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Mechanical reconfiguration mediates swallowing and rejection in *Aplysia californica*

Received: 16 November 2005 / Revised: 8 March 2006 / Accepted: 11 March 2006 / Published online: 4 April 2006
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Abstract Muscular hydrostats, such as tongues, trunks or tentacles, have fewer constraints on their degrees of freedom than musculoskeletal systems, so changes in a structure's shape may alter the positions and lengths of other components (i.e., induce *mechanical reconfiguration*). We studied mechanical reconfiguration during rejection and swallowing in the marine mollusk *Aplysia californica*. During *rejection*, inedible material is pushed out of an animal's buccal cavity. The grasper (radula/

odontophore) closes on inedible material, and then a posterior muscle, I2, pushes the grasper toward the jaws (protracts it). After the material is released, an anterior muscle complex (the I1/I3/jaw complex) pushes the grasper toward the esophagus (retracts it). During *swallowing*, the grasper is protracted open, and then retracts closed, pulling in food. Grasper closure changes its shape. Magnetic resonance images show that grasper closure lengthens I2. A kinetic model quantified the changes in the ability of I2 and I1/I3 to exert force as grasper shape changed. Grasper closure increases I2's ability to protract during rejection, and increases I1/I3's ability to retract during swallowing. Motor neurons controlling radular closure may therefore affect the behavioral outputs of I2's and I1/I3's motor neurons. Thus, motor neurons may modulate the outputs of other motor neurons through mechanical reconfiguration.

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Keywords Muscular hydrostat · Biomechanics · Feeding · Soft tissue · Mollusk

Abbreviations I2: Intrinsic buccal muscle 2 · I1/I3: Intrinsic buccal muscles 1 and 3 · LT: Length/tension · FI2: Force in I2 · Fmax: Maximum force · BML: Buccal mass lengths · B8a,b, B61, B62, B63: Buccal ganglion motor neurons and interneurons

Introduction

Soft-bodied structures are capable of complex deformations that cannot easily be generated by musculoskeletal systems. For example, worms can conform to and locomote through tortuous spaces as they burrow (Brusca and Brusca 1990), frogs and squid can rapidly extend tongues or tentacles for predation (Kier and van Leeuwen 1997; Nishikawa 1999; Mallett et al. 2001), octopi can use complex deformations of their tentacles and feeding structures, and elephants can use their trunks for grasping and manipulating objects (Kier and Smith 1985; Wilson et al. 1991). Structures that consist

entirely of muscle, and use muscles for both force generation and structural support are referred to as “muscular hydrostats” (Kier and Smith 1985). Because structural components can change shape, they can potentially reconfigure surrounding or adjacent muscles; we refer to this process as “mechanical reconfiguration”. Mechanical reconfiguration of the musculature may provide soft-bodied structures with additional behavioral flexibility.

Some forms of reconfiguration in soft-bodied structures have been studied. For example, a change in the length of longitudinal muscles can alter the shape and thus the mechanical advantage of surrounding circumferential muscles (Chiel et al. 1992; Van Leeuwen and Kier 1997). This is similar to the agonist/antagonist relationship seen in musculo-skeletal systems (Zajac 1993). These are examples of changes in closely linked degrees of freedom. In addition, because deformations of one part of a soft-bodied structure can alter the positions and lengths of muscles surrounding that structure, more complex forms of mechanical reconfiguration may affect behavior.

In the feeding structure of the marine mollusk *Aplysia californica*, it is known that changes of shape of the central grasper, the radula/odontophore, largely determine the shape of the surrounding muscles of the entire feeding apparatus (Drushel et al. 1997, 1998, 2002; Neustadter et al. 2002a, b). More generally, the radula/odontophores of many mollusks change shape during feeding (e.g., in gastropods: Rose 1971; Rose and Benjamin 1979; in cephalopods: Uyeno and Kier 2005). Do these shape changes lead to mechanical reconfiguration of the surrounding musculature? We have found an example of mechanical reconfiguration in which the changing shape of one part of a soft-bodied structure alters both the mechanical advantage and length/tension properties of two completely distinct surrounding muscles (I2 and the I1/I3/jaw complex), allowing them to apply greater force during behavior.

The reconfiguration is likely to be behaviorally important. The feeding apparatus is capable of generating at least three qualitatively different behaviors: (1) biting, an attempt to grasp food, (2) swallowing, transferring food into the buccal cavity, and (3) rejection, moving inedible material out of the buccal cavity (Kupfermann 1974). In this paper, we use a kinetic model to examine the role of mechanical reconfiguration during swallowing and rejection. At the onset of rejection, the grasper closes on material to push it out of the buccal cavity, changing shape (Neustadter et al. 2002a). The change in grasper shape, in turn, enhances the mechanical advantage and tension producing ability of the I2 muscle, which can then push the grasper more strongly forward to the jaws (i.e., protract it more strongly). In contrast, during swallowing, after the grasper is protracted open, it retracts closed, pulling material to be ingested further into the buccal cavity. The change in grasper shape after it closes allows the surrounding I1/I3/jaw complex to push the grasper more

strongly backward toward the esophagus (i.e., retract it more strongly). These enhancements in muscle forces have important implications for the neural control of swallowing and rejection, in part because they allow the motor neurons of the grasper to mechanically modulate the functional outputs of motor neurons for the I2 and I1/I3/jaw muscles.

Materials and methods

Anatomy of *Aplysia*'s buccal mass

The feeding apparatus of *Aplysia*, which is known as the buccal mass, consists of a central grasper surrounded by muscles that can push it toward the jaws (protract it) or toward the esophagus (retract it) (anatomy shown in Fig. 1a). The central grasper consists of a thin flexible sheet of cartilage-like tissue covered by fine teeth (the radula), whose opening and closing are controlled by underlying musculature (the odontophore). Thus, the entire grasper is referred to as the radula/odontophore. Between the halves of the radula is a structure, the radular stalk (Fig. 1b–d), whose position is controlled by the odontophore. When the halves of the radula are open, the radular stalk is between the radular halves and surrounded by the odontophore musculature, so that the radula/odontophore assumes a roughly spherical shape. When the radular halves close, the radular stalk is pushed out of the ventral part of the odontophore musculature, and so the radula/odontophore assumes a roughly ellipsoidal shape (Neustadter et al. 2002b). Posterior to the radula/odontophore is the thin I2 muscle (nomenclature from Howells 1942) whose contraction protracts the radula/odontophore toward the jaws. Anterior to the radula/odontophore are the thick bands of the I3 muscle that overlay the cartilage of the jaws, and in turn are covered by the very thin I1 muscle; this structure is referred to as the “I1/I3/jaw complex” or “I1/I3”. On the ventral side of the odontophore, fibers of the I2 and the I1/I3 interdigitate with the odontophore; this connection between the radula/odontophore and the surrounding musculature is referred to as the “hinge” (Drushel et al. 1998; Sutton et al. 2004a; inset in Fig. 1a).

Magnetic resonance imaging of rejection

To measure in vivo movements of the feeding apparatus during rejection, we obtained magnetic resonance images of rejections (acquisition rate 3 Hz) in intact behaving animals (methods are described in Neustadter et al. 2002a and in Neustadter and Chiel 2004). The resolution of the images was 1 mm × 1 mm pixels using a total acquisition matrix of 64×128. This spatial resolution was adequate for the buccal masses that were imaged, whose size was on the order 3 cm × 3 cm × 3 cm, and made it possible to obtain images at 3 Hz, which was fast enough to monitor the rejection behavior. Rejection responses

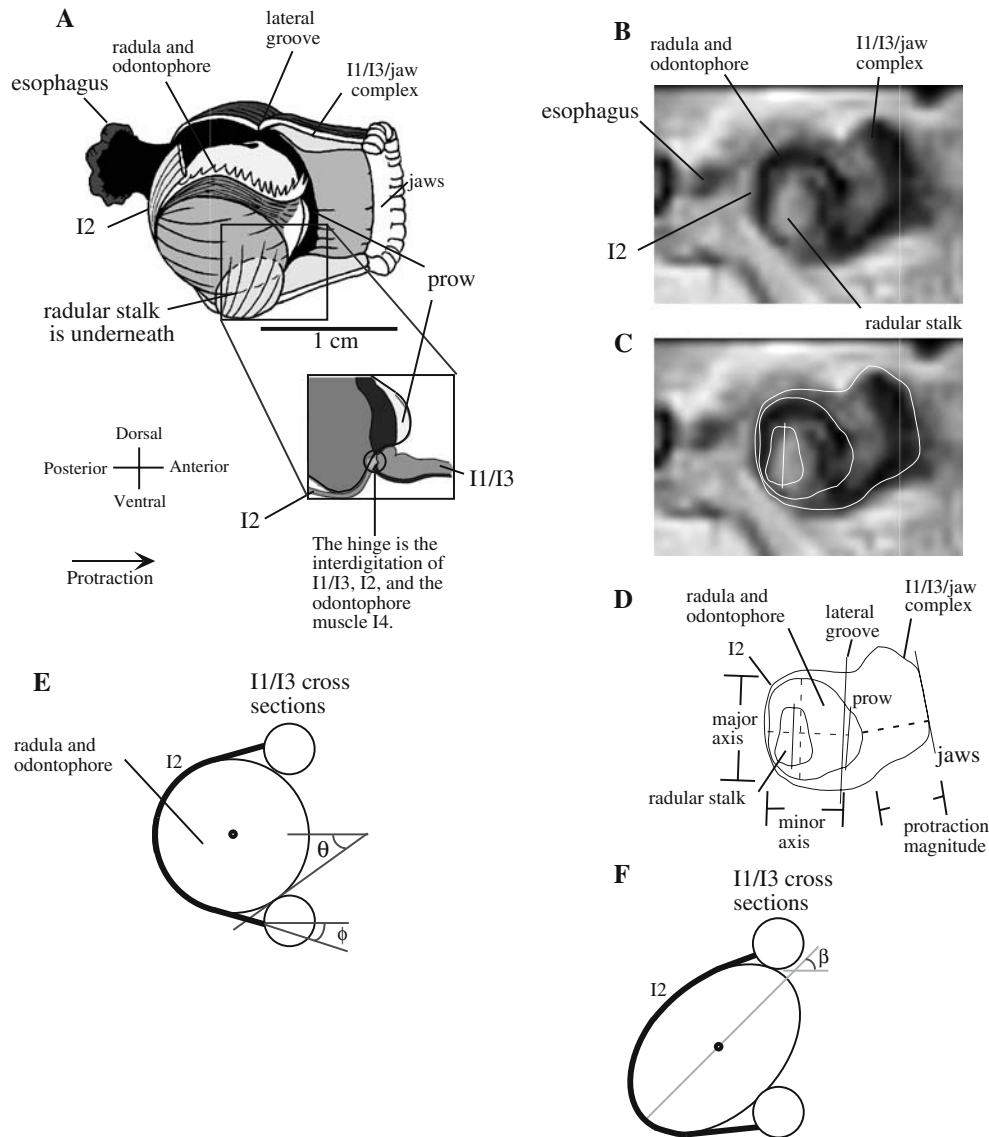


Fig. 1 Anatomy of the buccal mass and a schematic of the kinetic model. **a** Lateral cutaway view of the anatomy of the buccal mass (drawn by Dr. Richard Drushel). The radula is a thin, flexible sheet of cartilage-like material covered with fine teeth. The underlying odontophore consists of a mass of muscles that can open and close the radula. *Inset* shows hinge. **b** Mid-sagittal MRI of the buccal mass in a resting position with landmarks labeled. The radular stalk is a structure internal to the radula and odontophore that is used as a landmark to measure the angle of orientation of the radula/odontophore relative to the rest of the buccal mass. **c** Schematic drawing of outlines of odontophore, radular stalk, and of the buccal mass (including the I1/I3/jaw complex) superimposed on the MRI image shown in part **b**. **d** Schematic drawing of the buccal mass mid-sagittal anatomy based on the MRI picture shown in **b**. The major and minor axes of the radula/odontophore were

defined relative to the angle of the radular stalk. To be consistent with Neustadter et al. (2002a), the odontophore prow is not included in the minor axis of the radula and odontophore. The protraction magnitude was defined as the distance between the anterior-most portion of the radula/odontophore and the jaws. **e** A schematic of the kinetic model in a resting position. The model radula/odontophore is spherical when the radular halves are open. The posterior I1/I3 is represented as a torus anterior to the sphere. The I2 is represented as a sheet posterior to the radula/odontophore that attaches to the I1/I3. **f** Schematic of the kinetic model's representation of a more protracted and closed radula/odontophore. The model adjusts the aspect ratio and orientation of the radula/odontophore to reflect the changes in these measures seen in the MRI, and then estimates the observed muscle forces. See [Materials and methods](#) and [Fig. 2](#)

were induced in several ways: an animal was allowed to swallow a polyethylene tube; it was allowed to swallow seaweed attached to a string; or it was induced to swallow a string with seaweed wrapped around it. All of these stimuli induced rejection responses. We obtained a total of 11 rejection responses from four animals. During normal rejection responses, animals withdraw their head

and pull their body away from the stimulus. As a consequence of these whole body movements, only one of the eleven responses was sufficiently free of parallax and sufficiently close to the midline to be suitable for analysis (sequence 3229, slice 1, frames 85 through 103, induced by string wrapped with seaweed). Parameters were extracted from each frame of this sequence (MRI and

parameters shown in Fig. 1b–d; methods are described in Neustadter et al. 2002a).

Shape-changing kinetic model of the buccal mass

In previous work, we described a kinetic model of the buccal mass in which the grasper (radula/odontophore) was represented as a rigid sphere, the I2 protractor muscle was represented as a hemispherical sheet posterior to the sphere, the posterior of the I1/I3 was represented as a single torus (corresponding to a single circumferential muscle band of I3) that was anterior to the midline of the sphere when the structure was at rest, and the hinge was represented as a visco-elastic spring (Sutton et al. 2004b). In vivo, the odontophore both changes shape as it opens or closes, and rotates about the hinge. As described above, when the grasper is fully open, it assumes a roughly spherical shape, whereas when it is closed, it assumes a more ellipsoidal shape (Neustadter et al. 2002a). Thus, the model reported in this paper represented the ability of the central grasper to change from a spherical to an ellipsoidal shape, and also represented its ability to rotate about the hinge. In the model, the odontophore was an isovolumetric structure whose shape ranged from spherical (aspect ratio equal to 1.0) to ellipsoidal (aspect ratio equal to 2.0, based on MRI measurements in which the major axis was defined by the axis of the radular stalk). These values were chosen to match MRI data that showed that the ellipticity of the odontophore ranges from 1 (spherical) to 2 (ellipsoidal) (Neustadter et al. 2002a, ratio of data from left and right columns of Fig. 12 in that paper).

To place the components of the model in their correct orientation, the following sequence was followed: (1) the aspect ratio of the odontophore was set, (2) the displacement of the odontophore relative to the line of the center of the I3 torus was set, (3) the angle of rotation of the odontophore (β) was calculated based on a kinematic rule (see below), (4) the angles of contact between the top and bottom surfaces of the I3 torus were calculated using the Newton–Raphson root finding technique, (5) the I2 was placed so that it extended from the middle of the top of the I3 torus to the middle of its bottom (Fig. 1e, f, showing cross-sectional view of shape change model), and (6) the length of I2 was calculated from an exact geometric solution approximated by a fourth-order polynomial function.

The relationship between odontophore displacement and rotation was based on an analysis of the kinematics of rejection as observed in the single MRI recording described above, and the analysis of the kinematics of swallowing as previously described (Neustadter et al. 2002a). To transform the displacements and rotations into the coordinate system of the kinetic model, the lateral groove of the MR image was oriented to be vertical, and the angle of the radular stalk was measured relative to the lateral groove, leading to an equivalent

displacement and angle setting for the model odontophore (see Fig. 2 for the transformation of MR data into key model frames).

The mechanical advantages of the model I2 and I3 muscles were calculated as previously described (Sutton et al. 2004b). The net force exerted by I2 on the odontophore was proportional to the cosine of the angle (ϕ) between I2 and the odontophore (Fig. 1e), whereas the net force exerted by I3 on the odontophore was proportional to the tangent of the angle (θ) between I3 and the odontophore (Fig. 1e).

Given the input positions, and the length/tension properties of I2 and I3 (as defined in Sutton et al. 2004b, based on Yu et al. 1999), the model calculated the resultant forces on the odontophore. Results are reported as normalized forces.

Results

MRI kinematics of rejection

What is the odontophore's kinematics during rejection, and how does it compare with the kinematics observed during swallowing? Prior work has demonstrated that the odontophore shape, position and orientation determine the configuration of *Aplysia's* feeding apparatus (Drushel et al. 1997, 1998; Neustadter et al. 2002b) and has characterized these kinematic properties for swallowing (Neustadter et al. 2002a). To understand the kinematics of rejection, we measured kinematics of a single mid-sagittal rejection that we were able to record using magnetic resonance imaging (chosen from 11 behaviors because of its relatively low parallax; see Materials and methods). Several images from the MRI rejection behavior are shown in Fig. 2. We measured the shape of the odontophore (see Materials and methods for techniques), and observed that at the onset of protraction, the odontophore elongated dorso-ventrally and narrowed antero-posteriorly, leading to an increase in its aspect ratio (Fig. 3a). These results are consistent with previous observations that closure of the radular halves is associated with elongation of the odontophore during swallowing (Neustadter et al. 2002a, b). In turn, this suggests that we are observing an initial closure of the radular halves at the onset of rejection, consistent with previous observations that the radula is closed during the protraction phase of rejection, whereas it protracts open during biting or swallowing (Morton and Chiel 1993a). Note that in measuring the aspect ratio, we did not include either the prow or the radular stalk (to be consistent with Neustadter et al. 2002a). If these structures are included, the aspect ratio during rejection varies from 1.1 to 1.6.

We measured the position of the odontophore and observed that the anterior tip of the odontophore protracts past the jaws (Fig. 3b), similar to the protractions observed in biting (Morton and Chiel 1993a). We measured the orientation of the odontophore, and found

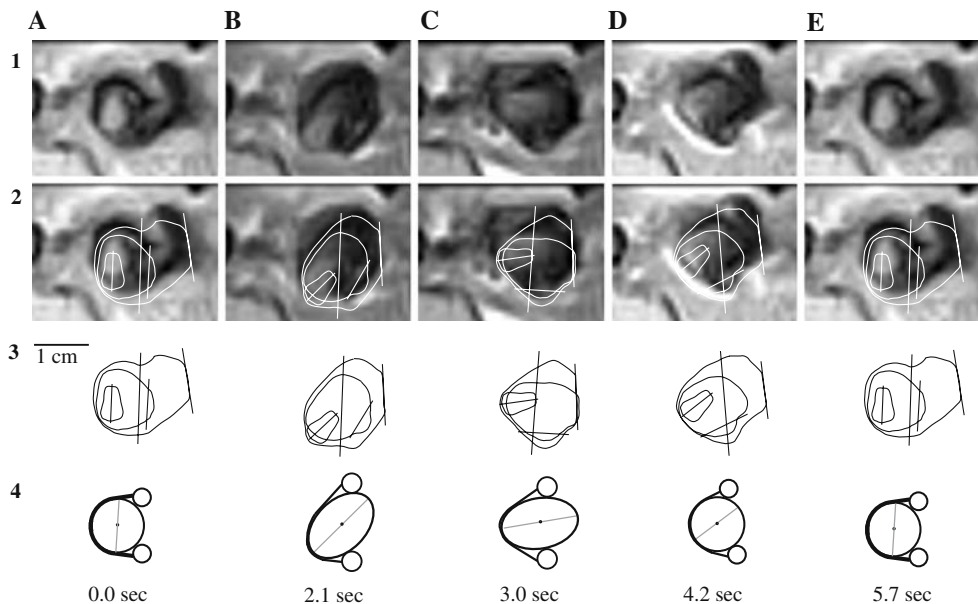


Fig. 2 Five frames from an MRI sequence of an in vivo rejection. *1* MR images of the behavior. *2* MR images with a sketch of the anatomical locations superimposed (same landmarks as presented in Fig. 1d). *3* Sketches of the anatomical orientations shown without the MRI. *4* Transformed kinetic model representation of these frames. Note that the major axis angle is based on radular stalk angle. **a** Rest position. The radula/odontophore is roughly spherical. **b** Mid-protraction. The radula/odontophore has become ellipsoidal in shape and has rotated clockwise. **c** Peak protraction.

The ellipsoidal radula/odontophore has rotated 80° clockwise, and the anterior-most portion of the radula/odontophore has extended past the jaws. Note that the torus representing the I3 muscle (i.e., the circles at the top and bottom of the diagram) models the most posterior part of the entire I1/I3/jaw complex. **d** Mid-retraction. The radula/odontophore has become more spherical and is rotating counterclockwise. **e** Return to rest position. Data are from images in set 3229, S1, F85–F103

that during protraction, the odontophore rotates toward the jaws through an angle of about 80°, similar to the rotation observed during swallowing (Fig. 3c; compare Neustadter et al. 2002a, Fig. 13, left column).

What mediates the very strong protraction of rejection? The major protractor muscle, I2, is a thin sheet posterior to the odontophore (Fig. 1a), and thus changing the shape of the odontophore could increase I2's length, changing I2's position on its length/tension curve, as well as increasing I2's mechanical advantage. We focused first on I2's length. We measured the length of I2 during the rejection response. During the onset of protraction, the I2 muscle elongated (Fig. 3d) at the same time that the odontophore's aspect ratio increased (Fig. 3a), approaching I2's optimal length to exert force ($0.98 l_{mto}$; Yu et al. 1999). The I2 then steadily shortened during protraction, reaching 68% of its optimal contractile length at the peak of protraction (so during rejection, I2 ranged from 0.98 to 0.68 l_{mto}). The odontophore was more protracted during rejection than it was during swallowing, and the I2 was longer throughout the protraction phase of rejection than it was during swallowing (in swallowing, I2 ranges from 0.86 l_{mto} at the onset of protraction to 0.69 l_{mto} at the peak of protraction; Neustadter et al. 2002a). The longer length of I2 throughout the protraction phase of rejection could allow I2 to exert the force necessary for generating a larger amplitude protraction (Yu et al.

1999; Sutton et al. 2004b; a general discussion of the role of length/tension properties in muscle is found in Zajac 1989). In contrast, at the peak of biting, a kinetic model predicts that I2's length will be too short to fully protract the odontophore unless it is either neuromodulated or assisted by another muscle (Sutton et al. 2004b). The I2 length observed at the peak protraction of rejection is much larger than that predicted for the peak protraction of biting, suggesting that the ability of I2 to exert protractive forces in rejection is much greater than in biting (Sutton et al. 2004b).

Grasper shape change enhances I2 force during protraction phase of rejection

Does the change in odontophore shape enhance I2's ability to exert force by increasing I2's length and I2's mechanical advantage? To answer this question, we simulated I2's length/tension properties and its mechanical advantage in a kinetic model in which the odontophore shape could be changed from spherical to ellipsoidal while maintaining a fixed volume (see Materials and methods). Increasing the aspect ratio of the odontophore from 1.0 (spherical) to 2.0 (ellipsoidal) increased the length of the I2 muscle for any given angle and displacement. If the odontophore was fixed at a

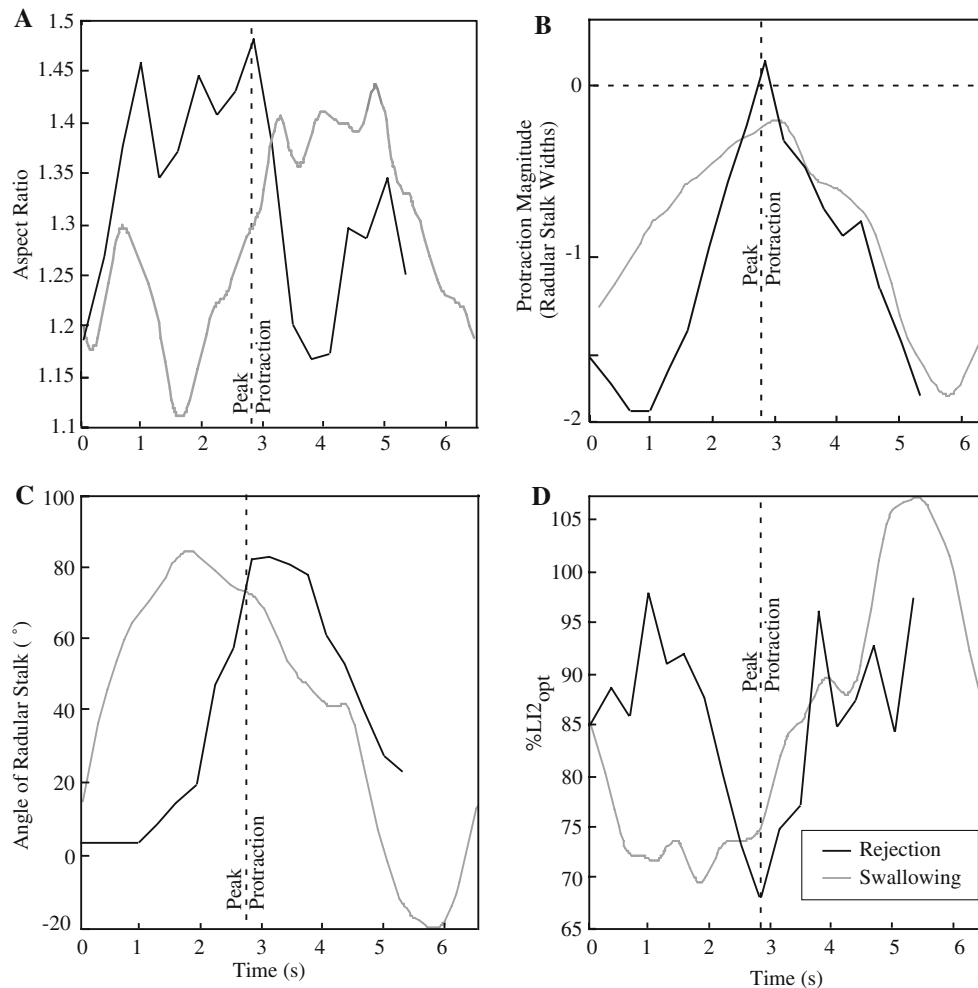


Fig. 3 MRI measurements of buccal mass kinematics during a single rejection behavior. For comparison, average measurements of swallowing are shown in gray (based on Neustadter et al. 2002a). **a** The aspect ratio is computed by dividing the major radula/odontophore axis length by the minor radula/odontophore axis length. In rejection, the aspect ratio increases during protraction, reaching a maximum of 1.48, and then decreases during retraction to a minimum value of 1.15. In contrast, note that the maximum aspect ratio for swallowing (1.42) occurs during retraction (when the grasper is closed on food that is pulled into the buccal cavity). **b** Protraction magnitude during rejection and swallowing. The radula/odontophore protracts past the jawline at peak protraction (indicated by horizontal dashed line), achieving a larger protraction magnitude than the protraction magnitude observed during swallowing. **c** Angle of orientation of the radular stalk during

rejection and swallowing. The radular stalk rotates clockwise during protraction (toward the jaws) and rotates counterclockwise during retraction (toward the esophagus). Note that rotation toward the jaws ends earlier in swallowing than in rejection, and that rotation toward the esophagus continues for longer in swallowing and reaches a larger magnitude. **d** Length of I2 muscle during rejection and swallowing. The initial increase in odontophore aspect ratio is accompanied by an initial increase in I2 length. As the odontophore continues to protract, the I2 length decreases. The I2 minimum rejection length is 68% of I2's optimal length, only slightly shorter than the minimum length of I2 observed during swallowing (69%). Note that during swallowing, I2 reaches its maximum length near the peak of retraction rather than early in protraction

given shape and was rotated and displaced forward based on the observed in vivo kinematics (see [Materials and methods](#)), the tension in I2 was greater as the aspect ratio increased for all displacements beyond the resting position (Fig. 4a). Under the same conditions, the mechanical advantage of I2 was also increased by increasing the odontophore's aspect ratio at all but the initial displacement past rest (Fig. 4b) because the angles of interaction between I2 and the odontophore decrease, so that more of I2's force component (which is pro-

portional to $\cos\phi$) is directly exerted on the odontophore (note schematic diagrams in Fig. 4a). Since the total force in I2 is a product of its tension and its mechanical advantage, the net force that I2 exerts as the odontophore protracts increases as the aspect ratio of the odontophore increases (Fig. 4c). These results hold true even if the odontophore changed shape without rotating (data not shown). Thus, the change of shape of the odontophore leads to an increase in the length and mechanical advantage of I2, and this reconfiguration

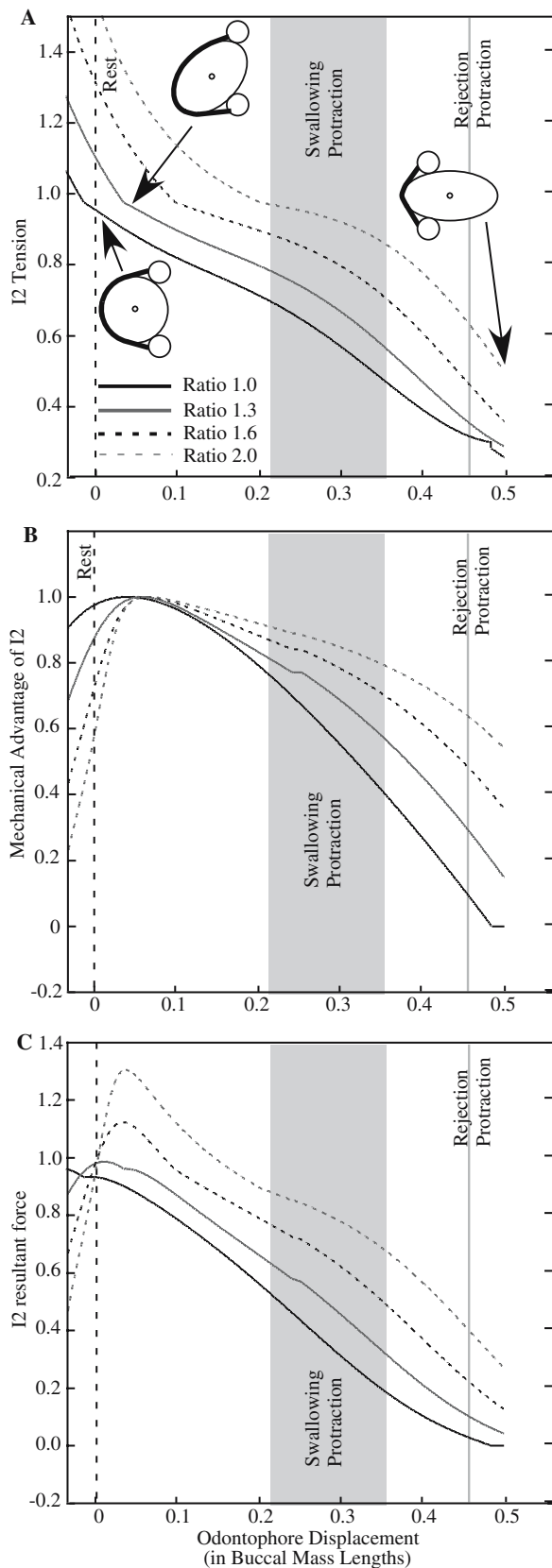


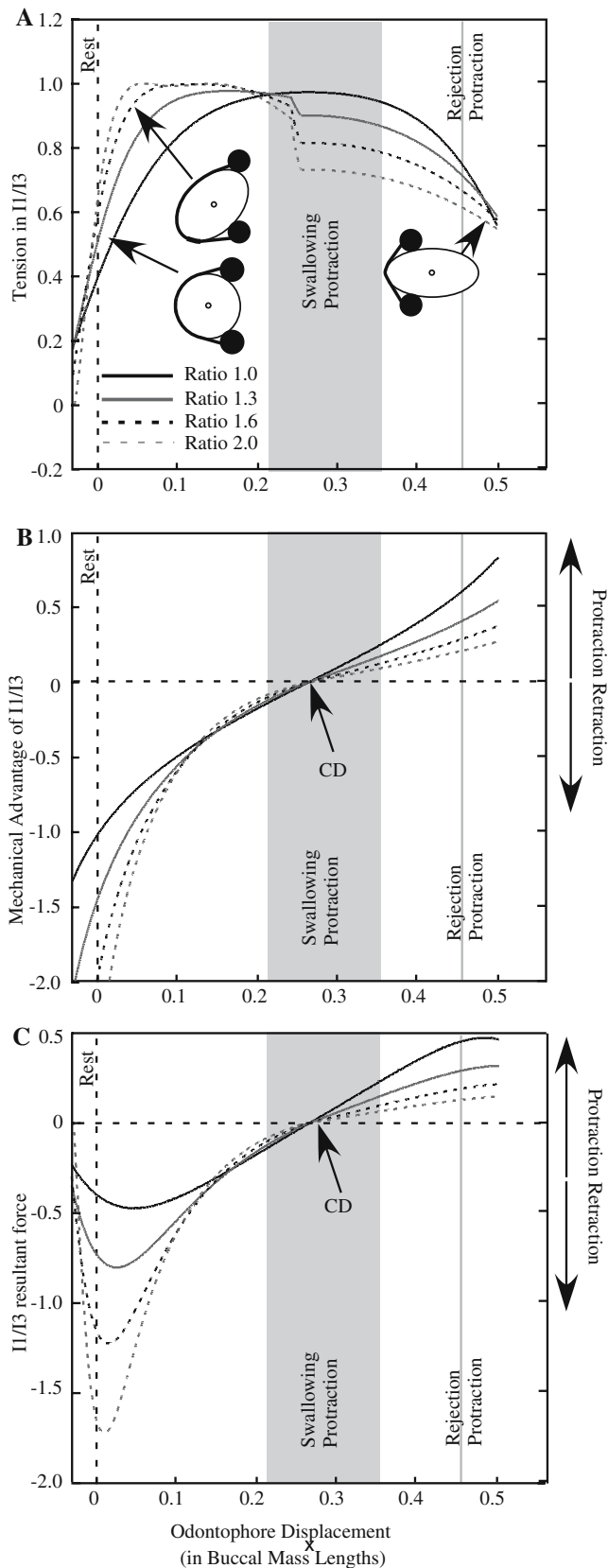
Fig. 4 Mechanical analysis of I2 at different odontophore aspect ratios and displacements. **a** Maximum tension that I2 can generate (calculated using I2's length/tension property for the given buccal mass configuration). Increasing the odontophore's aspect ratio increased the tension that I2 could generate. The tension in I2 increased past the optimal contractile tension (1.0) because passive forces are included in this calculation. **b** Mechanical advantage of I2. Maximal mechanical advantage is 1.0. At all displacements past the resting position by 13% of the peak protraction displacement, an increase in the odontophore's aspect ratio caused an increase in I2's mechanical advantage, increasing the amount of force that a given amount of I2 tension would apply to the radula/odontophore. **c** Resultant maximum force that I2 can apply to the radula/odontophore (i.e., the product of **a** and **b**). For all displacements beyond the resting position, an increase in the odontophore's aspect ratio increased the amount of force that I2 could apply to the radula/odontophore

allows I2 to exert greater force throughout the protraction phase of rejection.

Reconfiguration enhances I3's strength during retraction phase of swallowing

How does reconfiguration affect the other major muscle group (the I1/I3/jaw complex) that moves the grasper? We approached this question in two stages. We first examined the effects of shape change without rotation. The odontophore's shape was varied from spherical to ellipsoidal (aspect ratio varied from 1.0 to 2.0). The tension and mechanical advantage for the posterior I3 torus were calculated for positions ranging from full retraction to full protraction. We observed that both the mechanical advantage and tension in the I3 torus dropped as the shape of the odontophore changed from spherical to ellipsoidal (data not shown). The mechanical advantage dropped because the angle of contact (θ) between I3 and the odontophore decreased, and the force that I3 exerts on the odontophore is proportional to $\tan\theta$. The tension dropped because the cross-sectional area of the odontophore became smaller, thus shortening I3. Because of the changes in I3's mechanical advantage and the change of I3's position on its length/tension curve, the largest forces that I3 exerted were on the spherical odontophore, and the smallest were on the ellipsoidal odontophore.

In the second stage, as the odontophore's shape changed and it also rotated, we examined the tension in the I3 torus (Fig. 5a) as well as I3's mechanical advantage (Fig. 5b). The results were similar to the predictions obtained when the odontophore only changed shape and did not rotate, and predicted that I3 would become more effective at retraction as the aspect ratio of the odontophore increased for any displacements that were less than 28% of the peak protraction displacement



(Fig. 5c). The projected paths of the rejection and swallowing behaviors are shown on the mechanical force plots in Fig. 6.



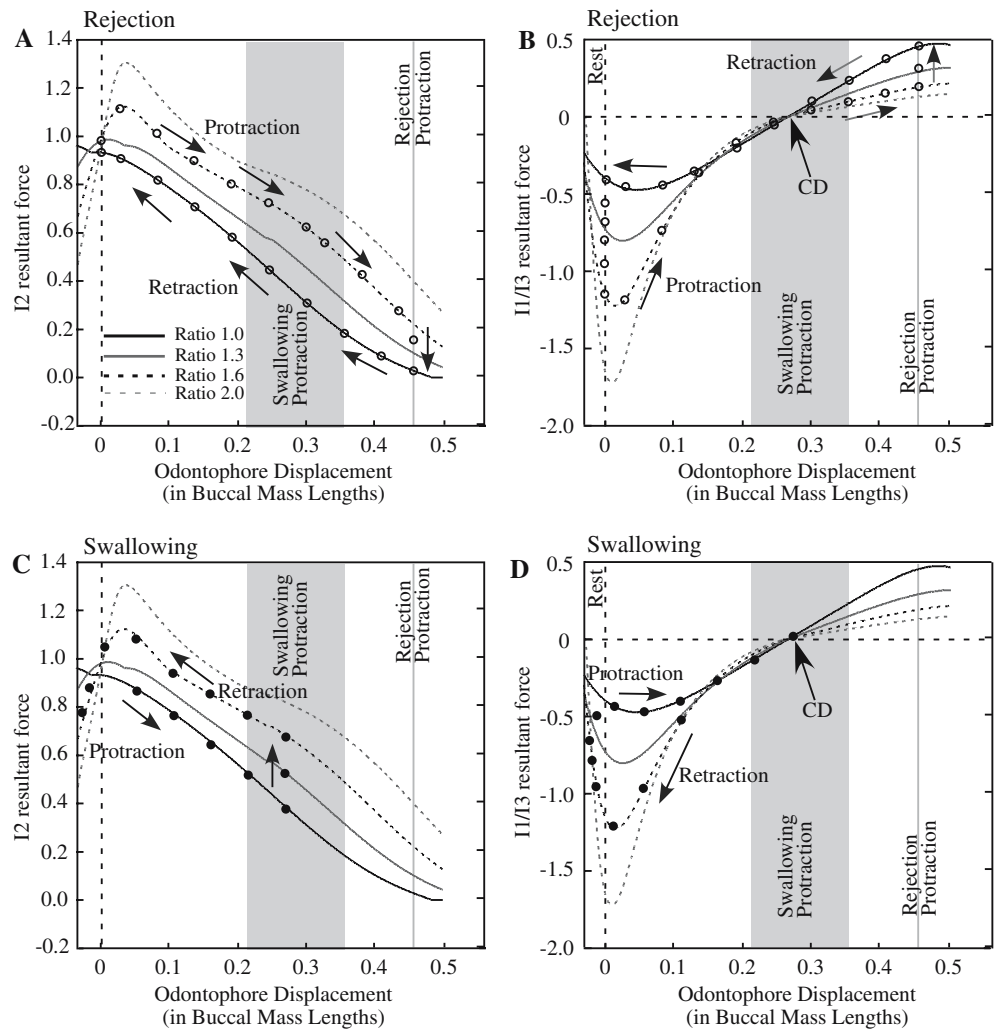
Fig. 5 Mechanical analysis of posterior part of the I1/I3/jaw complex at different odontophore aspect ratios and displacements. **a** Maximum tension that the I3 torus can generate (calculated using I3's length/tension property for the given buccal mass configuration; values are again normalized to the maximum contractile force). At large protractions, greater than the magnitude of those observed in swallowing, increases in odontophore aspect ratio decreased I1/I3's ability to generate tension. At small protractions or retractions, increases in odontophore aspect ratio increased the ability of the I3 torus to generate tension. **b** Mechanical advantage of I3 torus. Regardless of odontophore shape, there is still a context-dependent point (marked CD). If the odontophore is posterior to this point, contraction of the I3 torus will cause retraction, and if the odontophore is anterior to this point, contraction of the I3 torus will cause protraction (i.e., the direction of force exerted by the I3 torus reverses). Increases in odontophore aspect ratio decrease the mechanical advantage of the I3 torus in protraction (right side of the CD point), but they increase the magnitude of the mechanical advantage of the I3 torus in retraction (left side of the CD point). **c** Resultant maximum force that the I3 torus can apply to the radula/odontophore (the product of **a** and **b**). Increases in odontophore aspect ratio cause the I3 torus to become a weaker protractor (right side of the CD point), but a stronger retractor (left side of CD point)

Previous work had shown that the net forces generated by the posterior of I3 changed from protractive to retractive as the odontophore was moved beyond the context-dependent point (Fig. 5b, point marked "CD"; Sutton et al. 2004b). Changing the shape of the odontophore did not alter the location or the mechanical significance of the context-dependent point. Thus, the concept of a context-dependent point (Sutton et al. 2004b) can be extended to a larger behavioral regime than just the protraction phase of biting or swallowing. Moreover, the displacement of the odontophore anterior to the context-dependent point imposes an important constraint on the overall time of the behavioral cycle: the further anteriorly the odontophore is displaced relative to the context-dependent point, the longer it will take for the odontophore to return to that point. In turn, this implies that hinge forces may be important for speeding the return to the context-dependent point. Furthermore, this may impose a constraint on the timing of activation of the I2 protractor muscle relative to the onset of activation of the I1/I3/jaw complex. Ending I2 activation will permit the odontophore to retract in response to hinge forces and activation of the I1/I3/jaw complex for retraction may be delayed until the radula/odontophore has moved posterior to the context-dependent point (Fig. 7).

Discussion

In a soft tissue structure, changing the shape of one part may affect both the length tension property and the mechanical advantage of other muscles, and these effects are multiplicative. Kinematic measurements based on magnetic resonance imaging suggest that during the

Fig. 6 I2 and I1/I3 maximum resultant forces on the odontophore in rejection and swallowing based on the mechanical analysis of the musculature (Figs. 4, 5), and MRI. **a** I2's maximum resultant force during rejection. At the onset of protraction, the odontophore closes (assuming an ellipsoidal shape), increasing I2's strength. The odontophore then returns to a spherical shape during retraction (*open circles* show this path). **b** I1/I3's maximum resultant force during rejection. The odontophore protracts closed (i.e., with an ellipsoidal shape) and retracts open (i.e., with a spherical shape) (*open circles*). I1/I3 is a weak retractor during rejection. **c** I2's maximum resultant force during swallowing. The odontophore protracts open (i.e., with a spherical shape), and retracts closed (i.e., with an ellipsoidal shape) (*solid circles*). **d** I1/I3's maximum resultant force during swallowing. The odontophore protracts open (i.e., with a spherical shape) and retracts closed (i.e., with an ellipsoidal shape) (*solid circles*). The change in odontophore shape increases the resultant force that I1/I3 can generate in retraction during swallowing



protraction phase of rejection, the elongation of the odontophore may contribute to the larger amplitude protraction. We tested this hypothesis in a kinetic model, and found that I2's ability to exert force during protraction was enhanced as a consequence of the grasper's shape change because I2's elongation altered I2's position on its length/tension curve, and the grasper shape change increased I2's mechanical advantage.

We observed that the change in direction of I3's force at the context-dependent point was unaffected by changes in odontophore shape, suggesting that this point is significant not only for biting and swallowing (Sutton et al. 2004b) but also for rejection. Furthermore, the shape change and rotation of the odontophore may contribute to enhancing the ability of the I1/I3/jaw complex to retract the odontophore during swallowing. These results predict that during swallowing, when the odontophore is closed during retraction, the I1/I3/jaw complex will become a more effective retractor. Thus, structural reconfiguration of the I2 and I3 muscles surrounding the grasper as it changes shape and angle are likely to be behaviorally significant.

Limitations of results

Our previous study of swallowing analyzed four behaviors so as to provide statistical measures of the different kinematic parameters during the feeding cycle (Neustadter et al. 2002a, b). We were unable to do this for rejection because of the difficulty of obtaining mid-sagittal, parallax-free images. Of the eleven rejections, there were five in which radula/odontophore shape could be observed throughout the entire behavior. In all five of these rejections, the radula/odontophore elongated prior to and during the protraction phases of the behavior, and then shortened during the retraction phase, consistent with the behavior in the one rejection that we extensively analyzed in this paper. Furthermore, the results we have shown are qualitatively consistent with previously described features of rejection: (1) rejections are associated with strong protractions (Kupfermann 1974; Hurwitz et al. 1996); (2) during the protraction phase of rejection, the odontophore is closed, and opens during the retraction phase (Morton and Chiel 1993a); (3) closure of the odontophore is

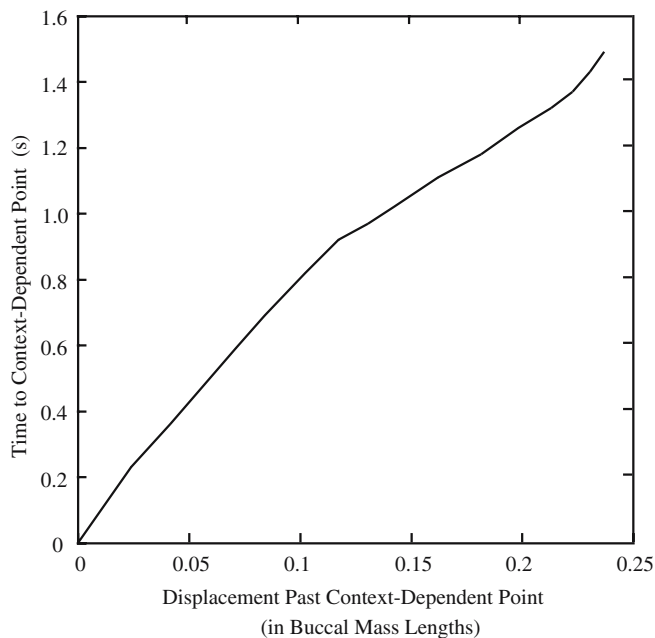


Fig. 7 Time required for the passive hinge forces to pull the radula/odontophore from a protracted position to the context-dependent point. The farther the radula/odontophore is protracted, the longer it takes the passive forces to pull the odontophore back. Active hinge forces would decrease but not eliminate this time delay

associated with its elongation in the mid-sagittal plane (Neustadter et al. 2002a). The mid-sagittal views of the one rejection that we have analyzed are consistent with all of these qualitative observations, and the MR images therefore allow us to estimate the kinematics of rejection.

Although the kinetic model simplifies many aspects of the feeding apparatus, it is likely that its conclusions are qualitatively valid. First, odontophore shape may be quantitatively inaccurate, because we track the mid-sagittal cross-section, but do not attempt to match its medio-lateral dimensions. Moreover, I2 divides and courses around the esophagus, which is also not represented in the model. Nevertheless, the mid-sagittal change in I2 length is directly observed in the MR images, and thus the model conclusions are likely to be qualitatively correct.

Second, the kinetic model represents I3 as a single torus, and thus only represents the posterior portion of the I1/I3/jaw complex. In *Aplysia kurodai*, differential activation of the I1/I3 musculature has been described (Nagahama and Takata 1988; Nagahama and Shin 1998), and motor neurons for the I1/I3 project to different regions of the muscle in *A. californica* (Scott et al. 1991; Church et al. 1991), suggesting that regions of the muscle may be differentially activated as well. Nevertheless, a more realistic representation that takes into account the extended lumen of the I1/I3/jaw complex still has a context-dependent point at which the net forces in the muscle shift from protraction to retraction. As a consequence, the I1/I3/jaw complex would still be shortened and show similar changes in mechanical

advantage due to the change in shape and rotation of the grasper. Thus, the results reported in this paper are likely to be qualitatively correct.

Third, the model prediction that retraction is initiated by a contraction of the hinge could be inaccurate because the hinge length was not directly measured. However, in our prior studies, we controlled the length of the hinge by pulling on the tip of the odontophore, elongating it, and thus changing the odontophore's shape to be more similar to that observed during rejection. Thus, our estimate of forces in the hinge is probably at least as accurate for rejection as it was for biting (Sutton et al. 2004a).

Fourth, it is possible that the passive forces in the model, especially of I3, are inaccurate, because we have not yet directly measured them. However, the mechanical advantage of the I3 on the shape changing and rotating odontophore will be unaffected by changes in I3's passive forces. Furthermore, the model's estimate of I3's tension assumes that I3 is operating on the ascending limb of its length/tension curve, which will not be affected by the passive properties. Since this is the region of operation for most muscles, the assumption is reasonable (Van Leeuwen 1991).

Fifth, our model does not take into account the effects of sensory input, either proprioceptive or exteroceptive, on the forces generated by the buccal mass. Behavioral studies of *Aplysia oculifera* have demonstrated that the duration and amplitude of the retraction phase of swallowing are changed by increases in load (Hurwitz and Susswein 1992). Mechanoaerents have been described for the buccal mass, and feedback from mechanoaerents is likely to control the switch from biting to swallowing and to control the intensity of the retraction phase of swallowing (Evans and Cropper 1998; Evans et al. 1999; Rosen et al. 2000a, b). Furthermore, increased facilitating activity, probably reflecting the activation of the I4 muscle, was observed in EMG records of the I2 muscle in intact animals when the animals exerted additional force against a load during swallowing (Hurwitz et al. 1996, Fig. 11C). In the analysis presented in this paper, we assumed that the I2 and the I3 muscles were receiving their maximal activation, and thus our results constitute an upper bound on the behavioral effects of the muscles. Sensory feedback may be very important in rapidly reaching this upper bound, but will not qualitatively change the results that we have presented. Of course, if sensory feedback reduces muscle force, then the upper bound will not be reached.

Finally, by using an ellipsoidal shape, the model assumes that the widest extent of the odontophore medio-laterally is always at its center throughout its changes in shape. The MRI data suggests that this is an oversimplification, and that the widest medio-lateral extent of the odontophore may shift anteriorly as it closes. Shifting the widest medio-lateral extent of the odontophore will shift the location of the context-dependent point. This inaccuracy does not affect our conclusions

about the enhanced ability of I2 to protract the radula/odontophore. However, if the widest lateral extent of the odontophore were shifted anteriorly, this would shift the context-dependent point, thus increasing the time for the radula/odontophore to move posterior to the I3. This would require an even larger pause in the activity from the end of I2 activation to the onset of I3 activation, further increasing the effect of mechanical reconfiguration on neural control. Furthermore, since the odontophore opens near the peak of protraction during rejection, so that the odontophore becomes more spherical, the model's predicted location for the context-dependent point is likely to correspond well with the *in vivo* location after the peak of protraction.

Biomechanical implications for feeding

Changing the shape of the odontophore reconfigures the musculature surrounding the odontophore so that those muscles can exert more force against external loads. Thus, during the power phase of rejection, which is protraction (i.e., the phase in which inedible material is pushed out of the buccal cavity), the change in shape of the odontophore as it closes stretches the I2 protractor muscle, allowing I2 to exert greater force during protraction (Figs. 4, 6a). Similarly, during the power phase of swallowing, which is retraction, the odontophore has closed on food that it is attempting to pull into the buccal cavity. The change in shape of the odontophore acts to stretch the I1/I3/jaw complex, enhancing its position on its length/tension curve; at the same time, that the grasper's rotated position and shape change enhance I1/I3's mechanical advantage. The product of these two factors enhance I1/I3's ability to exert force during the retraction phase of swallowing (Figs. 5, 6d).

Does mechanical reconfiguration affect behavior at the level of the whole organism? Several empirical tests could be done to address this question. Using an *in vitro* preparation, it would be possible to change the shape of the odontophore by opening or closing it, activate the I2 protractor muscle, and then measure whether the speed or distance of protraction was affected by the shape of the odontophore, as well as whether the movement was more forceful. Similarly, an *in vitro* preparation could be used to measure the effect of odontophore shape on the ability of the I1/I3/jaw complex to exert retractive forces on the odontophore.

Reconfiguration and neural control

Reconfiguration can change the interactions between motor neurons through mechanical coupling. For example, motor neurons for closing the odontophore can enhance the effectiveness of motor neurons for the protractor muscle, even though these neurons are not coupled synaptically within the ganglion (Church et al. 1991). In particular, activating the radula/odontophore closer motor neurons, B8a/b (Morton and Chiel 1993b)

prior to or during activity in the motor neurons for the I2 protractor muscle (B61, B62, B31, B32; Hurwitz et al. 1996) will change the shape of the odontophore as it is protracted, stretching I2 and enhancing both its tension and mechanical advantage (Fig. 4), and thus the mechanical effects of its motor neurons.

Reconfiguration and context-dependence are critical for the expression of forces in the I1/I3/jaw complex. In the model, the duration of activity in I2's motor neurons and the shape of the odontophore determine the position of the radula/odontophore relative to the middle of the I3 torus, which in turn determines whether the forces that I3 exerts will be protractive or retractive (Fig. 5). Activity of the radula/odontophore closer motor neurons, by changing the shape of the odontophore, also changes the length of the I3 torus and its mechanical advantage on the odontophore (Fig. 5), and thus the effectiveness with which I3 can exert force. As a consequence, the effects of the I1/I3/jaw complex motor neurons are coupled mechanically to the activity in motor neurons for the I2 protractor muscle and radular closer motor neurons. The model assumes that changing the shape of the odontophore does not change the location of the widest cross-section of the odontophore. However, as discussed above, *in vivo*, it is possible that as the radula/odontophore closes, the widest cross-section may shift from the middle to a more anterior position (Neustadter et al. 2002b). In turn, this suggests that activity in the radular closer motor neurons may not only affect the net force that the I1/I3 can exert, but also the location of the context-dependent point.

In addition to controlling the position of the I1/I3/jaw complex relative to the context-dependent point, the change in shape of the odontophore has other implications for neural control. During rejection, after the grasper closes and protracts to push inedible material out of the buccal cavity, it opens to release the material. If the I1/I3/jaw complex begins to contract shortly after the onset of protraction, it will act to close the halves of the grasper, which in turn will pull inedible material back into the buccal cavity. This implies that during rejection, contraction of the hinge initiates retraction, and that activation of the I1/I3/jaw complex will be delayed until its contraction will not induce closure of the grasper. In contrast, during swallowing, the grasper closes near the peak of protraction, and strong activation of the I1/I3/jaw complex will enhance the ability of the grasper to remain closed on food.

These results suggest that biomechanical interactions are likely to be critical for interpreting motor neuronal activity. For example, Ahn and Full (2002) have shown that two very similar muscles can act as a brake or a motor depending on their mechanical context. More generally, biomechanical coupling implies that behavioral outputs may only be deducible from looking at activity in multiple motor neuronal pools in the context of the appropriate biomechanics, and may create constraints or opportunities for the interneuronal coordination of multiple motor pools.

Given the low mass and low velocity of most molluscan feeding systems, inertial forces are low, and thus the time from neural activation to final movement is not dominated by inertial forces. As a consequence, it would be reasonable to assume that the transformation of neural activity to behavior would be fairly transparent. Indeed, because the system is quasi-static (Sutton et al. 2004b), the time for a muscle to change position is dominated by the activation and de-activation dynamics of the muscles, which supports the importance of understanding the neuromuscular transform (Brezina et al. 2000a, b). However, the reconfiguration of the musculature creates important interdependencies between different muscles, so that the net behavioral output becomes a function of the peripheral configuration, not just neural activation. For example, a recent study of swallowing in *Aplysia* demonstrated that the functions of motor neurons B7 (for the hinge) and B8 (for closing the halves of the radula) depend on mechanical context (Ye et al. 2006). Another example is the timing of onset of retraction relative to protraction in rejection, which is largely a function of the timing of deactivation in the I2 muscle and the time for the odontophore to move posterior to the context-dependent point, and thus depends on active and passive forces in the hinge (Fig. 7 illustrates the time dependence for the passive hinge forces). More generally, the duration of rhythmic behaviors will emerge both from the time constants of activation of the musculature, and the time for peripheral interactions to occur (e.g., the time for the system to pass the context-dependent point).

Many forms of modulation have been described in *Aplysia*'s nervous system. Neuromodulators that are extrinsic or intrinsic to the neural circuitry controlling feeding (Katz and Frost 1996) may act to alter transmitter release, or may act directly on a muscle to alter its response to conventional transmitters, thereby altering the neuromuscular transform (Brezina et al. 1996; 2000b; 2003; 2005). In particular, modulation has been described in both the I2 muscle (Hurwitz et al. 2000) and in the I1/I3 muscle (Fox and Lloyd 1997, 1998).

The term "neuromodulation" is currently used in two senses: the alteration of a neuron's intrinsic or synaptic properties by chemicals (neurotransmitters or hormones: Katz and Frost 1996; LeBeau et al. 2005), or the use of artificial electrical stimulation of neurons to alter some aspect of the periphery (e.g., reduce pain or improve bladder function; Scheepens et al. 2002). We have demonstrated a novel mechanism for modulation that is due to the system's mechanics: changing shape (firing of motor neuron B8) potentiates the amount of protractive force caused by firing of I2's motor neurons (B31/32 and B61/62), so that I2 can push the radula/odontophore toward the jaws (protract) with greater force. Thus, our results suggest a new form of interaction between neurons: *neuromechanical modulation*, in which the actions of one neuron are influenced by the outputs of another neuron through mechanical coupling. Neuromodulation of individual motor neurons and muscles through

chemical influences (from other neurons, or from circulating hormones) combined with mechanical reconfiguration of individual muscles by other muscles demonstrates the flexibility that this neuromuscular system has in generating behavior, and the importance of understanding the interactions between the nervous system and biomechanics for understanding behavior (Zajac 1989; Chiel and Beer 1997; Dickinson et al. 2000).

Reconfiguration in molluscs

Understanding reconfiguration, in which contraction of one muscle affects the forces generated by other muscles, may be important for understanding the feeding mechanisms of both gastropod and cephalopod molluscs. For example, the gastropods *Helisoma*, *Archidoris*, and *Lymnea*, and the cephalopods *Octopus*, *Sepia*, *Loligo*, and *Nautilus* all have radula/odontophores that either rotate or change shape significantly during behavior, which could affect the ability of the surrounding musculature to generate specific behaviors (Rose 1971; Rose and Benjamin 1979; Smith 1988; Messenger and Young 1999). A study of the buccal masses of *Octopus bimaculoides*, *Sepia officinalis*, and *Loliguncula brevis* demonstrated that the posterior mandibular muscle closes the beak when the lateral mandibular muscles are relaxed. In contrast, when the lateral mandibular muscles are contracted, creating a more rigid structure, the posterior mandibular muscle opens the beak, a form of reconfiguration that has been termed "muscular articulation" (Uyeno and Kier 2005). Given these examples, understanding mechanical reconfiguration may be critical to understanding the biomechanics of molluscan feeding structures.

Reconfiguration in other systems

Reconfiguration may also play an important role in other behaviors. In musculo-skeletal systems, hard skeletal structures cannot change shape significantly, but a muscle may alter the shape of several skeletal components, and this shape change may in turn alter the forces generated by multiarticular muscles. For example, in the snake, body curvature affects the behavior generated by phasic contractions of the epaxial muscles. If the body is straight, phasic contraction of the epaxial muscles induces swallowing. If the body is curved, phasic contraction of the epaxial muscles induces locomotion (Moon 2000). Alternatively, a muscle may act to alter another muscle's ability to exert force, and even the direction in which force is exerted. For example, in apheid shrimp, muscle CL1 controls whether contraction of muscle CL2 causes claw closure or claw opening (Ritzmann 1974). Similarly, the crayfish dorsolateral and transverse muscles use a pulley system to enhance the power of the central and lateral oblique muscles (Wine and Krasne 1982). Thus, mechanical reconfiguration may be a more

general mechanism that can allow muscular interactions in the periphery to enhance or change the effectiveness of other muscles.

Acknowledgements We thank the NSF (IBN-0218386 to HJC) and the NIH (NS-047073 to HJC), and the NSF IGERT program (Grant 345-1898) for their support of this research. We also thank Richard Drushel for the illustration of the buccal mass anatomy (Fig. 1a), and for his helpful comments on the research in this paper, and Robert Herman for his sketches of the MRI. Experiments described in this study comply with the *Principles of animal care*, publication No. 86-23, revised 1985, of the National Institute of Health, and also with the current laws of the United States.

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