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TOPICAL REVIEW

A review of linkage mechanisms in animal joints and related bioinspired designs

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Abstract

This paper presents a review of biological mechanical linkage mechanisms. One purpose is to identify the range of kinematic functions that they are able to perform. A second purpose is to review progress in bioinspired designs. Ten different linkage mechanisms are presented. They are chosen because they cover a wide range of functionality and because they have potential for bioinspired design. Linkage mechanisms enable animal joints to perform highly sophisticated and optimised motions. A key function of animal linkage mechanisms is the optimisation of actuator location and mechanical advantage. This is crucially important for animals where space is highly constrained. Many of the design features used by engineers in linkage mechanisms are seen in nature, such as short coupler links, extended bars, elastic energy storage and latch mechanisms. However, animal joints contain some features rarely seen in engineering such as integrated cam and linkage mechanisms, nonplanar four-bar mechanisms, resonant hinges and highly redundant actuators. The extreme performance of animal joints together with the unusual design features makes them an important area of investigation for bioinspired designs. Whilst there has been significant progress in bioinspiration, there is the potential for more, especially in robotics where compactness is a key design driver.

1. Introduction

This paper presents a review of biological mechanical linkage mechanisms. One purpose is to identify the range of kinematic functions that they are able to perform. A second purpose is to review progress in bioinspired designs. Ten different linkage mechanisms are presented. They are chosen because they cover a wide range of functionality and because they have potential for bioinspired design.

Linkage mechanisms such as four-bar mechanisms are common in animal joints, particularly in fish jaws [1], lizard jaws [2], snake jaws [3], bird wings [4] and mammalian limbs [5]. A comprehensive study of the linkage mechanisms in animal joints was carried out in 1996 by Muller [6]. However, several new mechanisms in nature have been discovered since then [7–12]. Also, the work in [6] did not discuss bioinspired designs. There has been much recent research on bioinspired linkages, especially in the areas of air vehicles and robotics.

Several types of articulating joints are found in animals such as hinge joints (planar rotation), spherical joints (rotation in any plane), gliding joints (linear movements), saddle joints (biaxial rotation) and condyloid joints (movements in two planes). These joints can act individually, such as when a finger is moved just at the metacarpophalangeal joint, or they can act in tandem such as when all three finger joints move together to curl or straighten the fingers. In the case of linkage mechanisms, a number of joints are constrained to move together via rigid links. When hinge joints are used in a linkage mechanism, the motions are planar. When spherical joints are used, the motion can be nonplanar.

Linkage mechanisms are very important in mechanical systems because they enable the optimisation of forces and motions [13–15]. One of the first recorded designs of linkage mechanisms was in 1784 when James Watt published his parallel four-bar linkage for converting rotary into linear motion in steam engines [16]. Since this time, four-bar

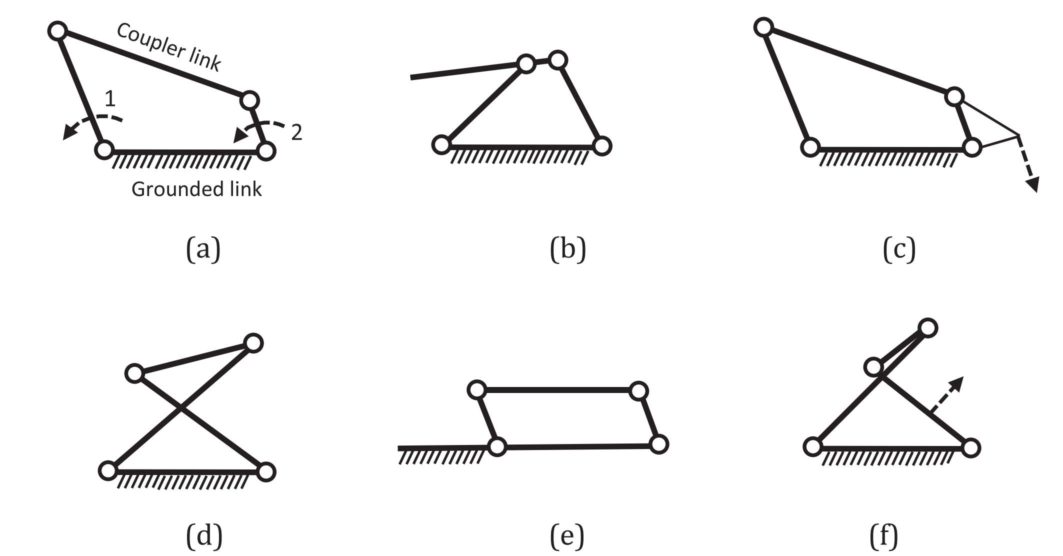

Figure 1. Some key design functions and features of four-bar mechanisms: (a) amplification of force or movement via links of different lengths; (b) amplification of rotation via a short coupler link; (c) optimisation of direction of linear actuator via an extension bar; (d) compact layout through inversion; (e) remote grounding position via an extended bar; (f) locked mechanism through an over-centre position.

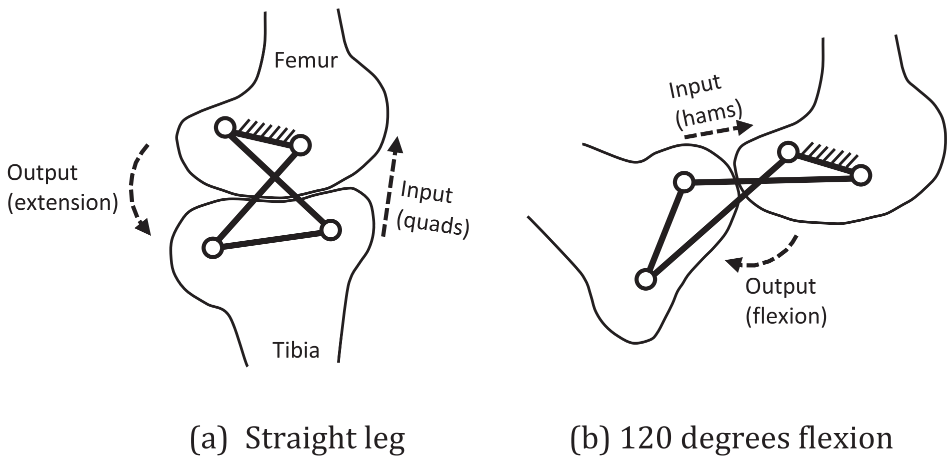

Figure 2. Schematic of the inverted four-bar mechanism in the human knee joint [17] (quads = quadricep muscles; hams = hamstring muscles). (a) Straight leg. (b) 120 degrees flexion.

linkages have been used extensively in a wide range of applications including: vehicle steering units, windscreen wiper drives, vehicle window lifting mechanisms, crane level luffing systems, angle poise lamps, riser recliner chairs, up-and-over doors and double-glazing window hinges.

The ability of linkage mechanisms to fine-tune mechanical performance is due to the very large range of possible layouts. To illustrate this, figure 1 summarises some of the key functions and features four-bar linkages. As is common practice, one link is shown as grounded, whilst the opposite link is referred to as the coupler link. There is normally one input link and one output link. In general, the input and output links can be any of the three links which are not the grounded link.

Figure 1(a) shows how a four-bar mechanism can be used to amplify force (bar 1 input) or amplify movement (bar 2 input). By adjusting the length of the bars, a vast range of motions of the coupler link is possible. Figure 1(b) shows that if the coupler link is made relatively short, then the rotation of the coupler link is greatly amplified for a given rotation of bar 1 or 2. Figure 1(b) also shows that by extending the coupler bar beyond the link, a large linear movement can be obtained. Figure 1(c) illustrates how the location and orientation of a linear actuator can be fine-tuned by creating an extension bar to the input link.

Figure 1(d) shows an inverted four-bar arrangement which creates a compact hinge with a moving centre of rotation. Figure 1(e) shows that when the grounded bar is extended, it can be grounded behind

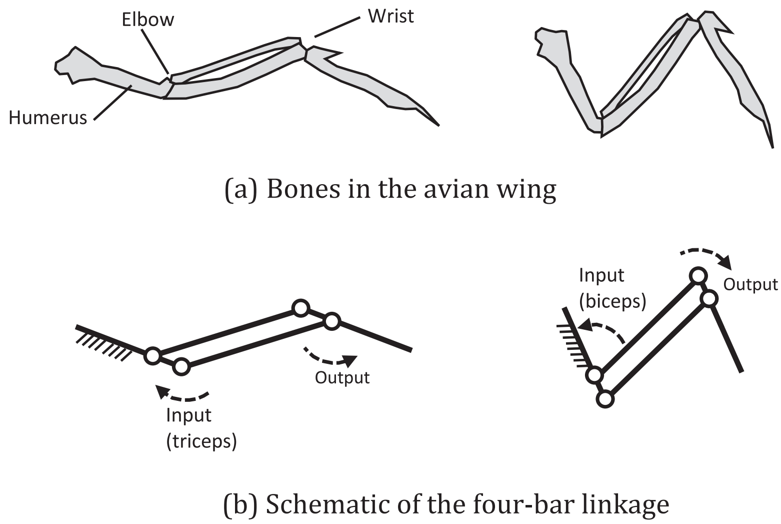

Figure 3. The four-bar pantograph mechanism in the avian wing joint [21]. (a) Bones in the avian wing. (b) Schematic of the four-bar linkage.

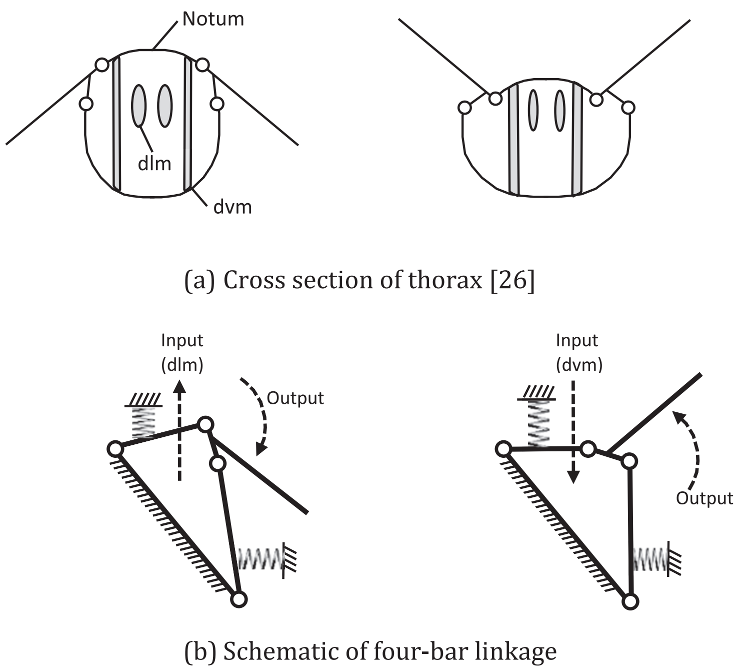

Figure 4. The wing joint of flies (Dipteran). (a) Cross section of thorax [26]. (b) Schematic of four-bar linkage.

one of the pivot points, thus enabling the mechanism to be located away from a grounding area. Figure 1(f) shows that when the coupler link is nearly in line with the output link (an over-centre position) the mechanism can be made to be self-locking. The configuration in figure 1(f) is also bi-stable because it can develop in one of two ways (inverted or noninverted).

It will be shown that all the design features illustrated in figure 1 are found in animal joints. The descriptions of the first four linkage mechanisms are based on the author's own research whilst the remaining six are based on the literature.

All the linkage mechanisms have been completely redrawn from original sources and put into a consistent format to aid comparison. In particular, the input and output motions and forces are specified as these are often incomplete in the original sources. An attempt has been made to draw the linkage mechanisms approximately to scale.

Unless otherwise stated, the mechanisms are assumed to be planar with revolute joints and rigid links. However, virtually all biological linkage mechanisms have a degree of out-of-plane movement. In addition, biological links sometimes undergo significant changes in length, especially when they are composed of soft tissue such as ligaments. For example, it has been found that the coupler link in the largemouth bass (see section 3.2) stretches by around 5%

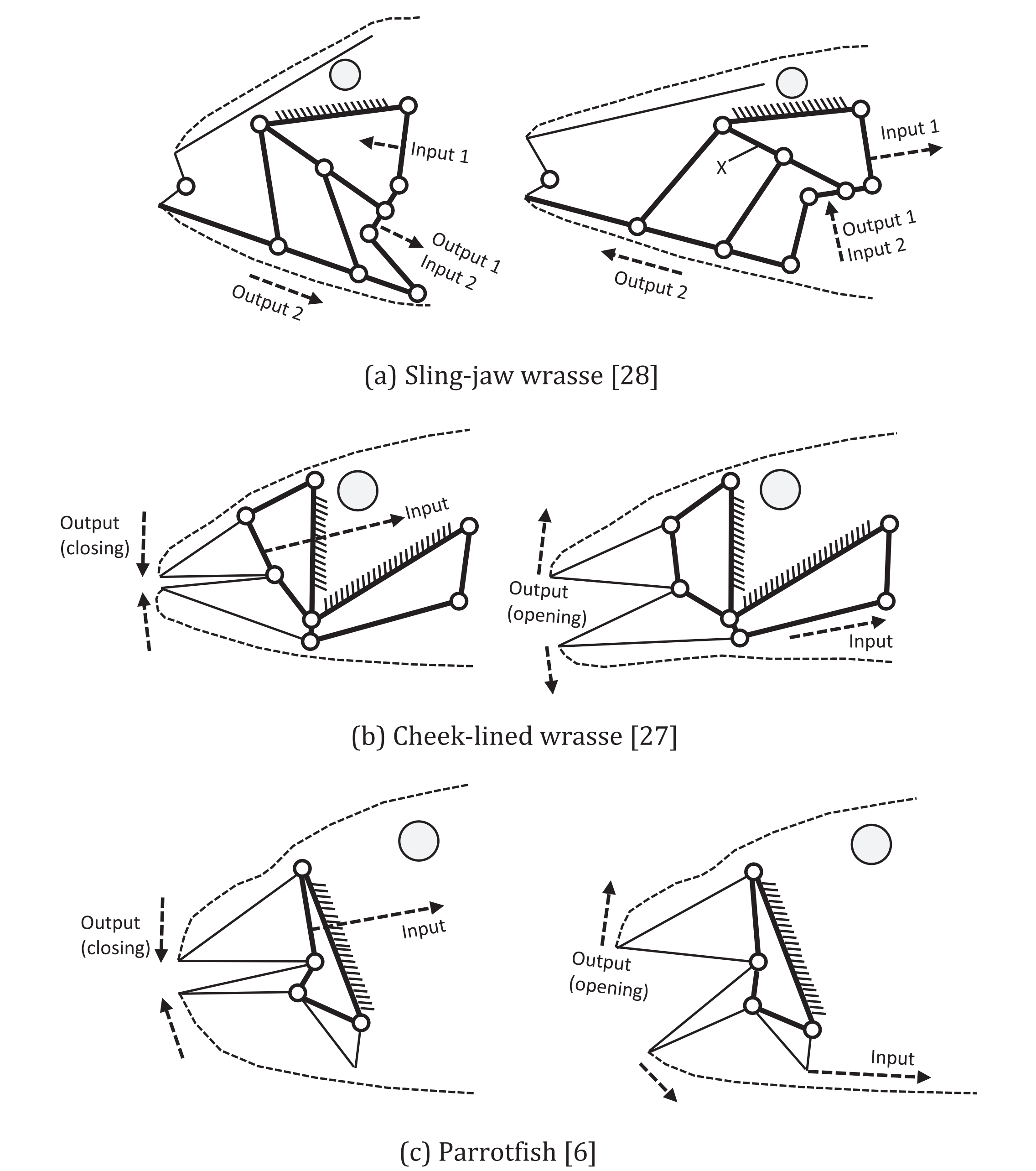

Figure 5. Schematics of the linkage mechanisms in wrasse jaws. (a) Sling-jaw wrasse [28]. (b) Cheek-lined wrasse [27]. (c) Parrotfish [6].

at peak gape (mouth opening) [7]. The linkage mechanisms of snakes have also been found to be highly flexible [3].

2. Limb and wing joints

2.1. Mammalian knee joint

The mammalian knee joint can be modelled approximately by a planar inverted four-bar mechanism and cam with a moving centre of rotation [6]. Figure 2 shows a schematic of the linkage mechanism in the human knee joint [17]. The crossed links of the mechanism are formed by the cruciate ligaments (anterior and posterior) whilst the remaining two bars are effectively formed by the bones (femur and tibia). The 'hinges' are formed by the flexibility of the cruciate ligaments where they join the bones. The cruciate ligaments are located between the two condyles of the femur bone which enables the linkage mechanism to operate in parallel with the cam mechanism. The cruciate ligaments are kept taut in tension and cannot take compression loads.

The cam mechanism consists of a cam (femur) and follower (tibia) and has a mixture of rolling and sliding during hinge movement [18]. The moving centre of rotation of the four-bar mechanism must be compatible with the cam motion during the required range of motion, otherwise the joint will not move freely.

The main function of the knee joint is to form a cam-type hinge. A key feature of this type of hinge

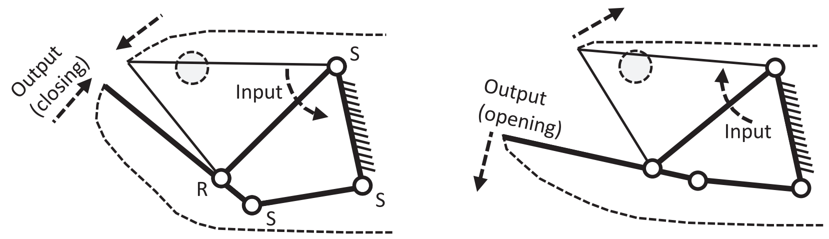

Figure 6. Schematic of the four-bar mechanism in the jaw of the largemouth bass. Reproduced with permission from [7]. (Note that Muller [6] has a different format with the grounded link and input link swopped compared to this diagram.)

is that it enables a relatively large range of movement of typically up to 145 degrees flexion due to the way the tibia rolls around the femur [17]. Without a moving centre of rotation, the range would be significantly reduced. (This will be discussed further in section 5.2.) Muscles of the quadricep group cause extension (straightening) of the knee whilst muscles of the hamstring group cause flexion (bending) of the knee.

A second important function of the joint is to transfer loads. The cam mechanism gives a large area of contact between the femur and tibia, thus allowing large loads to be transferred through the knee joint whilst bypassing the linkage mechanism. A third function of the linkage mechanism is to produce a favourable change in mechanical advantage during knee rotation. The moving centre of rotation is such that the distance between the instantaneous centre of the knee and the quadricep muscles increases with an increasing squat position (bent knees), thus reducing the force requirement in the muscles [17]. One study showed that the increase in mechanical advantage reduces muscular effort by up to 35% when rising from a squat position [17].

A fourth function of the linkage mechanism is to create an end-stop to prevent extension beyond a straight leg. The end-stop function is produced by the profile of the cam mechanism which locks the knee in the upright position [18]. This locking function reduces the effort required by muscles to stand upright. A similar locking function is found in horse knee joints which also has the effect of reducing the muscular effort required to stand [19].

2.2. Bird wing joints

The motion of bird wing deployment and retraction can be approximated by a pantograph four-bar mechanism as shown in figure 3. Bird wings are constrained such that the elbow joint drives the wrist joint like a pantograph mechanism [4, 20, 21]. Horses also have a four-bar pantograph mechanism in their hind legs with similar constrained motion [6]. A particular design feature of a pantograph-type mechanism is that grounding is achieved through an extended link. In the case of bird wings, this is the humerus bone. The elbow joint is driven through a pair of antagonistic muscles (biceps and triceps).

The main function of the avian elbow joint is to provide a deployment and retraction mechanism to allow the wing to be deployed for flight and stowed for non-flight activities. A second function of the mechanism is to reduce wing inertia by reducing the quantity of wrist muscles. In a case study of gulls, it was found that the reduced need for wrist muscles due to the pantograph mechanisms resulted in up to 12.3% reduction in power during flapping flight [21]. A third function of the mechanism is to reduce the degrees of freedom during gliding. This saves energy because it makes it easier to hold the wings in the gliding position [21]. A fourth possible function is increased aerodynamic stability due to the decreased degrees of freedom of the wings [21].

The modelling of joints in bird wings using a planar four-bar pantograph mechanism has been carried out since 1839 [20]. However, in 2017 experiments on the wing joints of racing pigeons were published showing significant out-of-plane movements [22]. In order to model this out-of-plane movement, the researchers developed a more refined model of the wing linkage mechanism based on a six-bar mechanism concept [22]. The short bar at the wrist joint was replaced by three bars and four of the planar hinges were replaced by spherical hinges. The new model was demonstrated to model the out-of-plane motion with a high degree of accuracy. Whilst the new model represents an important refinement, and is likely to be applicable to other bird species, the four-bar pantograph mechanism remains a reasonable approximation.

2.3. Insect wing joints

Flying insects generate aerodynamic lift by rapidly flapping and twisting their wings through large angles. The frequency of flapping is typically in the range of 20 to 1000 Hz with the higher frequencies being produced by smaller insects [23].

The hinges that enable wing flapping are integrated into the shell of the thorax. Figure 4 shows a schematic of the wing hinge of a typical fly (*Dipteran*) [24]. Like most species of flying insect, flies use indirect dorsoventral (dvm) and dorsolateral (dlm) muscles to elevate and depress their wings respectively. The muscles shown in figure 4 are described as indirect because they do not directly attach to

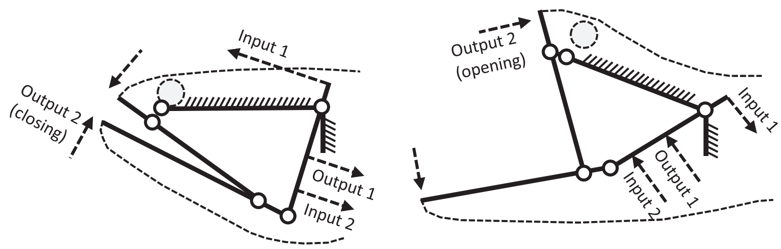

Figure 7. Schematic of the linkage mechanism in the jaw of deep-sea dragonfish. Reproduced from [8]. CC BY 4.0.

the wings. Instead, they manipulate the top plate of the thorax (known as the notum) which drives the wings [25].

A particular design feature of many insect wing joints is that the coupler link is relatively very short, thus greatly amplifying wing rotation for a given input angle. The wing is extended from the short coupler link, so that a relatively small distortion in the thorax causes a large flapping angle.

The thorax shell of the insect acts like an elastic spring and this enables the wing to flap at resonant frequency. Flapping at resonance is more efficient because the wings are continually storing and releasing elastic energy to change direction. This means that the inertial energy component that would be required to accelerate and decelerate the wings during wing reversal is greatly reduced.

3. Jaw mechanisms

Whereas birds of prey can use their feet to hold food, grab prey and fight, fish generally can only use their mouths for these survival functions. Therefore, there is great benefit to fish in having highly agile and functional jaws. One of the main ways in which fish obtain speed, strength and agility in their jaws is through linkage mechanisms.

Linkage mechanisms are mainly found in teleost fish [27] which are a type of ray-finned fish (*Actinopterygii*). Teleost fish are the most common type of marine and river fish and include wrasse, tuna, salmon, trout and bass.

3.1. Wrasse

Wrasse (*Labridae*) are a family of marine ray-finned fish within the teleost class. The jaw mechanisms of three types of wrasse are shown in figure 5.

The jaw linkage mechanism in the sling-jaw wrasse is shown schematically in figure 5(a). The fish lives off small fish and crustaceans. The fish has two distinct linkage mechanisms, a six-bar mechanism to open and close the mouth and a four-bar mechanism to drive the six-bar mechanism [28, 29]. The name ‘sling jaw’ derives from the slinging action of the six-bar mechanism that enables the mouth to be extended by a large distance. The jaw can extend up to 65% of the head length [30].

Mouth protrusion has two main functions. Firstly, it enables the fish to capture prey by a combination of a rapid approach and a suction effect. Suction is created due to the speed of movement of the jaw [31, 32]. A second function of mouth protrusion is that it saves energy by reducing the amount of swimming that the fish has to carry out to get to its food. When retrieving food that is within mouth-grasping distance, protruding the mouth requires far less energy (by at least an order of magnitude) than swimming forwards [28].

One interesting feature of the sling-jaw wrasse is how the two linkage mechanisms are connected with shared links. The link denoted x in figure 5(a) is one of the ‘rockers’ of the four-bar mechanism but it is also the effective ‘grounded’ bar of the six-bar mechanism. In addition, the coupler bar of the four-bar mechanism is extended to form the input bar of the six-bar mechanism. The coupler link length is also relatively very short in order to give a large kinematic amplification and hence fast deployment.

The jaw linkage mechanism in the cheek-lined wrasse is shown schematically in figure 5(b) [27]. This fish eats sea urchins, molluscs and crustaceans. As with the sling-jaw wrasse, the output bar of the rear four-bar mechanism drives the input bar of the mouth opening mechanism (although in this case it is not the coupler link but one of the rocker links). The four-bar mechanism in the jaw has two features that create a powerful bite. Firstly, the mechanism has a mechanical advantage to give force amplification. Secondly, the mechanism enables the actuator to be placed behind the jaw, thus accommodating a large muscle for closing the jaw. These two features will be explained more fully in section 5.1. The rear four-bar mechanism produces kinematic amplification to allow rapid opening of the mouth.

The jaw mechanism of large parrotfish (such as the green humphead) is shown schematically in figure 5(c). The fish feed mostly by crushing and eating live corals. The parrotfish jaw mechanism is similar to the cheek-lined wrasse although without the second four-bar mechanism behind the jaw. During biting, the jaw is drawn backwards due to the motion of the four-bar mechanism. This produces a pulling force during biting which is an advantage for pulling corals away from the reef. As with the cheek-lined wrasse, the parrot fish has a powerful

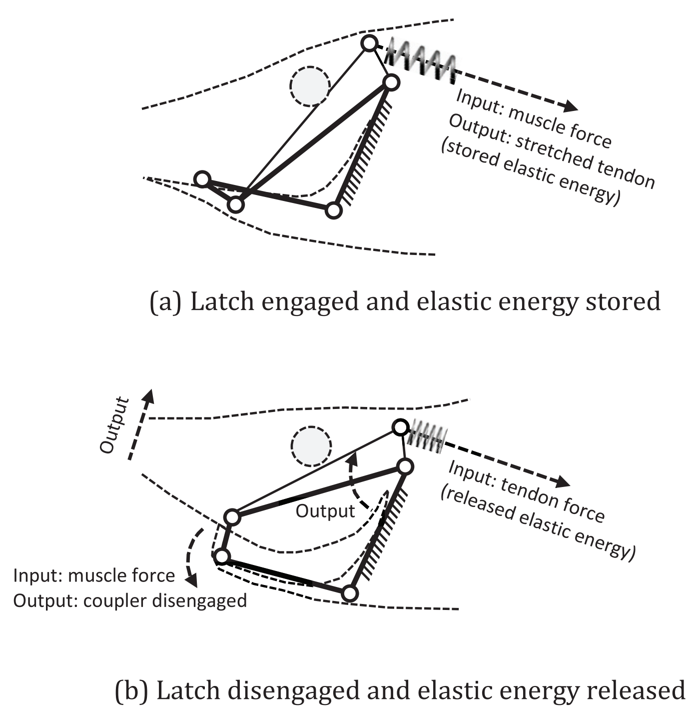

Figure 8. Schematic of the four-bar mechanism and latch mechanism in snipefish. Reproduced with permission from [12]. (a) Latch engaged and elastic energy stored. (b) Latch disengaged and elastic energy released.

bite due to force amplification and optimal actuator location.

3.2. Largemouth bass

The jaw linkage mechanism in the largemouth bass is shown schematically in figure 6. Largemouth bass are from the sunfish (*Centrarchidae*) family of freshwater ray-finned fish. As with the sling-jaw wrasse, the largemouth bass has a relatively short coupler link, giving high kinematic amplification. The largemouth bass has an unusual feature of significant out-of-plane rotations at the link pivot points of up to 12.5 degrees [7]. These rotations are possible because the mechanism can be approximated as a 3-degrees of freedom (DoF) four-bar linkage with three spherical joints (S) and one revolute joint (R), as shown in [7]. The out-of-plane motion enables a three-dimensional mouth-opening trajectory.

3.3. Deep-sea dragonfish

The jaw linkage mechanism of the deep-sea dragonfish is shown schematically in figure 7. Deep-sea dragonfish are from the (*Stomiidae*) family of ray-finned fish. The jaw mechanism is similar to that of the largemouth bass, although there is an additional hinge at the neck between the jaw and the spine. The four-bar mechanism only approximates to a four-bar because there is a small extra linkage at one end of the grounded link as shown in figure 7. The additional hinge in the neck [8] enables extended mouth opening of up to 120 degrees which is assumed to be for swallowing large prey [8]. As with the largemouth bass, the short coupler bar gives high kinematic amplification.

3.4. Snipefish

Snipefish use an energy storage and trigger mechanisms to carry out power amplification for rapid deployment of their head and jaw. By storing energy and releasing it in a controlled way, there is a decoupling between power delivery and power output. This makes it possible to achieve a high degree of power amplification. Using energy storage, it is possible to achieve powers and speeds that are much higher than what is possible through direct muscle action.

Snipefish (*Syngnathinae*) are a subfamily of small fish. To help capture small creatures, they place their mouth below the target prey and then suddenly and rapidly rotate their head and jaw towards the prey. This action is shown in figure 8 which also shows a schematic of the four-bar mechanism. This mechanism is unique to snipefish and seahorses [12].

The primary purpose of the four-bar mechanism is to form a quick-release latch system. This is achieved through an ‘over-centre’ design feature that makes the four-bar mechanism bi-stable. In figure 8(a) it can be seen that the coupler link is in an over-centre position and thus locks the four-bar mechanism. The coupler is the hyoid bone in the fish [12]. There are various muscles that can rotate the hyoid anticlockwise and hence unlock the mechanism and act as a trigger for deployment (figure 8(b)) [12].

The rotation of the input link is driven by a tendon spring which is preloaded in tension by large

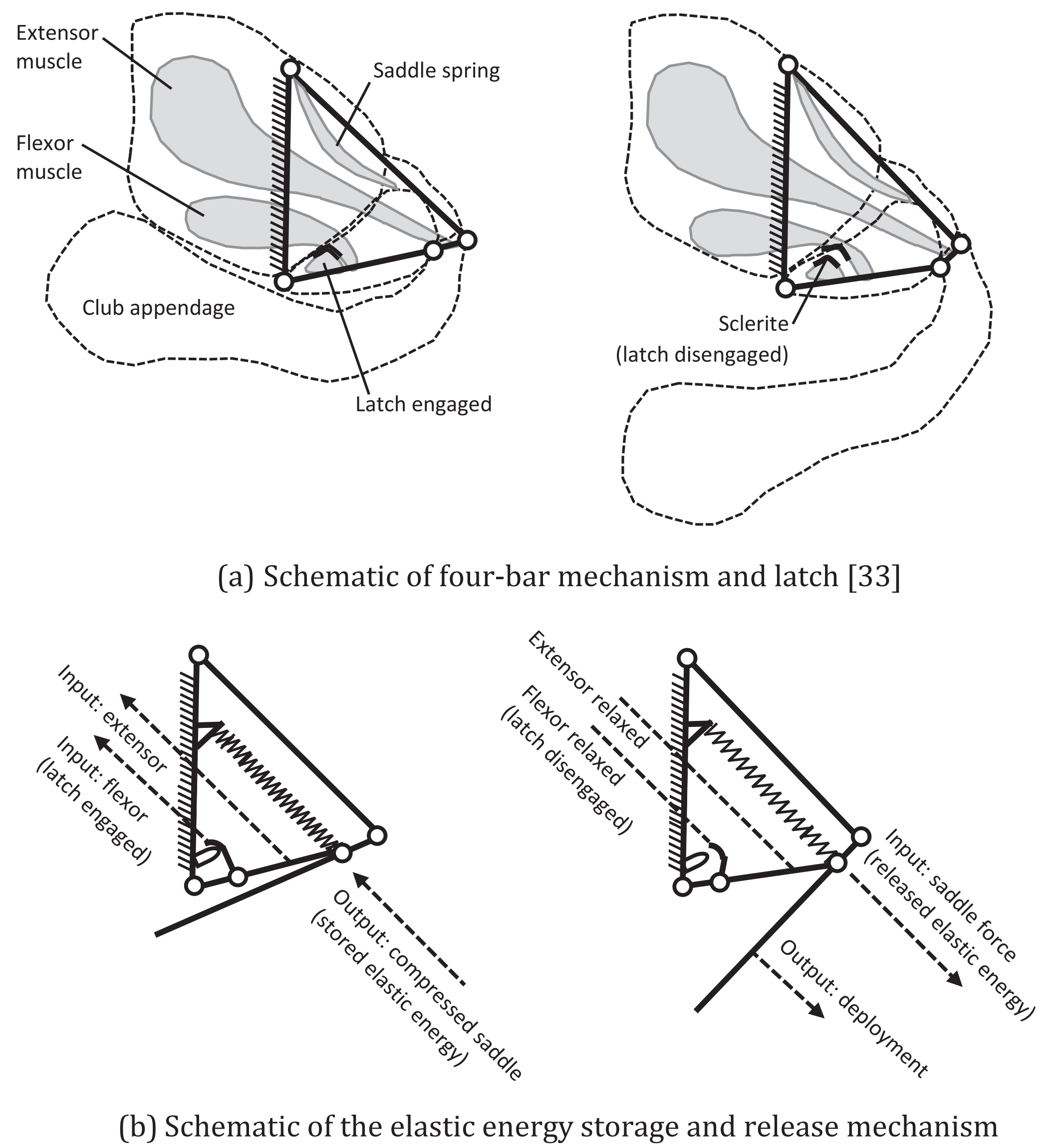

Figure 9. Mantis shrimp striking mechanism. (a) Schematic of four-bar mechanism and latch.Reproduced with permission from [33]. (b) Schematic of the elastic energy storage and release mechanism.

muscles (anterior epaxial and hypaxial muscles [12]) which act in series with the tendon. After stretching the tendon and storing energy, the input bar is prevented from moving until the hyoid is unlatched. When the hyoid is released from the over-centre position, it allows the stored energy to rapidly drive the head upwards.

The total rotation of the head is typically 20 degrees and happens in as little as 2 ms [12]. The head rotates extremely fast at speeds of up to 6090 degrees per second (1000 RPM). The hyoid bone has been observed to rotate at a rate of over 5000 RPM [12].

4. Appendage striking mechanism

The mantis shrimp (stomatopods) has an appendage that is used to smash shells and impale fish. The peacock mantis shrimp can directly deliver impact forces of over 1000 N which is several orders of magnitude greater than its bodyweight [33].

The mantis shrimp is able to generate the extremely fast strike using an energy storage mechanism together with a four-bar linkage mechanism. These mechanisms are shown schematically in figure 9. The main function of the four-bar mechanism is kinematic amplification, i.e. to make the coupler (output link) rotate faster than the input bar. The coupler link is able to achieve kinematic amplification because it is relatively short compared to the other three bars. In addition, the coupler link is greatly extended so that the end of the appendage has a large linear velocity. The actual rotational amplification (kinematic transmission) has been measured to be around 2.0 [34]. If the appendage was just part of a two-bar hinge, then it would not have any amplification.

Elastic energy is stored in cuticle exoskeletal material, especially a saddle-shaped exoskeletal spring mechanism [35], as shown in figure 9. In contrast to the snipefish, energy is stored in compression rather than tension.

A large, slow extensor muscle contracts to compress the saddle spring, while a flexor muscle simultaneously contracts to prevent the appendage from extending. The flexor muscle does not have to work as hard as the extensor muscle because there is a latch that locks the appendage in place. The latch takes the form of a pair of sclerites (hardened parts) [36], as shown in figure 9(a). When the shrimp is ready to strike, the flexor muscle relaxes, releasing the latch (the sclerites) which causes the stored elastic energy to be suddenly released and the appendage to be rapidly rotated.

An interesting and sophisticated design feature of the mantis shrimp is that it has a compression spring in 'parallel', in contrast to the 'series' configuration of the snipefish. Having an extensor muscle in parallel with the spring means that the extensor muscle does not need to be fully activated to keep the spring compressed, which means that it requires less energy to keep the mechanism loaded.

Two other examples of the rapid deployment of appendages in nature have been recently investigated [9–11]. Flea beetles use an energy storage mechanism to power their legs for large leaps [9, 10]. Dracula ants use an energy storage mechanism to snap their jaws onto prey [11]. However, in both these cases there is no four-bar mechanism to fine-tune forces or motions and so they are not presented in this paper.

5. Discussion

5.1. Functional analysis of biological linkage mechanisms

Table 1 summarises the functions and features of the linkage mechanisms considered in this paper. 14 different functions are identified, which illustrates the functional versatility of linkage mechanisms. Fish jaws in particular contain a wide range of linkage designs and functions [37, 38].

Table 1 shows how multi-functioning is common in biological linkage mechanisms. Every animal joint has at least two functions, with the knee joint having four distinct functions. Multi-functioning helps to produce packaging efficiency by placing a high degree of functionality into a small space. This is crucially important for animal joints where space is highly constrained.

One interesting feature of some animal joints is that of two separate mechanisms used either in series or parallel. Having two mechanisms in series enables more extreme displacements in the case of the dragonfish. In the case of the cheek-lined wrasse, two mechanisms are used to achieve two contrasting functions: force amplification for closing and kinematic amplification for opening. Having two mechanisms in parallel helps packaging efficiency as in the case of the knee joint and mantis shrimp striking mechanism.

Another reason for the high packaging efficiency is high levels of integration. For example, three of the fish jaws contain two linkages mechanisms integrated through at least one shared link. In addition, other parts such as ligaments, tendons and muscles are highly integrated into the joint.

One of the most important functions of linkage mechanisms in animals is allowing muscles to be placed in an optimal position for mechanical advantage and space utilisation. One of the clearest examples of this is found in fish jaws where space is extremely limited due to the hydrodynamic constraints on the shape of the mouth.

Figure 10(a) shows the mechanical advantage for the jaw-closing muscle in the parrotfish. For contrast, figure 10(b) shows approximately what the mechanical advantage would be if the parrotfish had a simple hinge joint (like a mammalian jaw joint) where a masseter muscle is used to pull the jaw directly together. The approximate relative sizes of the muscles are also shown.

The mechanical advantage of the four-bar mechanism in the parrotfish is around double that of a mammalian type jaw joint, thus producing twice the force for a given actuator. However, the actuator itself (the closing muscle) can also be very much larger [6]. By being located behind the jaw, the muscle can be an order of magnitude greater in size. So overall the actuator force is at least an order of magnitude greater.

The opening muscle of the parrotfish is also optimised in position and size. The bottom bar is extended so that the actuator is away from the four-bar system. The opening actuator is much smaller because opening does not require as much force as closing.

5.2. Current bioinspired linkage designs

Table 2 gives examples of bioinspired designs for the linkage mechanisms considered in this paper. It also shows related existing engineering systems to give an idea of how much overlap there is with current engineering.

The highly optimised linkage mechanisms found in animals have potential for bioinspired engineering applications, especially where there are tight space constraints or where multi-functionality is desired. Such objectives are common in mobile robots and so this is an area with significant potential for bioinspired designs.

There are several existing similarities between the linkage mechanisms in biology and engineering. For example, the parallelogram pantograph mechanism of the bird wing is analogous to the pantograph mechanism of an angle poise lamp, and the over-centre

Table 1. Functions and features of biological linkage mechanisms.

Biological example	Main function	Other functions	Special features
Knee joint	Cam hinge with moving centre of rotation	Transfer loads Force amplification End stop	Four-bar mechanism and cam mechanism in parallel
Bird wing elbow joint	Deployment mechanism	Reduce wing inertia Reduce DoF	Extended grounded link
Insect wing joint	Resonant hinge	Fine-tune actuator locations	Elastic energy storage Short coupler link
Sling-jaw wrasse jaw	Rotary to linear motion	Fine-tune actuator loc. Kinematic amplification	Two mechanisms in series with two shared links
Cheek-lined wrasse jaw	Force amplification	Fine-tune actuator loc. Kinematic amplification	Two mechanisms in series with one shared link
Parrotfish jaw	Force amplification	Fine-tune actuator loc. Pull action	Extended bar (opening)
Largemouth bass jaw	Kinematic amplification	Fine-tune actuator loc. Out-of-plane motion	Spherical joints Short coupler link
Dragonfish jaw	Kinematic amplification	Fine-tune actuator loc.	Two mechanisms in series with one shared link
Snipefish head joint	Mechanical latch (over-centre)	Fine-tune actuator loc.	Latch in series with spring
Mantis shrimp appendage	Mechanical latch (hook)	Fine-tune actuator loc. Kinematic amplification	Latch in parallel with spring Short coupler link

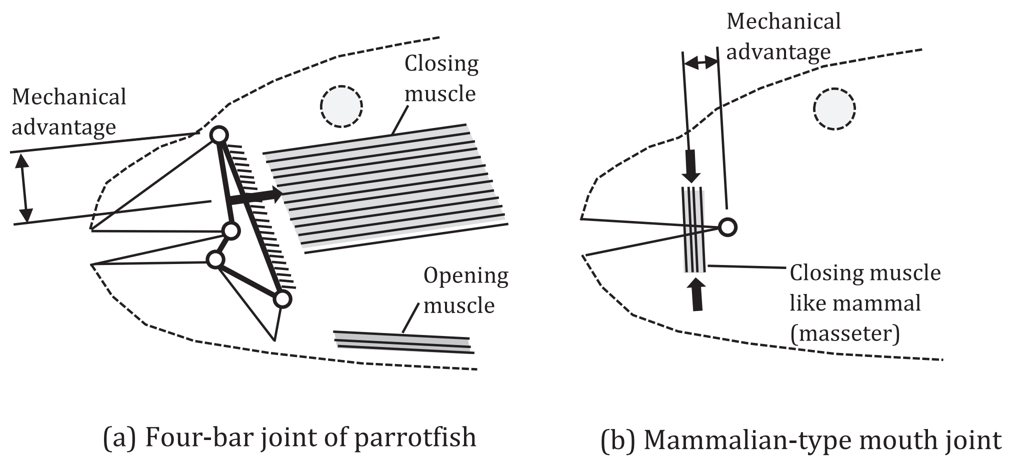

Figure 10. Actuator size and position for a four-bar linkage and a simple hinge joint. (a) Four-bar joint of parrotfish. (b) Mammalian-type mouth joint.

locking feature in the snipefish is analogous to the locking mechanism in locking pliers. The force amplification achieved in the parrotfish has conceptual parallels with the force amplification in geared four-bar robotic claws used in robots [59] and also the gearing system used in geared shears. However, of the ten linkage mechanisms presented in this paper, six do not have clear existing analogous engineering counterparts. These mechanisms have particular potential for bioinspired design.

Table 2 shows that there have been bioinspired projects in several areas, particularly with insect-inspired micro air vehicles (MAVS) and the pantograph mechanism of bird wings and/or horse hind legs.

Bioinspired knee joints have been produced that give a similar range of movement to the human knee of up to 145 degrees [17, 18]. Even though the current range of prosthetic knee joints of up to 120 degrees [60] is just enough for daily activities, it would be preferable for prosthetic knee joints to have the same range as the human knee [60]. An interesting feature of these knee joint-inspired designs is that they require a compression member for the anterior cruciate ligament to prevent instability in the joint [17]. The reason for the instability is that the bioinspired designs do not replicate the whole ligament and muscle anatomy of a mammalian knee [17].

Prosthetic knee joints have also been developed with five-bar and six-bar mechanisms [40, 41]. In the case of the five-bar mechanism, the researchers were able to achieve a hinge motion that better matched the actual motion of the human knee joint compared to a four-bar system [40]. However, their design relied on a geared actuation system. In the case of the six-bar prosthetic knee joint, the researchers were able to achieve a highly optimised trajectory of the ankle

Table 2. Animal linkage mechanisms and bioinspired designs.

Biological example	Related existing engineering designs	Example bioinspired designs	Potential future bioinspired designs
Mammalian knee joint	—	[17, 39–41]	Prosthetics, robotics
Bird wing joint	Angle-poise lamps	[42–49]	micro air vehicles (MAVs)
Horse hind leg	Scissor lifts		
Insect wing joint	—	[50–55]	MAVs
Sling-jaw wrasse jaw	—	—	Robotic grabber
Cheek-lined wrasse jaw	—	—	
Parrotfish jaw	Four-bar robotic claw Geared shears	[56, 57]	Robotic jaws
Dragonfish jaw	—	—	Robotic jaws
Largemouth bass jaw	—	[58]	Three-dimensional trajectories
Snipefish head rotation mechanism	Over-centre locking pliers	—	Robotic striking mechanism
Mantis shrimp striking mechanism	Latch trigger mechanism	[9]	Robotic striking mechanism

joint in the swing phase and also greater stability in standing [41].

The ability of birds to adjust their wing configuration for optimising flight [4] or for morphing between different modes of location [61] has led to much interest in bioinspired applications. Several bird wing-inspired folding wing mechanisms have been developed [42–49]. These are useful for optimising wing configuration during flight [42, 43] and also for morphing land-air or air-water vehicles [44–46]. Several leg walking mechanisms using four-bar mechanisms similar to horse linkage mechanisms have also been developed [47–49].

Insect-inspired flapping flight is known to have advantages for high manoeuvrability, high stability and low noise compared to propeller-driven aircraft. These favourable performance characteristics are produced by having flapping frequencies that are much lower than the frequencies of propeller-driven counterparts. The lower flapping frequencies are possible mainly because of the vortices produced by wing twisting. There have been many attempts to produce insect-inspired air vehicles [50–55]. A recent example of a resonant flapping mechanism using linkage mechanisms and antagonistic actuators is given in [50]. Other recent examples of MAVS (micro air vehicles) utilising energy storage are given in [51, 52].

5.3. Future potential bioinspired linkage designs

An important reason for the highly optimised performance of animal joints is the outstanding characteristics of muscle actuators. Biological muscle compares very favourably with engineering actuators in terms of power density and strain rates [62–64]. In addition, animals have high redundancy in actuators with multiple muscles being used to drive an input [65] as well as redundancy within individual muscles through hierarchical muscle bundles [66]. A bioinspired redundant actuator system has recently been developed [67]. However, there is still much scope for improving the performance of large-strain engineering actuators.

The recent discovery of spherical joints in the linkage mechanisms of bird wings and fish jaws opens up a whole extra dimension of possible motions of linkage mechanisms. The more accurate three-dimensional modelling of bird wing joints [22] could have important applications for the morphing of aircraft wings. A bioinspired non-planar linkage mechanism using spherical joints has been developed for an insect-inspired flapping mechanism with complex three-dimensional motions [58]. However, there is scope for more such bioinspired applications.

Jaw mechanisms have potential use in robotic manipulators where a high clamping force is required in a confined space. Whilst there are some linkage mechanisms used in robotic hands [56, 57, 59], these are not as compact as the biological examples considered in this paper. For example, in [56], whilst the four-bar mechanism simulates thumb movements well, the mechanism requires several bulky gearboxes. The exoskeleton [57] also uses a four-bar mechanism to simulate human thumb motion and achieves compactness through the use of remotely placed pneumatic actuators.

Striking mechanisms inspired by the snipefish or mantis shrimp also have potential use in robotics, for example for production tasks like hole punching or stapling. Since autonomous mobile robots are lightweight, they have limited ability to apply force in the absence of special mechanisms. Trigger mechanisms have the potential to provide very significant force and power amplification by using mechanical springs to store energy and trigger mechanisms for triggering.

The design of biological hinges within the linkages mechanisms has potential for biomimicking. An important difference between linkage mechanisms in nature and engineering (such as robotic joints) is that biological hinges have elements held together by ligaments rather than having shafts fully enclosed in a hole. In addition, biological hinges use notched profiles to take axial loads rather than using separate end-caps that are assembled onto the shafts.

The design features of biological hinges are illustrated in figure 11 which shows a frontal view of the human knee joint. The knee joint is held together by

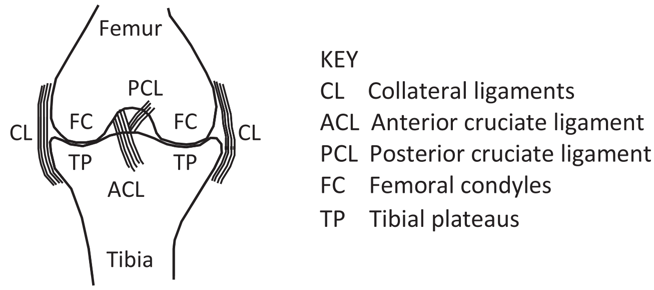

Figure 11. Front view of human knee joint showing two condyle notches.

ligaments such as the collateral ligaments and sideways movement is prevented by two condyles that fit into two notches in the tibia. The elbow joint has a similar trochlea notch to prevent sideways movement.

Biological mechanisms cannot have shafts and end-caps because growth constraints dictate that parts must be assembled as they are being formed. Such constraints make it very difficult to assemble parts like a shaft inside a hole. In contrast, engineering systems do not usually have such growth constraints.

However, one engineering application where there are potentially growth-like constraints is in the area of self-replicating machines. Whilst there have been significant advances in technology for 3D printing, there are not yet many technical solutions for the self-assembly of machines. There has been some progress in the self-assembly of materials using bioinspired approaches [68]. However, there has not been much progress on the self-assembly of mechanical parts. One approach to creating a self-assembling machine is to use bioinspired features like parts connected by ligaments and restrained by notches.

6. Conclusions

Linkage mechanisms enable animal joints to perform highly sophisticated and optimised motions. A central finding of this research has been identifying how biological linkage mechanisms achieve extreme levels of compactness in joints. The main reasons for optimal packaging are:

(a) The use of linkage mechanisms to position actuators away from the joint.
(b) The positioning of actuators to give optimal mechanical advantage.
(c) High levels of integration such as shared links and parallel operation.
(d) The use of power amplification through energy storage and release devices.

Other key design features of linkage mechanisms in animal joints include: kinematic amplification through a very short coupler link, separate kinematic and force amplification through two linkage mechanisms, variable mechanical advantage and optimised three-dimensional motions using spherical joints.

Many of the design features used by engineers in linkage mechanisms are seen in nature, such as short coupler links, extended bars, elastic energy storage and latch mechanisms. However, animal joints contain some features rarely seen in engineering such as integrated cam and linkage mechanisms, nonplanar four-bar mechanisms, resonant hinges and highly redundant actuators. The layout of biological hinges is particularly different from engineering hinges with ligaments used for attachment and curved notches used for axial restraints.

The extreme performance of animal joints together with unusual design features makes them an important area of investigation for bioinspired designs. Whilst there has been significant progress in bioinspiration, there is potential for more, especially in robotics where compactness is a key design driver.

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Data availability statement

All data that support the findings of this study are included within the article (and any supplementary files).

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