

COMMENTARY

A mobility-based classification of closed kinematic chains in biomechanics and implications for motor control

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ABSTRACT

Closed kinematic chains (CKCs), links connected to form one or more closed loops, are used as simple models of musculoskeletal systems (e.g. the four-bar linkage). Previous applications of CKCs have primarily focused on biomechanical systems with rigid links and permanently closed chains, which results in constant mobility (the total degrees of freedom of a system). However, systems with non-rigid elements (e.g. ligaments and muscles) and that alternate between open and closed chains (e.g. standing on one foot versus two) can also be treated as CKCs with changing mobility. Given that, in general, systems that have fewer degrees of freedom are easier to control, what implications might such dynamic changes in mobility have for motor control? Here, I propose a CKC classification to explain the different ways in which mobility of musculoskeletal systems can change dynamically during behavior. This classification is based on the mobility formula, taking into account the number of loops in the CKC and the nature of the constituent joint mobilities. I apply this mobility-based classification to five biomechanical systems: the human lower limbs, the operculum–lower jaw mechanism of fishes, the upper beak rotation mechanism of birds, antagonistic muscles at the human ankle joint and the human jaw processing a food item. I discuss the implications of this classification, including that mobility itself may be dynamically manipulated to simplify motor control. The principal aim of this Commentary is to provide a framework for quantifying mobility across diverse musculoskeletal systems to evaluate its potentially key role in motor control.

KEY WORDS: Linkage, Kinematics, Closed kinematic chain, Musculoskeletal systems, Degrees of freedom

Introduction

When first learning to stand, young humans quickly realize that two feet are better than one. Add a one- or two-hand grip on a nearby piece of furniture and you become especially tumble-proof. Why does increasing the number of contacts with a fixed frame increase an organism's stability? Adding contacts does not change the body's mass, lower the center of gravity, shift the projection of the center of gravity or increase friction – all factors typically associated with increasing stability (Tanaka et al., 1996; Holbein and Chaffin, 1997; Hoffman et al., 1998; Whiting and Rugg, 2006; Hof, 2007). And while additional contacts do expand the base of support, this may not account entirely for the increased stability. Rather, these contacts may increase stability in part by transforming the limbs from open kinematic chains (OKCs; see Glossary) into a transient

closed kinematic chain (CKC; see Glossary). Transforming an OKC into a CKC (e.g. by standing on two feet instead of one) reduces the system's mobility (see Glossary) but also increases the stability (i.e. decreases the likelihood of falling). Throughout musculoskeletal systems, one can find many similar examples of CKCs; these may be formed transiently as animals contact the substrate (Vaughan et al., 1982; Schneider et al., 2005; Nyakatura and Andrada, 2013) or they may be permanent structures composed of skeletal elements, ligaments and muscles (Westneat, 1990; Van Gennip and Berkhoudt, 1992; Hoese and Westneat, 1996; Patek et al., 2007; Roos et al., 2009; McHenry et al., 2012; Camp et al., 2015; Laitenberg et al., 2015; Niyetkaliyev et al., 2017; Levin et al., 2017; Olsen et al., 2017).

Previous studies have primarily used CKCs as models to understand how force and motion are transmitted in musculoskeletal systems. For example, four-bar linkages (see Glossary) in the skulls of fishes transform force from the body muscles into motion of the cranial elements for suction feeding and prey processing (Westneat, 1990; Van Wassenbergh et al., 2005; Konow and Sanford, 2008; Camp et al., 2015; Kenaley and Lauder, 2016; Olsen et al., 2017). Closed chains of skeletal elements in the skulls of birds explain how jaw muscles drive upper beak rotation (Van Gennip and Berkhoudt, 1992; Hoese and Westneat, 1996; Dawson et al., 2011; Gussekloo and Bout, 2005; Olsen and Westneat, 2016). And a CKC in mantis shrimps shows how energy stored in compression of an exoskeletal segment can drive extremely rapid extension of an appendage (Patek et al., 2007; McHenry et al., 2012). However, relative to an equivalent OKC, CKCs also reduce mobility, defined as the total degrees of freedom (DoF; see Glossary) or the total number of independently variable ways in which a system can move. It is this role of CKCs in reducing mobility that has been underappreciated and relatively unexplored across a range of musculoskeletal systems. In addition, previous work has focused mostly on structurally permanent CKCs; thus, the commonalities between permanent and transient CKCs have not been fully appreciated.

In this Commentary, I propose a classification of how the mobility of biological CKCs can (or cannot) change during behaviors (Fig. 1). This classification is based on two properties from the linkage mobility formula (see below): the number of loops and the nature of the constituent joint mobilities. I use 'permanent' and 'transient' to refer to a constant versus variable number of loops, respectively, and 'constant' and 'conditional' to refer to constituent joint mobilities that are constant versus variable, respectively. This classification is important because it distinguishes the reasons for dynamic changes (or lack thereof) in mobility during and across behaviors. I illustrate each category using examples from various musculoskeletal systems. Mobility has direct implications for motor control: greater DoF give an organism a greater number of ways in which to move but also a greater number of DoF that must be controlled (Turvey et al., 1982; Newell and McDonald, 1994;

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Glossary**Closed kinematic chain (CKC)**

Two or more links connected by joints to form a continuous loop; also known as a 'closed-chain linkage'.

Degrees of freedom (DoF)

The number of different ways in which a mechanical system can change conformation, or the number of parameters needed to fully specify the conformation of a system.

Four-bar linkage

Mechanical system composed of four rigid links connected in a loop by four joints; one of the most commonly used linkages in engineering applications.

Linkage

A mechanical system consisting of two or more links connected by joints, as an open or closed kinematic chain.

Mechanism

Generally used interchangeably with 'linkage'; however, 'mechanism' *sensu stricto* may refer to a linkage in which one link is stationary. Here, 'mechanism' is used to refer to a biological system with a particular function (e.g. 'jaw opening mechanism'), whereas 'linkage' is used to refer to an OKC or CKC model of a particular mechanism.

Mobility

Here, the total DoF of a joint or linkage; 'full mobility' for a particular body means three rotational and three translational DoF. Elsewhere, 'mobility' can also be used to refer to the full range of motion of a system.

Open kinematic chain (OKC)

Two or more links connected by joints that do not loop back on themselves; also known as a 'open-chain linkage'.

Parallel linkage

A linkage containing two or more closed loops; also known as a 'multiloop linkage'.

Todorov and Jordan, 2002; Berthouze and Lungarella, 2004; Hong and Newell, 2006). Thus, I also discuss implications of this classification for motor control. It is my hope that considering CKCs across diverse musculoskeletal systems will demonstrate the power of a simple mathematical framework to (1) quantify mobility, (2) generate hypotheses regarding the control of these systems and (3) identify commonalities in structure and function.

Defining the organization and mobility of kinematic chains

OKCs and CKCs can be thought of as having three levels of organization: (1) 'configuration', referring to the types of joints in the linkage (see Glossary) and which of these joints are connected by which links, (2) 'geometry', referring to the size or shape of the links, and (3) 'conformation', referring to a particular state of the linkage across its range of motion. These levels form a descriptive hierarchy: for a single configuration there are multiple potential geometries and for a single geometry there are multiple potential conformations. Thus, one can think of mobility, or total DoF, as the total number of ways in which to change the conformation of a linkage.

Linkage mobility can be calculated from an equation known as the Chebychev–Grübler–Kutzbach criterion (Müller, 2009):

$$M = \sum_{i=1}^j f_i - dn, \quad (1)$$

where M is the total mobility, j is the number of joints, f_i is the DoF of each joint i , d is a dimensionality constant ($d=3$ for 2D linkages and $d=6$ for 3D linkages) and n is the number of loops (closed chains) in the linkage. More intuitively, one can think of 'closing' a linkage as equivalent to fixing one link. From Eqn 1, the mobility of

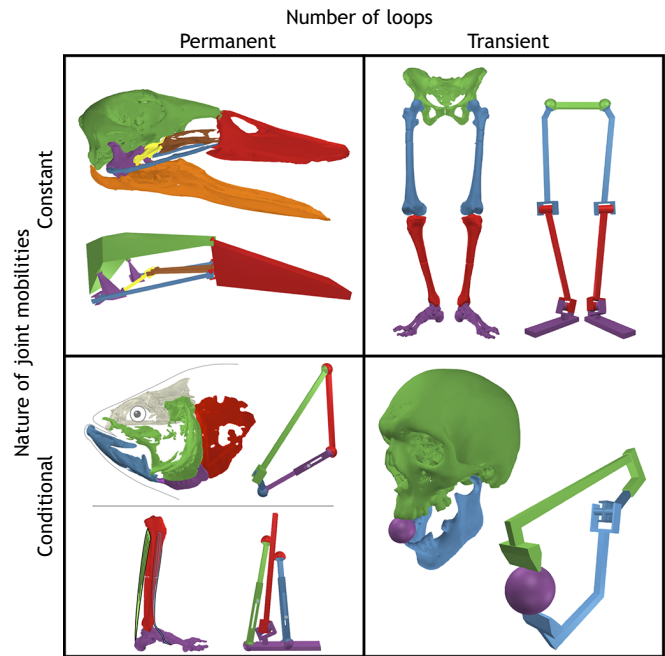


Fig. 1. A proposed mobility-based classification of closed kinematic chains (CKCs) based on the number of loops and nature of the joint mobilities. CKCs can have either a permanent or a transient number of loops and have constituent joint mobilities that are either constant or conditional. Each quadrant features the example musculoskeletal system(s) chosen for detailed consideration in this Commentary, showing both the anatomy and corresponding model. Clockwise from top left: the cranial kinetic mechanism of mallards, the human lower limbs, the human upper jaw and mandible with a food item, and the four-bar opercular mechanism of largemouth bass (top) and antagonistic muscles that act at the human ankle (bottom).

an open-chain linkage (no loops, $n=0$) is simply the sum of the DoF of each joint; thus, given the same set of joints, a closed chain will always have fewer DoF than an open chain.

There are linkages for which the Chebychev–Grübler–Kutzbach equation does not return the correct mobility, such as some multiloop linkages with parallel, in-series hinge and linear sliding joints (Gogu, 2005). For such linkages, mobility must be calculated from the kinematic constraint equations or using a virtual loop approach (Zhang and Mu, 2010). And for some 3D four-bar linkages with hinge joints at particular orientations (Chen and You, 2005), the equation only works if the linkage is treated as a special type of planar (2D) linkage ($d=3$). However, the equation works for all examples here and, to my knowledge, there is no linkage representing a musculoskeletal system reported to violate the mobility equation. Yet, this is certainly worth further investigation given the interest in such 'paradoxical linkages' in engineering (Gogu, 2005; Zhang and Mu, 2010). Lastly, the mobility equation also assumes that each joint has not reached the limit of its range of motion, which can substantially reduce the potential range of conformations (Gatesy et al., 2009; Manafzadeh and Padian, 2018). In the following sections, I discuss the application of the mobility formula to each of the four classes of CKCs that I propose.

Transient CKCs with constant mobility

If the equation presented in the previous section is applied to the human lower limbs, they can be categorized as a transient CKC with constant mobility (Fig. 2A). The CKC formed when both feet contact the ground is structurally transient because n changes depending on whether one or both feet are in contact with the

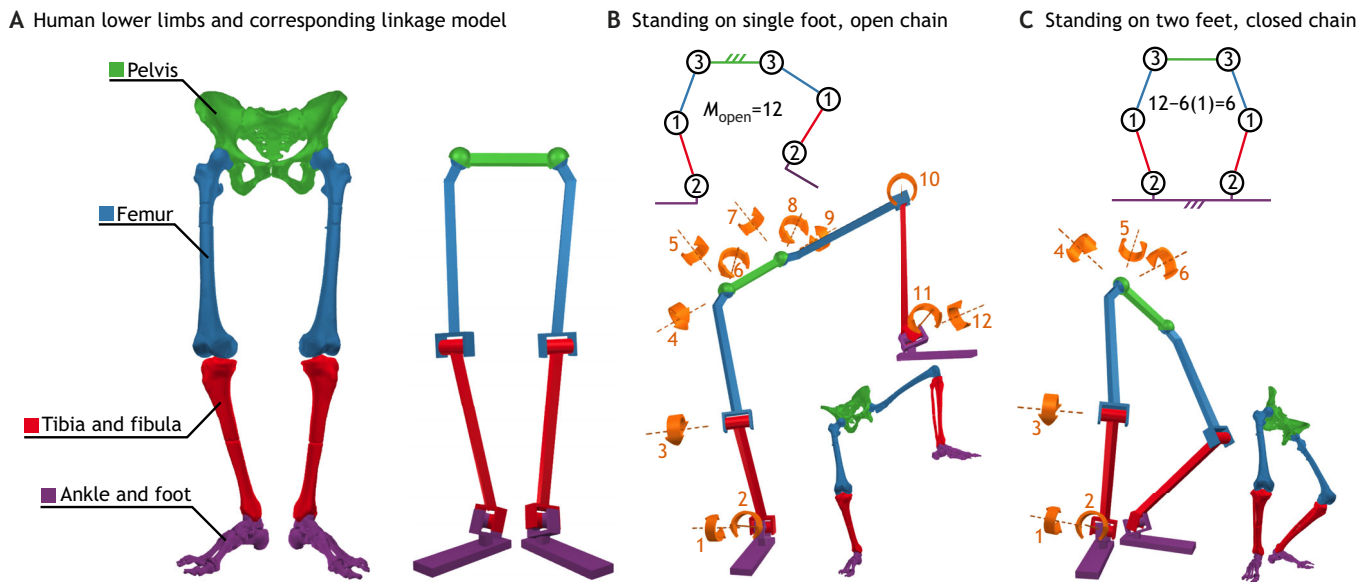


Fig. 2. The human lower limbs can form a transient closed chain, dynamically decreasing system mobility. The human lower limbs (A) form a 12-degrees of freedom (DoF) open kinematic chain (OKC) when standing on one foot (B) and a six-DoF CKC when standing on both feet (C). For this and all remaining figures, circle and line drawings (here at the top of B and C) represent a simple schematic diagram of each linkage model: circles represent the joints (with the number indicating the DoF of the joint), lines represent the links (in colors corresponding to the 3D schematics) and three short parallel lines indicate the fixed link. Also, for all remaining figures, numbered orange arrows indicate one possible set of parameters (DoF) for specifying the system conformation, and equations correspond to Eqn 1 (where M is the total mobility).

ground: standing on a single foot forms an OKC, in which case $n=0$, whereas standing on both feet forms a single-loop CKC ($n=1$). How much is mobility reduced by a biped standing on two feet versus one? Standing on a single foot and assuming the hip, knee and ankle joints have three, one and two rotational DoF, respectively (e.g. Arnold et al., 2010), the lower limbs and pelvis have a total of 12 DoF (Eqn 1; Fig. 2B). By planting the second foot and closing the open chain, the mobility is reduced by six ($n=1$ and $d=6$), giving the lower limbs and pelvis six DoF when standing on two feet (Fig. 2C), a 50% reduction. In addition, because this linkage is composed entirely of rigid skeletal elements, the mobility of the transient CKC remains constant regardless of the distribution of forces. This is because a rigid element will faithfully transmit forces and torques in any direction (compare this with the conditional mobility of CKCs containing compliant elements, discussed below).

With an increasing number of limbs contacting a fixed frame, organisms lose mobility but gain stability. For example, the six DoF of the lower limbs during two-foot standing also limits the pelvis to six DoF, such that any particular position and orientation of the pelvis is achieved by a unique conformation of the lower limbs. These six DoF can be specified by defining six axis rotations at multiple sets of joints in the lower limb; one of many possible sets is shown in Fig. 2C. Each DoF in a musculoskeletal system represents a dimension or axis along which the organism can move but also a dimension along which the neural system must control motion, unless that dimension is redundant or irrelevant for a particular task (Todorov and Jordan, 2002). A trade-off between mobility and stability has been proposed for the functional evolution of the shoulder joint in quadrupedal versus bipedal tetrapods (Sylvester, 2006; Veeger and Van Der Helm, 2007), although ‘mobility’ in these studies includes range of motion and DoF. Whether there exists a more general trade-off between mobility and stability in musculoskeletal systems remains unclear. For the particular example highlighted here, at least, by standing on two feet a

biped reduces its mobility (e.g. it can no longer kick with its free foot) but increases its stability in response to perturbations if, for example, the biped itself is the recipient of a kick.

Permanent CKCs with constant mobility

In contrast to transient CKCs, for a permanent CKC the value of n is constant; that is, the number of loops remains the same. In this way, the distinction between a structurally transient versus permanent CKC (Fig. 1) follows from a distinction between a variable versus constant n in the mobility equation (Eqn 1). Examples of permanent CKCs in biological musculoskeletal systems include CKCs formed entirely by rigid skeletal elements, such as the amniote rib cage when the ribs are joined by a sternum (e.g. Claessens, 2009; Brainerd et al., 2016; Brocklehurst et al., 2017; Capano et al., 2019). A second example can be found in the skull of birds (Fig. 3A), where the bones of the palate (jugal, palatine, pterygoid and quadrate) form four- and five-bar parallel linkages (see Glossary) that elevate and depress the upper beak (Bock, 1964; Van Gennip and Berkhoudt, 1992; Hoese and Westneat, 1996; Dawson et al., 2011; Olsen and Westneat, 2016). Because these skeletal elements remain permanently articulated, the number of loops, n , does not change across behaviors.

The bird cranial linkage demonstrates the mobility-reducing effect not only of closed chains but also of a multiloop linkage ($n>1$). Using the mallard duck as an example (Fig. 3A), one loop is a four-bar linkage formed by the neurocranium, quadrate, jugal and upper beak (Fig. 3B). In mallards, the quadrate articulates with the neurocranium by a single process that appears to allow three DoF of rotation (Dawson et al., 2011). However, the joints at either end of the jugal appear to allow only two DoF of rotation. From Eqn 1, the total mobility of the four-bar linkage is two DoF. Parallel to this four-bar linkage, the neurocranium, quadrate, pterygoid, palatine and upper beak form a five-bar linkage (Fig. 3C). This five-bar linkage does not limit the rotational mobility of the quadrate, and it

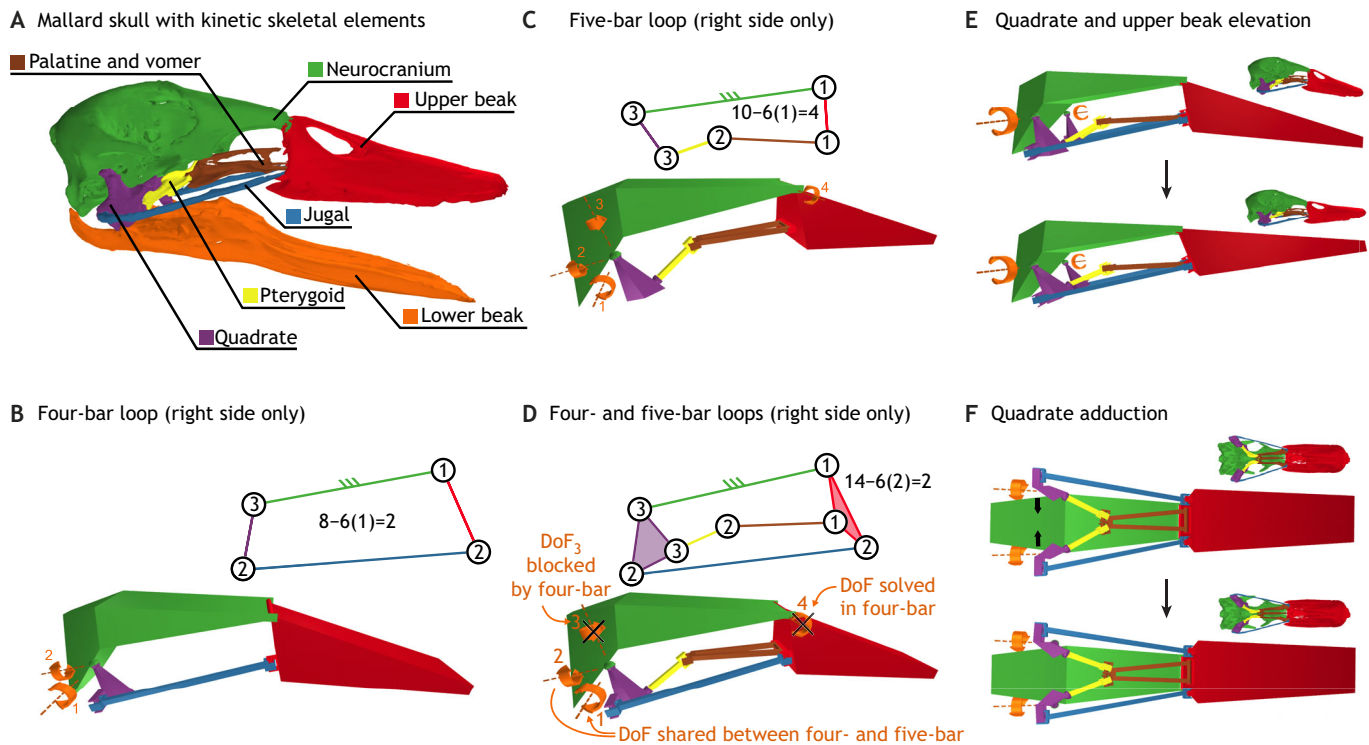


Fig. 3. The kinetic skeletal elements of the bird skull form a permanent closed chain with permanent mobility. The lower beak is shown only for reference. The skeletal elements of the bird jaw apparatus (A) form a two-DoF four-bar linkage (B) and a four-DoF five-bar linkage (C) on each side of the skull (orange arrows indicate DoF). The four- and five-bar linkages connect to form a multiloop linkage with two DoF (D) that couples rostral rotation of the quadrates with upper beak elevation (E) and permits quadrate adduction–abduction independent of upper rotation (F).

would allow the upper beak to rotate independent of the quadrate, for a total of four DoF. However, once combined ($n=2$), the four-bar linkage effectively eliminates two of the DoF of the five-bar linkage, resulting in a total mobility of two DoF for one side of the skull (Fig. 3D). This permits the quadrate to rotate forward and backward with upper beak rotation (Fig. 3E) and adduct–abduct independently of upper beak rotation (Fig. 3F).

By definition, the mobility of a structurally permanent CKC with constant mobility cannot be altered by the neural system. For this reason, a more interesting comparison of mobility in permanent CKCs as it relates to motor control can be found not within an individual but among species with homologous CKCs of differing mobility. For example, the nature of the neurocranium–quadrate joint, formed by one or two processes of the quadrate that fit into a socket or sockets on the neurocranium, varies among birds (Hendrickx et al., 2015). Unlike mallards (Fig. 3), some species (e.g. owls; Olsen and Westneat, 2016) have two widely spaced processes that limit quadrate rotation to a single axis and reduce the linkage mobility to one DoF. As the quadrates suspend the lower beak (Fig. 3A), birds with greater linkage mobility likely have the ability to rotate the lower beak about a dorsoventral axis (yaw) and to control spreading between the left and right sides of the lower beak (wishboning).

Permanent CKCs with conditional mobility

The examples presented so far have considered CKCs composed entirely of rigid elements for which the mobility is constant; that is, Eqn 1 holds under all conditions as long as the system remains a CKC. In contrast, a CKC formed by one or more compliant elements has mobility that varies under different conditions. For example, ligaments cannot resist compression, resist tension only

when they are taut, and can be twisted about their long axis. Although ligaments have complicated dynamic properties (e.g. Barrett and Callaghan, 2017), including the ability to strain in tension, for the purpose of calculating mobility I represent them here as two links joined by a one-DoF sliding (prismatic) joint and two spherical joints at either end (purple in Fig. 4A). If the sliding joint has not reached its maximum excursion, it has one DoF and the link represents a slack ligament. However, when the sliding joint reaches its maximum excursion and is under tension, its mobility becomes 0 and the link represents a taut ligament. Thus, in the case of a CKC containing a ligamentous link, the CKC is permanently closed but the value of f_i in Eqn 1 changes; the magnitude of this change is conditional on the direction of forces transmitted through the ligament, the conformation of the system and the material properties of the ligament.

A well-documented example of a CKC containing a ligamentous link is the four-bar opercular linkage (Fig. 4A), which functions to depress the lower jaw in some fishes (Westneat, 1990; Camp and Brainerd, 2015; Olsen et al., 2017, 2019). The linkage is formed by three rigid links (the suspensorium, operculum and lower jaw) and a compliant link (the interoperculo-mandibular ligament and interoperculum) between the operculum and lower jaw. The suspensorium–operculum joint allows full rotational DoF, while the suspensorium–lower jaw joint allows at least one DoF of rotation for lower jaw depression. When the ligament is slack, the four-bar linkage has five DoF (Fig. 4B), allowing the lower jaw to be depressed independent of the operculum (Fig. 4C). However, when the ligament becomes taut, the mobility of the system is reduced to four DoF (Fig. 4D) and lower jaw depression becomes coupled with opercular elevation (Fig. 4E). For simple coupling (i.e. without elastic energy storage), the ligament must be sufficiently stiff that

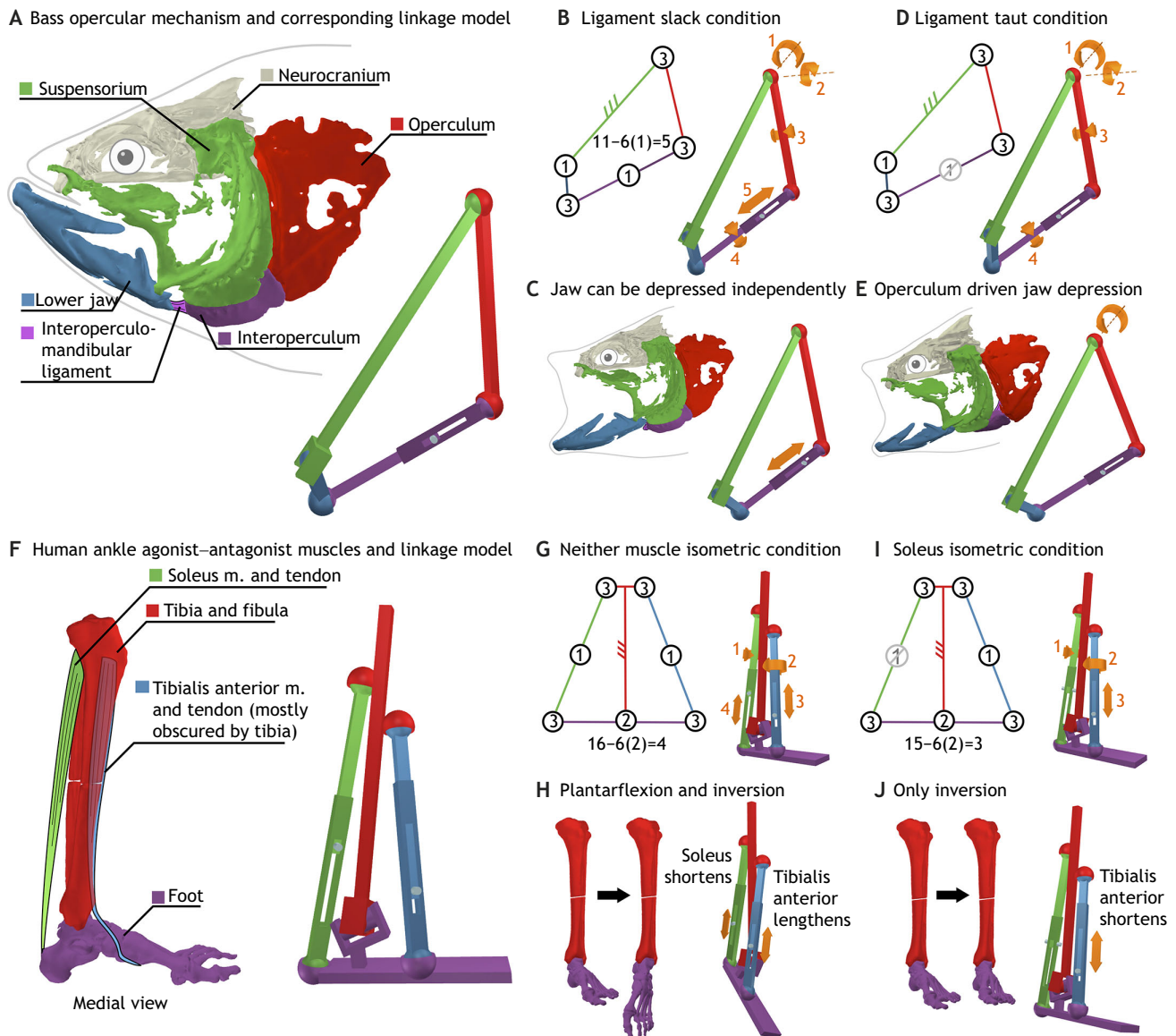


Fig. 4. Both the opercular mechanism in fishes and the human ankle joint have dynamic mobilities that depend on the mobilities of the constituent joints. The four-bar opercular linkage of largemouth bass (A) includes a link composed of ligamentous and bony elements (purple). When the ligament is slack (B), the linkage has five DoF (orange arrows) and the lower jaw can be depressed independent of opercular rotations (C). If the ligament is taut and in tension, the mobility decreases to four DoF (D) and opercular elevation can drive lower jaw depression (E). An antagonistic muscle pair at the human ankle (F) can be modeled as a multiloop linkage. When both muscles are non-isometric, the system has four DoF (G), including two rotational DoF at the ankle joint (H). If one muscle contracts isometrically, the mobility decreases to three DoF (I), allowing the other muscle to control the remaining one DoF at the ankle (J).

tension is transmitted through the ligament and not diverted into lengthening of the ligament.

Similar to a ligamentous link, an isometrically contracting muscle (a muscle that is actively generating tension but maintains a constant length) conditionally reduces the mobility of a CKC by one DoF. However, a difference is that the taut length of a muscle is neurally controlled. Take, for example, the tibialis anterior and soleus, an antagonistic muscle pair that is involved in rotating the foot about the ankle (Fig. 4F). The ankle joint has two DoF – plantarflexion–dorsiflexion and inversion–eversion – and the soleus acts to plantarflex the foot whereas the tibialis anterior acts to dorsiflex and invert the foot. When both muscles are non-isometric, this CKC has four DoF (two DoF of motion at the ankle joint and two DoF for ‘twisting’ of the soleus and tibialis anterior muscles, which can be disregarded; Fig. 4G). In this state, one muscle alone cannot control

ankle rotation because the system is underactuated (i.e. a single muscle controlling a two-DoF joint; Fig. 4H). However, if the soleus activates isometrically, it reduces the DoF of the system by one, turning the CKC into a one-DoF system (excluding two DoF of muscle ‘twisting’; Fig. 4I) and allows the tibialis anterior to control the remaining single DoF at the ankle joint (Fig. 4J). Additionally, isometric contraction of both muscles locks both DoF, reducing the mobility to zero, and allows the CKC to transfer energy from muscles outside the CKC (Biewener and Daley, 2007; Roberts and Azizi, 2011). In the case of a CKC containing a muscular link, the mobility of the system is conditional on the activation of the muscle, the material properties of the muscle and whether the muscle is in tension.

The two preceding examples show that mobility can be a dynamic property of musculoskeletal systems, even for

structurally permanent CKCs, and thus may be a motor control parameter. Other examples of conditional mobility CKCs include energy-storing systems with locking mechanisms (see Glossary) such as the mantis shrimp striking appendage (Patek et al., 2007) or the neurocranium-rotation mechanism of snipefish (Longo et al., 2018). With passive compliant structures, mobility can only be controlled indirectly: the neural system can vary mobility by changing the conformation of the system to place the compliant element in or out of tension. In contrast, for CKCs with muscular components, the neural system can directly control mobility by muscle activation. The concept of ‘freezing’ DoF is used throughout the motor coordination literature (e.g. Vereijken et al., 1992; Newell and McDonald, 1994; Scholz et al., 2000; Todorov and Jordan, 2002; Verrel et al., 2013), usually based on the observation that motion is reduced or prohibited along a particular joint axis. Freezing DoF is thought to be advantageous when a system has more DoF than needed to perform a particular task (Todorov and Jordan, 2002; Domkin et al., 2005) or during the early stages of learning a motor task when precise control of all DoF is not yet possible (Berthouze and Lungarella, 2004). But such observations do not test whether muscles are activated with the direct objective of reducing system mobility, raising the question of whether mobility is itself a motor control parameter or simply a consequence of other motor control strategies (Daley and Biewener, 2006; Biewener and Daley, 2007; Daley et al., 2007; Nishikawa et al., 2007).

Transient CKCs with conditional mobility

The CKC classification in Fig. 1 implies the existence of a fourth class: a transient CKC with conditional mobility. Can such a class of CKCs be found in nature? Feeding systems provide one example, as they generally consist of an open kinematic chain that ‘closes’ around a compliant food item. Taking the human upper jaw and

mandible as an example, motion at the human temporomandibular joint appears to occur predominantly along three DoF (Fig. 5A; Gallo et al., 2006; Iriarte-Díaz et al., 2017; Menegaz et al., 2015): two rotational DoF (depression–elevation and yaw) and one translational DoF (protraction–retraction). And if the mandible is assumed to behave as a single rigid body, a single ‘virtual joint’ can be used to represent the left and right temporomandibular joints for the purposes of mobility analysis. However, during food processing, if a food item is grasped between the upper and lower teeth, it closes a loop between the upper and lower mandible (Fig. 5B) and forms a transient CKC (the reader can verify this with the aid of a soft food item, such as a grape). As long as the food contacts the teeth, the joint between the food and teeth can be represented as a 3D sliding joint with five DoF, permitting the food item full rotational DoF and two translational DoF along the tooth surface (Fig. 5B, inset). Applying Eqn 1, the resulting CKC has a total of seven DoF, five for food motion and two for jaw joint motion (Fig. 5B). As long as the food is simply held and not punctured, the mandible can protrude or retrude and yaw but not depress or elevate substantially. In forming (and maintaining) this transient CKC, the mandible has lost a DoF.

For relatively tough foods, the mandible can continue to maintain this three-DoF system, exerting a force sufficiently strong to hold the food in place, but not so strong that the teeth begin to puncture the food item. However, if the force exerted by the teeth on the food exceeds the puncture force, the system gains additional mobility as the mandible can now elevate to drive the teeth through the food. Analogous to the previous examples of intrinsic compliant tissues (e.g. ligaments, muscles), the compliance of an extrinsic link (i.e. the food) creates a variable f_i in the mobility equation (Eqn 1), giving this transient CKC conditional mobility; in this case, conditional on whether the bite force is sufficient to permit motion of the teeth through the food. A CKC analysis brings an interesting perspective to the mechanics of feeding. Firstly, the mobility of this

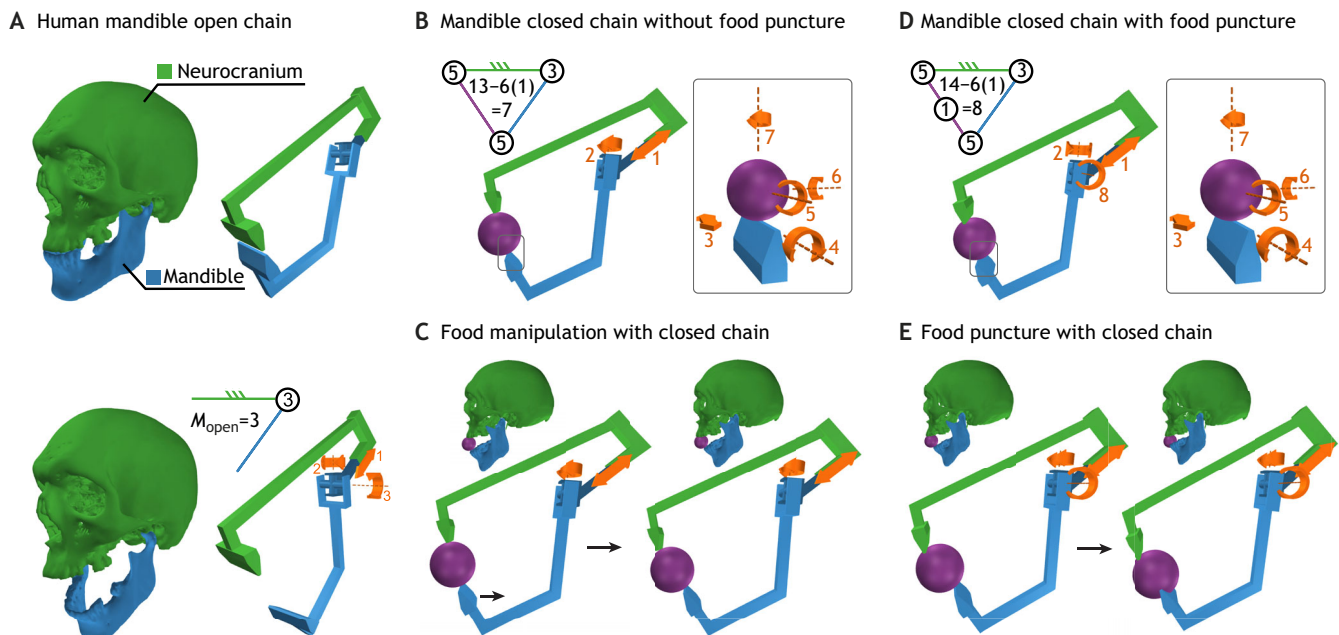


Fig. 5. The human mandible with a food item has a mobility that changes with food contact and manipulation. Without a food item, the mandible is a single-link three-DoF open chain (A). If a food item is simply held between the teeth without puncture (B), the tooth–food joint acts as a 3D sliding joint with five DoF (inset), and the system becomes a seven-DoF closed chain (orange arrows). This closed chain decreases mobility at the jaw joint to two DoF, permitting primarily yaw and protrusion (C). Food puncture adds at least one additional DoF, increasing the mobility to at least eight DoF (D) and restoring three rotational DoF to the jaw joint, including mandibular elevation (E).

transient CKC indicates the number of DoF the organism has for manipulating the food item (while maintaining a biting grasp) to best align the trajectory of the teeth with the fracture plane of the food. Secondly, treating the food item as a link in a CKC provides one approach to including tooth–food interactions in the study of feeding systems (Brainerd and Camp, 2019). And thirdly, placing the feeding system in a CKC classification scheme (Fig. 1) highlights how feeding requires particularly complex motor control, given the constantly changing mobility of the system, and identifies a commonality between feeding and locomotor systems (but see Granatosky et al., 2019).

Implications

Although the classification of CKCs laid out here may be well grounded in the mobility equation and comprehensively demonstrated, it serves little purpose if it is not biologically relevant. This relevance depends on a still partially unresolved question: is mobility manipulated, either evolutionarily or dynamically through neural control, to improve motor control? Considering each of the four categories of CKC discussed here provides a means of answering this question. For permanent CKCs with constant mobility (Fig. 1, top left), such as the kinetic cranial mechanism of birds, does mobility evolve under selection for motor control? If so, one would expect the mobility of a system to change through evolution in association with the DoF required for that system. For transient CKCs with constant mobility (Fig. 1, top right), like the human lower limbs, it remains unresolved whether two-leg standing is more stable because it expands the base of support or because the legs form a CKC. An experimental setup in which the base of support can be modified independently of the number of ground contacts (e.g. using specially designed footwear) would enable each factor to be evaluated independently.

For permanent CKCs with conditional mobility (Fig. 1, bottom left), such as those with isometrically contracting muscles, are the ‘frozen DoF’ observed during particular behaviors the result of muscles activating isometrically to directly reduce mobility or simply the result of reduced motion along a particular dimension? After all, maintaining isometry under a changing force regime is a sufficiently complex control problem in itself that it may not simplify the larger control problem. This could be tested by applying external forces to such a musculoskeletal system to probe whether reduced mobility is dynamically maintained during a particular behavior and whether this mobility also varies as expected with different behavioral tasks. Lastly, for transient CKCs with conditional mobility (Fig. 1, bottom right), where a compliant structure closes the kinematic chain, does the system increase in stability as a result of a decrease in mobility? This could be tested by perturbing systems while also varying the compliance and mobility of the chain-closing element; for example, a feeding system processing foods with different material properties (e.g. Reed and Ross, 2010).

These experiments presuppose a means of clearly quantifying the mobility of a musculoskeletal system, a topic also in need of further investigation. How can mobility be considered in combination with range of motion? For example, a joint may allow motion along a particular DoF, but if the allowed motion is too small to be biologically relevant, that DoF is hardly significant. Additionally, the mobility observed during *in vivo* motion is a subset of the total mobility; thus, passive manipulation should play a role in establishing mobility. And lastly, more work is needed to determine how to represent the mobility of compliant structures. For example, do muscular hydrostats have finite mobility? And how should the mobility of a ligament under tension but still capable of

strain be represented? This Commentary extends mobility to systems with non-rigid elements, but the general usefulness of applying linkages with rigid links to systems with compliant elements warrants further exploration.

Conclusion

The power of the linkage mobility analysis presented here lies in its ability to combine diverse musculoskeletal systems into a single framework. In this Commentary, I have shown how a simple equation (Eqn 1) can be used to quantify mobility in various biomechanical systems. This common framework allows dynamic changes in mobility to be compared across systems. For example, the existence of transient CKCs with conditional mobility suggests that different motor control strategies may be employed to dynamically change mobility. This can be achieved by, for example, adding fixed substrate contacts to form transient CKCs, shifting the force balance to engage a ligamentous coupling or using isometric muscle contraction to freeze a DoF. Given the centrality of mobility to motor control (Saltzman, 1979; Turvey et al., 1982; Newell and McDonald, 1994; Zatsiorsky, 1998; Todorov and Jordan, 2002; Hong and Newell, 2006), one would expect mobility to be a relevant control parameter. But do motor control programs manipulate mobility directly or does mobility change simply as a consequence of other motor control strategies (Daley and Biewener, 2006; Biewener and Daley, 2007; Daley et al., 2007; Nishikawa et al., 2007)? A consideration of such different examples of CKCs from the perspective of mobility broadens our traditional conception of what constitutes a CKC and expands the potential functions of CKCs from transmitting force and motion to include their dynamic and substantial effect on mobility. I hope that in demonstrating the ways in which mobility can vary structurally and dynamically in musculoskeletal systems, this Commentary encourages the study of mobility both as a potential explanation for different motor control strategies and as a useful concept for comparing otherwise seemingly disparate musculoskeletal systems.

Appendix

Figure methods and source data

Figs 1–5 were created from computed tomography (CT) scans of a mallard, human and largemouth bass. The mallard CT scan was downloaded from digimorph.org, with thanks to the University of Texas High-Resolution X-ray CT Facility, Dave Dufeu and National Science Foundation grant IIS-9874781 to D. Dufeu. The human CT scan was downloaded from the Visible Human Project at the University of Iowa (mri.radiology.uiowa.edu/visible_human_datasets.html). The largemouth bass scan was downloaded from xmaportal.org in the study ‘Largemouth Bass Feeding’ (ID BROWN6; Camp and Brainerd, 2015). Linkage models were created and manipulated using the R package ‘linkR’ (v1.2; Olsen and Westneat, 2016), and mesh renderings were created using the R package ‘svgViewer’ (v1.4; <https://CRAN.R-project.org/package=svgViewer>).

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Competing interests

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