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Running title: Strong hand preference for gesturing in baboons

For Peer Review

1 Baboons' hand preference resist to spatial factors for a communicative
2 gesture but not for a simple manipulative action

3
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3 20 Olive baboons (*Papio anubis*) do acquire and use intentional requesting gestures in
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5 21 experimental contexts. Individual's hand preference for these gestures is consistent with that
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7 22 observed for typical communicative gestures, but not for manipulative actions. Here, we
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9 23 examine whether the strength of hand preference may also be a good marker of hemispheric
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11 24 specialization for communicative gestures, hence differing from the strength of hand
12
13 25 preference for manipulative actions. We compared the consistency of individuals' hand
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15 26 preference with regard to the variation in space of either (i) a communicative partner or (ii) a
16
17 27 food item to grasp using a controlled set-up. We report more consistent hand preference for
18
19 28 communicative gestures than for grasping actions. Established hand preference in the midline
20
21 29 was stronger for gesturing than for grasping and allowed to predict the consistency of hand
22
23 30 preference across positions. We found no significant relation between the direction of hand
24
25 31 preference and the task.
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33 Key words: Handedness, Laterality, Language, Gesture, Hand preference, Olive baboon
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3 41 Handedness is by far the most overwhelming manifestation of behavioral asymmetry in
4
5 42 humans. A right-hand preference is shown by approximately ninety percent of humans
6
7 43 (Annett, 1985; Knecht et al., 2000a), and this population-level bias is considered universal
8
9 44 because of its existence across all modern cultures (Coren & Porac, 1977; Raymond &
10
11 45 Pontier, 2004) and over the course of human evolution (Cashmore, Uomini, & Chapelain,
12
13 46 2008; Faurie & Raymond, 2004; Uomini, 2009). From a neurofunctional viewpoint,
14
15 47 handedness is also one robust manifestation of hemispheric specialization, the other one being
16
17 48 language lateralization (Hopkins & Vauclair, 2012). Indeed, right-handers are left-hemisphere
18
19 49 dominant for hand functions and most humans are also left hemisphere dominant for language
20
21 50 functions. Both features have hence been argued to evolve concomitantly during the course of
22
23 51 human evolution (Crow, 2004; Ettliger, 1988; Waren, 1980).

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28 52 However, recent studies have emphasized that handedness would actually be only a
29
30 53 poor predictor of hemispheric dominance for language. First, a majority of left-handers are
31
32 54 also left hemisphere dominant for language in humans (Knecht et al., 2000b; Khedr, Hamed,
33
34 55 Said, & Basahi, 2002). Moreover, asymmetries in the use of limbs are not specific to humans
35
36 56 but are widespread in vertebrates instead (Hopkins, 2007; Rogers & Andrew, 2002;
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38 57 Vallortigara, Rogers, & Bisazza, 1999). It has hence been proposed that handedness predated
39
40 58 language (Corballis, Badzakova-Trajkov, & Häberling, 2012; Forrester, Quaresmini, Leavens,
41
42 59 Mareschal, & Thomas, 2013) and there is still considerable debate about whether left-
43
44 60 hemisphere dominance for language was inherited from hemispheric specialization for its
45
46 61 motor components (Greenfield 1991; Forrester et al., 2013) or rather its communicative
47
48 62 components (Vauclair, 2004). In that respect, communicative gestures that imply both motor
49
50 63 and communicative hand functions have been of particular interest in the recent years.
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54 64 Children point more frequently with their right hand (Bates, O'Connell, Vaid, Sledge, &
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56 65 Oakes, 1986; Cochet & Vauclair, 2010), even if they are left-handers or ambidextrous for
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3 66 manipulating objects otherwise (Vauclair & Imbault, 2009). Interestingly hand preference
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5 67 may be more pronounced for communicative gestures such as pointing than for object
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7 68 manipulation, and both types of hand preference are usually poorly correlated in human
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9 69 infants (Cochet & Vauclair, 2010; Jacquet, Esseily, Rider, & Fagard, 2012; Vauclair &
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11 70 Imbault, 2009). This has led some to hypothesize that hand preference for communicative
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13 71 gestures may be a better marker of hemispheric specialization for language than handedness
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15 72 (Cochet & Vauclair, 2010; Kimura, 1993; Vauclair, 2004).

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19 73 Further support for this hypothesis comes from comparative work conducted with non-
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21 74 human primates. Several studies have for example found right-sided asymmetries at the
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23 75 population level in both the chimpanzee (Hopkins et al., 2005; Meguerditchian, Vauclair, &
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25 76 Hopkins, 2010) and the baboon (Meguerditchian, Molesti, & Vauclair, 2011b;
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27 77 Meguerditchian & Vauclair, 2006) for a range of manual tasks, including complex (i.e.,
28
29 78 bimanual) manipulations and communicative gestures. As it is the case for children (Esseily,
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31 79 Jacquet, & Fagard, 2011; Jacquet et al., 2012; Vauclair & Imbault, 2009), the population-level
32
33 80 right biases found in both species were stronger for communicative gestures than for object-
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35 81 directed manual actions, (e.g. baboons: Meguerditchian & Vauclair, 2009; chimpanzees:
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37 82 Hopkins et al., 2005; Meguerditchian et al., 2010). Consequently, a similar pattern of hand
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39 83 preference can be observed in human and in some non-human primates (see also Meunier,
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41 84 Vauclair, & Fagard, 2012b; Meunier et al., this issue), albeit in different proportions. Taken
42
43 85 together, these data suggest that the left-hemisphere dominance in linguistic functioning is not
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45 86 modality-specific and may have deep phylogenetic origins (Corballis et al., 2012;
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47 87 Meguerditchian, Cochet, & Vauclair, 2011a; Vauclair, 2004).

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53 88 In two studies conducted in our laboratory, we found that baboons were able to request
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55 89 food intentionally from a human partner using either pointing (Meunier, Prieur, & Vauclair,
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57 90 2012a) or food-begging gestures (Bourjade, Meguerditchian, Maille, & Vauclair, submitted).

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3 91 While both gestures are communicative, presumed difference exists since pointing, but not
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5 92 begging, requires attracting the attention of a human towards an external distinct target and
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7 93 has been suggested to involve higher cognitive demands in monkeys (e.g. Hattori, Kuroshima,
8
9 94 & Fujita, 2010). Interestingly, the pattern of laterality for pointing was similar in baboons and
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11 95 human infants (Meunier et al., 2012b), while it has not been investigated so far for food-
12
13 96 begging. As regards food-begging, baboons were shown to keep their hand preference
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15 97 consistent with a typical communicative gesture (i.e., hand slapping), but not with object-
16
17 98 directed manual actions (Meguerditchian & Vauclair, 2009). The authors hypothesized that
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19 99 baboons' communicative gestures, as regards the direction and consistency of hand
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21 100 preference, may rely on a specific left-lateralized cerebral system that would be independent
22
23 101 from the system controlling purely manipulative actions (Meguerditchian et al., 2011a).
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25 102 However, overall direction of hand preference may not be the only aspect that has
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27 103 neuropsychological significance. Handedness is commonly measured as a discrete variable
28
29 104 based on the predominant use of the right or the left hand, or equivalent use of both hands. In
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31 105 contrast, many have suggested that measuring handedness on a continuous scale accounted for
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33 106 both the direction and the strength of hand preference, with the latter also being a good
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35 107 marker of brain specialization (e.g. Bishop, Ross, Daniels, & Bright, 1996; Dassonville, Zhu,
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37 108 Ugurbil, Kim, & Ashe, 1997; Khedr et al., 2002; Vallortigara et al., 1999). Neurofunctional
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39 109 evidence supports this claim since the strength and direction of handedness seem to be coded
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41 110 separately in the human brain (Dassonville et al., 1997). Likewise, it could be alternately
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43 111 hypothesized that the strength of hand preference for communicative gestures, defined as the
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45 112 proportion of same-hand use for a given gesture, may be a good marker of hemispheric
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47 113 specialization for communicative hand functions in baboons, hence differing from the
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49 114 strength of hand preference for manipulative actions.
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3 115 In this contribution, we examine these two hypotheses alternately using a standardized
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5 116 measure for quantifying consistency of hand preference as a tool towards validation (i.e.,
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7 117 QHP task, Bishop et al., 1996). The initial task developed in humans was to pick up playing
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9
10 118 cards. The use of the non-preferred hand was encouraged by varying the spatial position of
11
12 119 the cards in relation to the body midline. The prediction was that switching hand across
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14 120 positions indicated weaker preferences than keeping hand consistent across positions.
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16 121 Adaptations of this task for children (Esseily et al., 2011; Jacquet et al., 2012) and non-human
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18 122 primates (Chapelain et al., 2012; Meunier, Blois-Heulin, & Vauclair, 2011; Meunier et al.,
19
20 123 2012b; Meunier et al., this issue) have proved recently successful in highlighting the influence
21
22 124 of situational factors on handedness for reaching actions.

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26 125 Our aim of adapting this paradigm here was to use the sensitivity to situational factors
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28 126 as a means of measuring the robustness of hand preference of subjects predefined as right-
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30 127 handed, left-handed, ambiguously-handed, but also those established as exclusively-handed
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32 128 and non-exclusively handed irrespective of the direction of laterality. The rationale was then
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34 129 to determine the consistency of hand preference across spatial positions (herein: *consistency*
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36 130 of hand preference) in two different tasks, taking established hand preference (i.e., both in
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38 131 direction and strength) in the central position as a reference. We built on previously published
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40 132 data reporting hand preference for grasping in baboons (Meunier et al., 2011) to compare with
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42 133 novel data reporting hand preference for food-begging measured on same individuals within
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44 134 the same experimental setting. In order to portray the differential lateralization of
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46 135 communicative and non-communicative hand functions, we examined the *consistency* across
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48 136 positions of both the *direction* and the *strength* of individuals' hand preference with regards to
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50 137 the variation in space of (i) a communicative partner (i.e., food-begging) and (ii) a food item
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52 138 to grasp (i.e., grasping).
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3 139 Based on previously published research reporting stronger biases for communicative
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5 140 gestures than for grasping actions at the population level (Meguerditchian & Vauclair, 2009;
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7 141 Meunier et al., 2011; Meunier et al., 2012b), we expected hand preference to be more
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9 142 consistent across positions in the communicative than in the non-communicative context.
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11 143 Additionally, if the cerebral system controlling for communicative gestures differs from the
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13 144 system controlling manipulative actions on the basis of the *direction but not strength* of hand
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15 145 preference, we would expect more established right-handers than left-handers in the central
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17 146 position for food-begging than for grasping, and the direction of the established preference to
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19 147 predict the propensity to switch from preferred to non preferred hand. Alternately, if the two
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21 148 systems differ on the basis of the *strength but not direction* of hand preference, we would
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23 149 expect baboons to show stronger established hand preference for food-begging than for
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25 150 grasping, and the strength of the established preference to predict the propensity to switch
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27 151 from preferred to non preferred hand.
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35 153 **METHODS**

36 154 **Animals**

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39 155 The experiments took place in the Primate Station of the *Centre National de la Recherche*
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41 156 *Scientifique*, Rousset, France. Initially, 42 olive baboons (*Papio anubis*) were presented with
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43 157 the grasping task between September and December 2009 (see Meunier et al., 2011 for
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45 158 details). Two years later, 13 out of these subjects were presented with a food-begging task.
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47 159 These subjects had previously learnt to request food by extending an arm through the cage in
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49 160 former experiments (e.g. Bourjade et al., submitted; Meunier et al., 2012a). Only the data for
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51 161 these 13 subjects that have completed the two tasks are presented here. Subjects were five
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53 162 females and eight males, all adult. All lived in social groups and were housed either in
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3 163 outdoor parks or large cages with free access to an indoor shelter. Water was available *ad*
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5 164 *libitum* and subjects were never deprived of food or water during testing. All subjects had
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7 165 been tested in their outdoor area, and only females were partly isolated from dominant
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9 166 individuals (i.e., that were kept inside) during testing for the food-begging task. All
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11 167 procedures complied with the current French laws and the European directive 86/609/CEE.
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169 **Experimental procedure**

170 For the two tasks, the experimental set-up was an adaptation of the Bishop's QHP task
171 initially developed to test pre-defined human right-handers for their degree of hand preference
172 (Bishop et al., 1996). In the original task seven picture cards were placed on a semi-circle,
173 each positioned 30 degrees apart from one another, in front of- and within the reach of the
174 participant. Participants stood in front of the template and had to pick up specific cards one by
175 one to put them in a box located in front of them. Hand preference was sampled by recording
176 the hand used to pick up each card. This task has been thereafter adapted to non-human
177 primates in a very comparable set-up (Chapelain et al., 2012; Meunier et al., 2011; Meunier et
178 al., this issue). We provide a brief description of the experimental set-up here. Full details of
179 the methods and procedures are available elsewhere (Chapelain et al., 2012; Meunier et al.,
180 2011; Meunier et al., 2012b).

181 We used a similar apparatus for both tasks. Subjects sat down a concrete block fixed
182 perpendicularly to the mesh inside the cage at about 90 cm from the ground. There was a
183 10x60 cm hole in the wire-mesh that allowed the subject to pass its arms through. Two video
184 cameras were placed 2 m in front of the cage on both sides of the experimenter with an angle
185 of 45° to the subject's midline. For the food-begging task only, subjects were additionally
186 provided with a bottle hung inside the cage, filled with diluted fruit juice to prevent them

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3 187 orienting their body towards the experimenter, particularly when she positioned laterally (see
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5 188 supplementary material).
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8 189 For the grasping task, the playing card was replaced by a food item that was randomly
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10 190 and successively placed at one of the seven positions placed at 30° from each other on a semi-
11
12 191 circle drawn on a tray fixed outside of the wire-mesh (Figure 1a). Only one item, i.e., a raisin,
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14 192 was placed at a time and the experimenter randomly used her right or left hand to place it.
15
16 193 Hand preference had been sampled by recording the hand used by subjects to grasp the raisin.
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19 194 For the food-begging task, the playing card was replaced by the experimenter herself
20
21 195 holding a piece of food in one hand. The experimenter randomly and successively positioned
22
23 196 herself at one of the positions placed at 30° from each other on a 1 m radius semi-circle drawn
24
25 197 on a textile sheet lying on the ground in front of the subject's cage (Figure 1b). The
26
27 198 experimenter approached the apparatus from one meter away, always starting from the
28
29 199 midline and heading towards the position to be tested. The experimenter randomly used her
30
31 200 right or left hand to hold the piece of food, i.e., a 2 cm piece of banana. Hand preference was
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33 201 sampled by recording the hand used by subjects to beg for food.
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38 202 Note that for the food-begging task five positions only could be reliably scored. The two
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40 203 most extreme positions that had not been tested for food-begging were therefore not
41
42 204 considered anymore in the present paper for grasping. Consequently, the five remaining
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44 205 positions (i.e., corresponding to positions 2 to 6 in Meunier et al., 2011) were: extreme left
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46 206 (LL), left (L), central (C), right (R) and extreme right (RR) from the left to the right of the
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48 207 subject (Figure 1). For each task, the order of presentation of the positions was randomized
49
50 208 beforehand and then, the same order was presented for all subjects. The trials were scored as
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52 209 valid or invalid on subsequent video analysis. A valid trial was considered when the subject
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54 210 sat in front of the setup aligned with the middle of the apparatus. Video material was coded by
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3 211 two independent observers whose one was naïve to the experimental procedure. We only kept
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5 212 the trials that have been scored as valid by the two observers for further analysis. Thus,
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7 213 subjects reached 20 to 60 valid trials per position for grasping and 8 to 35 valid trials per
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9 214 position for food-begging.
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14 15 16 216 **Data analysis**

17
18 217 The *direction* of hand preference was determined with binomial tests on the number of right
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20 218 and left responses of each individual for each task and each position to evaluate departure
21
22 219 from chance level and categorize individuals as right-, left- or ambiguously-handed
23
24 220 accordingly. Handedness Index (HI) was calculated for each task and position by subtracting
25
26 221 the number of left-handed responses from the number of right-handed responses and then
27
28 222 dividing by the total number of responses (Hopkins, 1999). HI ranged from -1.0 to +1.0 with
29
30 223 positive values indicating right-hand bias and negative values left-hand bias. The *strength* of
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32 224 hand preference was assessed thanks to the absolute value of HI (ABS_{HI}) ranging from 0 to 1.
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34 225 Subjects displaying a significant bias in any position were categorized as *lateralized* for these
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36 226 positions. Subjects with ABS_{HI} = 1 were categorized as *exclusively-handed*, the other
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38 227 subjects as *non-exclusively-handed*. When referring to individuals as right-, left-, exclusively-
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40 228 or non-exclusively-handed or as lateralized, we referred to individual's established hand
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42 229 preference in the central position for each task.
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49 230 We applied generalized linear mixed models (GLMM) to our data in order to
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51 231 investigate the influence of situational factors as a function of the task. Several models were
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53 232 fitted with the proportion of right-handed over total responses of each individual in each
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55 233 position and each task as dependent variable (see summary of models fitted as supplementary
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57 234 material). Depending on the models, fixed effects were alternately or simultaneously (i) the
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3 235 position, (ii) the task, (iii) the subject's sex and (iv) the interactions between them. The
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5 236 positive correlation amongst observations of the same individual was taken into consideration
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7 237 by adding the individual or the interaction between individual and position as random effect,
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9 238 which allowed each individual to respond differently to positions (Brown & Prescott, 2006).
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11 239 The family chosen for the dependent variable in the models was Binomial with a Logit link
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13 240 function; model selection was based on the Akaike Information Criteria (AIC; Onyango,
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15 241 2009).

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19 242 As the rationale of the QHP task was to foster subjects on to switch from their
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21 243 preferred to non-preferred hand in the contralateral hemisphere, we counted the number of
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23 244 subjects that switched hand at 30 and 60 degrees in the non-preferred contralateral hemisphere.
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25 245 As almost all subjects, but two, that switched hand did so at 30° in the contralateral
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27 246 hemisphere, we considered this angle only for statistical analysis. Non-parametric statistics
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29 247 (Siegel & Castellan, 1988) were performed on such categorical data, as well as ABSHI and
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31 248 individual's mean HI for each task and each position. All tests were performed with R 2.10.1
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33 249 software (<http://cran.r-project.org>) with level of significance set at 0.05.
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41 **RESULTS**

42 **Comparison between tasks on the basis of the direction of hand preference**

43
44 252 The baboons did not display similar patterns of direction of hand preference for food-begging
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46 253 and for grasping (i.e. best fitting model, AIC = 690.6; Table 1). There was a significant effect
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48 254 of the task on the proportion of right-handed responses (Wald Test, $z = -4.23$, $p < 0.001$), and
49
50 255 a significant interaction between task and position (Figure 2). It means that the direction of
51
52 256 hand preference varied as a function of both task and position, with baboons being more right-
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54 257 handed for food-begging than for grasping in the position LL (Wald test, $z = -9.92$, $p < 0.001$)
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3 259 and position L (Wald test, $z = -8.02$, $p < 0.001$), and more right-handed for grasping than for
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5 260 food-begging in the position R (Wald test, $z = 11.54$, $p < 0.001$) and position RR (Wald test, z
6
7 261 $= 10.83$, $p < 0.001$). Irrespective of the task, baboons were overall more right-handed than
8
9 262 left-handed for position R (Wald test, $z = 2.23$, $p = 0.026$), but not for positions RR (Wald
10
11 263 test, $z = 0.71$, $p = 0.473$), L (Wald test, $z = -0.81$, $p = 0.417$) and LL (Wald test, $z = -0.55$, $p =$
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13 264 0.583).

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17 265 Each baboon did not keep similar hand preference for food-begging and for grasping
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19 266 based on handedness index (HI). HI did not correlate between tasks for all positions
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21 267 (Spearman correlation coefficients, position LL: $r = 0.17$, $p = 0.573$; position L: $r = 0.21$, $p =$
22
23 268 0.483 ; position C: $r = 0.39$, $p = 0.184$; position RR: $r = 0.44$, $p = 0.127$), except position R
24
25 269 (Spearman correlation coefficient, $r = 0.58$, $p = 0.037$). The average HI across all positions for
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27 270 each individual did not correlate between tasks (Spearman correlation coefficient, $r = 0.34$, p
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29 271 $= 0.252$).

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34 273 **Comparison between tasks on the basis of the strength of hand preference**

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36 274 The baboons did not display similar patterns of strength of hand preference for food-begging
37
38 275 and for grasping when considering ABSHI across positions (Figure 4). The strength of hand
39
40 276 preference was affected overall by the position of the item to grasp (Friedman analysis of
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42 277 variance, $F(4) = 29.97$, $p < 0.001$) but not by the position of the experimenter whom to beg
43
44 278 from (Friedman analysis of variance, $F(4) = 1.55$, $p = 0.834$). Direct comparisons between the
45
46 279 two tasks in each position reveal that the strength of hand preference was significantly higher
47
48 280 for food-begging than for grasping in the central position (one-sample permutation test, $t =$
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50 281 2.01 , $p = 0.042$), while it was significantly lower in the position LL (one-sample permutation
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52 282 test, $t = -2.02$, $p = 0.039$). There was no significant difference in the strength of hand
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3 283 preference between the two tasks for the positions RR, R and L (one-sample permutation
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5 284 tests, $p > 0.05$ in all cases).
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9 285 This result is gaining support by the fact that the consistency of hand preference across
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11 286 positions also varied as a function of the task. Based on established hand preference in the
12
13 287 central position (Tables 2 & 3), lateralized baboons were more likely to switch from preferred
14
15 288 to non-preferred hand in the contralateral space for grasping than for food-begging,
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17 289 irrespective of the direction of laterality (Fisher exact probabilities test, $p = 0.002$).
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21 22 23 291 **Discriminatory power of direction versus strength of hand preference**

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26 292 For hand preference established in the central position (Tables 2 & 3), we found no significant
27
28 293 difference between the number of right-handed and left-handed baboons as a function of the
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30 294 task (Fisher exact probabilities test, $p = 1$), while we found more exclusively-handed baboons
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32 295 than non-exclusively handed baboons for food-begging than for grasping (Fisher exact
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34 296 probabilities test, $p = 0.002$). Eight subjects out of 13 displayed exclusive hand preference for
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36 297 food-begging whereas no subject displayed exclusive hand preference for grasping in the
37
38 298 midline.
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42 299 The strength of hand preference established in the central position for food-begging
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44 300 (i.e., as exclusively- or non-exclusively-handed baboons) allowed predicting the propensity of
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46 301 individuals to switch from preferred to non-preferred hand in the contralateral hemisphere
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48 302 (Fisher exact probabilities test, $p = 0.022$, Table 3). All the eight baboons that had exclusive
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50 303 hand preference for food-begging in the central position kept their preferred hand in the
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52 304 contralateral hemisphere, while the two lateralized baboons that had non-exclusive hand
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54 305 preference in the central position switched to non-preferred hand at 30 degrees in the
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56 306 contralateral hemisphere. However, the direction of hand preference established in the central
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3 307 position, did not allow predicting the propensity of individuals to switch from preferred to
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5 308 non-preferred hand in the contralateral hemispace for grasping (Fisher exact probabilities test,
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7 309 $p = 1$, Table 2), nor for food-begging (Fisher exact probabilities test, $p = 0.444$, Table 3).
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11 12 13 311 **DISCUSSION**

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16 312 Three main points are worth noting in the present contribution. First, the differential
17
18 313 distribution of hand biases for gesturing toward a partner and for grasping an item
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20 314 corroborates previous results obtained in baboons and other species (Meunier et al., 2012b;
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22 315 Meunier et al., this issue) and stresses that these two manual actions seem not to be processed
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24 316 similarly by the brain. Second, this investigation sheds light on the relative influence of the
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26 317 strength of hand preference in distinguishing communicative from non-communicative tasks
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28 318 in an old-world-monkey. Third, these results clearly state that situational factors have little
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30 319 influence on hand preference for gesturing in a communicative context, as reported in
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32 320 macaques (Meunier et al., this issue), chimpanzees (Hopkins & Wesley, 2002) and human
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34 321 infants (Jacquet et al., 2012).
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43 323 **Influence of the nature of the task on hand preference**

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45 324 Our examination that compared hand use for grasping and for food-begging pointed out
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47 325 differential use of the right hand according to situational factors. Baboons hardly ever used
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49 326 their right hand to grasp a raisin situated on their left side, but used more often their right hand
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51 327 for begging from an experimenter located at same positions. Conversely, subjects used their
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53 328 right hand more often to grasp a raisin situated on their right than to beg for food from an
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55 329 experimenter situated on their right. These findings indicate that the position in space largely
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3 330 influences hand use for grasping but not hand use for requesting food from a partner. This is
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5 331 supported by the fact that baboons did not keep the direction of their hand preference
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7 332 consistent between tasks. Handedness indices measured on same individuals for the two tasks
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9 333 were very poorly correlated, except for the position R. The reason why these two indices
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11 334 correlate for this position only is not straightforward. As observed in humans for different
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13 335 activities (Steenhuis, 1999), left-handed baboons may be more likely to switch hand for
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15 336 gesturing in the contralateral hemisphere than right-handed baboons, but it does not explain
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17 337 why a similar trend was not observed for the extreme right position.
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21 338 The tasks also elicited different patterns of strength of hand preference across
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23 339 positions. At the group level, the strength of hand preference for grasping a raisin in the
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25 340 extreme rightward and leftward positions was high, whereas it was low in the more central
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27 341 positions. Contrarily, the measures of strength for food-begging did not vary across positions.
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29 342 In other words, situational factors do not affect the strength of hand preference for food-
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31 343 begging while they affect the strength of hand preference for grasping. At the individual level,
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33 344 this task-related effect underlies two opposite patterns of occurrences of hand switch. In the
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35 345 contralateral hemisphere subjects kept their preferred hand for begging for food, but switched
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37 346 to non-preferred hand for grasping, irrespective of the direction of hand preference. Together,
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39 347 these findings illustrate that the more pronounced biases for communicative gestures than for
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41 348 object manipulation recorded at the population level (Meguerditchian & Vauclair, 2009;
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43 349 Meunier et al., 2011; Meunier et al., 2012b) are underpinned by stronger hand preference at
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45 350 the individual level for communicative gestures than for grasping.
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51 351 Such a differential effect of situational factors on hand preference is in line with the
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53 352 few available studies that have compared handedness for different manual tasks and/or
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55 353 species using the QHP task. For instance, it had been found that the direction of hand
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57 354 preference was strongly affected by the position of an item to grasp in mangabeys and
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3 355 Campbell's monkeys (Chapelain et al., 2012). In a comparative work, Meunier and colleagues
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5 356 (2012b; this issue) highlighted convergent distributions of hand biases in macaques, baboons
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7 357 and human infants, with patterns very similar to ours. Human infants have otherwise been
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9 358 shown to use more their right hand to point to objects than to grasp them and to be more
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11 359 willing to use their right hand in the contralateral left hemisphere for pointing than for grasping
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13 360 (Jacquet et al., 2012). These collective data, all gathered with a similar experimental set-up
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15 361 (the QHP task), support the hypothesis that functional asymmetries for gesturing in a
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17 362 communicative context and for grasping may develop quite independently in humans and
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19 363 non-human primates, perhaps due to differential constraints on their expression.
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25 26 27 365 **Significance of the direction and the strength of hand preference**

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29 366 Both right-handed and left-handed baboons for grasping switched from preferred to non-
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31 367 preferred hand in the contralateral hemisphere, while both right-handed and left-handed
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33 368 baboons for begging kept their preferred hand in the contralateral hemisphere. This suggests
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35 369 that the direction of hand preference does not discriminate between the tasks, at least in our
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37 370 sample. Our data show however that the strength of hand preference in the midline may be a
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39 371 good predictor of the consistency of hand preference across positions, at least for food-
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41 372 begging. Three results are worth noting. First, the strength of baboons' hand preference was
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43 373 higher for food-begging than for grasping in the midline. Second, none of the subjects had
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45 374 exclusive preferences for one hand in the grasping task, whereas almost all of them had
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47 375 exclusive preferences for one hand in the food-begging task. Third, the baboons with
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49 376 established exclusive preferences for food-begging in the midline were less likely to switch
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51 377 hand across positions than the baboons with established non-exclusive preferences. Therefore,
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3 378 baboons' hand preference seems to differ between tasks on the basis of the strength of hand
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5 379 preference, rather than the direction.
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8 These results are gaining support from neuroimaging evidence in humans of a
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10 381 continuous relation between the strength of handedness and functional activation of the motor
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12 382 cortex (Dassonville et al., 1997). These authors found both right and left-handers having
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14 383 similar contralateral activation of the motor cortex concomitant to the use of the dominant
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16 384 hand. However, the strength of hand preference correlated negatively with the cerebral
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18 385 activation ipsilateral to the dominant hand. It means that activation in the motor cortex is
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20 386 more lateralized with increasing strength of handedness in both right-handers and left-
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22 387 handers. Additional research is needed to confirm whether the strength of hand preference
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24 388 might have similar neurofunctional significance in non-human primates.
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29 389 Although human infants (Cochet & Vauclair, 2010; Esseily et al., 2011; Jacquet et al.,
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31 390 2012; Vauclair & Imbault, 2009), like chimpanzees and baboons (Hopkins et al., 2005;
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33 391 Meguerditchian et al., 2010; Meguerditchian & Vauclair, 2009), have been reported to be
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35 392 more right-handed for gesturing than for manipulating objects, it is worth noting that no
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37 393 population-level bias emerged in the present data. It is possible that our sample size was too
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39 394 small to detect any population-level bias for food-begging. As proposed above, it could
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41 395 alternately be that the strength of hand preference for communicative gestures may be a better
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43 396 marker of hemispheric specialization than the direction of hand preference for the use of
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45 397 learnt gestures in baboons. As the direction of hand preference may be partly determined by
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47 398 epigenetic constraints (Schaafsma, Riedstra, Pfannkuche, Bouma, & Groothuis, 2009;
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49 399 Vallortigara et al., 1999), it is possible that brain specialization for these gestures may have
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51 400 been constrained by individual learning history, leading to differential lateralization at the
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53 401 population level. It would explain why the population right-sided bias was found lower for
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3 402 food-begging than for typical gestures in baboons, though both indices correlate nevertheless
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5 403 (Meguerditchian & Vauclair, 2009).
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10 405 **Conclusion**

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14 406 Baboons show stronger hand preference for communicative gestures than for
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16 407 manipulative action irrespective of the direction of laterality. Hand preference for gesturing is
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18 408 little influenced by situational factors and this consistency can be predicted by the strength of
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20 409 hand preference in the midline. Based on these findings, we suggest that behavioral
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22 410 asymmetries for gestural communication and for manipulative actions in baboons rely on
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24 411 independent brain processes that differ with the strength of hand preference, possibly
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26 412 reflecting differential degrees of lateralization in brain activation. Additional research is
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28 413 needed to evaluate whether the apparent behavioral continuity that exists between baboons,
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30 414 chimpanzees and humans with respect to manual asymmetries has neurological
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32 415 underpinnings.
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40 417 **NOTES**

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52
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3 571 Table 1. Summary of models fitted with the proportion of right-handed responses as
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5 572 dependent variable. Interactions between two effects are represented by colons. Bold
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7 573 characters indicate the best fitting model, which significantly differed from the null model
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10 574 fitted without fixed effects (Chi-square tests for the log-likelihood ratios, $p < 0.001$).

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Dependent variable	Model	Fixed effects	Random effects	AIC
Proportion of right-handed responses				
	1	none	individual	4292
	2	task	individual	4283
	3	task	individual:position	1676
	4	position	individual	1717
	5	position	individual:position	1659
	6	task, position, task:position	individual	820
	7	task, position, task:position	individual:position	691
	8	task, sex, position, task:sex	individual	1624
	9	task, sex, position, task:sex	individual:position	1690

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578 Table 2. Raw data for each individual tested in the grasping task

Individual	Sex	LL				L				C				R				RR			
		LH	RH	B test	HI	LH	RH	B test	HI	LH	RH	B test	HI	LH	RH	B test	HI	LH	RH	B test	HI
Anelka	M	50	10	<0.001	-0.67	36	24	0.155	-0.20	19	41	0.006	0.37	1	59	<0.001	0.97	0	60	<0.001	1.00
Katy	F	60	0	<0.001	-1.00	53	7	<0.001	-0.77	17	43	0.001	0.43	2	58	<0.001	0.93	1	59	<0.001	0.97
Marius	M	60	0	<0.001	-1.00	60	0	<0.001	-1.00	29	31	0.897	0.03	1	59	<0.001	0.97	0	60	<0.001	1.00
Momo	M	60	0	<0.001	-1.00	60	0	<0.001	-1.00	54	6	<0.001	-0.80	0	60	<0.001	1.00	0	60	<0.001	1.00
Oscar	M	59	1	<0.001	-0.97	60	0	<0.001	-1.00	50	10	<0.001	-0.67	1	59	<0.001	0.97	0	60	<0.001	1.00
Perfide	F	60	0	<0.001	-1.00	57	3	<0.001	-0.90	37	23	0.092	-0.23	12	48	<0.001	0.60	0	60	<0.001	1.00
Prise	F	55	5	<0.001	-0.83	46	14	<0.001	-0.53	28	32	0.699	0.07	4	56	<0.001	0.87	4	56	<0.001	0.87
Rodolphe	M	60	0	<0.001	-1.00	60	0	<0.001	-1.00	57	3	<0.001	-0.90	5	55	<0.001	0.83	0	60	<0.001	1.00
Sestarde	F	18	2	<0.001	-0.80	9	11	0.412	0.10	2	18	<0.001	0.80	0	20	<0.001	1.00	0	20	<0.001	1.00
Toti	M	60	0	<0.001	-1.00	60	0	<0.001	-1.00	37	23	0.092	-0.23	1	59	<0.001	0.97	0	60	<0.001	1.00
Tulie	F	60	0	<0.001	-1.00	57	3	<0.001	-0.90	38	22	0.052	-0.27	10	50	<0.001	0.67	1	59	<0.001	0.97
Ubu	M	60	0	<0.001	-1.00	60	0	<0.001	-1.00	49	11	<0.001	-0.63	3	57	<0.001	0.90	2	58	<0.001	0.93
Uranus	M	60	0	<0.001	-1.00	51	9	<0.001	-0.70	32	28	0.698	-0.07	2	58	<0.001	0.93	0	60	<0.001	1.00
Handedness category																					
LH-RH		13	0			11	0			4	3			0	13			0	13		
LAT				13				11				7				13				13	
EXC					9				6				0				2				9

580 Sex: *M* male, *F* female. Main columns: *LH* number of left-handed responses, *RH* number of right-handed responses, *B test* p-value of the
581 binomial test performed on the number of right-handed and left-handed responses (when the test is significant the higher value is in bold), *HI*
582 handedness index (bold characters indicate exclusive hand preference). Handedness category: *LH-RH* number of left-handed and right-handed
583 baboons, *LAT* number of lateralized baboons irrespective of the direction of laterality, *EXC* number of exclusive right-handed and left-handed
584 baboons ($HI = 1$ or $HI = -1$).

585 Table 3. Raw data for each individual tested in the food-begging task

Individual	Sex	LL				L				C				R				RR			
		LH	RH	B test	HI	LH	RH	B test	HI	LH	RH	B test	HI	LH	RH	B test	HI	LH	RH	B test	HI
Anelka	M	0	17	<0.001	1.00	0	18	<0.001	1.00	0	20	<0.001	1.00	0	20	<0.001	1.00	0	20	<0.001	1.00
Katy	F	0	18	<0.001	1.00	1	19	<0.001	0.90	0	20	<0.001	1.00	0	19	<0.001	1.00	0	14	<0.001	1.00
Marius	M	0	17	<0.001	1.00	0	19	<0.001	1.00	0	20	<0.001	1.00	0	20	<0.001	1.00	0	16	<0.001	1.00
Momo	M	5	14	0.032	0.47	2	17	<0.001	0.79	0	19	<0.001	1.00	0	20	<0.001	1.00	0	15	<0.001	1.00
Oscar	M	11	4	0.059	-0.47	16	2	0.001	-0.78	13	4	0.025	-0.53	11	7	0.240	-0.22	14	1	<0.001	-0.87
Perfide	F	19	1	<0.001	-0.90	14	5	0.032	-0.47	10	7	0.315	-0.18	5	10	0.151	0.33	4	7	0.274	0.27
Prise	F	19	0	<0.001	-1.00	21	0	<0.001	-1.00	21	0	<0.001	-1.00	21	0	<0.001	-1.00	16	0	<0.001	-1.00
Rodolphe	M	11	4	0.059	-0.47	16	4	0.015	-0.60	15	3	0.004	-0.67	3	17	0.001	0.70	4	12	0.038	0.50
Sestarde	F	1	9	0.011	0.80	0	14	<0.001	1.00	0	22	<0.001	1.00	0	20	<0.001	1.00	0	10	0.001	1.00
Toti	M	3	7	0.172	0.40	9	13	0.262	0.18	4	10	0.090	0.43	0	20	<0.001	1.00	11	8	0.324	-0.16
Tulie	F	9	2	0.033	-0.64	7	11	0.240	0.22	13	17	0.292	0.13	11	13	0.419	0.08	7	2	0.090	-0.56
Ubu	M	12	4	0.038	-0.50	21	0	<0.001	-1.00	21	0	<0.001	-1.00	18	2	<0.001	-0.80	19	0	<0.001	-1.00
Uranus	M	14	0	<0.001	-1.00	19	0	<0.001	-1.00	13	0	<0.001	-1.00	12	0	<0.001	-1.00	8	0	0.004	-1.00
Handedness category																					
LH-RH		4 5		6 5		5 5		3 7		3 6											
LAT				9		11		10		10		9									
EXC				5		6		8		8		8									

587 Sex: *M* male, *F* female. Main columns: *LH* number of left-handed responses, *RH* number of right-handed responses, *B test* p-value of the
 588 binomial test performed on the number of right-handed and left-handed responses (when the test is significant the higher value is in bold), *HI*
 589 handedness index (bold characters indicate exclusive hand preference). Handedness category: *LH-RH* number of left-handed and right-handed
 590 baboons, *LAT* number of lateralized baboons irrespective of the direction of laterality, *EXC* number of exclusive right-handed and left-handed
 591 baboons (HI = 1 or HI = -1).

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3 592 Captions
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9 594 Figure 1. Experimental set-up of (a) the grasping task and (b) the food-begging task
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15 596 Figure 2. Mean percentages (\pm SEM) of right-hand use for each task in the five positions. LL:

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17 597 extreme left, L: left, C: central, R: right, RR: extreme right. Significant interactions between

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19 598 tasks and positions are noted by asterisks, Wald tests *** $p < 0.001$.
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25 600 Figure 3. Mean Handedness Indices (\pm SEM) for each task in the five positions. LL: extreme

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27 601 left, L: left, C: central, R: right, RR: extreme right. Significant correlations of individual HI

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29 602 values between tasks are noted by an asterisk, Spearman correlation coefficient * $p < 0.05$.
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36 604 Figure 4. Mean absolute values of HI (\pm SEM) for each task in the five positions. LL: extreme

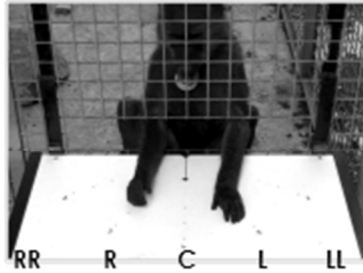
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38 605 left, L: left, C: central, R: right, RR: extreme right. Asterisks indicate significant variations of

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40 606 ABSHI across positions (Friedman analysis of variance *** $p < 0.001$) and between tasks

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42 607 (one-sample permutation test, (a) $p < 0.05$).
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(a) Grasping task



(b) Food-begging task

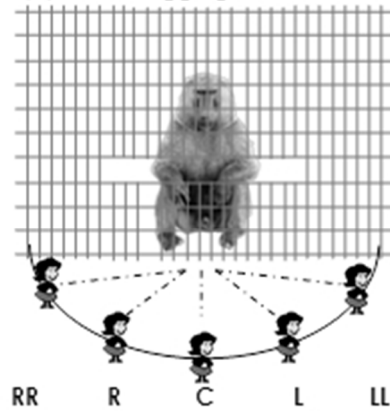


Figure 1
21x33mm (300 x 300 DPI)

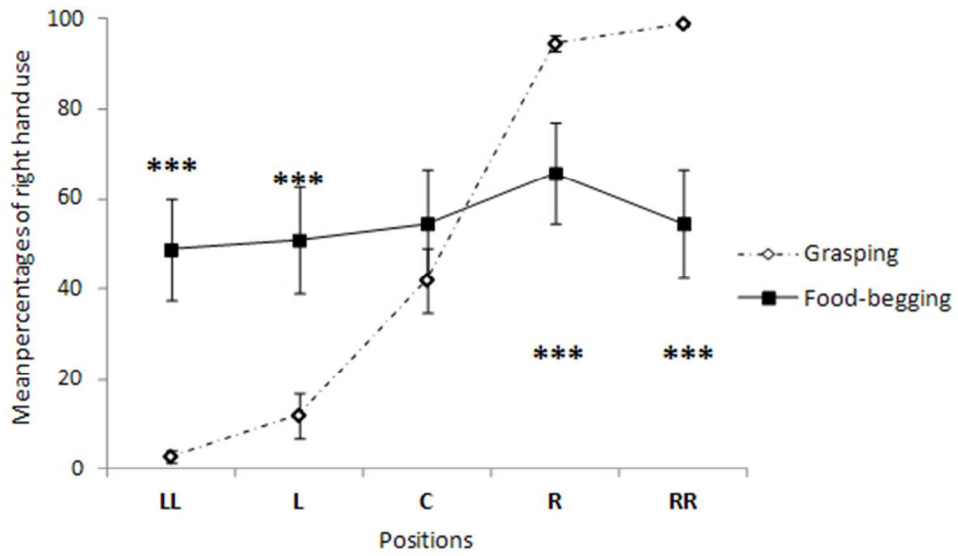


Figure 2
48x28mm (300 x 300 DPI)

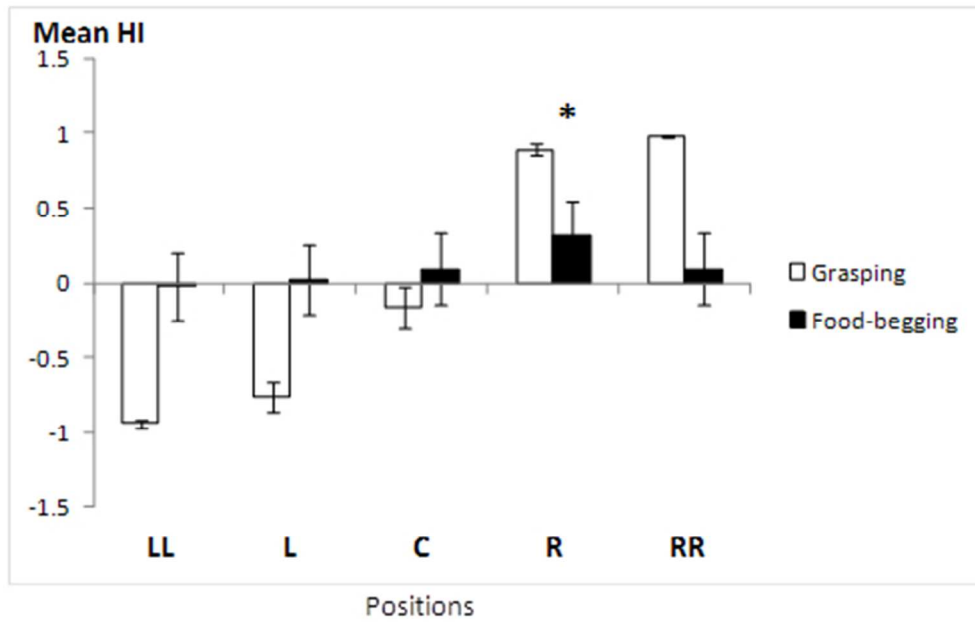


Figure 3
41x27mm (300 x 300 DPI)

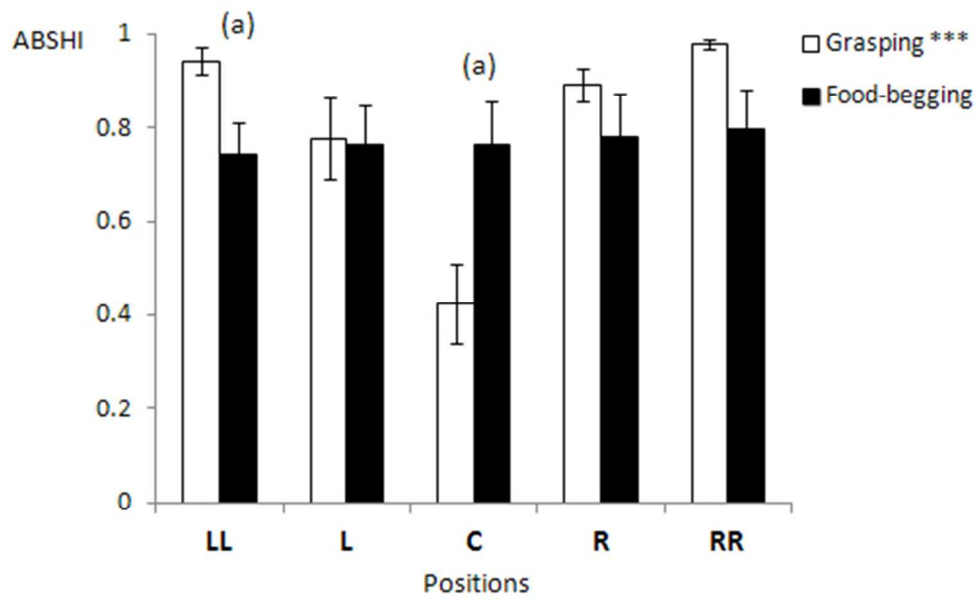


Figure 4. Mean absolute values of HI (\pm SEM) for each task in the five positions. LL: extreme left, L: left, C: central, R: right, RR: extreme right. Asterisks indicate significant variations of ABSHI across positions (Friedman analysis of variance *** $p < 0.001$) and between tasks (one-sample permutation test, (a) $p < 0.05$).

181x112mm (72 x 72 DPI)