How zoo-housed chimpanzees *(Pan troglodytes)* target gestural communication within and between age groups

Como os chimpanzés *(Pan troglodytes)* em cativeiro direcionam a comunicação gestual de acordo com a faixa etária

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Abstract Gestural communication among nonhuman primates evolved as a response to their complex social environment. In this scope, males and females, adults and non-adults employ different gestures, probably due to their distinct social roles. In this study, a within and between age group analysis of the gestures produced in different contexts was carried out. For this purpose, a community of 16 captive chimpanzees (*Pan troglodytes*) was observed during a 3-month period. Initially, data were collected through *ad libitum* sampling in order to identify their gestural repertoire. Subsequently, focal sampling was used to identify who gesticulated with whom and in what context. Overall, the results showed that juvenile chimpanzees tend to direct their gestures to different age groups according to the context; more

Resumo A comunicação gestual nos primatas não-humanos evoluiu como uma resposta à complexidade social. Neste âmbito, machos e fêmeas tendem a usar diferentes tipos de gestos, provavelmente consequências das diferentes pressões sociais a que estão sujeitos. Neste estudo, realizou-se uma análise intra e interclasses etárias dos gestos produzidos em contextos distintos. Para tal, durante um período de 3 meses, observou-se uma colónia de chimpanzés (*Pan troglodytes*) em cativeiro. Inicialmente, os dados foram recolhidos através de uma amostragem *ad libitum*, para a elaboração do catálogo gestual. Posteriormente, a amostragem focal determinou quem gesticula com quem, e em que contexto. De um modo geral, os resultados mostraram que, em alguns casos, os chimpanzés juvenis tendem a gesticular para outros chimpanzés de

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specifically, juvenile chimpanzees frequently gesticulate within their age group in play contexts, and with older individuals in locomotion and affiliation contexts. Based on this, a certain degree of flexibility in juvenile chimpanzees gestural signalling is suggested, to the extent that they rather direct their gestural signs to chimpanzees of the same age group with the aim of involving themselves in the activities' context in which the gestural sign is produced.

Keywords: Gestures; chimpanzee; flexibility; play.

classes etárias semelhantes, tendo em conta o contexto; mais especificamente, estes direcionam gestos em contexto de brincadeira para outros chimpanzés juvenis, e comunicam com chimpanzés adultos em contexto de locomoção e afiliação. Com base nestas evidências, sugerimos a existência de um certo grau de flexibilidade na capacidade de comunicar por gestos dos chimpanzés juvenis, uma vez que estes tendem a direcionar os seus gestos para recetores de classes etárias aparentemente mais adequados, tendo em conta o contexto do sinal gestual.

Palavras-chave: Gestos; chimpanzé; flexibilidade; brincadeira.

Introduction

Over the past decades, research on gestural communication in nonhuman primates has become a rather appealing area due to the phylogenetic proximity between humans and other primates. Evidences on shared communication characteristics in nonhuman and human primates have emerged, regarding flexibility, intention, and learning opportunity (Liebal and Call, 2012), cultural variation and mutual understanding (e.g. chimpanzees and bonobos: Pollick and de Waal, 2007; bonobos: Graham et al., 2017) or even neuronal mechanisms underlying language production in humans and gestural production in nonhuman primates (e.g. southern pig-tailed macaques: Rizzolatti et al., 1996; chimpanzees, bonobos, and western gorilla: Cantalupo and Hopkins, 2001).

Besides the hypothesized association with the human language, gestural communication used by nonhuman primates plays a fundamental role in the transmission of information among individuals. Therefore, its study allows for a deeper understanding of how primates interact with conspecifics, and how they deal with a vast group of challenges, mainly of a social nature (Liebal et al., 2013). In fact, according to some authors (Maestripieri, 1999; Call and Tomasello, 2007), the gestural communication of nonhuman primates is influenced by the complexity of their social environment. That is, the higher the social complexity of a particular species, the greater will be the complexity and variety of its gestural reper-

toire. Taking chimpanzees as an example, their gestural repertoire is one of the most varied (i.e., in terms of the number of different gestures produced) and complex (in meaning and morphology), reflecting an adaptation to the innumerable demands of their social systems (Roberts et al., 2012a), which comprises formation of coalitions (Gilby et al., 2012), conflict resolution (Fuentes et al., 2002), and mating strategies (Duffy et al., 2007).

Lately, new data supporting the hypothesis that social complexity affects gestural communication of nonhuman primates arose. Scott (2013) found differences in the use of gestural signs by opposite sex chimpanzees when subjected to social pressures. In intersexual interactions, males resorted more often to agonistic gestural signs, as a control attitude toward females, while females gesticulated more frequently in affiliation contexts, to avoid retaliation and aggressive behaviour of males. On the other hand, Roberts and Roberts (2015) found that, in mating circumstances and also for chimpanzees, there was an adaptation in the sensory modality of subordinate males' gestural communication in the absence or presence of alpha males. In the presence of alpha males, subtle tactile gestural or visual signs were used to address females, whereas in their absence, acoustic gestural signs were preferentially used to get females attention.

Gestural communication also differs according to the nonhuman primate ontogeny. In this sense, Tomasello et al. (1989) stressed that some gestural signs used by juvenile chimpanzees were not adopted by adults and vice-versa; and that other gestural signs were used by individuals of distinct age groups, though with different purposes. For example, the *arm raise* (an individual raises his arm, as if to hit, and then charges other) gestural sign is made by juvenile chimpanzees only to engage in play activities (Tomasello et al., 1985), and the *throwback head* is used both by young siamangs (*Symphalangus syndactylus*) to play and by adults to start copulation (Liebal et al., 2004a).

Additionally, Call and Tomasello (2007) also suggested that, in chimpanzees, gestural repertoire tends to increase during infancy and youth, but it decreases once the individual becomes an adult. Hobaiter and Byrne (2011a) proposed that the reduction of gestural repertoire in adulthood may be explained by a higher capacity of understanding gestural signs, restricting communication to more effective gestures, in a phenomenon called *repertoire tunning*. On the other hand, younger individuals are less experienced and thus incapable of understanding gestures efficacy; accordingly, they use a greater number of signs that constitute a larger gestural repertoire, although with a smaller efficiency in comparison to adults. Call and Tomasello (2007) and Liebal et al. (2013) added that younger chimpanzees are highly involved in play activities, which require a higher flux of communi-

cation. Actually, according to Frohlich et al. (2016a; 2017), playing is a decisive element in the acquisition of gestural signs in an early phase of the individual's ontogeny. They state that playing provides socialization opportunities as well as the necessary experiences to stimulate the development of a complete gestural repertoire — flexible and intentional — and to improve, simultaneously, the capacity of using proper gestural signs for the accomplishment of a specific goal.

Although individuals in different ontogeny stages also suffer distinct social pressures (Hamada and Udono, 2006; Watts and Pusey, 2002), very little is known about the pattern of gestural communication in individuals of different age groups. Liebal and Call (2012) underlined this idea when alerting for the scarcity of published data on differences in gestural signs use among independent groups of the same community of non-human primates. As mentioned above, some evidences about these differences — e.g., between males and females — have been reported (e.g. Scott, 2013; Roberts and Roberts, 2015). Nevertheless, on what concerns age groups, research has been mostly focused on the effect of social complexity in the use of gestural signs, as well as on the development of gestural repertoire throughout the ontogeny of individuals, namely on how signs are acquired in the first years of life.

Endeavouring to overcome this lacuna, the present study aims to analyse how individuals from a chimpanzee (*Pan troglodytes*) captive colony produce gestural signs between and within distinct age groups in different contexts. For this purpose, we hypothesized that the context of gesture communication would differ between and within age groups interactions, for both juvenile and adult chimpanzees, and match their social priorities. To this end, we predicted that, on the one hand, adult chimpanzees would be more likely to employ sex and grooming within age group interactions, and, on the other hand, juvenile chimpanzees would be more likely to use play gestures within age group interactions, but locomotion, food and affiliation gestures between age group interactions.

Methods

Subjects

The colony studied was composed by 7 male and 9 female chimpanzees, from which 5 were juveniles (aged between 4 and 7 years old) and 11 were adults (aged between 13 and 30 years old), all living at the Lisbon Zoo (Portugal). Neither kinship, nor the dominance rank in the colony were known. During the day, chimpanzees had unrestricted access to the outdoor captivity (1220 m^2, approximately), composed by a grass field delimited by a stream and made up of tree trunks, a wooden climbing facility, ropes, blankets and stairs leading to the indoor captivity (470 m^2, approximately) that also contained a wooden climbing facility and where chimpanzees stayed

overnight and during heavy rain days, and cleaning and feeding operations (every day between 9 am and 10 am).

Procedures

Data was collected by the first author (MO) of this study between 10 am and 4 pm, during a 3-month period, from December 2nd, 2015 to February 23rd, 2016.

Data Collection

With the aim of recording interactions during which chimpanzees displayed gestural signs to communicate with each other, *ad libitum* sampling was adopted in a first phase, followed by a focal sampling (Altmann, 1974; Martin and Bateson, 1993), each one serving a different purpose. *Ad libitum* sampling allowed the elaboration of the gestural repertoire. In order to guarantee the accuracy of the data collected, the observation in this phase was based on the protocol described in table 1.

At the end of the first phase, the gestural repertoire (table 2) was produced according to the following procedures: (1) morphological description of gestural signs [analogous to Hobaiter and Byrne (2011b), or Roberts et al. (2014)] always

Table 1. *Ad libitum* observation sampling protocol.

Item	Operational Definition	Criteria
Gesture	The communication signal produced by the expressive movements of the head, limbs, or other body parts and directed to a recipient with the purpose of influencing their behaviour in a specific way (Liebal et al., 2004b; Roberts et al., 2014).	(1) Gesture production towards an individual (Liebal et al., 2013; Roberts et al., 2012b). (2) Gesture production in a way that ensures the recipient can visualize it. Otherwise, the signaller manipulates the recipient's attention via auditory and/or tactile signs or by moving forward to the recipient before gesture production (Liebal et al., 2013; Roberts et al., 2012b). (3) Persistence or production of additional gestures in response to an unsuccessful communication attempt (Liebal et al., 2013; Roberts et al., 2012b).
Apparently Satisfactory Outcome	An outcome that ends the signaller's intention to communicate, if the purpose of the gesture was satisfied (Hobaiter and Byrne, 2014).	Based on the observation of the impact of the recipient's behavioural response towards the signaller, according to the functional context of the interaction (Roberts et al., 2012b; Moore, 2014; Cartmill and Byrne, 2010).

beginning the designation attributed to each gestural sign by a verb in the infinitive form, as proposed by Nishida et al. (2010); (2) allocation of the functional context to each gesture; and (3) correspondence between each gestural sign and the respective and apparently satisfactory outcome. The functional context of each gesture was also determined based on its apparently satisfactory outcome (Tomasello et al., 1997) and in line with the definitions proposed by Pollick and de Wall (2007), namely for play, affiliative, agonistic, feed, locomotion, sexual and groom contexts. As an example of these procedures, the *direct upper limb* gestural sign is morphologically described by the stretch of one of the upper limbs towards the receiver or another location, and it is performed by a chimpanzee who looks to move to another location, in the context of locomotion (see table 2).

It should be noted that intra- or inter-observer tests were not carried out. Not only the geomorphological characteristics of the chimpanzees' enclosure were not suitable for video equipment installation, but also the viewing angle did not allow for an observation spectrum capable of covering the entire space. Hence, the observer was forced to change position on several occasions, during date collection. Plus, no gestural repertoires on the population under study were available. Alternatively, in an attempt at minimizing this handicap, the gestural repertoire obtained through *ad libitum* sampling was compared with the ones gathered by Roberts et al. (2014), Scott (2013), McCarthy et al. (2013), and Hobaiter and Byrne (2011b). From the 30 gestural signs identified, only one did not have a partial or total correspondence with the morphological descriptions presented by the above mentioned authors.

Subsequently, focal samplings were collected. During each 15 minutes session, a focal chimpanzee was followed and observed as a signaller (the chimpanzee who produces an intentional gesture, Roberts et al. 2012a) or a recipient (the chimpanzee to whom the gesture was directed, as determined through the orientation of the head and the body of the signaller, during or immediately after the gesture production, Roberts et al. 2012a) of a gestural sign. In each interaction, along with the gestural signs, the identification of the recipient (if the focal chimpanzee was the signaller) or the signaller (if the focal chimpanzee was the recipient) was registered. The behavioural response of the recipient was also registered (present or absent). The focal sampling sessions were not randomized. The selection of the focal chimpanzee was based on the criterion of the number of focal sessions already done to ensure that all subjects had the same number of focal sessions and identical observation times, as suggested by Martin and Bateson (1993).

The gestures previously identified and described at the gestural repertoire

Table 2. Gestural repertoire with all gestures observed during *ad libitum* sampling for the chimpanzee colony, living at the Lisbon Zoo (Jardim Zoológico de Lisboa). This repertoire encompasses the gesture designation, its morphological description, functional context and apparently satisfied outcome, and the age group who produced the gesture.

Gesture	Morphological Description	Performed by	Context	Apparently Satisfied Outcome
Bite	Bite smoothly into a random part of the receiver's body.	Juvenile and adults	Play	Get engaged in play
Pull limbs	Grasp the upper or the lower limb of the receiver with one hand and then pull that limb vigorously.	Juvenile and adults	Locomotion	Move to another location
Hit the back	Slap consecutively on the receiver's back, with one of the following configurations: only with one hand, with both hands simultaneously or alternately.	Juvenile and adults	Play	Get engaged in play
Push	Put one hand on a random part of the receiver body and push moderately smooth.	Juvenile and adults	Locomotion	Put away receiver
Hit the ground	Slap consecutively the floor producing an audible contact, with one of the following configurations: with both hands simultaneously or with both hands but alternately.	Juvenile	Play	Draw attention and/or get engaged in play
Grasp limb	Grasp vigorously, with one hand, the upper or the lower limb of the receiver.	Juvenile and adults	Locomotion	Immobilize receiver
Throw soil	"Sweep" vigorously the ground with both hands in a way that dirt debris is thrown towards the receiver.	Juvenile and adults	Locomotion /Play	Move to another location; Draw attention and/or get engaged in play
Fling upper limbs	Get in bipedal posture, walk towards the receiver and then flex the upper limbs, preceded by its extension, projecting the upper limbs against the receiver's body.	Juvenile	Play	Get engaged in play
Hit the head	Slap smoothly on the head of the receiver, with only one hand.	Juvenile and adults	Play	Draw attention and/or get engaged play
Direct upper limb	Stretch one of the upperlimbs towards the receiver or another location.	Juvenile and adults	Locomotion	Move to another location

Table 2. (cont.)

Gesture	Morphological Description	Performed by	Context	Apparently Satisfied Outcome
Shake rope bed	Get in a bipedal posture with the hands grasping the wood trunk that holds the ropes, and wag the rope bed with vertical movements of the feet and look to the receiver who is lying down or sitting under the signaller.	Juvenile	Play	Get engaged in play
Shake rope	Take the rope of the wood stairs leading to the inner captivity, with both hands and shake it sideway to touch the receiver, who is sitting or lying on that stairs.	Juvenile	Play	Get engaged in play
Show genitals	Move towards the receiver, lie down near with lower limbs flexed and opened, keep the feet on the ground and display the genitals.	Adults	Sex	Initiate copulation
Shake wood trunk	Take one of the wood trunks of the stairs leading to the inner captivity, with both hands and shake it in a way to disturb the receiver, who is sitting or lying on that trunk.	Juvenile and adults	Play	Get engaged in play
Raise upper limb	Get in a bipedal posture and lift one of the upperlimbs in the vertical direction, accompanied by small crunches of the lower limbs.	Juvenile	Play	Get engaged in play
Put on the back	Place both hands on the upper back of the recipient that is in slow walking.	Juvenile	Locomotion	Move to another location
Hit the wood trunk	Clap on one of the wood trunks of the stairs leading to the inner captivity, with both hands simultaneously, producing an audible contact.	Juvenile	Play	Draw attention and/or get engaged in play
Show lower limb	Hang, with both hands, on one of the suspended ropes, make circular movements around the wood trunks and move one of the lower limbs towards to the receiver's head, whenever the sender passes over the latter, who is sitting or lying under the rope.	Juvenile	Play	Get engaged in play
Rub penis	Get in a bipedal posture, with one hand grasp the suspended rope while the other massage and rub the genital area with the erected penis.	Adults	Sex	Initiate copulation

Table 2. (cont.)

Gesture	Morphological Description	Performed by	Context	Apparently Satisfied Outcome
Lift upper limbs	Stretch both upper limbs, in a front and slightly shoulder level way, toward the receiver.	Juvenile	Affiliative	Get affection
Direct lips	Approach the face towards the receiver's face, with the lips projected in a way to form a small extension.	Juvenile and adults	Affiliative	Get affection
Provide upper limb	Stretch one of the upperlimbs toward the receiver, with the palm of the hand facing up.	Juvenile	Locomotion	Move to another location
Run upside down	Run toward the receiver, with the head and shoulders bent toward the ground.	Juvenile	Play	Get engaged in play
Show back	Move toward the receiver and then sit with the back facing the receiver.	Juvenile and adults	Groom	Get groomed
Touch the head	Touch smoothly with the tip of the foot on the receiver's head (the signaller is suspended on the rope and above the receiver).	Juvenile	Play	Get engaged in play
Get up	Get in a bipedal posture, projecting the body vertically through the extension of the lower limbs and only one upper limb towards one of the receiver's lower limbs, who is an upper position suspended in the rope.	Juvenile and adults	Locomotion	Immobilize receiver
Show rear	Crouch down near the receiver and stretch the lower limbs to direct the buttock to receiver's facial area.	Juvenile and adults	Groom	Get groomed
Swag	Get in a bipedal posture and walk slowly toward the receiver by swinging the body alternately to either sides.	Juvenile and adults	Affiliative/ Play	Get submission/ Get engaged in play
Show upper limb	Stretch the upperlimb at eye level of the receiver.	Juvenile and adults	Groom	Get groomed
Put on the shoulder	Extend one of the upper limbs and place a hand on the receiver's shoulder.	Juvenile and adults	Affiliative	Get affection

were converted into 3-letter codes [analogously to Liebal et al. (2004b) and Roberts et al. (2014)] in order to avoid redundancies and to improve data collection efficiency (Lehner, 1996). For example, the *direct upper limb* was coded into *dul*.

Data Analysis

Gesture Rate

Only data collected during the focal sampling were considered for calculation of the gesture rate. This rate (*g*) was calculated for each individual in the sample, by dividing the total number of gestural signs produced under focal sampling (*n*) by the total number of hours of observation (*t*). Regarding the total number of hours of observation, each chimpanzee was observed during 12 focal sessions. In most chimpanzees, 12 focal sessions are equivalent of three hours of observation. However, in some cases, during the observation session, the focal chimpanzee temporarily was no longer in sight. This out of sight amount of time was not accounted. That is, the observation time, in hours, ranges from 2.75 hours to 3 hours — i.e., all chimpanzees had the same number of focal sessions, but not all had the same observation time.

The gesture rate was measure for the situational contexts described in table 3.

Besides gesture rate analysis, the behavioural response of the recipients was also analysed. For this responsiveness rate (r), the total number of interactions with recipient's behavioural response (n^1) was divided by the total number of interactions (n^2) in three situational contexts: overall interactions, overall intra-age group interactions (juvenile-juvenile, adult-adult), and overall inter-age group interactions (juvenile-adult, adult-juvenile).

Statistical Analysis

Collected data was statistically processed and analysed using *IBM SPSS Statistics 23*. The gesture rate for each chimpanzee and for each situational context was first measured, as described above. Then, and given the small sample size (N=16), the Shapiro-Wilk test was run and all variables in study were not normally distributed. Subsequently, the Mann-Whitney test was used to compare the gesture rate between juvenile and adult chimpanzees in all interactions (overall and for each functional context), in same age group interactions (overall and for each functional context) and in different age group interactions (overall and for each functional context). The same procedure was used to compare the responsiveness rate in overall, intra-age group and inter-age group interactions. Finally, the Wilcoxon test was used to compare the gesture rate between same age groups and different age groups interactions (overall and for each functional context).

Table 3. Situational contexts in which gesture rate was measured and its requirements.

Situational context	Functional context	Recipient
All interactions (overall)	All	All
All intra-age group interactions (overall)	All	Only same age group recipients
All inter-age group interactions (overall)	All	Only different age group recipients
All playing interactions	Only play	All
All intra-age group playing interactions	Only play	Only same age group recipients
All inter-age group playing interactions	Only play	Only different age group recipients
All feeding interactions	Only feed	All
All intra-age group feeding interactions	Only feed	Only same age group recipients
All inter-age group feeding interactions	Only feed	Only different age group recipients
All affiliative interactions	Only affiliative	All
All intra-age group affiliative interactions	Only affiliative	Only same age group recipients
All inter-age group affiliative interactions	Only affiliative	Only different age group recipients
All agonistic interactions	Only agonistic	All
All intra-age group agonistic interactions	Only agonistic	Only same age group recipients
All inter-age group agonistic interactions	Only agonistic	Only different age group recipients
All sex interactions	Only sex	All
All intra-age group sex interactions	Only sex	Only same age group recipients
All inter-age group sex interactions	Only sex	Only different age group recipients
All locomotion interactions	Only locomotion	All
All intra-age group locomotion interactions	Only locomotion	Only same age group recipients
All inter-age group locomotion interactions	Only locomotion	Only different age group recipients
All grooming interactions	Only groom	All
All intra-age group grooming interactions	Only groom	Only same age group recipients
All inter-age group grooming interactions	Only groom	Only different age group recipients

Results

First of all, no gestures were found in either feeding or agonistic contexts. Overall, almost 75% of the gestures observed were produced by juvenile chimpanzees. Table 4 briefly summarizes the percentage of gestures produced in each functional context. On the one hand, from an age group view, play and locomotion were the contexts in which most gestures were displayed by juvenile and adult chimpanzees, respectively. On the other hand, from a context view, play and locomotion, and sex and groom were the contexts in which there was a greater predominance of gestures employed by juvenile and adult chimpanzees, respectively.

All Interactions

When all individuals are considered, significant differences were found for the global gestures rate (U=0.000; z=-3.162; $p \leq 0.001$) as well as for the gestures rates in the following contexts: play (U=0.000; z=-3.433; $p \leq 0.001$) and locomotion (U=2.500; z=-2.847; p=0.002). As shown in figure 1, in both cases, juvenile chimpanzees presented considerably higher gestures rates compared to adults. For the remaining contexts, no significant differences were observed (affiliation: U=10.000; z=-2.036; p=0.052; grooming: U=23.500; z=-0.481; p=0.661; and sexual: U=17.500; z=-1.490; p=0.267).

Within Age Group Interactions

When considering only interactions within the same age group (juvenile-juvenile, adult-adult), significant differences were obtained between the individuals' global gesture rates (U=0.000; z=-3.136; $p \leq 0.001$). However, when each context was analysed separately, significant differences were only obtained for the play context (U=0.000; z=3.580; $p \leq 0.001$). In this particular case, as shown in figure 2, the gesture rate was considerably higher

Table 4. Brief overview of the gestures by age group and context.

	Juvenile		Adult		Sum (context)	
	n	%	n	%	n	%
Play	146	97.6	5	3.3	151	46.3
Locomotion	75	65.2	40	34.8	115	35.3
Feed	0	0.0	0	0.0	0	0.0
Sex	0	0.0	7	100.0	7	2.1
Affiliative	16	50.0	16	50.0	32	9.9
Groom	5	23.8	16	76.2	21	6.4
Agonistic	0	0.0	0	0.0	0	0.0
Sum (age group)	242	74.2	84	25.8	326	100.0

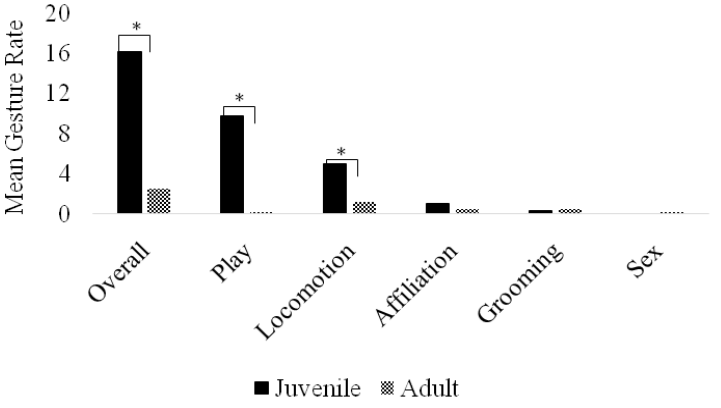

Figure 1. Gesture rate comparison of juvenile and adult chimpanzees for each functional context; * $p<0.05$.

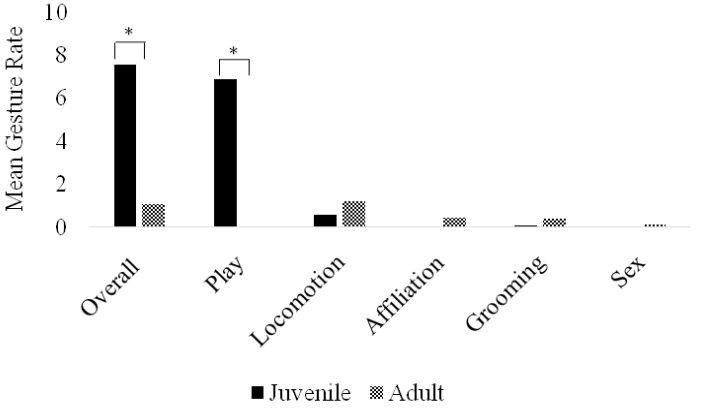

Figure 2. Gesture rate comparison of juvenile and adult chimpanzees in same age group (juvenile-juvenile, adult-adult) interactions, for each functional context; * $p<0.05$.

in juvenile chimpanzees. In the remaining contexts, no statistically significant differences were found: affiliation (U=12.500; z=-1.972; p=0.090), locomotion (U=24.500; z=-2.906; p=0.743), grooming (U=14.500; z=-1.621; p=0.145) and sexual (U=20.000; z=-1.248; p=0.441).

Between Age Group Interactions

As for the interactions between individuals of different age groups (juvenile-adult; adult-juvenile), significant differences were also obtained in the global gesture rates (U=0.000; z=-3.127; $p \leq 0.001$). Regarding each context, differences were found in affiliation (U=1.000; z=-3.233; p=0.001) and locomotion (U=2.000; z=-2.906; p=0.002), where the gesture rate of juvenile chimpanzees was higher, as shown in figure 3.

Within vs Between Age Group Interactions

When each age group was analysed separately (Figure 4) — and once more with the aim of comparing the gesture rate intra- and inter-age group in different contexts —, statistically significant differences were only obtained for juvenile individuals in play (z=-2.023; p=0.031), locomotion (z=-2.086; p=0.036) and affiliation (z=-2.023; p=0.031) contexts. In the first case, intra-age group gestural communication was significantly higher than the recorded for the inter-age group. The opposite was found for the locomotion and affiliation contexts. No significant differences were found in the grooming context for juvenile individuals (z=-0.816; p=0.375). Regarding adult individuals, no differences were found between the rate of gestures intra- and inter- age group in play (z=-0.447; p=0.500), locomotion (z=-1.137; p=0.155), affiliation (z=-1.725; p=0.078), grooming (z=-1.580; p=0.070) or sexual (z=-0.184; p=0.500) contexts.

Overall Responsiveness Rate

To evaluate the responsiveness rate, only three situational contexts were considered: overall interactions and only intra- and inter-age group interactions. In any of these, no significant differences were found: overall (U=23.000; z=-0.518; p=0.661), intra-age group (U=21.000; z=-0.757; p=0.510) and inter-age group (U=4.000; z=-2.711; p=0.008) (Figure 5).

Discussion and conclusions

The main aim of this study was to investigate the differences in gestural communication within and between age groups of the chimpanzee community living at the Lisbon Zoo (Lisbon, Portugal). In order to ascertain these differences and to analyse in which contexts there was a higher frequency of intra- and inter-age group gestural communication, the observation focused on three parameters: age group of the signaller, the gesture produced (and respective functional context) and the age group of the receiver. In general, the obtained results revealed that, in some cases, juvenile chimpanzees tended to direct their gestures to chimpanzees of apparently more adequate age group to particular contexts.

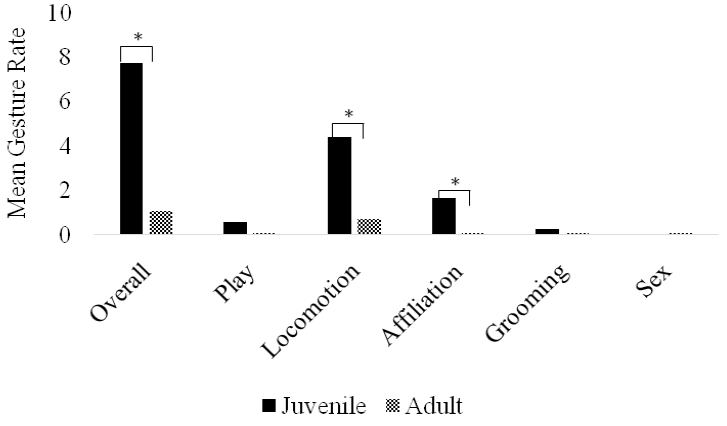

Figure 3. Gesture rate comparison of juvenile and adult chimpanzees in different age groups (juvenile-adult, adult-juvenile) interactions, for each functional context; * $p<0.05$.

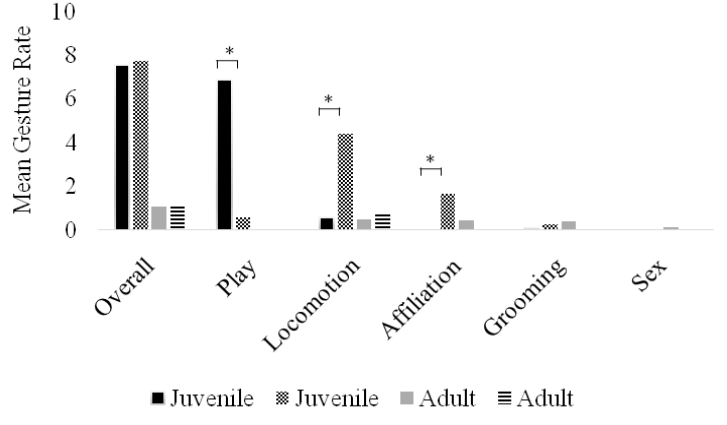

Figure 4. Gesture rate comparison of juvenile and adult chimpanzees in same and different age group interactions, for each functional context; * $p<0.05$.

The within and between age groups analyses have shown that juvenile chimpanzees strongly prefer to communicate by gestures in a play context, but also to direct the same gestures to conspecifics of the same age group. These evidences corroborate the results obtained by Tomasello et al. (1985) and Frohlich et al.

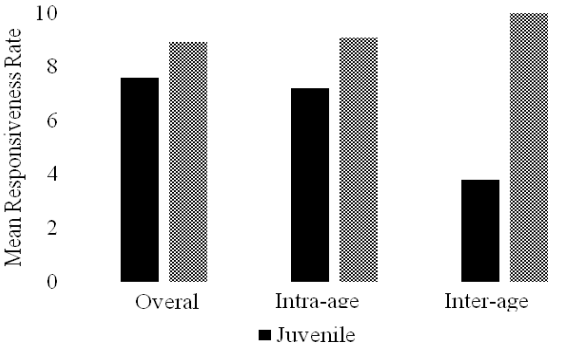

Figure 5. Responsiveness rate comparison of juvenile and adult chimpanzees in overall, intra-age group and inter-age group interactions.

(2016a). As such, two plausible and complementary motives emerge to explain why young chimpanzees gesticulate substantially more to others of the same age group in play context.

First of all, several authors (Hobaiter and Byrne, 2011b; Tomasello et al., 1997; King et al., 1980; Palagi et al., 2004; Shimada and Sueur, 2014) state that playing is the main context in which younger individuals of several primate species get involved. Generally, the evolutionary function of playing fosters the development of social, physical and cognitive capacities (Davila-Ross et al., 2011; Cordoni and Palagi, 2011), and promotes the necessary behavioural flexibility to deal with social and ecological needs (Palagi and Paoli, 2007). Therefore, play activities between juvenile individuals bring several benefits, namely socialization, sensori-motor stimulation and physical and cognitive exercising (Bekoff and Byers, 1981). They might also influence future dominance hierarchy (Byers and Walker, 1996; Palagi and Cordoni, 2012), stimulate the learning of behaviour and communication elements from other chimpanzees (Fagen, 1981), reduces social conflicts (Palagi, 2007), and potentiate the practice and testing of communication signs as well as the establishment of social relationships (Goodall, 1968).

Secondly, adult chimpanzees do not show much physical and cognitive availability to get involved in non-priority activities such as playing. That is why younger chimpanzees tend to choose other young individuals to play (Mendonza-Granados and Sommer, 1995; Flack et al., 2004).

Moreover, the results obtained in this study apparently support the *social*

negotiation hypothesis, which, according to Frolich et al. (2016a), suggests that "gestures are the output of social shaping, shared understanding, and mutual construction in real time by both interactants". The results here presented clearly provide evidence of a high prevalence of gestural signalling in play interactions among young chimpanzees. This suggests that they devote a great part of their time to playing, which is, according to Frohlich et al. (2016a; 2017), an essential component in the early stages of chimpanzees' ontogeny, not only for the development of a functional and complete gestural repertoire, but also for the effective learning of the appropriate gestural signs. The latter should be based on mutual and shared understanding and exhibited to produce different meanings, specific for different contexts.

In play context, the gestural communication pattern of juvenile individuals is compatible with what is considered, in the literature aforementioned, as a typical behaviour of young chimpanzees. In other words, the involvement among young individuals in play activities is rather common and the results obtained corroborate that tendency, attested by a significant rate of gestural signs within the group of juvenile chimpanzees in play context.

On the other hand, on what concerns inter-age groups interactions, the results revealed differences in locomotion and affiliation contexts, in which the gesture rate of juvenile chimpanzees has surpassed the one of adult individuals. Apparently, the fact that locomotion and affiliation include diverse and regular parenting activities may explain why, in these contexts, juvenile chimpanzees tend to direct their gestures to adults. For instances, in locomotion context, younger chimpanzees frequently request 'joint-travel' to adults, with the intent of exploring the surrounding environment, even when they are already physically independent (Tomasello et al., 1989; Tomasello et al., 1985; Flack et al., 2004). This pattern of gestural communication is similar to that found by Halina et al. (2013) in bonobos (*Pan paniscus*) living in captivity. However, Frohlich et al. (2016b) verified the opposite in wild chimpanzees, i.e., that the initiative of gesticulating in order to require 'joint-travel' was performed by the progenitors. In sum, data here presented do not sustain potential interspecific differences on what concerns maternal styles related to locomotion, as stated by Frohlich et al. (2016b). For this motive, it is suggested that possible socioecological discrepancies between captivity and wild environment might be at the base of the differences found.

The same gestural communication pattern was verified in affiliation context. Younger chimpanzees usually seek their parents or other adult chimpanzees for affiliative activities (Tomasello et al., 1989; Goodall, 1968; Pusey, 1990; Langergraber et al., 2007). This occurs not only due to

the affective relationship between them, but because the latter are the most suitable to provide affiliative care. Hayashi and Matsuzawa (2017) also argue that, even after becoming independent and beginning to explore the social and physical environment around them, younger chimpanzees continue to request affiliation activities to their mothers quite often, taking them as a 'secure base'.

As emphasized by Roberts et al. (2012b), gestural communication plays an important role in the way nonhuman primates deal with social complexity. In fact, the results here presented suggest a certain degree of flexibility in gestural signalization of juvenile chimpanzees, showing their tendency to direct gestural signs to get involved with individuals of a similar age-group depending on the context in which the gestural sign is produced.

Finally, the following constraints should be taken into account when interpreting the obtained results: the relatively short period of data collection; the possible kinship and/or dominance rank between the individuals (according to some authors, this may influence several interactions in diverse contexts — e.g. Goodall, 1968; 1986; Boeschet al., 2006; Lonsdorf et al., 2014; Foerster et al., 2016; Murray et al., 2006), and, more important, the fact that the data collected was not validated through analyses intra- and inter-observer. To attain a holistic understanding of gestural communication in nonhuman primates, similar analyses, i.e., between/within age-groups, should be carried out both in the wild, where primates are exposed to selective active pressures (Frohlich et al., 2016b), and in captive populations.

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