choosing between two different movements that solve the task albeit with different rewarding rates. Interestingly, despite the difference in reward rate in the reaching movement no learning was
demonstrated. This suggests that the reward does not affect the decision between the two type of reaching (the waving and direct). An intriguing finding that requires further investigation, is the demonstrated the ability of the octopus to direct its arm to the target even though the movement starts from the hole rather than for the base of the arm. This proposes that the octopus uses sensory feedback to gather information about its environment and incorporate them in its feed-forward inverse model to compute adequate actions and trajectories. With respect to fetching it seems that the octopus has two alternative behaviors to solve the task (direct and indirect pulling). In this task there also seems to be a fixed decision ratio that also does not change over time (but here the reward is equal for the two movements).

MATERIALS AND METHODS

Subjects and holding

Subjects were six wild-caught Octopus vulgaris (Lamarck, 1798) (2 females, 4 males; between 250-450g bodyweight) collected by fishermen from the Israeli coast of the Mediterranean Sea. The animals were housed individually in 100 liter artificial sea water tanks within a closed circulation system and held according to the guidelines for the EU Directive 2010/63/EU for cephalopod welfare (Fiorito et al., 2014). Tanks were enriched with clay-pot dens, gravel, rocks and green algae (Caulerpa prolifera), temperature of the holding rooms was held constant at about 19°C. Day and night cycles were simulated by artificial illumination for 12 hours. Animals were fed every other day with either dead shrimps or pieces of fish.

All animals acclimatized for at least 14 days in the holding tanks before they were transferred to an experiment tank (400 liter), where they acclimatized for another day before experiments started. Animals were preselected for motivation and general health.

Experiments

Each animal was placed separately inside a custom made transparent Perspex box (40x40x40 cm) with a hole (1.5 cm in diameter) at the center of one side that
allowed the insertion of only a single arm. The animal had to reach out through the
hole to retrieve a food reward and pull it back in. Success criterion for the reaching
task was the touching of a target (white Perspex disc on a transparent Perspex stick).
A piece of shrimp was placed on the tip of the arm, which had to be completely pulled
through the hole for a successful fetching task. The reaching task onset was marked
by the insertion of the target into the water. Fetching tasks followed successful
reaching tasks or were initiated by letting the animal grip the target and then being
pulled to stretch the arm to average fetching distance. The target was presented
approximately at the level of the hole and the distance varied between 2-40 cm to
motivate the animals to reach for it.

Kinematic Analysis

The experiment was constructed according to the publication by Gutfreund et
al. (1996). The sessions were recorded with two digital video cameras (SONY
Handycam HDR-XR550; Tokyo, Japan) in an angle of about 90 degrees and later
formatted, cut and transformed into picture sequences (25 frames per second) with
video editing software (Adobe Premiere CS5; San Jose, California, USA).

For the 3D reconstruction of trajectories and tangential velocity profiles, the
visual information of the two cameras was transformed to 3D coordinates, applying
the direct linear transformation (DLT) method (Wood and Marshall, 1986; Woltring
and Huiskes, 1990). A calibration body was used to obtain 11 parameters that were
used to define the image coordinates of the two cameras in the following DLT
equations:

$$x_1 = \frac{P_3 X + P_4 Y + P_5 Z + P_6}{P_6 X + P_{10} Y + P_1 Z + 1} \quad (1),$$

$$y_1 = \frac{P_8 X + P_9 Y + P_7 Z + P_8}{P_8 X + P_{10} Y + P_1 Z + 1} \quad (2),$$

with $x_1$ and $y_1$ as image coordinates of a designated point of camera 1 and the
unknown 3D coordinates $X$, $Y$ and $Z$. The variables $P_{1-11}$ represent the 11 parameters
obtained from defined points of the calibration body.

Three points of interest were then marked in the image sequences using
MATLAB (MathWorks; Natick, Massachusetts, USA.) to reconstruct arm movement:
two reference points and either the bend or tip of the arm during reaching tasks or the
food item, which was typically put on the distal quartile of the arm, during fetching
tasks. This positional data was then used to calculate the tangential velocity profile.
The data was smoothed by fitting a fifth order polynomial to the projections of the
points on the three axes as a function of time. The coefficients were obtained by
calculating the least-square equation, using the singular value decomposition
algorithm. Then $V_{\text{tan}}$ was calculated from the derivatives of the smoothed coordinates
$X(t)$, $Y(t)$ and $Z(t)$ with:

$$V_{\text{tan}} = \sqrt{\left(\frac{dX}{dt}\right)^2 + \left(\frac{dY}{dt}\right)^2 + \left(\frac{dZ}{dt}\right)^2} \quad (3),$$

To account for invariances, the tangential velocity $[V(t)]$ and time $(t)$ were normalized
according to the maximum velocity ($V_{\text{max}}$) and travel distance ($D$), following
procedure after Atkeson and Hollerbach (1985) and Gutfreund et al. (1996):

$$V_{\text{normalized}} = \frac{V(t)}{V_{\text{max}}} \quad (4),$$

$$T_{\text{normalized}} = \frac{V_{\text{max}} \cdot x_t}{D} \quad (5),$$

$$D = \sum_t \sqrt{(X_t - X_{t-1})^2 + (Z_t - Z_{t-1})^2} \quad (6),$$

with the smoothed coordinates $X$ and $Z$ and the index $t$ as image number or time.

Further data analysis was done with SPSS 19 (IBM Software; Armonk, New
York, USA) and Microsoft Excel 2011 for Mac OS (Redmond, Washington, USA). A
inter-rater reliability test was done in order to calculate rating similarities between
two independent observers. For this purpose two observers categorized the same trials
according to the categorization rules and differences were calculated according to

REFERENCES

229, 204-206.

Differences in context and feedback result in different trajectories and adaptation


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COMPETING INTERESTS

The authors declare no competing financial interests.

AUTHOR CONTRIBUTIONS

J.N.R. and M. J.K. designed the study and carried out the behavioral experiments, J.N.R. analyzed the data, J.N.R, B.H. and M.J.K. discussed the results and drafted the manuscript.

Table 1: Distribution of categories among the first ten trials

<table>
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<td>Straight</td>
<td>Straight</td>
<td>Straight</td>
<td>Deflected</td>
<td>Deflected</td>
<td>Deflected</td>
</tr>
</tbody>
</table>

One-sample runs test

\[ r = 4 \quad 6 \quad 7 \quad 4 \quad 4 \quad 4 \]

\[ p = 1 \quad 1 \quad 0.287 \quad 1 \quad 1 \quad 1 \]

Figure texts

Figure 1 Picture sequence of typical straight reaching and fetching movements in a constrained situation. Octopuses are behind a Perspex wall and reach or fetch through a hole with a single arm (indicated in red). A Straight reaching toward a target is done with a typical bend propagation, which is set up by building up an arm loop at the
hole. White arrow points at arm bend. Seconds 0.3 – 0.6 show building up of the arm
loop; seconds 1.4 - 1.8 show bend propagation toward the target; seconds 2.4 show
arm hitting the target. Blue ring highlights the hole; B Straight fetching of a food item
(white object). Frame at 0.2 seconds shows the arm attached to target; seconds 0.4 –
1.5 show linear point-to-point pull-in movement. Arrows at second 0.8 mark two
bends of the S-shape grip of the food item (white). Colors, brightness and contrast
were altered to highlight arm movements.

Figure 2 Comparison of normalized tangential velocity profiles during reaching tasks.
A unconstrained animals (taken from Gutfreund et al., 1996) and B constrained
animals. Both graphs show bell shaped curves, aligned at peak velocity and with axes
normalized for time and velocity.

Figure 3 Kinematic profiles of typical waving-like motions. A 3D reconstruction of
the trajectory of an arm. One circle represents the site of the attached food item on the
arm in a single frame of a picture sequence with 25fps. Red circle marks the site of
the target. The axes are in cm. B Normalized tangential velocity profile

Figure 4 Comparison of reaching durations. Reaching durations (in seconds) for
reaching of the straight and waving-like category. Asterisk denotes significance p<
0.05

Figure 5 Number of choices in respective reaching category waving and straight, split
in three trial bins for each animal. Significant differences between the first and third
trial bin were recorded in Animal 3 and Animal 5. Asterisks denote significance p<
0.05.

Figure 6 Kinematic profiles of fetchings of the straight and the deflected category. A,
C 3D reconstruction of typical arm trajectories for each respective category. One
circle represents the site of the attached food on the arm in a single frame of a picture
sequence with 25 fps. Red circles mark the site of the hole. The axes are in cm. B, D
Normalized tangential velocity profiles. One trial is shown for clarity in the deflected category.

**Figure 7** Number of choices in respective fetching category straight and deflected, split in three trial bins for each animal. No significant differences were recorded between the first and third trial bin in each category per animal.
A. Unconstrained animals

B. Constrained animals

Normalized time

Normalized velocity