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The significance of closed kinematic chains to biological movement and dynamic stability

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ABSTRACT

Closed kinematic chains (CKCs) are widely used in mechanical engineering because they provide a simple and efficient mechanism with multiple applications, but they are much less appreciated in living tissues. Biomechanical research has been dominated by the use of lever models and their kinematic analysis, which has largely ignored the geometric organization of these ubiquitous and evolutionary-conserved systems, yet CKCs contribute substantially to our understanding of biological motion.

Closed-chain kinematics couple multiple parts into continuous mechanical loops that allow the structure itself to regulate complex movements, and are described in a wide variety of different organisms, including humans. In a biological context, CKCs are modular units nested within others at multiple size scales as part of an integrated movement system that extends throughout the organism and can act in synergy with the nervous system, where present. They provide an energy-efficient mechanism that enables multiple mechanical functions to be optimized during embryological development and increases evolutionary diversity.

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1. Introduction

Closed kinematic chains (CKCs) have been used in mechanical engineering since at least the beginning of the Industrial Revolution because they provide a simple and efficient mechanism with multiple applications (Phelan, 1962). They combine multiple parts into continuous mechanical loops, with each influencing the mechanical behaviour of all the others in the system, and enabling the controlled transfer and amplification (or attenuation) of force, speed and kinetic energy (Fig. 1). However, while CKC linkages have been referred to as 'complex lever systems' (Alfaro et al., 2004), this description does not do them justice in a biological context because of the particular ways in which they relate to each other.

Modern anatomy has taken many centuries to accumulate a vast body of knowledge. It has classified structures according to the thinking of the day and sought to understand their functions using the latest technologies, but established conventions have allowed many important issues to be overlooked. The dissections of Vesalius

* Corresponding author. E-mail address: gscarr3@ntlworld.com (G. Scarr). (1514–1564) were important in overturning the dominant (but largely erroneous) anatomical wisdom that had prevailed since the time of Galen (c129–c200 CE), but his depictions of the musculo-skeletal duality have dominated our assessments of motion (Rifkin and Ackerman, 2006) and it is only relatively recently that the connective tissues have received the attention they deserve (Gracovetsky, 2008; Guimberteau and Armstrong, 2015; Schleip et al., 2012; Still, 1899).

Similarly, orthodox views of movement are essentially based on the mechanics of man-made machines described in the seventeenth century and a numerical system of kinematic analysis that greatly simplifies the anatomy (Brown and Loeb, 2000; Scarr and Harrison, 2016; Van Ingen Schenau, 1994), and although this approach has become the standard method of examining the forces and torques involved in joint motion (Rankin et al., 2016; Zajac et al., 2003), much less attention has been paid to the morphological geometry.

Biological CKCs are now examined from a more qualitative perspective that considers them as modular units nested within others at every size scale and part of an integrated movement system that extends throughout the organism (Levin, 2006; Turvey







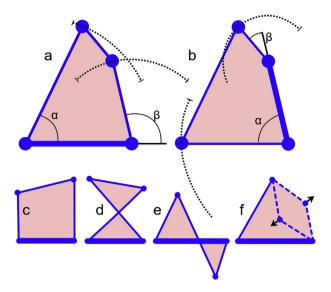


Fig. 1. a) and b) **Planar four-bar mechanics.** Two 4-bar shapes showing the pin-joints, trajectories and limits of three moving bars in relation to a fixed reference bar (bold) for each one, and how the motion of each bar is controlled by the relative positions of all the others, with the non-linear relationship between the changing angles (α and β) defining its mechanical properties (see later *Simple analysis* section). Some common 4-bar arrangements: c) uncrossed; d) conversely crossed; e) inversely crossed; f) inward (delta) and outward (kite) folding.

and Fonseca, 2014; Wilson and Kiely, 2016). Each part is structurally and functionally connected with all the others and contains a sequence of nested sub-systems that extends down to the cellular and molecular levels and is evolutionarily designed to respond to the specific loadings imposed (Simon, 1962; Clune et al., 2013; Kiely and Collins, 2016).

These linkage systems show how the position and orientation of each anatomical part results from the mechanical behaviour of a huge number of inter-linked tissues. They enable the structure itself to respond instantly to rapidly changing conditions and regulate complex movements in ways that are beyond the sole capability of the nervous system (Brown and Loeb, 2000; Kiely and Collins, 2016; Valero-Cuevas et al., 2007). The analysis of CKC geometries then reveals how multiple mechanical properties can be functionally compared between different parts of the body and other species, and optimized between different tissues during embryological development. It also provides a mechanism for increasing evolutionary diversity (Alfaro et al., 2004, 2005; Wainwright et al., 2005).

CKC geometries have been described in the feeding mechanisms of crustaceans (Claverie et al., 2011; Summers, 2004), fish (Alfaro et al., 2004; Hulsey et al., 2005), amphibians (Kleinteich et al., 2008), reptiles (Kardong, 2003), the flight mechanics of insects (Miyan and Ewing, 1988; Walker et al., 2012) and birds (Biewener, 2011; Hedrick et al., 2012), and the limbs of mammals (Van Weeren et al., 1990) but are much less recognized in humans (Bradley et al., 1988; Huson, 1997).

Although 'kinematic analysis' and the lever model are widely used in biomechanics, the qualitative assessment of CKC geometries in living tissues has received little attention, with Vogel (2013, p. 401) declaring that "we mammals make no great use of multi-bar linkages". It is thus the intention of this paper to highlight their significance as ubiquitous, mechanically-efficient and evolutionary-conserved structural arrangements with many advantages to human physiology, because kinematics is all about the geometry of motion.

1.1. The 4-BAR kinematic chain

The simplest geometric arrangement that enables the structure itself to control motion is the planar 4-bar, where the length and position of each bar (linkage) determines the behaviour of all the others in the system, and the angular relationships between them define its mechanical properties (Fig. 1). In comparison, 3-bar shapes (triangles) are crucially important because of their inherent stability, while those with five and more bars are uncontrollable on their own (although their importance in more complex systems is described later), which makes the planar 4-bar the best model to start describing this mechanism in biology (Muller, 1996).

1.2. The coupling of multiple tissues

The most thoroughly investigated 4-bar mechanisms in biology have been described in the feeding mechanisms of fish (Alfaro et al., 2004; Hulsey et al., 2005; Muller, 1996) (Fig. 2) where the jaws, neurocranium, hyoid, suspensoria (cheeks) and opercula (gill covers) are part of multiple CKCs that are coupled together and mutually change shape; and permit the rapid expansion of the head and buccal cavity, mouth opening, sucking in and containment of the prey (Roos et al., 2009; Konow and Sanford, 2008). These mechanisms are also very efficient because they use a relatively small number of muscles to initiate complex movements in structures that are coupled together and operate in different planes.

Although there is considerable variation between species, such mechanisms enable those structures without direct muscular attachments to move with remarkable force and speed, and with a total prey capture period of less than fifty milliseconds in the largemouth bass (Westneat and Olsen, 2015) and twenty-five milliseconds in the seahorse (Roos et al., 2009). Such quadratic feeding systems that couple upper jaw motion relative to the braincase have also been described in reptiles (Herrel et al., 1999; Montuelle and Williams, 2015) and birds (Bock, 1964; Gussekloo et al., 2001).

1.3. Amplification of force and speed

This ability of the 4-bar mechanism to amplify force and speed is well illustrated in the pantograph, where the output pen is able to move a greater distance and at a faster rate than the input stylus (Fig. 3a). Its non-linear behaviour is intrinsically related to the geometry and is an emergent property that in a biological context enables the system to amplify muscular input and produce considerably greater amounts of force and speed, with the structure itself guiding motion. It is well demonstrated in the feeding mechanism of the mantis shrimp (Claverie et al., 2011; Summers, 2004) (Fig. 3b).

Here, the large muscle situated within the thorax causes the chitinous 4-bar mechanism to change shape and propel the long raptorial appendage towards the target prey with a force of 1500 N and within just three milliseconds; and with devastating effect (Patek and Caldwell, 2005). Such rapid jaw-closing movements are also found in ants (0.13 ms) (Patek et al., 2006), spiders (0.12 ms) (Wood et al., 2016) and termites (0.025 ms) (Seid et al., 2008) although the underlying mechanics have not been detailed as yet.

While many of these linkages in fish are constructed from stiff bone and cartilage (and chitin in the shrimp) it should be noted that the bars of some species are replaced by more flexible ligaments and/or variable length muscles (Hulsey et al., 2005; Roos et al., 2009), both of which enable other possibilities. Download English Version:

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