

1 Running head: CHIMPANZEES' INTERNAL AROUSAL AND HELPING

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3 **Chimpanzees' (*Pan troglodytes*) internal arousal remains elevated if they cannot**
4 ***themselves help a conspecific***

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31 Comparative Psychology. In addition, we thank Ramona Frickel and Anna-Lina Rauschenbach for their
32 help coding the videos.

33 The data and analysis scripts can be accessed here: *OSF* (<https://osf.io/pf6q4/>)

34
35 The research was carried out between February 2014 and June 2016.

36
37 Authors' Contribution

38 R.H., A.V., F. K., A. A.-S., L. B., J.C., & M.T. designed the studies and contributed equally to writing and
39 revising the manuscript. R.H. conducted Study 1. L.B. conducted Study 2. R.H. analysed the data for both
40 studies.

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45 Abstract

46 Chimpanzees help conspecifics achieve their goals in instrumental situations but neither their
47 immediate motivation nor the evolutionary basis of their motivation are clear. In the current
48 study, we gave chimpanzees the opportunity to instrumentally help a conspecific to obtain
49 food. Following recent studies with human children, we measured their pupil diameter at
50 various points in the process. Like young children, chimpanzees' pupil diameter decreased
51 soon after they had helped. However, unlike children, chimpanzees' pupils remained more
52 dilated upon watching a third party provide the needed help instead of them. Our
53 interpretation is that chimpanzees are motivated to help others, and the evolutionary basis is
54 direct or indirect reciprocity, since providing help oneself sets the conditions for a payback.
55 This is in contrast to young children whose goal is to see others being helped – by whomever
56 – presumably because their helping is based not on reciprocity.

57 *Keywords:* chimpanzees, helping, internal arousal, pupil dilation

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62 Chimpanzees' (*Pan troglodytes*) internal arousal remains elevated if they cannot *themselves*
63 help a conspecific

64 All great ape species exhibit some form of prosocial behavior (e.g., Albiach-Serrano,
65 2015; Cronin, 2012; Schmelz & Call, 2016). However, the underlying motivation of their
66 helping behavior is heavily debated, especially in chimpanzees, the most studied non-human
67 primate species (de Waal & Suchak, 2010; Schmelz & Call, 2016). Two distinct but related
68 questions have been raised in the literature: What is chimpanzees' immediate motivation
69 when carrying out behavior that benefits others, and what is the evolutionary basis of their
70 motivation?

71 With regards to the immediate goal of chimpanzees' prosocial behavior, two
72 theoretical accounts have been put forward. The *prosocial motivation* account holds that
73 chimpanzees show a genuine concern for others (humans and conspecifics) and therefore
74 help to alleviate their needs (de Waal, 2009; Melis, 2018). In favour of this account, there is
75 evidence that chimpanzees inform conspecifics of potentially harmful situations (Crockford
76 et al., 2012), they support their allies consoling others when they are distressed (Harcourt &
77 de Waal, 1992), and they trust their close allies to return food in a cooperative sharing task
78 (Engelmann et al., 2015). In addition, experimental studies have shown that chimpanzees
79 remove physical barriers allowing conspecifics to have access to food (Melis et al., 2011;
80 Warneken et al., 2007) and also that they exchange tools with those who need them most
81 (Yamamoto et al., 2009). Furthermore, chimpanzee helping seems flexibly coordinated
82 toward conspecifics' actual needs: They provide the specific tool (among several tools) that
83 appropriately fulfils the conspecific's need (Yamamoto et al., 2012). Together, these studies
84 suggest that chimpanzees show a *prosocial motivation* to alleviate others' needs (Melis,
85 2018; see Tan & Hare, 2013, for similar findings with bonobos).

86 The alternative, *non-prosocial motivation* accounts of chimpanzee helping suggest

87 that individuals are primarily motivated by the degree of the requester's harassment (Gilby,
88 2006; Silk et al., 2005; Stevens, 2004) or, more generally, by situational constraints. One
89 argument is that the 'standard' instrumental helping paradigms used in experimental studies
90 may have introduced methodological constraints related to both the physical and the social
91 aspects of the tasks, the types of measures taken, and the control of extraneous variables,
92 which could compromise the validity of the studies and potentially call into question the
93 prosocial interpretation of the respective results (Albiach-Serrano, 2015). Along these lines,
94 the stimulus enhancement hypothesis suggests that individual chimpanzees are primarily
95 motivated by the situational constraints, e.g., made salient through the presence of the
96 conspecific, but irrespective of his/her actual needs (Tennie, Jensen, & Call, 2016; see
97 Schmelz & Call, 2016 for a review). In the above mentioned experimental studies, for
98 example, the helping individuals were often confronted by recipient behaviors such as
99 vocalizing, clapping hands (Yamamoto et al., 2009, 2012), or rattling a chain which, if
100 released, would provide access to food (Melis et al., 2011). This might have drawn subjects'
101 attention toward specific contextual features of the experimental situation, thus enhancing the
102 probability of them performing the helping actions. Such alternative explanations of these
103 studies' results have challenged the claim that chimpanzees genuinely concern themselves
104 with others' needs. This interpretation is supported by studies that confront helpers with the
105 choice to deliver (or not) a reward to a conspecific (whilst conferring the identical reward to
106 themselves in both cases). In these studies chimpanzees do not show a robust preference for
107 choices that systematically improve the well-being of others (House, Silk, Lambeth, &
108 Schapiro, 2014; Jensen, Hare, Call, & Tomasello, 2006; Silk et al., 2005; Vonk et al., 2008;
109 see Horner, Carter, Suchak, & de Waal, 2011, for different results). However, it is possible
110 that in the respective studies the absence of a preference for prosocial choices resulted from
111 subjects being focused exclusively on their own rewards thus neglecting the partner's

112 situation and opportunity for rewards (Albiach-Serrano, 2015).

113 Focusing on the evolutionary bases of prosocial motivation and based on previous
114 empirical work with chimpanzees, it might be possible to reconcile the prosocial and non-
115 prosocial accounts. Chimpanzees may respond to others' need for help at an emotional and
116 physiological level (Bonnie & de Waal, 2004a; Schino & Aureli, 2009), but their immediate
117 motivation to help may be more based on wanting to complete the helping action themselves
118 rather than seeing the others' need fulfilled (i.e., regardless of who provides the help).
119 Situations in which others need help provide the individual with an opportunity to potentially
120 'receive credit' for their helping. On a proximate level it is not necessary that chimpanzees
121 perceive the situation as an opportunity to 'get credit' – in fact they may be unaware of the
122 benefits of their actions (Schino & Aureli, 2017). This question about the proximate
123 mechanisms of chimpanzees' instrumental helping builds on prior work on reciprocal helping
124 through mechanisms such as 'attitudinal reciprocity' (de Waal, 2009) and 'emotional
125 bookkeeping', which have been suggested to account for the range of chimpanzees' prosocial
126 behaviors (see Schino & Aureli, 2009 for an extensive review).

127 Many of chimpanzees' social exchanges are thought to be based on reciprocity, where
128 individuals return favours to help those who have helped them (Gomes et al., 2009; Muller &
129 Mitani, 2005), but the empirical evidence on reciprocal helping is mixed (for reviews see
130 Massen et al., 2010; Preston & de Waal, 2002; Schino & Aureli, 2017; Schmelz & Call,
131 2016; Schweinfurth & Call, 2019; Silk, 2003; Stevens & Hauser, 2004). On the one hand,
132 there is mounting evidence that chimpanzees show a preference toward prosocial choices that
133 deliver food to others if the conspecific is a close ally or friend (Engelmann & Herrmann,
134 2016) or if the conspecific has previously helped them (Schmelz et al., 2017; see also Melis
135 et al., 2008; Yamamoto & Tanaka, 2009 for weaker effects). On the other hand, other studies
136 found little to no reciprocal helping in chimpanzees (Brosnan et al., 2009; Silk et al., 2005;

137 Yamamoto & Tanaka, 2010). On the whole, however, and based on a review of more than
138 100 primate studies, there is more positive than negative evidence for reciprocal helping in
139 chimpanzees (Schweinfurth & Call, 2019). One conclusion is that in studies measuring the
140 behavioral rates, reciprocal helping may depend on task demands such that situations which
141 emphasize reciprocation can increase chimpanzees' helping and prosocial choices (e.g.,
142 Engelmann & Herrmann, 2016; Schmelz et al., 2017). More generally, chimpanzees may
143 view a helping situation more as an opportunity to 'get credit' as well as to initiate direct
144 reciprocation and to lesser degree help out of genuine concern for the other individual's
145 welfare (although the two motivations are certainly not mutually exclusive). Addressing this
146 possibility requires assessing individuals' underlying motivation, for example, via changes in
147 physiological arousal in response to others in need.

148 Such a non-invasive paradigm has been developed in the study of human children's
149 motivation to help others. During their second year of life, children begin to help adults and
150 peers to overcome physical obstacles and provide out of reach objects (Hepach, Kante, et al.,
151 2017; Warneken & Tomasello, 2006), and they warn unaware others of potentially dangerous
152 locations (Knudsen & Liszkowski, 2013), thus showing a similar instrumental helping
153 repertoire as chimpanzees and bonobos (Melis, 2018). It has been shown that at least in
154 young children, the underlying motivation to provide help is a concern to see the individual
155 in need be helped. Evidence for this comes from studies demonstrating that 18-months- to 3-
156 year-old children's internal arousal, assessed via changes in pupil diameter, increases in
157 response to seeing others needing help and decreases as long as the need is fulfilled
158 appropriately (Hepach et al., 2016; Hepach, Vaish, & Tomasello, 2017a; Hepach et al.,
159 2019). However, 2-year-old children do not seem primarily motivated to get credit for
160 helping, given that their internal arousal decreases both when they provide the help and when
161 they see another person help (Hepach et al., 2012). This intrinsic motivation is flexible such

162 that 2- and 3-year-old children become motivated to actively help after they have accidentally
163 harmed others (Hepach, Vaish, & Tomasello, 2017a). Changes in pupil diameter, therefore,
164 can provide access to the kind of ‘motivational substrate’ underlying behavior (Schmelz &
165 Call, 2016). Both humans and non-human primates show increases in pupil diameter in
166 response to emotionally charged or motivationally significant stimuli (Aston-Jones & Cohen,
167 2005; Bradley et al., 2008; Henderson et al., 2014; Nieuwenhuis et al., 2011). This
168 physiological variable thus provides a unique opportunity to study the underlying motivation
169 of behavior, including helping behavior, in particular given that greater increases in pupil
170 diameter have been linked to faster helping in children (Hepach, Vaish, Müller, et al., 2017).

171 Here we carried out two studies to investigate the underlying mechanisms of
172 chimpanzee helping in which we directly measured chimpanzees’ internal arousal via
173 changes in pupil diameter. Broadly construed, we addressed two questions: (1) Do
174 chimpanzees have the goal to help others? and (2) Does seeing a third party providing the
175 help satisfy that goal just as well? In each study, we measured subjects’ pupil diameter twice:
176 once at the beginning of the test trial and a second time at the end of the test trial. In both
177 studies, we experimentally manipulated whether chimpanzees could carry out an initiated
178 action (*subject-delivers-food*) or whether the human experimenter was faster to achieve the
179 outcome before the subject chimpanzee could finish his or her action (*experimenter-delivers-*
180 *food*). What differed across the two studies were the situational constraints. Specifically, we
181 conducted study 2 to address alternative explanations for the changes in pupil dilation found
182 in study 1.

183

184

Study 1

185 In study 1 the chimpanzees could pull a rope to deliver food to an empty experimental
186 booth (*control: empty-booth*) or to a conspecific inside the booth (*helping: stooge-present*).

187 Subjects never themselves gained access to the food and participated in 4 experimental
188 conditions in a full within-subjects design. We hypothesized that subjects would be more
189 motivated to carry out the action in the *helping: stooge-present* condition so as to get credit
190 by the conspecific for their helpful action. This would be reflected in greater internal arousal
191 when the behavior and thus the goals were frustrated because the experimenter was faster to
192 help (*experimenter-delivers-food*) compared to when the subject could complete the action
193 (*subject-delivers-food*) in this condition. On the other hand, we expected no difference in
194 pupil diameter change between the condition where subjects delivered the food item
195 themselves (*subject-delivers-food*) and the condition where the experimenter delivered the
196 food item (*experimenter-delivers-food*) in the *control: empty-booth* condition.

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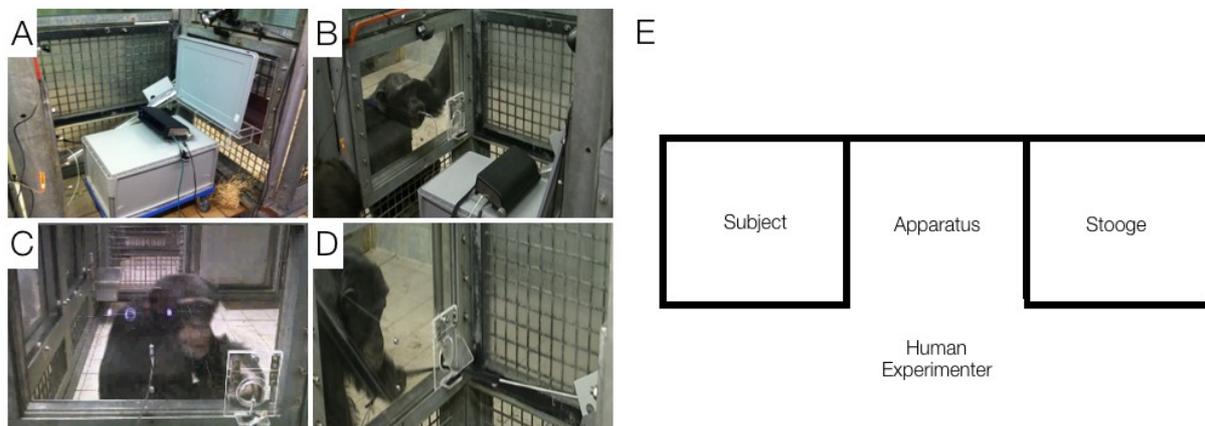
199 **Participants**

200 Subjects were 19 chimpanzees (*Pan troglodytes verus*; *P. t. schweinfurthii*; *P. t.*
201 *verus-schweinfurthii hybrid*) living in two separated social groups at the Wolfgang Köhler
202 Primate Research Center (WKPRC) in Leipzig, Germany. Two chimpanzees (one female for
203 one group and one male for the other group) were assigned the role of the stooge recipient
204 because they could be tested together with each of the subject chimpanzees with one
205 exception (see below). The other 17 individuals were assigned the role of the subject. Of the
206 17 subject individuals, 2 did not enter the familiarization phase because they could not be
207 separated from the group and 3 passed the familiarization phase but were not motivated to
208 participate in the test phase of the study. Of these 12 remaining subjects, 7 provided data on
209 each of the 4 experimental conditions thus comprising the final sample (5 females; mean age
210 = 18.6 y; range: 10 to 30 y). The study was conducted between February 2014 and February
211 2015.

212 **Ethical Note**

213 The study was approved by an internal ethics committee at the Wolfgang Köhler
 214 Primate Research Center at the Max Planck Institute for Evolutionary Anthropology. At the
 215 center, animal research is in compliance with the ‘EAZA Minimum Standards for the
 216 Accommodation and Care of Animals in Zoos and Aquaria’, the ‘WAZA Ethical Guidelines
 217 for the Conduct of Research on Animals by Zoos and Aquariums’ as well as the ASAB/ABS
 218 ‘Guidelines for the Treatment of Animals in Behavioral Research and Teaching’.
 219 Chimpanzees at the WKPRC live in zoo conditions with indoor and outdoor enclosures,
 220 ranging between 1500 and 4500 m², the latter containing natural features like trees, plants,
 221 water currents and rocks. Chimpanzees were tested individually in the familiar environment
 222 of their sleeping rooms, and their participation was strictly voluntary. Subjects were neither
 223 food- nor water-deprived.

224



226 *Figure 1.* Overview of Materials used in Study 1. **A.** View of the compartment between the
 227 two booths (in this picture, the subject is in the left booth and the stooge is in the right booth).
 228 The eye tracker is positioned to record the subjects’ eyes. The grey occluder is blocking the
 229 subject’s view of the stooge during the baseline measure, during the post-trial measure and
 230 between trials. On the very left of the image one sees the orange juice flow regulator. A lamp
 231 above the stooge’s panel was manually turned on and off during measurements. Note that
 232 study 2 additionally included a tube connecting the Stooge-panel with the Subject-panel (see
 233 supplementary materials for an image). **B.** The eye tracker is recording the subject’s eyes

234 while the subject is drinking from the juice dispenser (Kano & Call, 2014). **C.** The subject is
235 opening the latch to access the rope. **D.** The subject is pulling the rope to move food toward
236 the opposite booth. **E.** A birds-eye perspective of the testing booths. Larger versions of the
237 photos are provided in the supplementary materials.

238

239 **Materials & Design**

240 Subjects were presented with an apparatus that delivered food if a rope was pulled.
241 The apparatus was placed in a compartment space between two chimpanzee booths. The rope
242 could be pulled from one booth, whereas the food could be retrieved from the other booth.
243 Crucially, the pulling and receiving ends of the apparatus were opposite of one another but
244 visible from all sides. On the pulling end of the apparatus, the rope was attached to the testing
245 panel with Velcro in order to prevent it from falling to the ground and thus to ensure the
246 subject's access to it. Subjects had to reach through a small Plexiglas window to touch the
247 rope, though, and this window could be blocked by the experimenter with a screw. The
248 window contraption allowed us to slow down the chimpanzees' responses and give the
249 experimenter enough time to deliver the food to the stooge or the empty booth in the
250 respective condition. The food was placed on a Plexiglas cylinder that moved along a track.
251 On the receiving end of the apparatus, a hole in the Plexiglas safety panel provided access to
252 the food once it was pulled in front of it. This hole could be blocked with a small plastic
253 piece to prevent the stooge from accessing the food.

254 In order to capture the chimpanzees' eye movement, we drilled a small hole in the
255 subject's Plexiglas safety panel and attached a mouthpiece connected to a juice box to allow
256 subjects to drink diluted grape juice (75 % water, 25 % juice) provided they were close
257 enough to the panel (see Fig. 1 for details). While drinking, subjects remained in a steady
258 position, so head movement was minimized as much as possible. We recorded chimpanzees'
259 eye movement with a Tobii X120 (60 Hz; Tobii Technology AB, Stockholm, Sweden) eye

260 tracking unit directed at the subject at a distance of approximately 70 cm (see Kano & Call,
261 2014; Kano & Tomonaga, 2009, 2010). In addition, we positioned a webcam above the
262 subject to record the receiving end of the apparatus. The eye tracking software (Tobii Studio)
263 synchronizes subjects' gaze and pupil diameter with the live-scene recorded by the webcam.
264 A second webcam was positioned opposite of the subject's seating position to record a live
265 video and to monitor subjects while they were drinking. Finally, we placed a small lamp
266 opposite of the subject's seating position. The lamp (with a standard E27 light bulb) was
267 turned on at specific time points during an experimental trial to elicit a pupillary light reflex
268 in subjects (see Fig. 1 and 2 for details). This allowed us to identify the pupillary minimum of
269 the induced reflex as described in the analysis section (see also Henderson et al., 2014;
270 Hepach, Vaish, Müller, et al., 2017; Hepach, Vaish, & Tomasello, 2015).

271 Each chimpanzee participated in a 2 x 2 within-subjects design. The conditions were:
272 1) *helping: stooge-present / subject-delivers-food*, 2) *helping: stooge-present / experimenter-*
273 *delivers-food*, 3) *control: empty-booth/ subject-delivers-food* and 4) *control: empty-booth/*
274 *experimenter-delivers-food*. With the exception of one subject (see *Participants*) all
275 chimpanzees were tested in each of the 4 conditions. Only those instances in which subjects
276 started to pull the rope (for the sake of clarity in the following referred to as 'pulling') were
277 included in the pupil-diameter-change focussed analyses. Therefore, we designed the study to
278 create opportunities for subjects to pull the rope until each subject provided at least 4
279 instances of pulling the rope within each of the 4 conditions (see the supplementary online
280 materials for more details).

281 Sessions were carried on different, if possible consecutive, days. On each test session,
282 subjects were presented with up to six trials. However, a session ended if the subject did not
283 respond on the first 4 trials. Since only few subjects participated in more than four test trials
284 per day, we did not consider trials 5 to 6 but focussed only on the first 4 trials of each session.

285 The maximum number of test sessions within each condition was 10. Therefore, subjects
286 were given a maximum number of 40 (10 days x 4 trials) opportunities to pull the rope per
287 condition (a maximum of 160 opportunities in total across all 4 conditions).

288 If this criterion was reached for either the *experimenter-delivers-food* or the *subject-*
289 *delivers-food* condition, we stopped the alternating order of both conditions and presented the
290 subject only with the remaining condition until subjects pulled 4 times or until the subject
291 reached the maximum number of 10 sessions for that condition. To illustrate, a subject who
292 pulled the rope on each of the 4 trials within a session would participate in 4 sessions (16
293 rope pulls) in total while a subject who never attempted to pull the rope in any of the 4
294 experimental conditions would participate in 40 sessions in total.

295

296 **Procedure**

297 ***Familiarization Phase.*** Before the actual test, we conducted a familiarization phase to
298 ensure that subjects understood the main premises of the apparatus and how food was
299 delivered. Chimpanzees participated individually in this phase. On each familiarization trial
300 (8 per session, being different sessions held on different days), subjects were given the
301 opportunity to pull the rope that moved the cylinder with food towards the opening on the
302 receiving end of the apparatus. The study room could be set up such that the door between
303 the two booths was open or closed, to prevent the subject from walking from the pulling end
304 to the receiving end of the apparatus and obtain the food. In each familiarization session, we
305 presented subjects with one of two sequences of open-door (*OD*) and closed-door (*CD*) trials:
306 *OD-OD- CD-CD- OD-OD- CD-CD* or *CD-CD- OD-OD-CD-CD-OD-OD* (counterbalanced
307 across subjects). The sequence of trials was not fully randomized to keep subjects engaged
308 throughout the procedure. At the beginning of a familiarization trial, independently of
309 whether the door was open (*OD*) or closed (*CD*), the rope was attached to the pulling end of

310 the testing panel, the Plexiglas-window on the pulling end of the apparatus was blocked with
311 a screw, and the plastic slider on the receiving end was removed, so that the food could be
312 potentially accessed if the cylinder was moved in front of the opening. The experimenter
313 picked up one piece of food (either a grape, a slice of banana, a pellet or a peanut, depending
314 on the food preference of the individual chimpanzee, which was assessed prior to the study)
315 and held it in his/her hand until the subject looked at it. The experimenter then placed the
316 food item on the cylinder, picked up the rope, re-attached it on the pulling end of the testing
317 panel and removed the screw from the Plexiglas-window, so that the subject could open it.
318 The procedure continued only once chimpanzees' attention was drawn to the rope. The
319 subjects were given 20 seconds to open the Plexiglas-window and pull the rope. We noted
320 down whether the subject pulled the rope. Each subject was exposed to a maximum number
321 of 10 familiarization sessions. The familiarization phase was ended earlier if subjects
322 performed above chance in *not* pulling the rope on *CD*-trials and *do* pulling the rope on *OD*-
323 trials in two consecutive sessions (tested with a *Fisher's exact test*). In other words, if the
324 subject performed correctly in the two back-to-back sessions, he/she passed the test. Of the
325 12 subjects that took part in the test phase, only one subject participated in 10 familiarization
326 sessions meaning that it pulled the rope similarly often on *CD*- and *OD*-trials. This subject
327 was not excluded from the analysis to avoid further reducing the sample size.

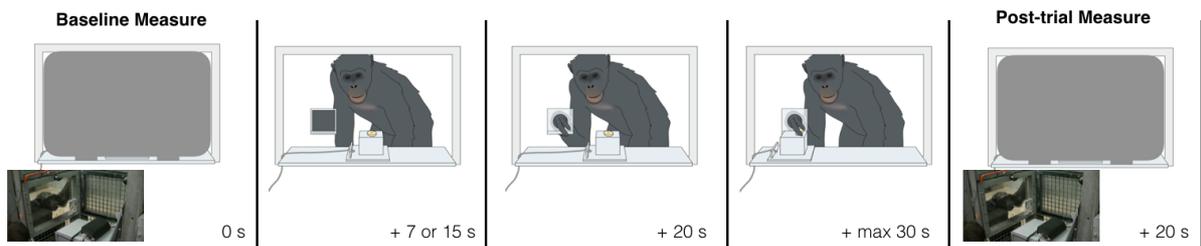
328 ***Test Phase.*** At the beginning of each test session (there was one session per day for
329 subjects and a maximum of 2 sessions per day for stooges), the experimenter started the eye
330 tracker and filled the juice dispenser with the diluted juice-mix (see above). The eye tracking
331 system had been calibrated to each subject's eyes in prior separate sessions, using a so-called
332 five-point calibration following published procedures (Kano & Call, 2014; Kano &
333 Tomonaga, 2010). Test trials in a session followed the same time course of events. Each trial
334 began with the experimenter placing a grey occluder in front of the panel on the receiving

335 end of the apparatus, thus blocking the subject's view of the opposite booth (but not blocking
336 the lamp). The experimenter waited until the subject began drinking and until the eye tracker
337 captured his or her eye. Next, the light switch was turned on in the following standardized
338 order: Light on (1 second) – Light off – wait 2 seconds - Light on (1 second) – Light off –
339 wait 2 seconds (baseline measure of pupil diameter). The experimenter then removed the
340 occluder, placed the food on the cylinder and waited either 7 or 15 seconds (depending on the
341 counterbalancing, to alternate the exposure time of food and avoid training effects). The light
342 sequence was initiated again to draw the subject's attention to the opposite booth. Then, the
343 experimenter removed the plastic slider and moved the cylinder toward the opening, but not
344 within reach of the stooge (in the *helping: stooge-present*). After 20 seconds, the light
345 sequence initiated again. Next, the experimenter picked up the piece of food and held it up in
346 sight of both the subject and the stooge. The experimenter then placed the food back on the
347 cylinder, attached the rope to the panel and removed the screw on the pulling end of the
348 apparatus. The subject was now given a maximum of 30 seconds to open the Plexiglas-
349 window and pull the rope. In the *subject-delivers-food* condition the chimpanzee could put
350 her fingers through the opening on her side of the Plexiglas panel to pull the rope thus
351 moving the food item in reach of the conspecific (*helping: stooge-present* condition) or
352 dropping the food in the empty booth (*control: empty-booth* condition). In the *experimenter-*
353 *delivers-food* condition the experimenter waited until the subject reached through the whole
354 and touched the rope until the experimenter picked up the food item and gave it to the stooge
355 (*helping: stooge-present* condition) or threw it in the empty booth (*control: empty-booth*
356 condition).

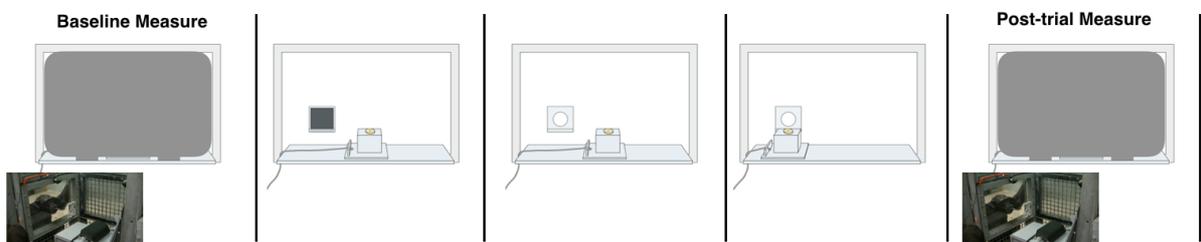
357 If subjects did not attempt to pull the rope within 30s, the experimenter picked up the
358 food and threw it in a bucket next to him/her. The experimenter turned on the light to draw
359 the subject's attention to the opposite panel and then placed the grey occluder on the

360 receiving end of the apparatus to block the subjects' view of the opposite booth and provide
361 the sample visual plane for the crucial pupil diameter measurement. After 20 seconds, the
362 light was turned on again (post-trial measure of pupil diameter). Note that although five
363 identical light sequences were elicited during a test trial, we only measured subjects' pupil
364 diameter on the first and fifth sequence because only in those instances did the grey occluder
365 provide a similar luminance surface in the subject's gaze direction. The purpose of the
366 remaining three light sequences was to keep subjects familiarized to the light and draw their
367 attention forward to the panel. This sequence of events was carried out in this pre-specified
368 order irrespective of whether the subject's eye could be tracked during the crucial
369 measurement phases and whether the stooge approached the opening. Trials were never
370 repeated.
371

Study 1: *Helping: Stooge-present*



Study 1: *Control: Empty-booth*



372

373 *Figure 2.* Sequence of events in study 1. This figure shows the view of the apparatus and the

374 stooge from the subject's point of view. The timing was identical in the two contexts and

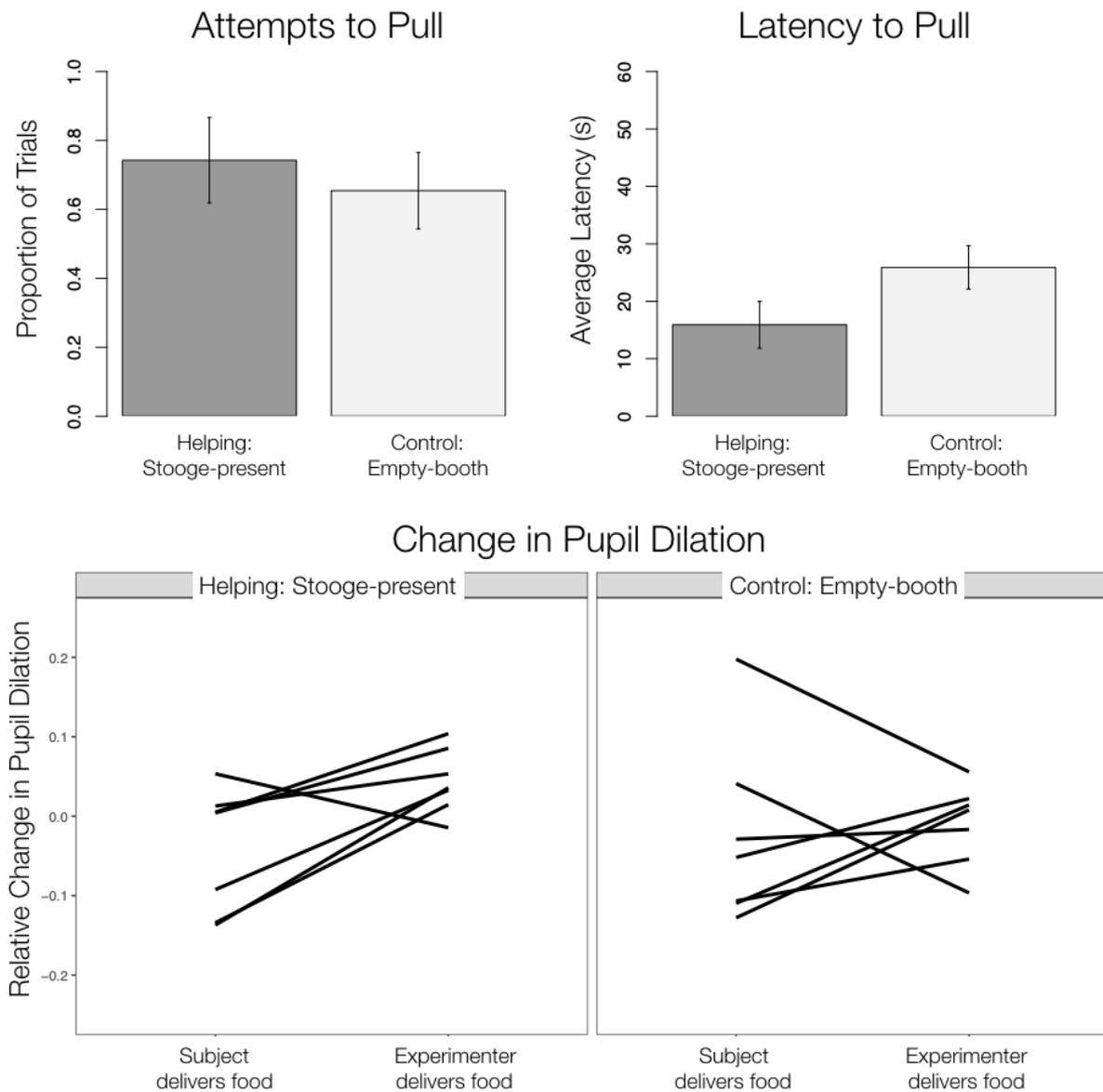
375 refers to the time elapsed, in incremental steps, from the initiation of the baseline measure.

376 The Baseline and Post-trial measurement lasted approx. 15 s. Pupil diameter was collected

377 continuously but we focused on the change in pupil diameter from the Baseline to the Post-

378 trial measure.

379



380

381

382 *Figure 3.* Results of Study 1. **Top row.** Rate of pulling the rope and latency with which
 383 subjects attempted to pull the rope. Error bars represent standard errors of the mean. **Bottom**
 384 **row.** Change in pupil diameter. Each line represents an individual subject.

385

386 **Data Analysis**

387 The complete data set and analysis scripts are provided on *OSF* (Hepach, Vaish,
 388 Kano, Albiach-Serrano, Benziad, Call, & Tomasello, 2019). This includes all continuously
 389 recorded gaze and pupil diameter data recorded during each test session. Importantly, we

390 measured changes in subjects' pupil diameter from baseline to after the trial while they were
391 looking at the grey occluder (to reduce noise resulting from shifting gaze). For each test trial,
392 we were interested in three dependent variables: the attempt to pull the rope, the latency to
393 pull the rope, and the change in pupil diameter from the beginning (baseline measure) to the
394 end of the trial (post-trial measure). We noted down whether the stooge sat in front of the
395 panel (receiving end) during the trial. The attempt to pull was coded as '1' or '0' on each
396 trial. Two independent coders (main coder and reliability coder), both blind to hypotheses,
397 coded all the data with regards to whether the subject attempted to pull (Cohen's Kappa =
398 .85) and how fast subjects were to do so (i.e., latency to pull; Pearson's $\rho = .81$, $ICC = .74$).
399 Data from the main coder were used for all subsequent analyses.

400 To gather the change in pupil diameter we first identified, for each subject, the
401 pupillary minima, the local minimum of pupil diameter, during each of the size measurement
402 sequences. We then focused on the baseline and post-trial measures of pupil diameter,
403 subtracted the baseline pupillary minima (A) from the post-trial measure minima (B) and
404 divided the resulting difference by the same baseline value: $(A-B) / B$ (more details are
405 provided in the supplementary online materials). With regard to the statistical analysis of the
406 data we carried out both focussed and exploratory analyses. The same 7 subjects who
407 provided data for all the conditions in the focussed analyses were included in each of the
408 exploratory analyses. All analyses are based on Wilcoxon exact rank sum tests and for each
409 we report 95% confidence intervals as well as Cohen's d . All reported p -values are two-
410 tailed.

411 **Focussed analyses.** We compared subjects' change in pupil diameter between the
412 *helping: stooge-present/experimenter-delivers-food* and the *helping: stooge-present /subject-*
413 *delivers-food* condition, as well as between the *experimenter-delivers-food* and the *subject-*
414 *delivers-food* condition within the *control: empty-booth* context. We thus focussed our

415 analyses of pupil diameter on those two contrasts that allowed us to test our predictions.
 416 These analyses were carried for those trials on which the subject pulled the rope and, in the
 417 helping context, those trials on which the stooge reached for the food: $M_{\text{Helping/Subject-delivers}} =$
 418 2.3 sessions ($SD = 1.3$), $M_{\text{Helping/Experimenter-delivers}} = 1.6$ ($SD = 1.1$), $M_{\text{Control/Subject-delivers}} = 2.1$
 419 sessions ($SD = 1.5$), $M_{\text{Control/Experimenter-delivers}} = 2.3$ ($SD = 1.3$). The total number of sessions
 420 completed ranged between 4 and 16 sessions ($M = 8.3$, $SD = 4.4$).

421 **Exploratory analyses.** We first compared the average number of trials a subject
 422 pulled in the *helping: stooge-present* context when the stooge was reaching for the food
 423 compared to the *control: empty-booth* context. Next, we calculated the average latency for
 424 each subject in each condition and compared the latency to pull the rope between the *helping*
 425 and the *control* context. This analysis was only carried out on those trials on which the
 426 subject pulled the rope. In addition to the focussed analysis on the change in pupil diameter,
 427 we compared subjects' baseline pupil diameter at the beginning of a trial across the four
 428 conditions to investigate whether subjects differed in tonic arousal at the onset of each trial.

429

430

Results

431 **Focussed analyses.** Subjects showed a greater increase in pupil dilation after they
 432 could not carry out the action in the *helping: stooge-present / experimenter-delivers-food*
 433 condition ($M = 0.04$, $SD = 0.04$) compared to when they pulled the rope in the *helping:*
 434 *stooge-present / subject-delivers-food* condition ($M = -0.04$, $SD = 0.08$), $T = 26$, $[0.007 \ 0.15]$,
 435 $p = .047$, $d = 1.38$ (see Fig. 3). In contrast, in the *control: empty-booth* condition subjects
 436 showed similar levels in pupil dilation after they could not carry out the action in the
 437 *experimenter-delivers-food* condition ($M = -0.01$, $SD = 0.05$) and when they pulled the rope
 438 in the *subject-delivers-food* condition ($M = -0.03$, $SD = 0.11$), $T = 15$, $[-0.14 \ 0.12]$, $p = 0.94$,
 439 $d = 0.19$ (Fig. 3). There was no overall difference pupil diameter change between the *helping:*

440 *stooge-present* ($M = 0.002$, $SD = 0.05$) and *control: empty-booth* ($M = -0.02$, $SD = 0.07$)
 441 condition, $T = 17$, $[-0.04\ 0.1]$, $p = .69$, $d = 0.34$ suggesting that subjects' arousal did not
 442 overall remain increased when they saw the conspecific being helped.

443 **Exploratory analyses.** Chimpanzees pulled the rope at similar rates in the *helping:*
 444 *stooge-present* ($M = 0.74$, $SD = 0.33$) and in the *control: empty-booth* context ($M = 0.65$, SD
 445 $= 0.29$), $T = 14$, 95% CI $[-0.46\ 0.54]$, $p = .56$, $d = 0.28$ (Fig. 3). However, we found that
 446 chimpanzees were faster to pull the rope in the *helping: stooge-present* ($M = 15.92$ s, $SD =$
 447 10.77 s) compared to the *control: empty-booth* condition ($M = 25.9$ s, $SD = 9.97$ s), $T = 29$,
 448 $[2.73\ 16.46]$, $p = .047$, $d = 0.96$. In addition, we did not find differences in baseline pupil
 449 diameter at the beginning of test trials across the four conditions, $ds < .3$, $ps > .4$ (see
 450 supplementary online material for details).

451

452

Study 2

453 The goal of study 2 was to rule out the possibility that the increased internal arousal in
 454 the *helping: stooge-present / experimenter-delivers-food* condition (compared to the *helping:*
 455 *stooge-present / subject-delivers-food* condition) in study 1 was due to subjects being
 456 observed by a conspecific while carrying out the action or, alternatively, because the food
 457 was handled by the human experimenter in the presence of a conspecific. With this aim, in
 458 study 2 we modified the apparatus such that pulling the rope always resulted in the subject
 459 receiving the reward. Similar to study 1, we manipulated whether the subject could complete
 460 the action of delivering the food to themselves or whether the human experimenter was faster
 461 to deliver the food to the subject. In one context, a conspecific was present and observed
 462 (*observer present/subject-delivers-food* or *observer present/experimenter-delivers-food*)
 463 whereas in the other context the booth was empty (*empty-booth/subject-delivers-food* or
 464 *empty-booth/experimenter-delivers-food*).

465

466 Participants

467 Subjects were 17 chimpanzees (*Pan troglodytes verus*; *P. t. schweinfurthii*; *P. y.*
468 *verus-schweinfurthii hybrid*) and came from the same two populations as in study 1. The
469 study was conducted between February 2016 and June 2016. Of the 17 subjects three subjects
470 were assigned the role of the stooge observer, 1 in the smaller group and 2 in the larger group
471 (the latter allowed us to test all available subjects). Of the 16 subjects, 2 individuals did not
472 participate in the familiarization phase, 2 subjects did not participate in the test phase, and 3
473 individuals participated in both phases but did not provide pupillometry data for analysis.
474 Therefore, the final sample consisted of 9 subjects (5 females; mean age = 22 y; range: 12 y
475 to 44 y).

476

477 Materials & Design

478 We used the same apparatus employed in study 1 with two important modifications.
479 First, on the observer's side the chimpanzee could not access the food. An additional opaque
480 plastic piece blocked any access to it. Second, every time the rope was pulled the subject
481 received the reward. This was accomplished by attaching a tube that connected the apparatus
482 with the subject's side of the booth. When the rope was pulled with food on the cylinder, the
483 cylinder would slide to the side (identical to study 1) and then hit a plastic piece which
484 dropped the food reward from the cylinder into the tube which made the food item roll to the
485 subject. The capture of eye movements and pupil diameter was identical to study 1.

486 Each chimpanzee participated in a 2 x 2 within-subjects design. The conditions were:
487 *observer present / subject-delivers-food*, *observer present / experimenter-delivers-food*,
488 *empty-booth / subject-delivers-food*, *empty-booth / experimenter-delivers-food* condition. All
489 chimpanzees were tested in each of the 4 conditions. We fixed the number of presentations of

490 conditions within one day and presented each subject with a maximum of 4 trials per day.
491 Similar to study 1, the presentation of the *observer present* and the *empty-booth* conditions
492 was organized in two blocks of sessions. Also, the presentation of the *subject-delivers-food*
493 and the *experimenter-delivers-food* conditions alternated from session to session (1 per day).
494 Specifically, one half of the subjects first participated in the *observer present* condition and
495 then in the *empty-booth* condition while the second half were tested in the *empty-booth*
496 condition first and then the *observer present* condition second. The counterbalancing and the
497 alternating presentation of conditions were identical to study 1.

498

499 **Procedure & Data Analysis**

500 After participating in a familiarization phase (more details are provided in the
501 supplementary online materials) subjects were paired with a stooge who sat in the booth
502 opposite to the subject (*observer-present* condition) or the opposite booth was empty (*empty-*
503 *booth* condition). The order of events within a test trial was identical to study 1. If the subject
504 pulled the rope, she/he always obtained the food (whereas in study 1 the food was always
505 moved to the booth opposite of and inaccessible to the subject). If the subject did not pull the
506 rope, the experimenter placed the food back into the bucket (similar to study 1). The
507 experimenter distributed bread crumbs on the observer's side to keep the observer sitting
508 opposite of the subject for the entire duration of the session.

509 The test trial began with the experimenter placing a grey occluder on the receiving
510 end of the apparatus, thus blocking the subject's view of the opposite booth. The
511 experimenter waited until the subject began drinking and until the eye tracker captured his or
512 her eye. Next, the experimenter initiated the light switch sequence for the baseline measure of
513 pupil diameter. The experimenter removed the occluder, placed the food on the cylinder and
514 then waited either 7 or 15 seconds, depending on the counterbalancing similar to study 1. The

515 light was turned on again to draw the subject's attention to the opposite booth. The
516 experimenter moved the cylinder along the panel until it was in center view of the subject and
517 briefly touched the panel (opposite of the subject) thus making a movement similar to the one
518 of removing the plastic block in Study 1. After 20 seconds, the light was turned on again.
519 Next, the experimenter picked up the piece of food and held it up to be visible to both the
520 subject and the stooge. She then placed the food back on the cylinder, attached the rope on
521 the pulling end of the apparatus and removed the screw. The remaining procedure during test
522 trials paralleled that of study 1 (see Fig. S1 and supplementary online materials for more
523 details).

524 Two independent coders (main coder and reliability coder), both blind to hypotheses,
525 coded the all the data with regards to whether the subject attempted to pull and how fast
526 subjects were to do so (i.e., latency to pull). The agreement among the two coders was high
527 for the attempts to pulls (Cohen's $Kappa = .94$) and good for the behavior latency (Pearson's
528 $rho = .85$, $ICC = .73$). Data from the main coder were used for all subsequent analyses.

529

530

Results

531 **Focussed analyses.** In the *observer-present* condition subjects showed similar pupil
532 diameter after they could not carry out the action in the *experimenter-delivers-food* condition
533 ($M = 0.06$, $SD = 0.16$) and when they pulled the rope in the *subject-delivers-food* condition
534 ($M = -0.04$, $SD = 0.11$), $T = 33$, $[-0.08\ 0.24]$, $p = .25$, $d = 0.68$. Likewise, in the *empty-booth*
535 condition subjects showed similar levels in pupil diameter after they could not carry out the
536 action in the *experimenter-delivers-food* condition ($M = 0.04$, $SD = 0.18$) and when they
537 pulled the rope in the *subject-delivers-food* condition ($M = -0.02$, $SD = 0.1$), $T = 27$, $[-0.13$
538 $0.25]$, $p = 0.65$, $d = 0.35$ (see Fig. S2C).

563 themselves thus providing them with an opportunity to ‘get credit’ for completing the helpful
564 action.

565 The present experiments are the first to explore the internal physiological mechanism
566 underlying non-human primate helping and it is important to consider number of points that
567 merit closer attention, including the sample size as well as alternative explanations for the
568 pattern in pupil dilation changes found in the present studies. In both studies, the sample size
569 of subjects who contributed data to the final statistical analyses was small, which reduced
570 statistical power. Collecting data on pupil diameter changes requires subjects to remain
571 within the tracking radius of the eye tracking system for at least 10 seconds at the beginning
572 (baseline measure) and again at the end of a test trial (post-trial measure). In addition, we
573 assessed changes in chimpanzees’ pupil diameter in an active helping paradigm in which
574 subjects were encouraged to move freely to manipulate the apparatus, which at the same time
575 interfered with the tracking ability of the eye tracking device. Therefore, an important next
576 step is to implement the current design with a larger sample of subjects and to include
577 different types of helping situations.

578 To address alternative explanations of the current pupil dilation results it is important
579 to note that we found no differences in chimpanzees’ pulling rates between the conditions
580 where they pulled food in reach of a conspecific (study 1: helping context) and where they
581 pulled food into an empty booth (study 1: empty-booth context). Therefore, it is important to
582 consider the question whether chimpanzees were in fact motivated to help their conspecific.
583 One possibility is that subjects did not understand the experimental apparatus. We think that
584 this is unlikely, given that all subjects underwent substantial training in the familiarization
585 phase. This involved pulling the rope, thus manipulating the mechanism, more often when it
586 was later accessible compared to when access to the food was blocked. This procedure of
587 training subjects models previous work on chimpanzee helping (Melis et al., 2011; Schmelz

588 et al., 2017). Alternatively, the pattern of behavioral results in study 1 may be explained by
589 the fact that there was nothing else in the room for the subjects to manipulate apart from the
590 apparatus (see Albiach-Serrano, 2015). In addition, chimpanzees received juice throughout
591 the trials in regular intervals - so as to track their eyes - which kept them close to the
592 apparatus, thus increasing the likelihood of interacting with it (irrespective of the
593 experimental context). In sum and crucially, the results found with regards to differences in
594 subjects' pupil dilation changes in study 1 cannot be explained by the pattern of
595 chimpanzees' pulling behavior.

596 In study 2 we found similar pulling rates between pulling in food for themselves with
597 a conspecific watching and with no conspecific watching. This suggests they were equally
598 motivated to obtain food in the presence and in the absence of a conspecific (study 2;
599 observer-present vs. empty-booth context). In addition, the physiological pattern of the
600 results in study 2, i.e., the absence of differences in subjects' pupil dilation depending on
601 whether they pulled themselves as opposed to having the experimenter provide the food,
602 suggests that - in the context of obtaining food for themselves – chimpanzees are intrinsically
603 motivated to get food irrespective of who provides it. Pupil data were analyzed only
604 including those trials on which the subject attempted to pull. Therefore, any distraction
605 created by the experimenter through moving the food into the bucket on no-pulling trials
606 could not affect the analyses of pupil diameter changes. Study 2 further allowed us to address
607 the possibility that, in study 1, subjects were more aroused (i.e., showed greater pupil
608 dilation) in the situation where the experimenter delivered the food to the conspecific because
609 the manipulation of the food by the experimenter in front of a conspecific was in itself
610 arousing. Crucially, in study 2 we did not find differences in chimpanzees' pupil diameter
611 changes when the experimenter delivered the food to them compared to when they could
612 complete the action themselves, while being watched by a conspecific. This suggests that, in

613 the context of conspecifics needing help, elevated levels of pupil dilation were a result of not
614 completing the action rather than the experimenter handling food (in which case pupil
615 dilation should have been elevated in the observer-present context/experimenter delivers food
616 condition).

617 Against the background of the current results we would like to propose the ‘getting
618 credit hypothesis’ of chimpanzee helping which is consistent with previous work in showing
619 that helping in chimpanzees may be motivated by concerns for reciprocation. This hypothesis
620 further reconciles the prosocial and non-prosocial explanations of chimpanzee helping. On
621 the one hand, we found support for the *prosocial motivation* account, given that subjects
622 seemed to be sensitive to whether manipulating the apparatus provided a conspecific with
623 food. This was reflected in (1) faster pulling to deliver food to the conspecific (compared to it
624 falling into the empty booth and (2) chimpanzees’ internal arousal being more elevated after
625 the experimenter delivered food to the conspecific compared to when subjects delivered the
626 food to the conspecific. On the other hand, we found support for the *non-prosocial*
627 *motivation* account, given that chimpanzees’ main concern when carrying out the helpful
628 behavior was not to see the conspecific being helped but rather to provide the help
629 themselves. That is, in the *helping* context chimpanzees were motivated to carry out the
630 action themselves, i.e., showed elevated internal arousal in the *experimenter-delivers-food*
631 condition, instead of wanting to see the conspecific being helped, in which case, subjects’
632 internal arousal would be expected to be similarly low in the *experimenter-delivers-food* and
633 *subject-delivers-food* conditions (see Hepach et al., 2012, for findings with young children).

634 Our findings dovetail with two suggested proximate mechanisms of chimpanzee
635 prosociality, namely emotional bookkeeping and attitudinal reciprocity, which contribute to
636 chimpanzees forming social and emotional bonds with allies with whom they engage in
637 repeated reciprocal interactions (Bonnie & de Waal, 2004; Schino & Aureli, 2009). Indeed,

638 while the evidence for reciprocal helping in chimpanzees is mixed, more studies report
639 positive than negative findings based both on observational and experimental studies
640 (Schweinfurth & Call, 2019). Previous work had suggested that chimpanzees are indifferent
641 to whether conspecifics are helped based on their performance in the so-called prosocial
642 choice tasks (House, Silk, Lambeth, & Schapiro, 2014; Jensen, Hare, Call, & Tomasello,
643 2006; Silk et al., 2005; Vonk et al., 2008; see Horner, Carter, Suchak, & de Waal, 2011, for
644 different results). However, it is possible that chimpanzees' concern for others welfare' was
645 underestimated in prosocial choice tasks given that the analysis focused on subjects' behavior
646 and not on physiological measures. In fact, one central conclusion that can be drawn from the
647 current results is that even in the absence of behavioral effects, i.e., same rate of pulling
648 between experimental and control conditions, chimpanzees may nevertheless view others'
649 need for help as opportunities to 'get credit' by carrying out the behavior themselves. This
650 raises an interesting question for future research employing the prosocial choice task. When
651 chimpanzees choose to benefit a conspecific as opposed to making a choice that only benefits
652 themselves, is their motivation seeing the other helped or rather to help the other *themselves*?
653 Given that chimpanzees in the current study 1 were motivated to provide the help themselves
654 (while the overall pulling rates were similar across contexts) it is possible that this motivation
655 spans across other helping situations, including the prosocial choice task. Based on the
656 current findings, the prediction would be that if chimpanzees attempt to make the prosocial
657 choice but someone else is faster and provides the help instead of them, then this should
658 result in increased pupil dilation compared to when they can carry out the action themselves
659 (Hepach, Vaish, & Tomasello, 2017a).

660 To what extent chimpanzees think about the kinds of credit they could receive from
661 helping others is another question for future research. For example, and using the same
662 measure of physiological arousal employed in the present study, one may ask whether

663 chimpanzees who carry out helping behaviors expect the conspecific to help them in return or
664 to choose them over another individual on subsequent occasions (see Schino & Aureli, 2017,
665 for a discussion on the respective mechanism of partner control and partner choice). This
666 could be measured based on the initial subjects' physiological arousal in response to the
667 conspecific not reciprocating. Building on work with human subjects (for reviews see Hepach
668 & Westermann, 2016; Laeng et al., 2012; Sirois & Brisson, 2014), unexpected outcomes
669 should trigger greater pupil dilation. Furthermore, it would be interesting to investigate the
670 influence of relationship quality, e.g., friendships, on changes in subjects' arousal to address
671 the question of whether the 'getting credit hypothesis' similarly applies to friendships and kin
672 relationships.

673 Finally, we propose using the paradigms developed for the present studies to compare
674 the underlying motivation of chimpanzees to that of other great apes, including humans.
675 Young children's internal arousal increases when seeing others needing help and decreases
676 upon seeing the person in need receive help (Hepach et al., 2012). At the same time, children
677 are motivated to get credit for helping others in guilt-like and gratitude-like situations, where
678 they have accidentally harmed others and are given the opportunity to provide help (Hepach
679 et al., 2017). Such a line of research could further address questions such as whether
680 chimpanzee (and human) children show positive emotions after helping (for recent paradigms
681 see Aknin et al., 2015; Hepach, Vaish, & Tomasello, 2017b), and to what extent there are
682 reputational effects on these species' helping. For example, in young children reputational
683 concerns increase from toddlerhood to preschool and school age such that children will help
684 more if reputational incentives are high (Engelmann et al., 2013). In the current study 2, there
685 was a potential reputational cost for the subject pulling food toward themselves and away
686 from the conspecific. The 'observer present' condition in study 2 provides a means to
687 investigate reputation effects - which could drive chimpanzees' reciprocation - and this

688 needs to be followed up on with studies that include a larger sample and vary the relationship
 689 between the subject and the conspecific.

690 In sum, in the current studies we found that chimpanzees helped others by completing
 691 the necessary instrumental action fastest when this fulfilled the conspecific's need. In
 692 addition, our data suggest that chimpanzees were motivated to carry out the helping action
 693 themselves, given that their internal arousal remained increased if they merely saw a third
 694 party provide the help. In comparison to previous work with young human children, the
 695 present results suggest that while both species help others reach their goals, the intrinsic
 696 motivation for *why* they help is different.

697

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