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Title:

How humans grasp three-dimensional objects

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Author Contributions:

GM, LKK, VCP and RWF conceived and designed the study. LKK collected the data. LKK and GM analyzed the data. GM developed the computational model of grasp selection. All authors wrote the manuscript.

1 **Abstract**

2 We rarely experience difficulty picking up objects, yet of all potential grasp points on an object's
3 surface, only a small proportion yield stable, comfortable grasps. Here, we present extensive
4 behavioral data alongside a computational model that correctly predicts human precision
5 grasping of unfamiliar 3D objects. We tracked participants' forefinger and thumb as they picked
6 up objects of 10 wood and brass cubes configured to tease apart effects of shape, weight,
7 orientation, and mass distribution. Grasps were highly systematic and consistent across
8 repetitions and participants. The model combines five cost functions related to force closure,
9 torque, natural grasp axis, grasp aperture, and visibility. Even without free parameters, we find
10 that the model predicts human grasps with striking fidelity: indeed, it predicts individual grasps
11 almost as well as different individuals predict one another's. Adding fittable weights to the model
12 reveals the relative importance of the different constraints: the combination of force closure,
13 hand posture, and grasp size explains most of human grasping behavior, while our participants
14 cared surprisingly little about minimizing torque and optimizing object visibility. Together, these
15 findings provide a unified account of how we derive effective grasps from objects' 3D shape and
16 material properties to interact with them successfully.

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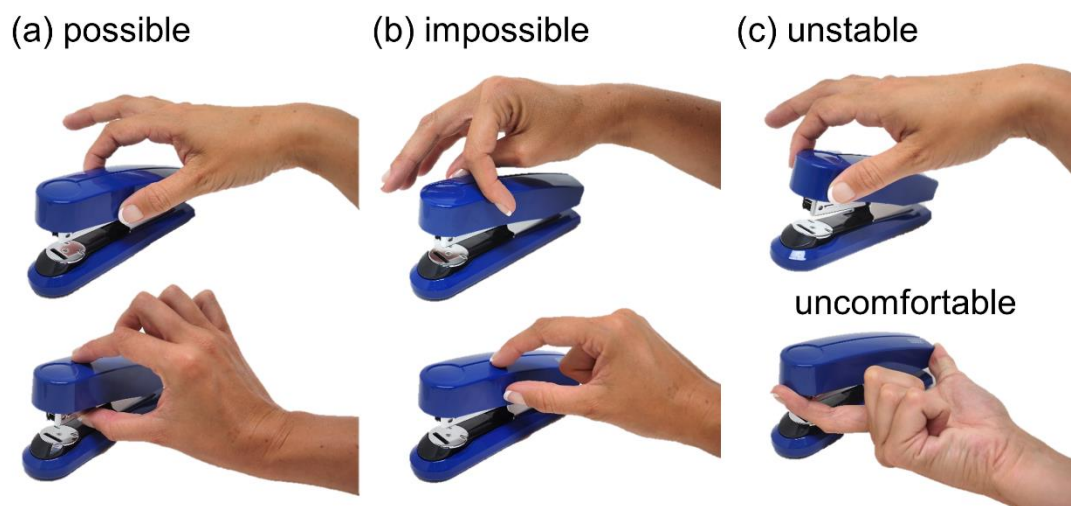
18 **Significance Statement**

19 Working out how we pick up and interact with objects effectively is one of the most important
20 challenges in behavioral science. Of all the potential contact points on an object's surface, only
21 a small proportion yield effective grasps. Despite this, we rarely experience any difficulty
22 choosing where and how to pick objects up. Here, we present a computational model that
23 unifies the varied and fragmented literature on human grasp selection. We find that the model
24 correctly predicts human grasps across a wide variety of conditions, taking into account the
25 object's 3D shape, material properties and orientation.

26

27 Introduction

28 In everyday life, we effortlessly grasp and pick up objects without much thought.
29 However, this ease belies its computational complexity. Even state of the art robotic AIs fail to
30 grip objects nearly 20% of the time(1). To pick something up, our brains must work out which
31 locations on the object will lead to stable, comfortable grasps, so we can perform desired
32 actions (Figure 1a). Most potential grasps would actually be unsuccessful, e.g., requiring thumb
33 and forefinger to cross, or failing to exert useful forces (Figure 1b). Even many possible grasps
34 would be unstable, e.g., grasping an object too far from its center, so that it rotates once we try
35 to lift it (Figure 1c). Somehow, the brain must infer which, of all potential grasps, would actually
36 succeed. Despite this, we rarely drop objects or find ourselves unable to complete actions
37 because we are holding them inappropriately. How does the brain select stable, comfortable
38 grasps onto arbitrary 3D objects, particularly objects we have never seen before?



39
40 **Figure 1.** The computational complexity of grasp selection. (a) Possible (b) Impossible (c)
41 Possible but uncomfortable or unstable grasps.

42
43 Despite the extensive literature describing human grasping patterns and movement
44 kinematics(2–11), little is understood about the computational basis of human grasp selection.

45 Few authors have attempted to study and model how humans select grasps (e.g. (12, 13)), and
46 even then, only for 2D shapes. This is because, even for two-digit precision grip, many factors
47 influence how we grasp objects. Object shape must be considered, since the surface normals at
48 thumb and index finger contact locations must be approximately aligned (a concept known as
49 force closure(14)), otherwise the object will slip through our fingertips (Figure 1b, bottom). The
50 object's mass and mass distribution must be evaluated, since for grips with high torques (i.e. far
51 from the object's center of mass, or CoM(15–19)) the object will tend to rotate under gravity and
52 potentially slip out of our grasp (Figure 1c, top). The orientation(16, 20–22) and size(23) of each
53 grasp must be considered, since our arm and hand can move and apply forces only in specific
54 ways, and grasps that do not conform to the natural configuration of our hand in 3D space might
55 be impossible (Figure 1b, top), or uncomfortable (Figure 1c, bottom). The hand's positioning
56 may also determine an object's visibility(9, 24–27).

57 Most previous research on visually guided grasping did not assess the relative
58 importance of these factors, nor how they interact. Here we sought to unify these varied and
59 fragmented findings into a single theoretical and computational framework. We therefore
60 constructed a rich dataset in which we could tease apart how an object's 3D shape, mass, mass
61 distribution, and orientation influence grasp selection. We devised a set of objects made of
62 wood and brass cubes in various 3D configurations (Figure 2), and asked participants to pick
63 them up with a precision grip, move them a short distance and place them at a target location,
64 while we tracked their thumb and forefinger. By varying the spatial configurations of the cubes
65 and orientation of the objects in Experiment 1 we could (1) determine how consistent
66 participants are with themselves and other people, and (2) measure the interactions between
67 allocentric 3D shape and egocentric perspective on those shapes. If actors take the properties
68 of their own effectors into account (e.g., hand orientation, grasp size), we should expect the
69 same 3D shape to be grasped at different locations depending on its orientation relative to the
70 observer(16). In Experiment 2, we varied the mass and mass distribution of the objects (Figure

71 2c) to test the relative role of 3D shape and mass properties on grasp point selection. If
72 participants take torques into account, identical shapes with different mass distributions should
73 yield systematically different grasps(15, 17–19).

74 Next, we employed this rich dataset to develop a computational model to predict human
75 grasp patterns. We reasoned that grasps are selected to minimize costs associated with
76 instability and discomfort. Accordingly, we implemented a model that combines five factors
77 computed from the object's shape, mass distribution, and orientation: (i) force closure(14), (ii)
78 torque(15–19) (iii) natural grasp axis(16, 20–22), (iv) natural grasp aperture for precision
79 grip(23) and (v) visibility(24, 25). We find that the model predicts human grasp patterns strikingly
80 well.

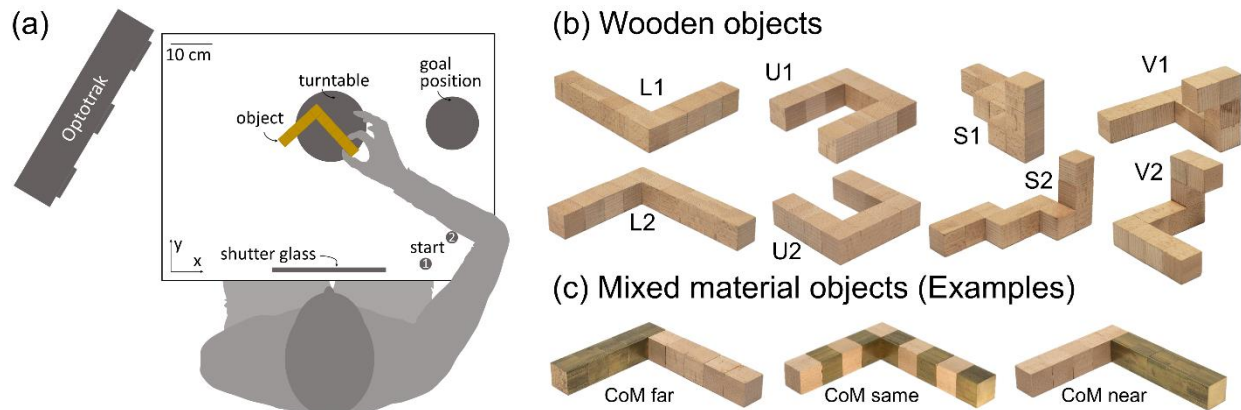
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82 **Results:**

83 ***Experiment 1: 3D shape and orientation***

84 **Human grasps are tightly clustered and represent a highly constrained sample from the**
85 **space of potential grasps.** We asked 12 participants to grasp four objects made of beech
86 wood presented at two orientations (*Figure 2*; see **Methods**). *Figure 3a* shows how grasp
87 patterns tend to be highly clustered. In each condition, different grasps have similar size (finger-
88 to-thumb distance) and orientation, and also cover the same portions of the objects. Fitting
89 multivariate Gaussian mixture models to the responses reveals that grasps cluster around only
90 1, 2, or 3 modes. In *Figure 3b* we can observe these distinct modes for object U at orientation 2
91 in a 2D representation of grasp space, where we can also note that human grasps cover only a
92 minute portion of the space of potential grasps. *Figure 3c* also shows how, for one
93 representative condition, different grasps from the same subjects are more clustered than
94 grasps from different subjects, since individuals predominantly selected only one (70%) or two
95 (27%) modes, and only rarely (3%) grasped objects in three separate locations.

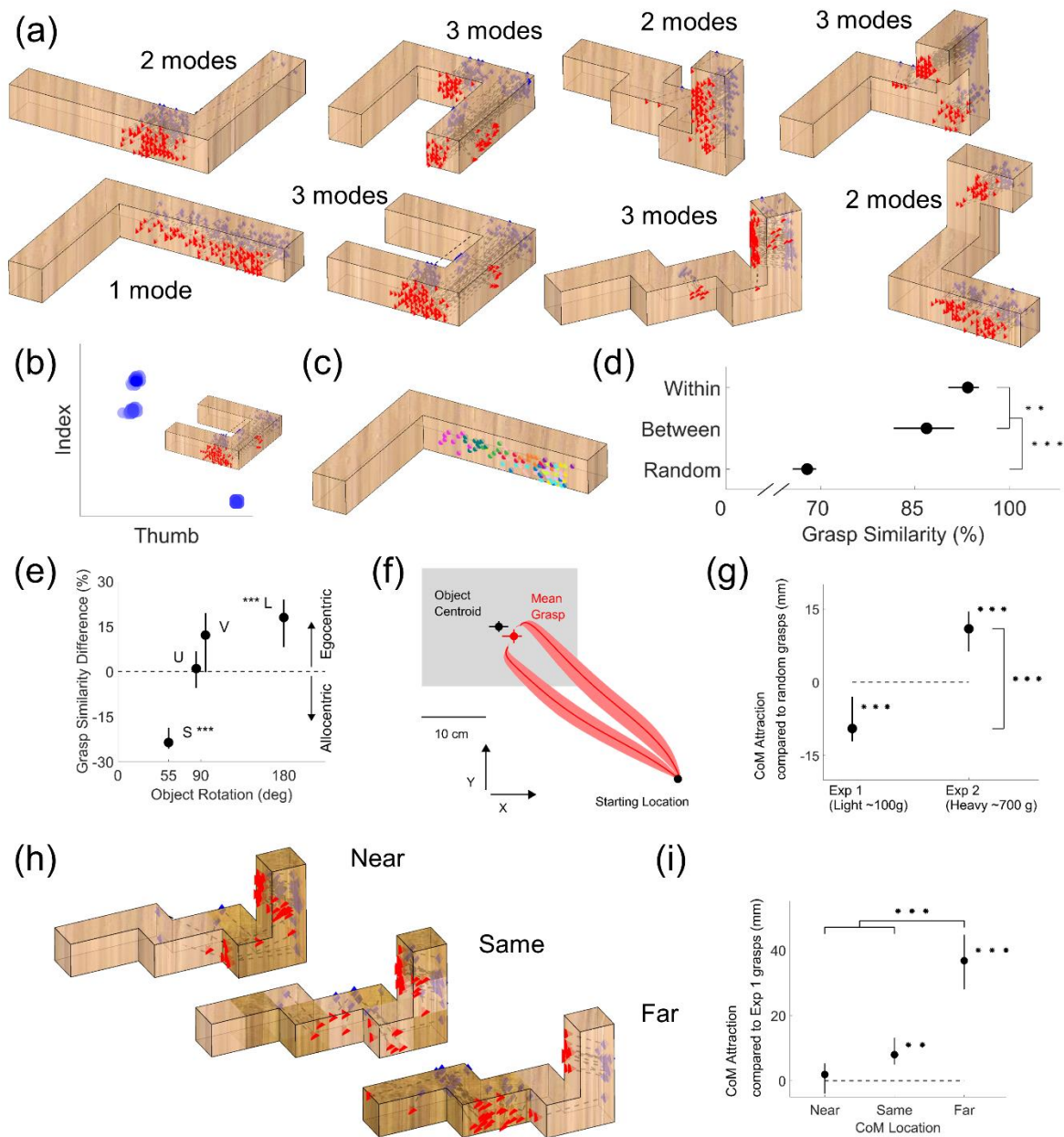
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97

98 **Figure 2.** Setup and stimuli. (a) Experimental setup. Seated participants performed grasping
99 movements with their right hand. Following an auditory signal (coinciding with the shutter
100 window turning transparent) they moved from one of the starting positions to the object and
101 grasped it with a precision grip. They transported and released the object at the goal position
102 and returned to the start position. (b) In Experiment 1 we employed four objects made of
103 wooden cubes. Each object had a unique shape (that here we name L, U, S, V) and was
104 presented at one of two different orientations with respect to the participant. (c) In Experiment 2
105 the objects had the same shapes as in Experiment 1, but now were made of wood and brass
106 cubes. The brass and wood cubes were organized either in an alternate pattern (middle), so
107 that the CoM of the object would remain approximately the same as for the wooden object, or
108 grouped so that the CoM would be shifted either closer to (right) or away from (left) the
109 participant's hand starting location.

110



111

112 **Figure 3. Empirical Results. (a)** Human grasps from Experiment 1. Grasps are represented as

113 thumb (red triangles) and index finger (blue diamonds) contact positions, connected by dotted

114 black lines. (b) Human grasps (blue blobs) for object U, orientation 2, when projected in a 2D

115 representation of the space of potential grasps, cluster around three distinct modes. (c)

116 Distribution of thumb contact points on object L, orientation 2. Different colors represent grasps

117 from different participants. **(d)** The level (%) of grasp similarity expected for grasps randomly
118 distributed on the object surface and the observed level of between- and within-participant grasp
119 similarity **(e)** Difference in grasp similarity across orientations when grasps were encoded in
120 object-centered (allocentric) vs human-centered (egocentric) coordinates, as a function of
121 magnitude of rotation across the two orientation conditions. **(f)** Average grasp trajectories
122 viewed in the x-y plane (red curves) from start location towards the objects (always contained
123 within the gray shaded region). The average human grasp (red dot) across conditions is biased
124 toward shorter reaching movements compared to the object centroids (black dot). **(g)** Attraction
125 towards the object CoM for grasps executed onto light (Experiment 1) and heavy (Experiment 2)
126 objects compared to grasps uniformly distributed on the object surfaces (zero reference). **(h)**
127 Human grasps from Experiment 2 onto object S presented at orientation 2. **(i)** Attraction towards
128 the object CoM compared to Experiment 1 grasps (zero reference), for Experiment 2 grasps
129 onto heavy objects whose CoM is closer, the same distance as, or farther than the light wooden
130 objects from Experiment 1. In all panels, error bars/regions represent 95% bootstrapped
131 confidence intervals. ** $p < 0.01$, *** $p < 0.001$

132
133 To further quantify how clustered these grasping patterns are we designed a simple
134 metric of similarity between grasps (see **Methods**). Figure 3d shows how both between- and
135 within-subject grasp similarity are significantly higher than the similarity between random grasps
136 due to object geometry ($t(7)=9.76$, $p=2.5 \times 10^{-5}$ and $t(7)=25.11$, $p=4.1 \times 10^{-8}$ respectively).
137 Additionally, within-subject grasp similarity is significantly higher than between subjects
138 ($t(7)=3.89$, $p=0.0060$). Nevertheless, the high level of similarity between grasps from different
139 participants demonstrates that different humans tend to grasp objects in similar ways. The even
140 higher level of within-subject grasp similarity further demonstrates that grasp patterns from
141 individual participants are idiosyncratic, which may reflect differences in the strategies employed
142 by individual participants.

143 **Findings reproduce several known effects in grasp selection.** First, previous research
144 suggests haptic space is encoded in both egocentric and allocentric coordinates(28), and that
145 grasps are at least partly encoded in egocentric coordinates to account for the biomechanical
146 constraints of our arm and hand(16). Our findings reproduce and extend these observations.
147 For each object we computed grasp similarity across the two orientations in both egocentric and
148 allocentric coordinates. Figure 3e shows that, as the extent of the object rotation increases,
149 grasp encoding shifts from allocentric to egocentric coordinates. Across small rotations (object
150 S, 55 deg rotation), grasps are more similar if encoded in allocentric coordinates ($t(11)=13.90$,
151 $p=2.5*10^{-8}$), whereas for large rotations (object L, 180 degrees) grasps are more similar if
152 encoded in egocentric coordinates ($t(11)=4.59$, $p=7.8*10^{-4}$). Therefore, both 3D shape as well
153 as movement constraints influence grasps.

154 Second, Figure 3f shows that participants selected grasps locations that were on
155 average 26 mm closer to the starting location than the object centroid ($t(11)=9.74$, $p=9.6*10^{-7}$),
156 reproducing known spatial biases in human grasp selection (12, 25, 27, 29, 30).

157 Third, consistent with Kleinholdermann et al (12) but contrary to previous claims(15–19),
158 our findings suggest humans care little about torque when grasping light objects. If actors
159 sought to minimize torque, the selected grasps should be as close as possible to the CoM. In
160 contrast, Figure 3g shows that for the light weight objects in Experiment 1, grasps were on
161 average 9 mm farther from the CoM than the average distance to the object's CoM of grasps
162 uniformly sampled onto the surface of the objects ($t(11)=4.53$, $p=8.6*10^{-4}$).

163

164 ***Experiment 2: Mass and Mass Distribution***

165 **Humans grasp objects close their center of mass when high grip torques are possible.**

166 Due to the low density of beech wood, even the grasps farthest from the CoM in Experiment 1
167 would produce relatively low torques. Therefore, in Experiment 2 we tested whether participants
168 grasp objects closer to the CoM when higher torques are possible. We did this by using objects

169 of greater mass and asymmetric mass distributions. Specifically, for each of the shapes in
170 Experiment 1, we made three new objects, each made of five brass and five wooden cubes: two
171 'bipartite' objects, with brass clustered on one or the other half of the object, and one
172 'alternating' object, with brass and wood alternating along the object's length. These objects had
173 the same 3D shapes as in Experiment 1, but were nearly tenfold heavier (Figure 2c, see
174 **Methods**).

175 Figure 3g shows how human grasps are indeed significantly attracted towards the CoM
176 of heavy objects, presumably to counteract the larger torques associated with higher mass. In
177 Experiment 2, grasps were on average 11 mm closer to the object CoM than grasps sampled
178 uniformly from the objects' surfaces ($t(13)=4.94$, $p=2.7 \times 10^{-4}$), and on average 20 mm closer
179 than the grasps from Experiment 1 ($t(24)=6.63$, $p=7.4 \times 10^{-7}$). Importantly, participants shifted
180 their grasps towards the CoM—not the geometrical centroid—of the objects (observe how the
181 grasp patterns shift in Figure 3h). Figure 3i shows that when the object CoM was shifted
182 towards the hand starting location, participants did not significantly adjust their grasping strategy
183 compared to Experiment 1 ($t(13)=0.81$, $p=0.43$). Conversely, when the object CoM was in the
184 same position as in Experiment 1, participants shifted their grasps on average by 8 mm towards
185 the CoM ($t(13)=3.92$, $p=0.0017$). When the object CoM was shifted away from the hand starting
186 position, participant grasps were on average 37 mm closer to the object CoM compared to
187 Experiment 1 grasps ($t(13)=8.49$, $p=1.2 \times 10^{-6}$), a significantly greater shift than both the near and
188 same CoM conditions ($t(13)=8.66$, $p=9.2 \times 10^{-7}$ and $t(13)=7.58$, $p=4.0 \times 10^{-6}$). These differential
189 shifts indicate that participants explicitly estimated each object's CoM from visual material cues.

190 Even with the heavier objects, participants still systematically selected grasp locations
191 that were closer to the starting location than the object centroid ($t(13)=4.03$, $p=0.0014$).
192 However, now participants exhibited only a 9 mm bias, which was significantly smaller than the
193 26 mm bias observed for the light wooden objects in Experiment 1 ($t(24)=4.67$, $p=9.6 \times 10^{-5}$).

194 Together these findings suggest that participants combine multiple constraints to select
195 grasp locations, taking into consideration the shape, weight, orientation, and mass distribution of
196 objects, as well as properties of their own body to decide where to grasp objects. We next
197 sought to develop a unifying model that could predict these diverse effects based on a few
198 simple underlying principles.

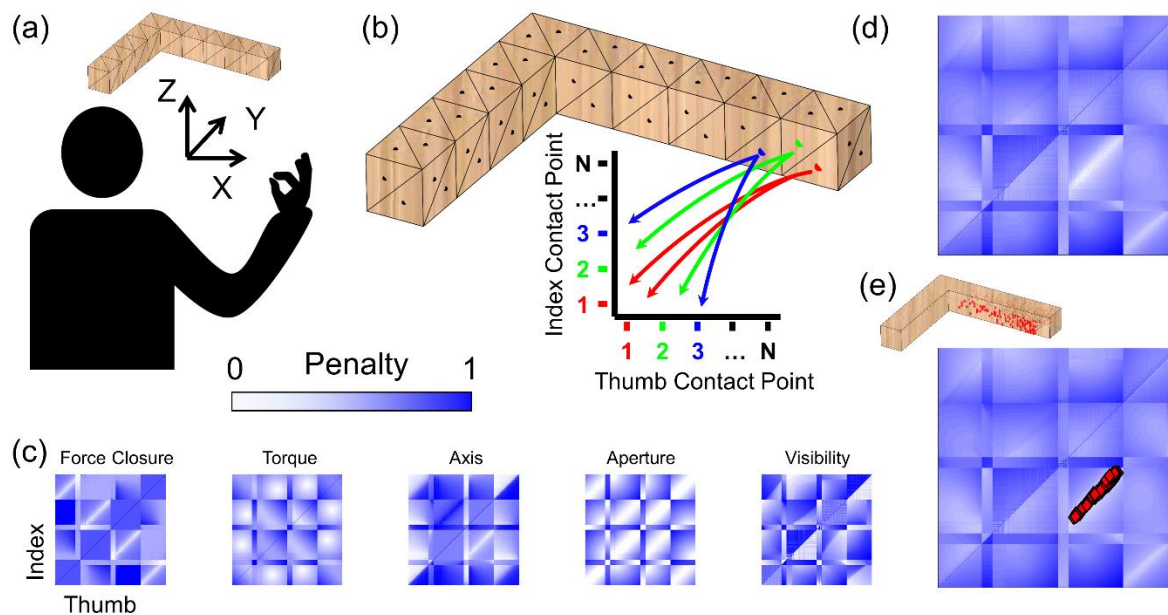
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200 ***Computational model of human grasp selection.***

201 Based on the insights gained from our empirical findings, we developed a computational
202 model to predict human grasp locations. The model takes as input 3D descriptions of the
203 objects' shape, mass distribution, orientation, and position relative to the participant, and
204 computes as output a *grasp cost function*, describing the costs associated with every possible
205 combination of finger and thumb position on accessible surface locations (i.e., those not in
206 contact with table). We reasoned that humans would tend to grasp objects at or close to the
207 minima of this cost function, as these would yield the most stable, comfortable grasps. Low cost
208 grasps can then be projected back onto the object to compare against human grasps. It is
209 important to note that this is not intended as a process model describing internal visual or motor
210 representations (i.e., we do not suggest that the human brain explicitly evaluates grasp cost for
211 all possible surface locations). Rather, the model is a way of combining a subset of the factors
212 which are known to influence human grasp selection into a single, unifying framework (12).

213 For each object, we create a triangulated mesh model in a 3D coordinate frame, from
214 which we can sample (Figure 4a-b). For precision grip, we assume one contact point each for
215 thumb and index finger. Thus, all possible precision grip grasps can be ordered on a 2D plane,
216 with all possible thumb contact points along the x-axis, and on the y-axis, all possible index
217 contacts in the same ordering as for the thumb.

218



219

220 **Figure 4.** A framework that unifies distinct aspects of grasp selection. (a) Mesh model of object
221 in same 3D reference frame as participant poised to execute grasp. (b) Discrete sampling of the
222 surface defines a 2D space containing all potential combinations of index and thumb contact
223 points on the object. (c) Color-coded maps showing penalty values for each potential grasp for
224 each penalty function. (d) Overall penalty function computed as the linear combination of maps
225 in (c). (e) Human grasps projected into 2D penalty-function space neatly align with minimum of
226 combined penalty map.

227

228 To estimate the cost associated with each grasp, we take a (weighted) linear combination of five
229 *penalty functions*, determined by the physical properties of the graspable object (surface shape,
230 orientation, mass, mass distribution) as well by the physical constraints of the human actuator
231 (i.e. the human arm/hand). Specifically, we consider optimality criteria based on: (i) optimum
232 force closure(14), (ii) minimum torque(15–19), (iii) alignment with the natural grasp axis(16, 20–
233 22), (iv) optimal grasp aperture(23), and (v) optimal visibility(24, 25, 27). (see **Methods** for
234 mathematical definitions). Figure 5(c) shows maps for each penalty function: white indicates low

235 penalty, dark blue high penalty. To compare and combine penalty, values are always
236 normalized to [0,1].

237 **Force closure:** force closure is fulfilled when the two contact-point surface normals, along
238 which gripping forces are applied, are directed towards each other(14). Thus, we penalize
239 lateral offsets between the grasp point normals.

240 **Minimum torque:** grasping an object far from its CoM results in high torque, which causes the
241 object to rotate when picked up(15–19). Large gripping forces would be required to prevent the
242 object from rotating. We therefore penalize torque magnitude.

243 **Natural grasp axis:** when executing precision grip grasps, humans exhibit a preferred hand
244 posture known as the *natural grasp axis*(16, 20–22). Grasps that are rotated away from this axis
245 result in uncomfortable or restrictive hand/arm configurations. We therefore penalize angular
246 misalignment between each candidate grasp and the natural grasp axis (taken from (21)).
247 Unlike force closure and torque, this penalty map is asymmetric about the diagonal.

248 **Optimal grasp aperture:** humans prefer the distance between finger and thumb at contact
249 ('grasp aperture') to be below 2.5 cm(23). We therefore penalize grasp apertures above 2.5 cm.

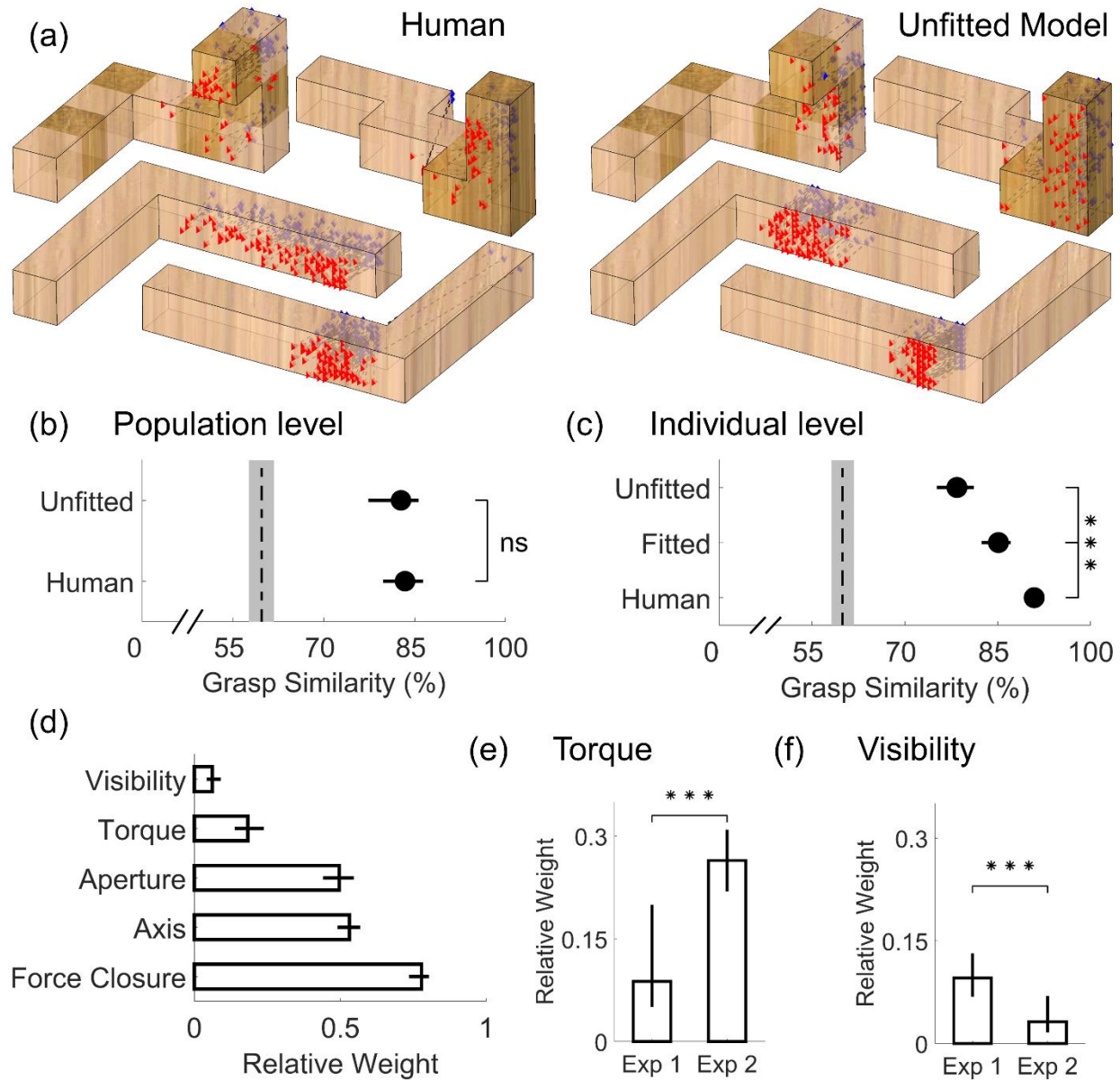
250 **Optimal visibility:** our behavioral data, and previous studies, suggest humans exhibit spatial
251 biases when grasping. It has been proposed that these may arise from an attempt to minimize
252 energy expenditures through shorter reach movements(24). However, Paulun et al (25) have
253 shown that these biases may in fact arise from participants attempting to optimize object
254 visibility. While our current dataset was not designed to untangle these competing hypotheses,
255 re-analyzing published data (19, 27) confirms that object visibility—not reach length—is most
256 likely responsible for the biases. We therefore penalized grasps that hindered object visibility.
257 We also designed a penalty function for reach length and verified that, since reach length and
258 object visibility are correlated in our dataset, employing one or the other penalty function yields
259 very similar results.

260

261 We assume that participants select grasps with low overall costs across all penalty
262 functions. Thus, to create the overall grasp penalty function, we take a (weighted) linear sum of
263 the individual penalty maps. The minima of this full penalty map represent grasps that best
264 satisfy all criteria simultaneously. The map in Figure 5d exhibits a clear minimum: the white
265 region in its lower right quadrant.

266 To assess the agreement between human and optimal grasps, we may visualize human
267 grasps in the 2D representation of the grasp manifold. The red markers in Figure 5(e) are the
268 human grasps from object L at orientation 2, projected in 2D and overlain onto the full penalty
269 map. Human grasps neatly align with the minima of the penalty map.

270 **Model Fitting.** The simple, equally-weighted combination of constraints considered thus far
271 agrees with human grasping behavior surprisingly well. However, it is unlikely that actors treat
272 all optimality criteria as equally important. Different persons likely weight the constraints
273 differently (e.g., due to strength or hand size). Therefore, we developed a method for fitting full
274 penalty maps to participants' responses. We assigned variable weights to each optimality
275 criterion, and fit these weights to the grasping data from each participant, to obtain a set of full
276 penalty maps whose minima best align with each participant's grasps (see **Methods**).



277

278 **Figure 5. Computational Results.** (a) Grasping patterns predicted through the computational
 279 framework (right) closely resemble human grasps onto real objects varying in shape,
 280 orientation, and material (left). Simulated grasp patterns are generated with no knowledge of our
 281 human data (i.e. model not fit to human grasps). (b) Population level grasp similarity, i.e.
 282 similarity of human and unfitted model grasps to median human grasp across all participants.
 283 (c) Individual level grasp similarity, i.e. similarity of human, unfitted, and fitted model grasps to
 284 the median grasp of each participant. In panels (b,c), dashed line is estimated chance level of

285 *grasp similarity due to object geometry, bounded by 95% bootstrapped confidence intervals. (d)*
286 *Pattern of fitted weights across Experiments 1 and 2. (e) Relative weight of the minimum torque*
287 *constraint in Experiments 1 and 2. (f) Relative weight of the visibility constraint in Experiments 1*
288 *and 2. Data are means; error bars, 95% bootstrapped confidence intervals. *** $p < 0.001$*

289

290 **Model grasps are nearly indistinguishable from measured human grasps.** To compare
291 human and optimal grasps directly, we can sample predicted optimal grasps from around the
292 minimum of the full penalty map (see **Methods**) and project back onto the objects. Figure 5a
293 shows human grasps (left) and unfitted model predictions (right) on a few representative objects
294 (see Supplementary Figure S1 for complete set). Human and predicted grasps have similar size
295 and orientation, and also cover similar portions of the objects.

296 Figure 5b depicts grasp similarity at the population level, i.e., across participants and
297 between human and unfitted model grasps. Grasp similarity between participants was computed
298 (for each object and condition), as the similarity between the median grasp of each participant
299 and the median grasp across all others. Grasp similarity between human and model grasps was
300 computed as the similarity between the median unfitted model grasp and the median grasp
301 across all participants.

302 Unfitted model grasps were significantly more similar to human grasps than chance
303 ($t(31)=10.79$, $p=5.0 \times 10^{-12}$), and effectively indistinguishable from human-level grasps similarity
304 ($t(31)=0.31$, $p=0.76$). Note that this does not mean our current approach perfectly describes
305 human grasping patterns; it suggests instead that our framework is able to predict the median
306 human grasping patterns nearly as well as the grasps of a random human on average
307 approximate the median human grasp.

308 **Fitting the model can account for individual grasp patterns.** In both Experiments,
309 participants repeatedly grasped the same objects in randomized order. Figure 5c depicts how
310 similar human and model grasps are to the median grasp of each individual participant in each

311 experimental condition. Individual subjects are highly consistent when grasping the same object
312 on separate trials. Grasps predicted through our framework with no knowledge of the empirical
313 data were significantly less similar to the median grasps of individual humans ($t(31)=9.33$,
314 $p=1.6*10^{-10}$). This is unsurprising, since the unfitted model predicts the average pattern across
315 observers, but there is no mechanism for it to capture idiosyncrasies of individual humans.
316 Fitting the model to the human data (see **Methods**) significantly improved grasp similarity
317 ($t(31)=5.00$, $p=2.1*10^{-5}$). Note however that model grasp patterns fit to a single participant are
318 still distinguishable from random real grasps by the same individual ($t(31)=4.85$, $p=3.3*10^{-5}$).

319 **Force closure, hand posture, and grasp size explain most of human grasp point**

320 **selection.** The pattern of fitted weights across both experiments (Figure 5d) reveals the relative
321 importance of the different constraints. Specifically, we find that force closure is the most
322 important constraint on human grasping, which makes sense because force closure is a
323 physical requirement for a stable grasp. Next in importance are natural grasp axis and optimal
324 grasp aperture, both constraints given by the posture and size of our actuator (our hand). In
325 comparison, participants appear to care only marginally about minimizing torque, and almost
326 negligibly about object visibility.

327 **Analyzing the patterns of fitted weights confirms our empirical findings.** The model also
328 replicates our main empirical findings in a single step. Figure 5e shows that the relative
329 importance of torque was much greater for the heavy objects tested in Experiment 2 compared
330 to the light objects from Experiment 1 ($t(24)=4.40$, $p=1.9*10^{-4}$). Conversely, Figure 5f shows that
331 the relative importance of object visibility instead decreased significantly from Experiment 1 to
332 Experiment 2 ($t(24)=3.07$, $p=0.0053$). Additionally, by simulating grasps from the fitted model,
333 we are able to recreate the qualitative patterns of all behavioral results presented in Figure 3
334 (see Supplementary Figure S2).

335

336

337 **Discussion:**

338 We investigated how an object's 3D shape, orientation, mass, and mass distribution jointly
339 influence how humans select grasps. Our empirical analyses showed that grasping patterns are
340 highly systematic, both within and across participants, suggesting that a common set of rules
341 governs human grasp selection of complex, novel 3D objects. Our findings reproduce, unify,
342 and generalize many effects observed previously: (1) both 3D shape and orientation determine
343 which portion of the object people grasp (8, 12, 15, 16, 31–34).; (2) humans exhibit spatial
344 biases even with complex 3D objects varying in shape and mass(12, 25, 27, 29, 30); (3) object
345 weight modulates how much humans take torque into account when selecting where to grasp
346 objects(15–19). We then combined this diverse set of observations into a unified theoretical
347 framework that predicts human grasping patterns strikingly well, even with no free parameters.
348 By fitting the computational model to human behavioral data, we showed that force closure,
349 hand posture, and grasp size are the primary determinants of human grasp selection, whereas
350 torque and visibility modulate grasping behavior to a much lesser extent.

351 **3D Shape** Behavioral research on the influence of shape on grasping is surprisingly scarce,
352 primarily employs 2D or simple geometric 3D stimuli of uniform materials, and rarely
353 investigates grasp selection (8, 15, 16, 31–34). For example, by using 3D stimuli that only
354 varied in shape by a few centimeters, Schettino et al(33) concluded that object shape influences
355 hand configuration only during later phases of a reaching movement during which subjects use
356 visual feedback to optimize their grasp. Here, we show that distinct 3D shapes are grasped in
357 systematically distinct object locations, and our behavioral and model analyses can predict
358 these locations directly from the object 3D shape.

359 **Orientation** When grasping spheres or simple geometrical shapes, humans exhibit a preferred
360 grasp orientation (the NGA) (16, 20–22), and most previous work on how object orientation
361 influences grasping has primarily focused on hand kinematics(15, 19, 32, 35). Conversely, with
362 more complex 3D shapes we show that the same portion of an object is selected within a range

363 of orientations relative to the observer, whereas for more extreme rotations the grasp selection
364 strategy shifts significantly. Therefore, object shape and orientation together determine which
365 portion of an object will be grasped, and thus the final hand configuration.

366 **Spatial Biases** The spatial biases we observe are consistent with participants attempting to
367 increase object visibility(25, 27), and our data also replicate the finding that these biases are
368 reduced when object weight increases(19, 25).

369 **Material/Weight/Torque** Goodale et al(15) were among the first to show that participants tend
370 to grasp objects through their CoM, presumably to minimize torque. Lederman and Wing(16)
371 found similar results, yet in both studies low-torque grasps also correlated with grasps that
372 satisfied force closure and aligned with the natural grasp axis. Kleinholdermann et al(12) found
373 torque to be nearly irrelevant in grasp selection, yet Paulun et al(19) observed that grasp
374 distance to CoM was modulated by object weight and material. Our findings resolve these
375 conflicting findings. By using stimuli that decorrelate different aspects of grasp planning, we find
376 that shape and hand configuration are considerably more important than torque for light weight
377 objects, and that the importance of minimizing torque scales with mass. Additionally, shifting an
378 object's mass distribution significantly attracted grasp locations towards the object's shifted
379 CoM, demonstrating that participants could reliably combine global object shape and material
380 composition to successfully infer the object's CoM.

381 **Computational Modelling** Previous models of grasping have mainly focused on hand
382 kinematics and trajectory synthesis(2–6) whereas we attempt to predict which object locations
383 will be selected during grasping. Our modelling approach takes inspiration from
384 Kleinholdermann et al(12), which to the best of our knowledge is the only previous model of
385 human two-digit contact point selection, but only for 2D shape silhouettes. In addition to dealing
386 with 3D objects varying in mass, mass distribution, orientation, and position, our modeling
387 addresses several limitations of previous approaches. The fitting procedure quantifies the
388 relative importance of different constraints, and can be applied to any set of novel objects to test

389 how experimental manipulations affect this relative weighting. The modular nature of the model
390 allows additional constraints to be included, excluded or given variable importance. For
391 example, we know that end-state comfort of the hand plays a role in grip selection(36, 37), yet
392 the tradeoff between initial and final comfort is unclear(38). By varying the participants' task to
393 include object rotations, and by including a penalty function penalizing final hand rotations away
394 from the natural grasp axis, it would be possible to assess the relative importance of initial, final
395 (or indeed intermediate) hand configurations on grasp planning. The modelling could also be
396 extended to multi-digit grasping, by adding to each penalty function three dimensions for each
397 additional finger considered (the x,y,z coordinates of the contact point). This approach is
398 consistent with (and complementary to) the approach by Smeets and Brenner(2, 5), who posit
399 that grasping is a combination of multiple pointing movements. Future models should also
400 generalize from contact points to contact patches of nonzero area, as real human grasp
401 locations are not only points but larger areas of contact between digit and object. To facilitate
402 such developments, we provide all data and code (doi:xx.xxxx/zenodo.xxxxxxx upon
403 publication).

404 **Neuroscience of Grasping** While our model is not meant as a model of brain processes, there
405 are several parallels with known neural circuitry underlying visual grasp selection (for reviews
406 see(39–41)). Of particular relevance is the circuit formed between the Ventral Premotor Cortex
407 (Area F5), Dorsal Premotor Cortex (Area F2), and the Anterior Intraparietal Sulcus (AIP). Area
408 F5 exhibits 3D-shape-selectivity during grasping tasks and is thought to encode grip
409 configuration given object shape(42–44), whereas area F2 encodes the grip-wrist orientation
410 required to grasp objects under visual guidance(45). Both regions exhibit strong connections
411 with AIP, which has been shown to represent the shape, size, and orientation of 3D objects, as
412 well as the shape of the handgrip, grip size, and hand-orientation(46). Additionally, visual
413 material properties, including object weight, are thought to be encoded in the ventral visual
414 cortex(47–51), and it has been suggested that AIP might play a unique role in linking

415 components of the ventral visual stream involved in object recognition to hand motor
416 system(52). Therefore, the neural circuit formed between F5, F2, and particularly AIP is a strong
417 candidate for combining the multifaceted components of visually guided grasping identified in
418 this work(53–57). Combining targeted investigations of brain activity with the behavioral and
419 modelling framework presented here holds the potential to develop a unified theory of visually
420 guided grasp selection.

421

422 **Materials and Methods:**

423 ***Participants***

424 Twelve naïve participants (5 males and 7 females between the ages of 20 – 31, mean age: 25.2
425 years) participated in Experiment 1. Fourteen naïve participants (9 males and 5 females
426 between the ages of 21 and 30, mean age: 24.4 years) participated in Experiment 2.

427 Participants were students at the Justus-Liebig-University Giessen, Germany and received
428 monetary compensation for participating. All participants reported having normal or corrected to
429 normal vision and being right handed. All procedures were approved by the local ethics board
430 and adhered to the declaration of Helsinki. All participants provided written informed consent
431 prior to participating.

432 ***Apparatus***

433 Experiments were programmed in Matlab version R2007a using the Optotrak Toolbox by V. H.
434 Franz(58). Participants were seated at a table with their head positioned in a chinrest (Figure
435 2a), in front of an electronically controlled pane of liquid crystal shutter glass(59), through which
436 only part of the table was visible and which became transparent only for the duration of a trial.
437 Objects were placed at a target location, 34 cm from the chinrest in the participant's sagittal
438 plane. Small plastic knobs placed on participants' right side specified the hand starting
439 positions. A plate (28.5 cm to the right of the goal location and with a 13 cm diameter at 26 cm

440 from start position 1 in the participant's sagittal plane) specified the movement goal location. We
441 tracked participants' fingertip movements using an Optotrak 3020 infrared tracking system. The
442 Optotrak cameras were located to the left of the participants. To record index finger and thumb
443 movement, sets of three infrared markers (forming a rigid body) were attached to the base of
444 the participants' nails. The fingertip and tip of the thumb were calibrated in relation to the marker
445 position, as participants grasped a wooden bar with a precision grip, placing their fingertips at
446 two known locations on the bar.

447 ***Stimuli***

448 **Experiment 1: Light objects made of wood.** Four differently shaped objects (defined as
449 objects L, U, S and V; Figure 2b) each composed of 10 wooden (beech) cubes (2.5^3 cm^3),
450 served as stimuli. Objects were fairly light with a mass of 97 g. Two of the objects featured
451 cubes stacked on top of each other, whereas the other two objects were composed exclusively
452 of cubes lying flat on the ground. The objects were presented to the participants at one of two
453 orientations. Across orientations, object L was rotated by 180 degrees, objects U and V were
454 rotated by 90 degrees, and object S was rotated by 55 degrees. Figure 2b shows the objects
455 positioned as if viewed by a participant.

456 **Experiment 2: Heavy composite objects made of wood and brass.** For each of the 4 shapes
457 from Experiment 1, we created 3 new objects (12 in total) to serve as stimuli for Experiment 2
458 (Figure 2c). Individual cubes were made of either wood or brass. The objects were composed of
459 5 cubes of each material, which made them fairly heavy with a mass of 716g. By reordering the
460 sequence of wood and brass cubes, we shifted the location of each shape's CoM. For each
461 shape we made one object in which brass and wooden cubes alternated with one another, and
462 two bipartite objects, where the 5 brass cubes were connected to one another to make up one
463 side of the object with the wooden cubes making up the other side. This configuration was also
464 inverted, (i.e., wooden and brass cubes switched locations). All objects were presented at the
465 same two orientations as Experiment 1.

466 **Object meshes.** Triangulated mesh replicas of all objects were created in Matlab; each cube
467 face consisted of 128 triangles. To calibrate mesh orientation and position, we measured, using
468 the Optotrack, four non planar points on each object at each orientation. We aligned the model
469 to the same coordinate frame employed by the Optotrack using Procrustes analysis.

470 ***Procedure***

471 Prior to each trial, participants placed thumb and index finger at a pre-specified starting location.
472 In Experiment 1, two start locations were used (start 1 at 28 cm to the right of the chinrest in the
473 participant's coronal plane and 9.5 cm forward in the sagittal plane; start 2 9 cm further to the
474 right and 3 cm further forward, 23 cm from the center of the goal plate). Given that we observed
475 no effect of starting position in our data, in Experiment 2 only the first starting location was
476 employed. When the subject was at the correct start position, the experimenter placed one of
477 the stimulus objects at the target location behind the opaque shutter screen. Each object could
478 be presented at one of two orientations with respect to the participant. The experimenter could
479 very precisely position each object at the correct location and orientation by aligning two small
480 grooves under each object with two small pins on the table surface.

481 Once both stimulus and participant were positioned correctly, a tone indicated the beginning of
482 a trial, at which point the shutter window turned translucent. Participants were then required to
483 pick up the object using only forefinger and thumb and place it at the goal location. Participants
484 had 3 seconds to complete the task before the shutter window turned opaque. In Experiment 1,
485 no instructions were given regarding how the objects had to be picked up. In Experiment 2,
486 participants were instructed to keep the objects as level as possible.

487 Experiment 1 had sixteen conditions: two starting locations, four wooden objects of different
488 shapes, each object presented at two orientations. Each participant repeated each condition five
489 times (eighty trials per participant).

490 Experiment 2 had thirty-six conditions: twelve distinct objects (four shapes in three material
491 configurations) presented at two orientations. Half of the participants handled only shapes L and

492 V, the other half handled shapes U and S. Each participant repeated each condition seven
493 times (eighty-four trials per participant). In both experiments trial order was randomized.
494 Following each trial, the experimenter visually inspected the movement traces to determine
495 whether a grasp was successful or not. Grasps were deemed unsuccessful when the movement
496 was too slow, when an object was dropped, or when tracking was lost. Unsuccessful grasps
497 were marked as error trials, added to the randomization queue, and repeated. A total of 368
498 error trials (13.8% of trials from Experiment 1 and 13.9% from Experiment 2) were not analyzed.

499 ***Training***

500 Each participant completed six practice trials (using a Styrofoam cylinder in Experiment 1, and
501 by lifting random objects from the shapes not used in that participant's run in Experiment 2) prior
502 to the experiment to give them a sense for how fast their movement should be in order to
503 complete the entire movement within three seconds. Practice trial data were not used in
504 analyses. Prior to Experiment 2, participants were familiarized with the relative weight of brass
505 and wood using two rectangular cuboids of dimensions 12.5x2.5x2.5 cm, one of wood (50 g)
506 and one of brass (670 g).

507 ***Analyses***

508 All analyses were performed in Matlab version R2018a. Differences between group means were
509 assessed via paired or unpaired t-tests, as appropriate. Values of $p < 0.05$ were considered
510 statistically significant.

511 **Contact points.** Contact points of both fingers with the object were determined as the fingertip
512 coordinates at the time of first contact, projected onto the surface of the triangulated mesh
513 models of the object. The time of contact with the object was determined using the methods
514 developed by Schot et al (60) and previously described in Paulun et al (19).

515 **Grasp similarity.** We described each individual grasp \vec{G} as a 6D vector of the x,y,z coordinates
516 of the thumb and index finger contact points:

517
$$\vec{G} = [x_T, y_T, z_T, x_I, y_I, z_I]$$

518 To compute the similarity S between two grasps \vec{G}_1 and \vec{G}_2 , we first computed the Euclidian
519 distance between the two 6D grasp vectors. We then divided this distance by the largest
520 possible distance between two points on the specific object D_{max} , determined from the mesh
521 models of the objects. Finally, similarity was defined as 1 minus the normalized grasp distance,
522 times 100:

523
$$S = 100 * \left(1 - \frac{\|\vec{G}_1 - \vec{G}_2\|}{D_{max}} \right)$$

524 In this formulation, two identical grasps, which occupy the same point in a 6D space, will be
525 100% similar, whereas the two farthest possible grasps onto a specific object will be 0% similar.
526 Within-subject grasp similarity was the average similarity between grasps from the same
527 participant to the participant's own median grasp. Between-subject grasp similarity was the
528 similarity between the median grasp of each participant and the median grasp across all other
529 participants.

530 **Computational model**

531 The model takes as input 3D meshes of the stimuli and outputs a cost function describing the
532 costs associated with every possible combination of finger and thumb position on the accessible
533 surface locations of our objects (i.e., those not in contact with the table plane). First, we define
534 the center of each triangle in the mesh as a potential contact point. Then, given all possible
535 combinations of thumb and index finger contact points $\overline{CP}_T = [x_T, y_T, z_T]$; $\overline{CP}_I = [x_I, y_I, z_I]$, the
536 surface normal at both contact points $\vec{n}_T = [x_T^n, y_T^n, z_T^n]$; $\vec{n}_I = [x_I^n, y_I^n, z_I^n]$, and the CoM of the
537 object $\overline{CoM} = [x_{CoM}, y_{CoM}, z_{CoM}]$, the five penalty functions we combined into a computational
538 model of grasp selection were defined as follows:

539 **Force closure.** For two-digit grasping, a grasp fulfills force closure when the grasp axis
540 connecting thumb and index contact points lies within the friction cones resulting from the

541 friction coefficient between object and digits(14). A grasp perfectly fulfills force closure when the
 542 grasp axis is perfectly aligned with the vectors along which gripping forces are applied, which
 543 are the opposite of the contact-point surface normals. Therefore, we defined the force closure
 544 penalty function as the sum of the angular deviances (computed using the atan2 function) of the
 545 grasp axis from both force vectors $\vec{F}_T = -\vec{n}_T$; $\vec{F}_I = -\vec{n}_I$:

$$546 \quad P_{FC}(\vec{CP}_T, \vec{CP}_I) = \text{atan2}(\|\vec{F}_T \times (\vec{CP}_I - \vec{CP}_T)\|, \vec{F}_T \cdot (\vec{CP}_I - \vec{CP}_T)) \\ 547 \quad + \text{atan2}(\|\vec{F}_I \times (\vec{CP}_T - \vec{CP}_I)\|, \vec{F}_I \cdot (\vec{CP}_T - \vec{CP}_I))$$

548 **Torque.** If a force is applied at some position away from the CoM, the object will tend to rotate
 549 due to torque, given by the cross product of force vector and lever arm (the vector connecting
 550 CoM to the point of force application). Under the assumption that is possible to apply forces at
 551 the thumb and index contact points that counteract the force of gravity \vec{F}_g , we can compute the
 552 total torque of a grip as the sum of torques exerted by each contact point. Therefore, we defined
 553 the torque penalty function as the magnitude of the total torque exerted by a grip:

$$554 \quad P_T(\vec{CP}_T, \vec{CP}_I) = \|(\vec{CoM} - \vec{CP}_T) \times -\vec{F}_g + (\vec{CoM} - \vec{CP}_I) \times -\vec{F}_g\|$$

555 **Natural grasp axis.** Schot, Brenner and Smeets(21) have carefully mapped out how human
 556 participants grasp spheres placed at different positions throughout the peripersonal space, and
 557 provide a regression model that determines the naturally preferred posture of the arm when
 558 grasping a sphere. We input the configuration of our current experimental setup into the
 559 regression model developed by these authors, and found the natural grasp axis for our
 560 participants to be $\vec{NGA} = [0.49 \ 0.87 \ 0]$. We therefore defined the natural grasp axis penalty
 561 function as the angular deviance from this established natural grasp axis:

$$562 \quad P_{NGA}(\vec{CP}_T, \vec{CP}_I) = \text{atan2}(\|\vec{NGA} \times (\vec{CP}_I - \vec{CP}_T)\|, \vec{NGA} \cdot (\vec{CP}_I - \vec{CP}_T))$$

563 **Optimal grasp aperture for precision grip.** Cesari and Newell(23) have shown that, when free
 564 to employ any multi-digit grasp, human participants selected precision grip grasps only for
 565 cubes smaller than 2.5 cm in length. As cube size increases, humans progressively increase the

566 number of digits employed in a grasps. Therefore, since our participants were instructed only to
 567 employ precision grip grasps, we defined the optimal grasp aperture penalty function as 0 for
 568 grasp sizes smaller than 2.5 cm, and as a linearly increasing penalty for grasp sizes larger than
 569 2.5 cm:

$$570 \quad P_{OGA}(\overrightarrow{CP_T}, \overrightarrow{CP_I}) = \begin{cases} 0, & \text{if } \|\overrightarrow{CP_I} - \overrightarrow{CP_T}\| < 25mm \\ \|\overrightarrow{CP_I} - \overrightarrow{CP_T}\| - 25, & \text{if } \|\overrightarrow{CP_I} - \overrightarrow{CP_T}\| > 25mm \end{cases}$$

571 **Object Visibility.** Under the assumption that humans are attempting to minimize the portion of
 572 the objects hidden from view by their hand, we defined the optimal visibility penalty function as
 573 the proportion of object still visible during each possible grasp. We first defined the line on the
 574 XZ plane that passes through the thumb and index finger contact points. We made the
 575 simplifying assumption that, given all possible surface points on the object SP_{TOT} , the surface
 576 points $SP_{OCC}(\overrightarrow{CP_T}, \overrightarrow{CP_I})$ that fall to the side of the line where the hand is located will be
 577 occluded. Therefore, the object visibility penalty function was defined as:

$$578 \quad P_{OGA}(\overrightarrow{CP_T}, \overrightarrow{CP_I}) = \frac{Length(SP_{OCC}(\overrightarrow{CP_T}, \overrightarrow{CP_I}))}{Length(SP_{TOT})}$$

579 **Overall grasp penalty function.** To obtain the overall grasp penalty function, each grasp
 580 penalty function was first normalized to the [0 1] range (i.e., across all possible grasps for each
 581 given object, independently of the other objects). Then, we took a weighted linear sum of the
 582 individual penalty functions, with all weights equal to 1:

$$583 \quad P_O(\overrightarrow{CP_T}, \overrightarrow{CP_I}) = P_{FC}(\overrightarrow{CP_T}, \overrightarrow{CP_I}) + P_T(\overrightarrow{CP_T}, \overrightarrow{CP_I}) + P_{NGA}(\overrightarrow{CP_T}, \overrightarrow{CP_I}) + \\ 584 \quad P_{OGA}(\overrightarrow{CP_T}, \overrightarrow{CP_I}) + P_{RT}(\overrightarrow{CP_T}, \overrightarrow{CP_I})$$

585 For display purposes this final function was normalized to the [0 1] range. The minima of this
 586 overall grasp penalty function represent the set of grasps that best satisfy the largest number of
 587 constraints at the same time.

588 **Model fitting.** In both Experiments 1 and 2, human participants executed repeated grasps to
 589 the same objects at each orientation. To fit the overall grasp penalty function to these human
 590 data, for each participant in each condition we first defined a human grasp penalty function
 591 $P_H(\overrightarrow{CP_T}, \overrightarrow{CP_I})$ in which all grasps selected by a participant onto an object were set to have 0
 592 penalty, and all grasps that had not been selected were set to have a penalty of 1. Then, we fit
 593 the function:

$$594 \quad P_{O,fit}(\overrightarrow{CP_T}, \overrightarrow{CP_I}) = \sum_i C_i * P_i(\overrightarrow{CP_T}, \overrightarrow{CP_I})$$

595 to the human grasp penalty function. More specifically, we employed a nonlinear least-squares
 596 solver to search for the set of coefficients $C_i = [C_{FC}; C_T; C_{NGA}; C_{OGA}; C_{RT}]$ that minimized the
 597 function:

$$598 \quad F(C_i) = \sqrt{W(\overrightarrow{CP_T}, \overrightarrow{CP_I}) * \left[\left(\sum_i C_i * P_i(\overrightarrow{CP_T}, \overrightarrow{CP_I}) \right) - P_H(\overrightarrow{CP_T}, \overrightarrow{CP_I}) \right]}$$

599 i.e. we searched for the set of coefficients for which $P_{O,fit}$ best approximated the human grasp
 600 penalty function P_H . The solver employed the trust-region-reflective algorithm; we set the lower
 601 and upper bounds of the coefficients to be 0 and 1, and 0.2 as the starting value for all
 602 coefficients. Critically, $W(\overrightarrow{CP_T}, \overrightarrow{CP_I})$ was a weight function which served to give equal weight to
 603 high and low penalty grasps in the human grasp penalty function, since the number of non-
 604 selected grasps with $P_H(\overrightarrow{CP_T}, \overrightarrow{CP_I}) = 1$ vastly outnumbered the few selected grasps for which
 605 $P_H(\overrightarrow{CP_T}, \overrightarrow{CP_I}) = 0$. Thus, for grasps where $P_H(\overrightarrow{CP_T}, \overrightarrow{CP_I}) = 0$, $W(\overrightarrow{CP_T}, \overrightarrow{CP_I})$ was equal to the
 606 number of times the participant had selected that specific grasp. For grasps where
 607 $P_H(\overrightarrow{CP_T}, \overrightarrow{CP_I}) = 1$ instead, $W(\overrightarrow{CP_T}, \overrightarrow{CP_I}) = \frac{N_{G,selected}}{N_{G,non-selected}}$; where $N_{G,selected}$ was the total number
 608 of grasps performed by the participant onto the object, and $N_{G,non-selected}$ was the total number
 609 of non-selected grasps within the grasp manifold.

610 **Predicting Grasps.** The minima of both the equally weighted (non-fitted) and the fitted overall
611 grasp penalty functions represent the set of grasps predicted to be optimal under the weighted
612 linear combination of the five penalty functions included in our computational model. To
613 visualize these predicted optimal grasps, we sampled them from the minima of the penalty
614 functions. First, we removed all grasps with penalty values greater than the lower 0.1th
615 percentile. The remaining grasps were therefore all optimal or near-optimal. From this subset,
616 we then randomly selected (with replacement) a number of grasps equal to the number of
617 grasps executed by the human participants. The probability with which any one grasp was
618 selected was set to be 1 minus the grasp penalty, thus grasps with zero penalty had the highest
619 probability of being selected. These sampled grasps can then be projected back onto the
620 objects for visualization purposes (Figure 5a), or they can be directly compared to human grasp
621 using the grasp similarity metric described above (Figure 5b,c).

622

623 **Data availability.** Data and analysis scripts will be made available from the Zenodo database
624 (doi:xx.xxxx/zenodo.xxxxxxx upon publication).

625

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631

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764 Supplementary Information to

765 ***How humans grasp three-dimensional objects***

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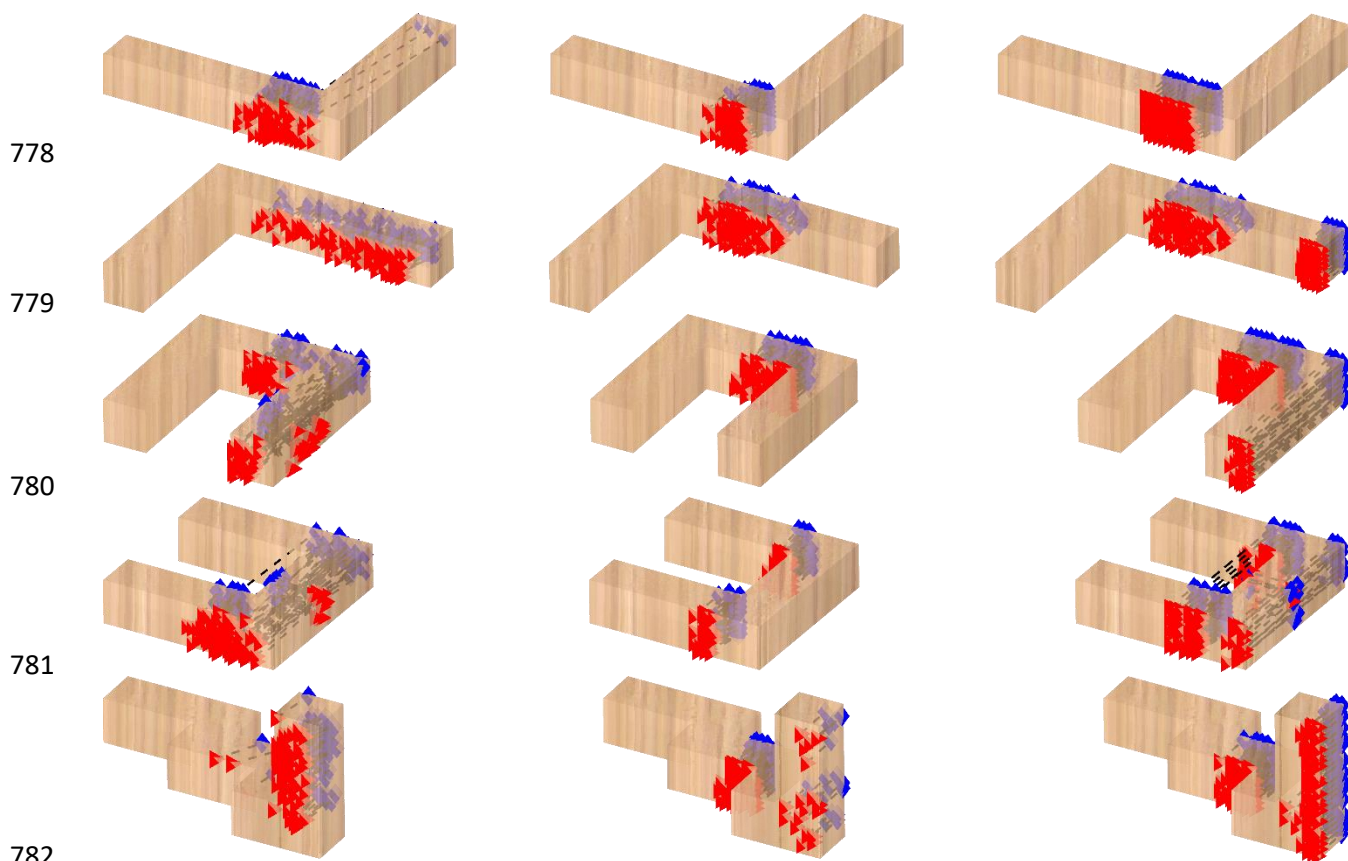
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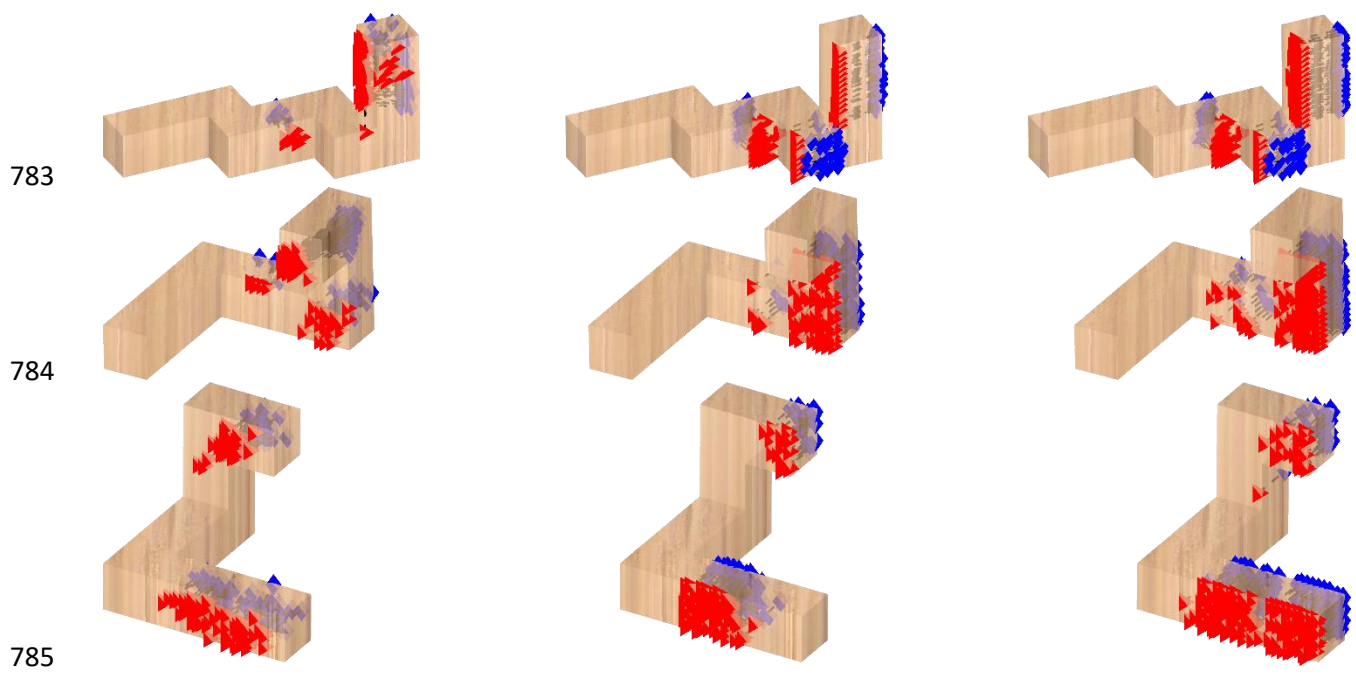
776 (a) Experiment 1

777 Human

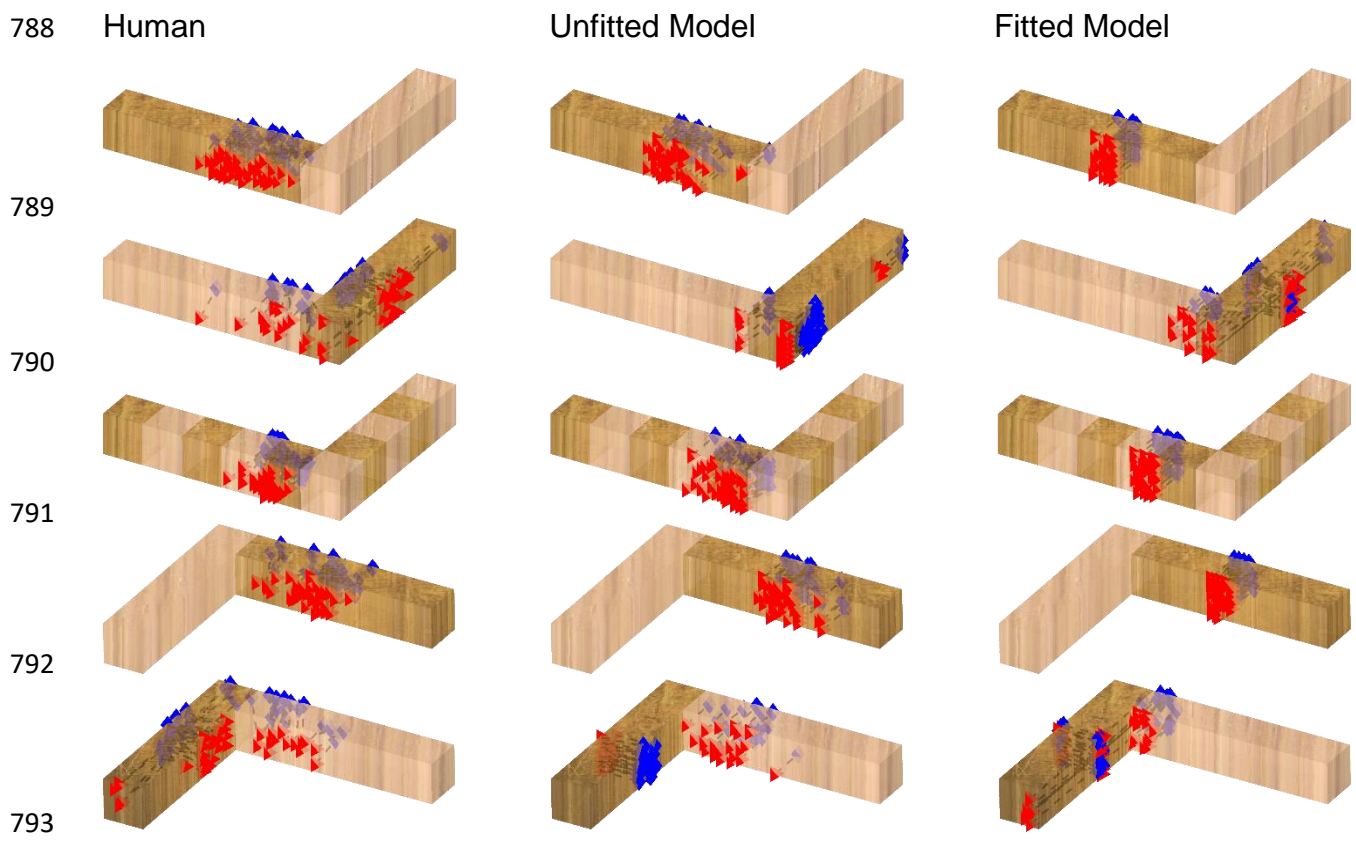
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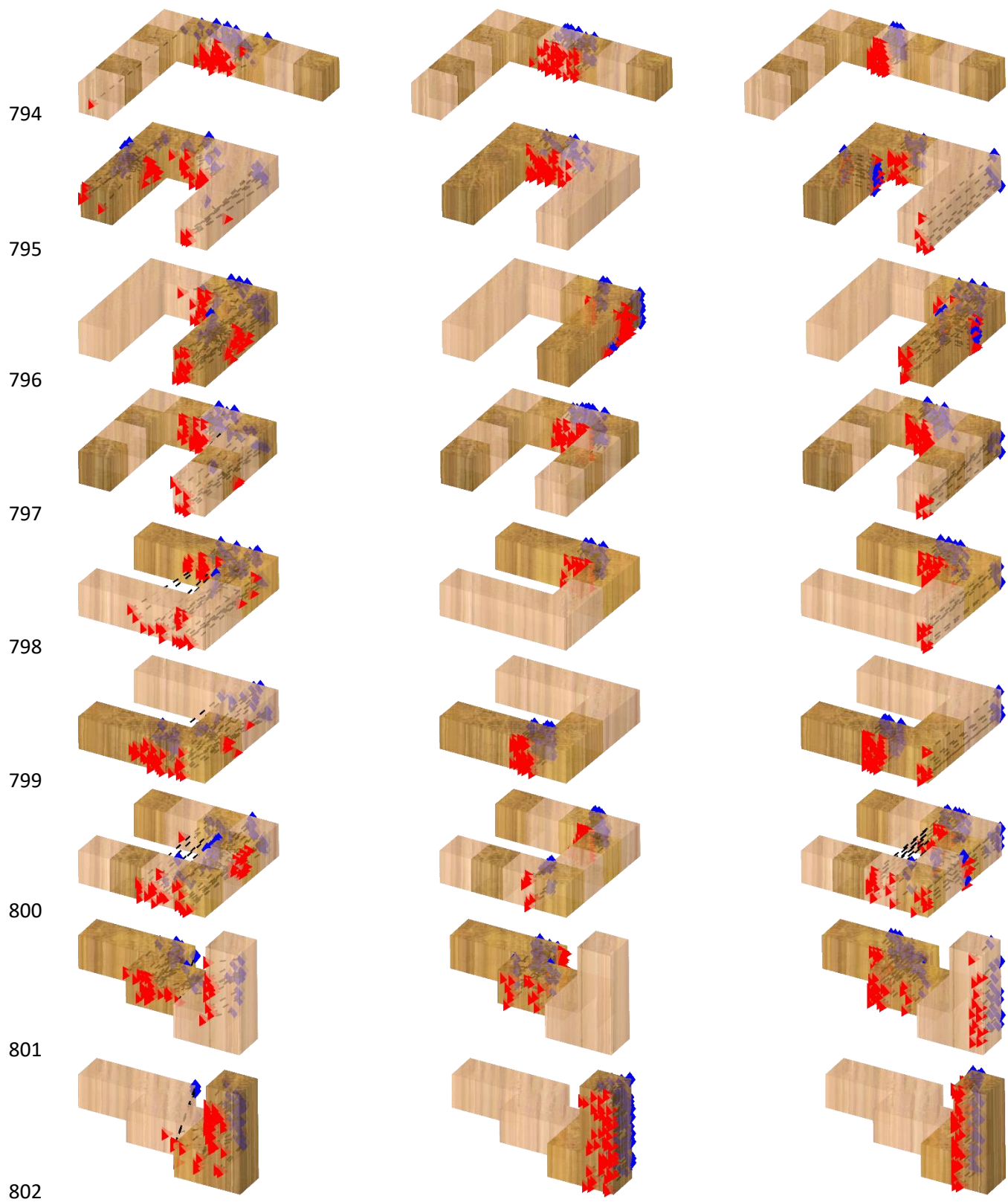
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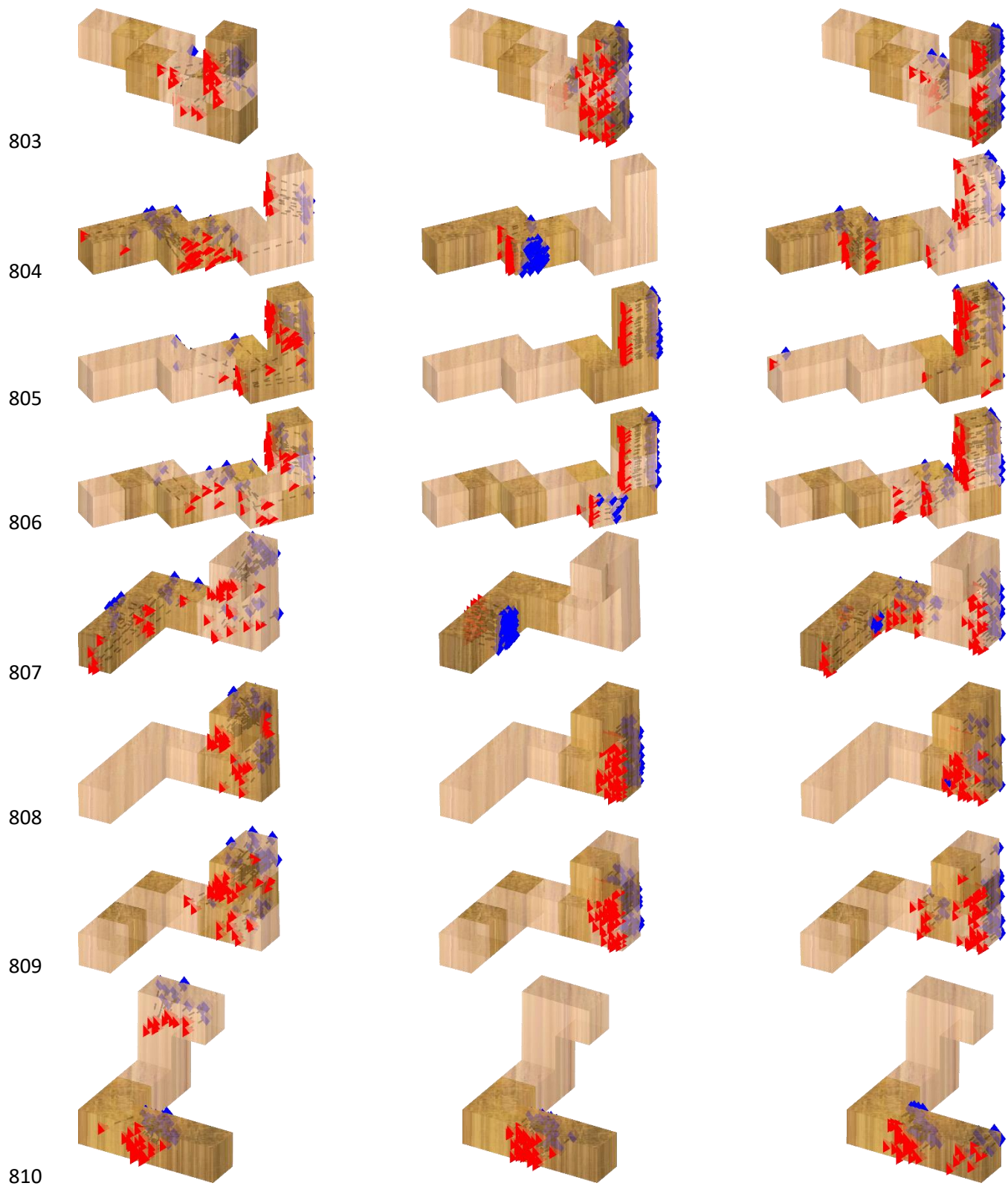




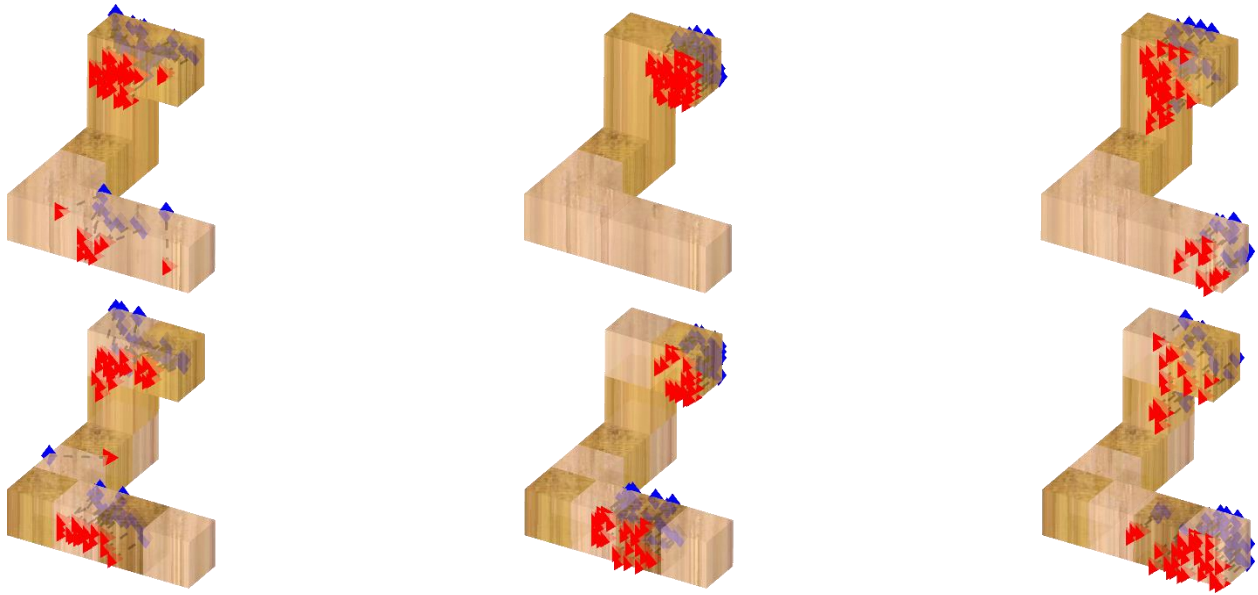
787 (b) Experiment 2







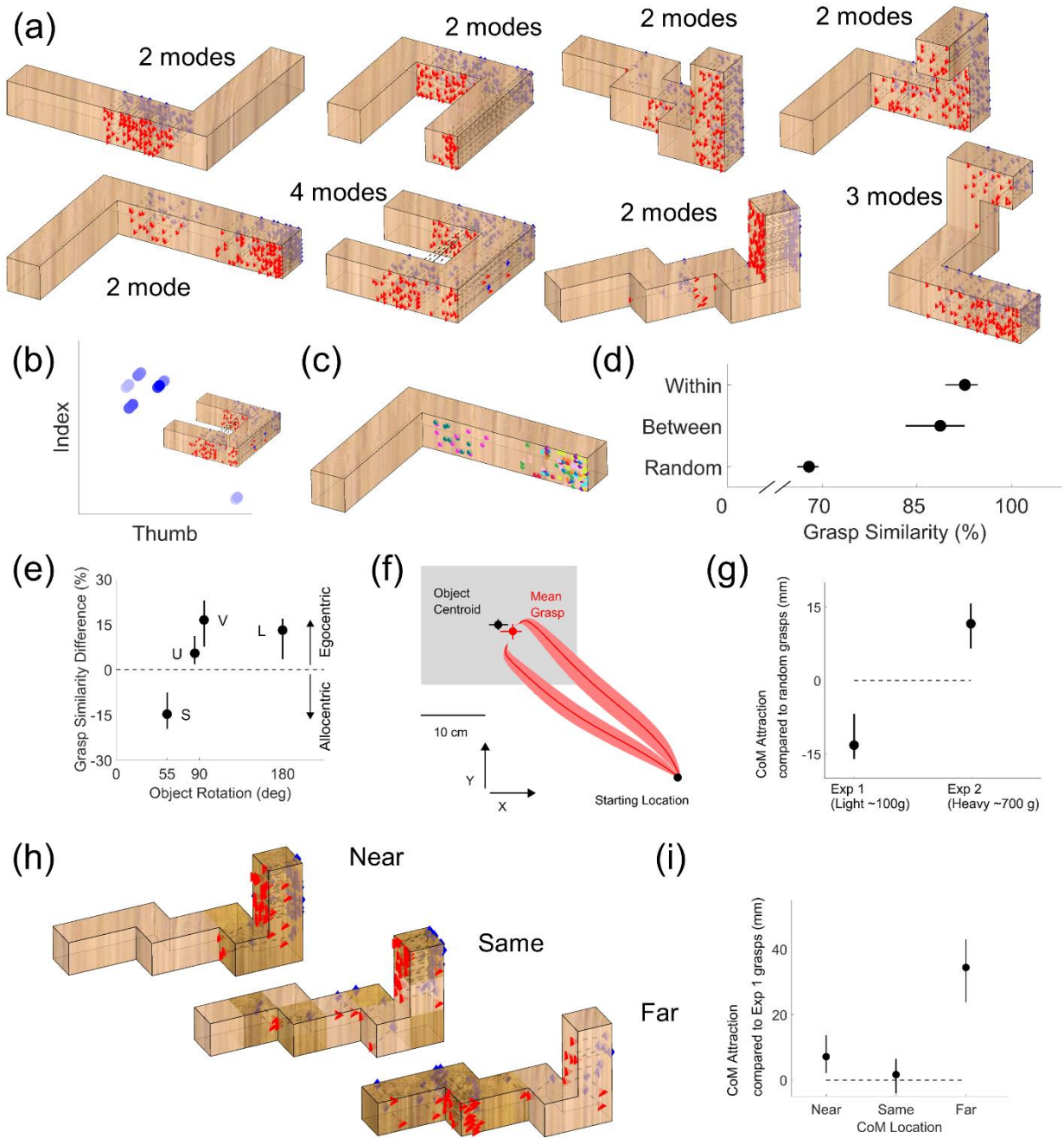
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812

813 **Figure S1.** Grasping patterns from human participants (left), unfitted model (middle), and fitted
814 model (right). (a) Grasping patterns on wooden objects from Experiment 1. (b) Grasping
815 patterns on mixed material objects from Experiment 2.

816



817

818 **Figure S2.** Pattern of empirical results recreated from simulating grasps from the fitted
 819 computational model. All panels are the same as in Figure 3 of the main manuscript, except that
 820 the data are simulated from the model. Only the grasp trajectories in panel (f) are from the
 821 human data, to highlight how the model correctly reproduces the biases in human grasping
 822 patterns.

823