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1 **Title: Object manipulation without hands**

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19 ABSTRACT

20 Our current understanding of manipulation is based on primate hands, resulting in a detailed but
21 narrow perspective of ways to handle objects. Although most other animals lack hands, they are still
22 capable of flexible manipulation of diverse objects, including food and nest materials, and depend on
23 dexterity in object handling to survive and reproduce. Birds, for instance, use their bills and feet to
24 forage and build nests, while insects carry food and construct nests with their mandibles and legs.
25 Bird bills and insect mandibles are much simpler than a primate hand, resembling simple robotic
26 grippers. A better understanding of manipulation in these and other species would provide a broader
27 comparative perspective on the origins of dexterity. Here we contrast data from primates, birds, and
28 insects, describing how they sense and grasp objects, and the neural architectures that control
29 manipulation. Finally, we outline techniques for collecting comparable manipulation data from
30 animals with diverse morphologies and describe the practical applications of studying manipulation
31 in a wide range of species, including providing inspiration for novel designs of robotic manipulators.

32

33 KEYWORDS: object manipulation, robot manipulation, functional morphology, motor control,
34 dexterity, sensory ecology.

35

36

37 *Introduction*

38 Manipulation or manual dexterity has been described as a ‘Rosetta Stone for cognition’ [1], because
39 it allows examination of cognitive abilities in naturally occurring, non-verbal behaviours. In
40 particular, the act of grasping an object forms the foundation of manipulation, as in order to
41 manipulate an object efficiently, an animal has to first establish a stable grip on the object. This
42 process of grasping involves a hierarchy of control decisions: what to grasp; how to position the
43 body and end effectors; precise continuous control to execute an action; dealing with uncertainty;
44 detecting success or failure and modifying subsequent actions. It also involves a close and
45 continuous interaction between body and brain, with the mechanics of end-effectors playing a
46 significant role in the dynamics of the behaviour. Thus, precise manipulation of objects requires
47 dynamic perception, control, and adjustment of the manipulator, as grasping imposes sharp
48 transitions in the state space of the animal’s and environment’s dynamics.

49 Having hands to manipulate objects has enabled humans to develop pivotal innovations,
50 including tools and shelters. Consequently, biological investigation into object manipulation has
51 been largely centred around tool use, typically those in the hands of human and non-human primates.
52 While manipulation using forelimbs is considered a broadly shared trait in tetrapods (e.g., rats, frogs;
53 [2]), and different morphological traits in forelimbs can improve manipulative abilities [3],
54 manipulation that occurs without hands has been largely neglected in current frameworks. The close
55 focus on primate hands has meant that the expectation for the manipulation skills of animals without
56 hands has been low, for instance: ‘[t]he special ability to pick things up and manipulate them ... [is]
57 something that porpoises can’t do at all and crows can’t do very well’ [4]. After all, the etymology of
58 the word ‘manipulate’ involves ‘manus’, the Latin word for hand, so it might only be natural to
59 expect animals without hands to lack skills for manipulation. However, perhaps this
60 anthropomorphised language may have deflected our eyes from the rich diversity of the physical
61 interactions between animals and their environment. Once we adopt a more general definition of

62 manipulation (e.g., ‘an agent's control of its environment through selective contact’ [5]), the absence
63 of hands no longer means the absence of manipulation.

64 Indeed, manipulation skills play a significant role in the fitness of many species that lack
65 hands. For example, a bird that fails to build a structurally sound nest might lose a safe roosting
66 space, its potential mate, or all its eggs if the nest falls apart. Alternatively, manipulation skills may
67 affect food-handling time, a key variable modulating energy intake rates in optimal foraging theory
68 [6,7]. Although the ability of animals to manipulate objects underpins much of their daily lives, there
69 is limited understanding of the underlying mechanisms that dictate successful performance, such as
70 the morphology and sensorimotor control of the relevant appendages in animals without hands. For
71 instance, birds typically use their bills and feet to forage and build nests, while insects such as ants,
72 termites and wasps carry food and construct nests with their mandibles and legs. The principal
73 appendages used, i.e. the bills in birds and the mandibles in insects, are much simpler than a hand,
74 resembling simple robot grippers; yet they are able to accomplish highly sophisticated actions on
75 objects in their environment.

76 Coincidentally, manipulation of natural objects is a major, and largely unsolved, problem for
77 robotics. Although recent advances in gripper design [8], new sensory systems [9], and new
78 algorithmic approaches [10], especially those that utilise machine learning [11], have improved
79 performance of robotic systems in these areas, many potential robotic applications are severely
80 limited by the inability of robots to grasp diverse objects with efficiency and reliability. It remains
81 the case that state-of-the-art robot systems are easily outperformed by animals, including those
82 without hands.

83 To initiate the integration of data and theories about manipulation with and without hands,
84 and to inspire new avenues for designing robots that can flexibly handle objects, we focus here on
85 manipulation in two groups of animals that achieve diverse manipulation without hands: birds and
86 insects. For example, most of *ca.* 10,000 species of birds build nests (Figure 1) to raise young, using

87 materials including grass, twigs, moss, mud and even artificial objects like cigarette butts [12,13].
88 Similarly, insects exhibit high competence in manipulating a wide variety of objects (Figure 1), to
89 provide a shelter and food for offspring [14], to collect nectar and pollen [15], and to break up and
90 transport large items [16–18]. We compare these two cases to the findings from primate hand
91 research in different steps involved in grasping: the perception of objects before and during grasping,
92 the neural basis of controlling grasp, and the act of grasping. We then discuss how recent
93 developments in automated tracking and quantification of animal behaviour provide opportunities to
94 move beyond simple descriptive accounts of these behaviours towards a more mechanistic
95 understanding, and how this may provide inspiration for robotic grasping.

96

97 *Seeing objects before contact*

98 Object manipulation starts with gathering sensory information about extrinsic (e.g., distance, angle)
99 and intrinsic (e.g., size, shape) properties of the object. How primates, birds and insects take in such
100 information is, however, rather different. Before coming into contact with the object, primates rely
101 primarily on visual information to generate motor commands for their forearms and hands to reach
102 the object (Figure 2a, left). This process is flexibly controlled so that if the environmental conditions
103 change (e.g., the object moves), the animal can adjust the hand trajectory accordingly, which plays a
104 crucial role in tool use [19]. While primates have an entire view of the object and their hands
105 interacting with the object, viewing both from a distance, birds and insects have both their eyes and
106 main manipulators attached to their head (Figure 2a, middle & right). This means that, ironically,
107 primates have a “bird’s eye view” of the manipulation process (Figure 2b, left), while birds do not
108 (Figure 2b, middle). Such sensory systems that are unique to each animal’s perceptual and motor
109 characteristics are referred to as ‘umwelt’ [20]. Taking account of variation in these sensory
110 characteristics would help us understand differences we see in behaviour of different animals [20].
111 For birds and insects, moving their manipulator also moves the eyes, and as a result the information

112 they can access. While this arrangement might not allow the all-encompassing view of manipulation
113 experienced by the primates, it affords birds and insects direct sensory information about the position
114 of their manipulator relative to the object. By perceiving changes in the relative size and angles of
115 the object as they move their manipulator towards the object, birds and insects can use simple
116 heuristics (e.g. keep an object's centre of mass in lower centre of visual field) to grasp the object in
117 an optimal fashion. This means that, as long as they keep their eyes open, they can control their
118 manipulator motions flexibly. Large-billed crows, for example, kept their eyes open during reaching,
119 quickly adjusting the pecking trajectory even when they were fitted with an artificial bill extension to
120 grasp food successfully [21]. Also, while pigeons show a relatively fixed response in grasping tasks
121 as they squint their eyes during reaching [22], they can adjust their motions to the size of the target
122 object, as long as they are given a chance to see the object before reaching [23].

123

124 *Sensing objects while grasping*

125 Once a primate grasps the target object, mechanoreceptors on the hand provides rich tactile
126 information to amass object properties like shape, substance, and texture [24, 25], which, combined
127 with proprioceptive information about the position and shaping of the hand, help them 'work out'
128 how to place the manipulator for a stable grip. Within primates, the capacity for a stable grasp of
129 objects may differ among species [26, 27], potentially due to variation in their ecology [24, 25].
130 Birds and insects have a similar haptic-sensing system to that of human hands, in the form of bills
131 and antennae, as they both combine touch and proprioception. Birds that perform elaborate
132 manipulations possess a highly developed somatic perception system in their bills, called bill tip
133 organs [28–30]. In parrots, for example, these somatosensory receptors are densely distributed on the
134 bill tip and may assist them to establish a stable grip on a tree trunk while climbing, even though they
135 are unable to see the trunk due to the extreme curvature of their bills [30]. This way tactile

136 information may help birds overcome the limited visual coverage of the target object, improving
137 accuracy and efficiency of manipulation.

138 In fact, even with their developed eyesight, both primates and birds require tactile feedback
139 for efficient manipulation. Not dissimilar to prosthetics users who experience a grasping problem
140 from the lack of tactile feedback [31], injured apes lacking digits struggle to feed at the rate of intact
141 individuals depending on the types of food [32], and chickens with clipped bills reduce their foraging
142 rate by 80% [33], although latter response may also be explained by the birds experiencing the pain
143 of clipping.

144 Similarly, insects rely heavily on touch and proprioception (Figure 2b, right) to control grasp.
145 This makes sense considering insects often handle objects that are far larger than their bodies, and so
146 exceed their visual field. Insects usually make the first contact with food with the antennae, then
147 follow with a series of probing movements before attempting a grasp. Insects' antennae hold a range
148 of different tactile sensors [34]: tactile hairs detect contact, with different mechanical thresholds and
149 directional sensitivity, while a specific chordotonal organ in antennae detects motion of the distal
150 joint, which makes antennae active sensors. Similar sensors are found on the mandibles used for
151 grasping and insects can be observed to 'handle' objects before finalising their grasp. Although it is
152 unclear if the handling behaviour is to assess quality or to find a good gripping point, insects do
153 respond to ergonomic properties of objects. Ants, for instance, preferentially use the 'handle'
154 provided by the elaisome on a seed, and artificial replacement handles increase the probability of
155 seed transport [35]. Leaf- and grass-cutting ants position the item in the ant's grip to improve the
156 load balance and adjust the head angle dynamically according to the terrain on which they walk [17].

157

158 *Neural basis of grasping control*

159 How the brain processes sensory information to control grasping may differ between animals.

160 Comparing the neurological architecture for grasping in primates, birds, and insects would help

161 identify how similar the pathways are between primates and birds, at which point differences become
162 distinct, as well as how insects solve similar manipulative problems with much smaller number of
163 neurons. In both primates and birds, the cerebellum is involved in motor control of the processes of
164 reaching and grasping, and cerebellar structural complexity is associated with the degree of
165 manipulation expressed by different species [36, 37]. This may mean either that the role of the
166 cerebellum in manipulation is conserved across vertebrate groups to some extent, or the convergence
167 in the neural underpinning of manipulation in primates and birds, despite differences in the
168 manipulator and sensory anatomy involved. But determining exactly which would require further
169 investigations.

170 In contrast, insects have drastically different neural structures from vertebrates. For
171 manipulation by insects, there is good evidence that the insect central complex (CX) circuit is
172 involved. For example, lesions and genetic modification of specific parts of the CX selectively affect
173 targeting behaviour in flies crossing gaps [38], cockroaches using their antennae to anticipate
174 obstacles [39], and praying mantis pursuing prey. All of such targeting behaviour requires the animal
175 to estimate their precise spatial relation to a target in 3D and take a well-timed and well-coordinated
176 action towards it. Also, the organisation of the various modules of the CX, such as the fan-shaped
177 body and protocerebral bridge, are more elaborate in nest-constructing social insects and insect
178 species that perform complex independent limb movements, whereas they tend to be reduced in
179 species that have simpler or more symmetrical patterns of movement [40]. Additionally, the dorsal
180 lobe antennal mechanosensory and motor centre control the antennal motion, suggesting that this is
181 the location for active sensing, and hence a useful focus for further attention for its role in grasping.

182

183 *Action-based representation of grasping*

184 As an animal contacts the target object with its manipulator, it kicks off a sequence of transient states
185 of grip. Using visual and tactile feedback, the animal might regrasp and adjust the way it holds the

186 object, to gather more information about the object, and/or to establish a more stable grip. In human
187 hand research, each of the grips in this sequence is defined based on which parts of a hand touch the
188 object [41]. Considering that a hand has six distinct parts including a palm and five digits, the
189 number of possible permutations of parts that could touch the target object soars quickly, resulting in
190 numerous entries in primate grasping repertoire. Does this diversity, however, really reflect variation
191 in the function and the underlying control mechanisms of grasping?

192 Even when all digits are in contact with the object, whether all the digits touching the object
193 in a grip play the same role depends on the task. For instance, on occasion all the digits and the palm
194 provide force to grasp a bottle, while on others only the thumb and the index finger provide essential
195 force to grip, and the other digits just ‘touch’ the bottle. In the latter, the thumb and the index finger
196 provide the functional grip, whereas others merely add support, or add almost no force at all. By
197 taking account of the amount and direction of force each component applies, one can reorganise
198 classic grip types functionally. And more importantly, describing grip using parameters like vectors
199 of force (Figure 2a) could illustrate grip in terms of the dynamic relationship between the
200 manipulator and the object (an analogous example of tool-use definition; [42]), making grasping by
201 hands comparable with grasping by non-hand manipulators like bills and mandibles.

202 An obvious example of this is grasping by bird bills and pinching by hands. They both stand
203 for the state in which an object is held between two components, a finger and the opposing thumb in
204 a hand [41], or upper and lower beaks in bird bills, with each component exerting force towards the
205 other. Interestingly, among primates modern humans are considered uniquely capable of strong
206 pinching, which aids tool making and using [43], while ‘pinching’ is a usual form of grasping for
207 many birds.

208 This, however, does not mean that ‘pinching’ is the only form of manipulation birds can do.
209 Actions like prying or pecking, for instance, also plays an important role in foraging of some birds
210 such as crossbills and woodpeckers. Further, birds can vary their grasp by changing where on the

211 object they hold and so how to apply the force. In fact, some birds seem to develop preferences for a
212 specific way of holding the target object. Some male weaver birds, for instance, consistently
213 preferred a specific side of their cheek on which they held grass to insert into a nest [44]. Similarly,
214 individual New Caledonian crows have a preferred side against which they hold a foraging tool [45].
215 Such preference could streamline the control process of grasping, by always taking sensory
216 information from the same side, and so over time, making it easy to detect deviation from the usual
217 set of visual and tactile information. In addition, birds and insects can expand their repertoire of grips
218 by using other body parts, increasing the number of body parts that support the target object. Parrots,
219 for instance, are some of the few birds that have intrinsic muscles to move tongues dexterously [46].
220 These birds use their fleshy tongue to rotate a food item like a seed while holding it in the bill, and to
221 stabilise it in a place while crushing the shell with its bill [46], whereby the tongue acts like a digit.
222 Additionally, feet and legs can play a static role such as stabilising an object, just like the thumb and
223 the middle finger while using chopsticks (the index finger plays the dynamic role of opening/closing
224 the chopsticks). This is indeed the case when a raptor or a praying mantis tears prey with its bill or
225 mandibles, while holding the prey in its feet or legs.

226

227 *Methodologies towards manipulation beyond hands*

228 What new methods could contribute to building a broader framework to compare and integrate
229 manipulation with and without hands? We suggest that one promising way is to make use of cutting-
230 edge image tracking methods, which allow describing and analysing a grasping process in terms of
231 motions (Figure 2a). The technology to record, extract, and analyse behavioural footage has become
232 cheaper and more powerful in recent years, including an upsurge of image-tracking methods to
233 extract motions from footage (reviewed in [47]). Well-known examples include DeepLabCut [48]
234 and DeepPoseKit [49], both of which use deep-learning algorithms to recognise the tracking target
235 even when it changes its shape and colour with movement. More suitable for analysing how different

236 skeletal parts move together is XMALab [50], an integrated programme to collect motion data from
237 2D x-ray videos and to reconstruct 3D motions.

238 These image-tracking methods produce large amounts of motion data, often in the form of the
239 target locations in each frame. Such data can be transformed into different parameters like velocity
240 and orientation [51], parameters that can then be analysed using methods developed in movement
241 ecology and engineering, such as Hidden Markov models [52] or spline regression models [53].
242 These methods categorise distinct behavioural elements, by detecting systematic and recurring
243 patterns in motions. Image tracking and clustering of behavioural elements would enable us to
244 visualise different aspects of motions like force and speed during manipulation. In so doing, these
245 methods would help us transfer what could only be captured as behavioural accounts into
246 quantitative data, just like spectrograms converted bird songs into acoustic data [54]. Indeed,
247 analytical tools that have been developed for categorising human grasping actions might be
248 successfully redeployed to this wider context.

249

250 *Robotic applications of manipulation with and without hands*

251 Grasping and manipulation have always been central to the study of robotics, but the problems of
252 manipulation in unconstrained environments are yet to be solved [55, 56]. A robot typically follows a
253 similar series of steps in grasping as animals do: ‘sensing the object and environment’ (constructing
254 an accurate representation of the space), ‘reaching and grasping’ (selecting an efficient and effective
255 action), and ‘sensing the outcome’ (assessing the success or failure of actions). Success on this task
256 remains limited, with higher performances ranging from around 80% in rather constrained situations
257 (e.g. only translation and rotation of the gripper needs to be determined before grasping; [57]) to
258 nearer 50% in dense 3D clutter with naturalistic objects [58]. In contrast to these low success rates of
259 robots, animals show generally high success rates in grasping (e.g., >98% in tool grasping by New
260 Caledonian crows; [59]). Learning how animals’ manipulators are built and how animals move the

261 manipulators could provide hints for designing new hardware and software for more successful
262 robotic manipulation.

263 As such, a number of bioinspired approaches have been tested in robotic grasping, but
264 perhaps surprisingly, neither insects nor birds have received much consideration as a potential model
265 [60, 61]. Some bioinspired approaches have focussed on the human hand, to develop robotic systems
266 able to operate in unstructured environments, arguing that it is important to make better use of
267 integrated position, force, tactile and proximity sensing [62]. But if that is the case, these are equally
268 compelling reasons to consider manipulation by mandibles as inspiration (Figure 2a&b). Currently
269 most bioinspired work focuses on use of soft or compliant actuators [63, 64], such as grippers
270 inspired by soft fingers [8]. Similarly, inspired from unique flexible manipulators of some animals
271 (e.g., elephant trunks, octopus arms, and monkey tails), some attempts have been made to model and
272 design robotic actuators based on these prehensile appendages [65, 66]. But as the design and control
273 of such devices for specific applications remain a major challenge, an obvious alternative is to
274 consider animals such as birds and insects that use rigid structures to grasp (Figure 2c). As birds and
275 insects manage skilled manipulation only using their structurally simple manipulators and fewer
276 neurons, their bills and mandibles could inspire the development of efficient robotic mandibles in a
277 novel way (Figure 2d). For instance, most primates share the basic structures of wrists (the base of
278 the manipulator; [67]), while birds are exceptionally variable in the structure of their manipulator's
279 base, the number of cervical vertebrae [68]. This might mean that a bird's neck structure corresponds
280 to the manipulative task (e.g., picking up a seed, tearing soft tissue, or weaving a grass nest) in which
281 the species engages, providing a starting point for designing specialist robotic bills.

282

283 *Conclusion*

284 Effective manipulation of objects is essential for many animals' survival and breeding. While the
285 vast majority of manipulation research has revolved around primate hands, most animals lack hands

286 as a manipulator. By actively integrating theories and findings from previous research to include
287 manipulation without hands, we will gain a more general insight into how animals interact with the
288 physical world. Such research could both refine our understanding of what is special about human
289 hands, and inspire novel designs for grasping robots or prosthetic grippers. Together, these avenues
290 of research into manipulation with and without hands can serve as a link between the fields of animal
291 behaviour, animal cognition, functional morphology, and biomechanics.

292

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471 AUTHORS' CONTRIBUTIONS

472 S.S. conceived the concept for the review. S.H. and B.W. contributed to the original text, with S.S.
473 assembling the initial draft. All authors jointly edited the paper.

474

475 COMPETING INTERESTS

476 We declare no competing interests.

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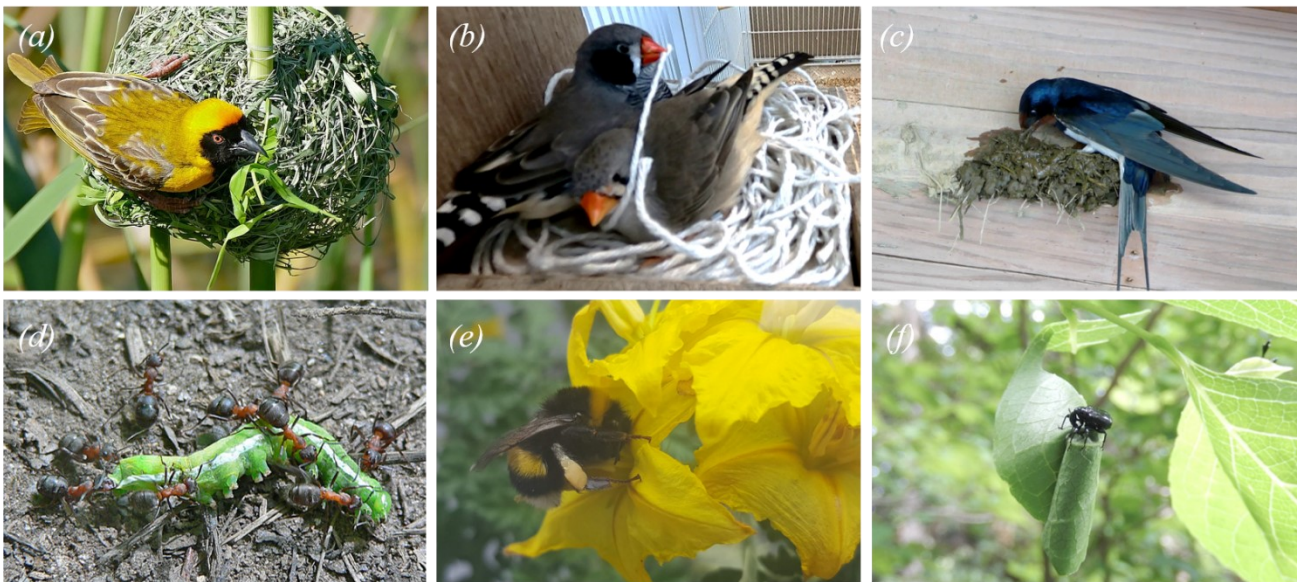
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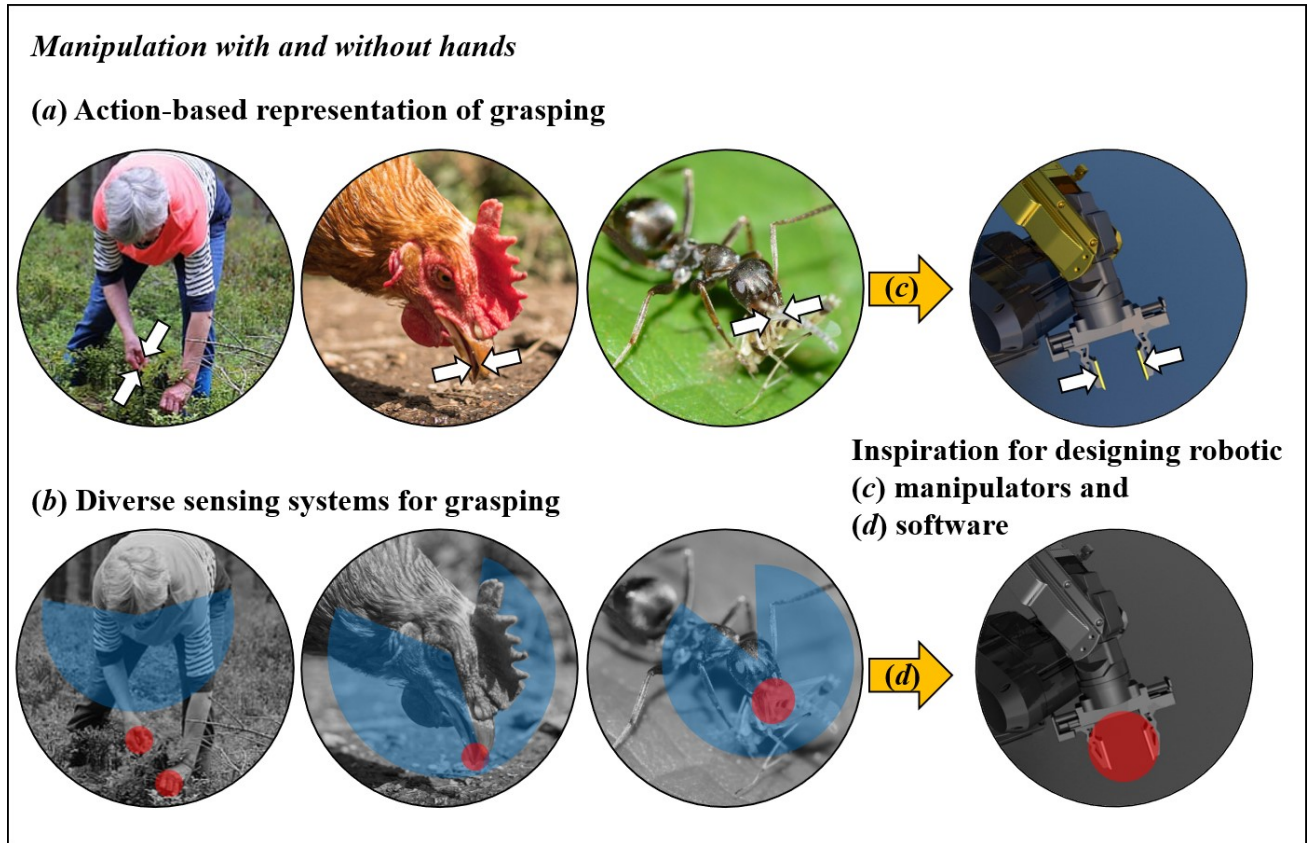
483 FIGURES



484

485 Figure 1. Examples of object manipulation in birds and insects. Manipulation of: (a) grass strips by a
486 southern-masked weaver bird (*Ploceus velatus*); (b) cotton strings by a zebra finch (*Taeniopygia*
487 *guttata*); (c) mud pellets by a barn swallow (*Hirundo rustica*); (d) a worm by a group of wood ants
488 (*Formica rufa*); (e) a flower by a bumble bee (*Bombus terrestris audax*); and (f) a leaf to lay eggs in

489 by a leaf-rolling weevil (*Cycnotrachelus roelofsi*). Photographs by (a) B Dupont; (b)&(c) S
490 Sugasawa; (d) P Dickson; (e) DJ Pritchard; and (f) Y Higuchi.
491



492
493 Figure 2. Description of physical and sensory components of manipulation with and without hands.
494 (a) A human, a bird, and an ant engaging in a similar task (i.e., picking up food items). White arrows
495 show the direction of force applied by different parts of manipulators, specifically, the person's index
496 finger and thumb, the hen's bill, and the ant's mandibles. (b) Even in similar manipulative tasks, the
497 way the person, the bird, and the ant take in and process sensory information is different. The
498 contacts between the manipulators and the object are marked with red, and the approximate range of
499 visual fields are marked with blue. While the person has an entire view of the hands, the eyes and
500 manipulators of the bird and the ant are attached to the head, providing direct sensory information
501 about the position of their manipulator relative to the object. Data from manipulation in these

502 biological systems may provide inspiration for designs (*c*) and necessary sensory input and operation
503 sequences (*d*) of robotic grippers. All photographs used in this figure are royalty free.
504