RESEARCH ARTICLE

Vocal Signature in Wild Infant Chimpanzees

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A large array of communication signals supports the fission/fusion social organization in chimpanzees, and among them the acoustic channel plays a large part because of their forest habitat. Adult vocalizations convey social and ecological information to their recipients allowing them to obtain cues about an ongoing event from calls only. In contrast to adult vocalizations, information encoded in infant calls had been hardly investigated. Studies mainly focused on vocal development. The present article aims at assessing the acoustic cues that support individual identity coding in infant chimpanzees. By analyzing recordings performed in the wild from seven 3-year-old infant chimpanzees, we showed that their calls support a well-defined individual vocal signature relying on spectral cues. To assess the reliability of the signature across the calls of an individual, we defined two subsets of recordings on the basis of the characteristics of the frequency modulation (whimpers and screams) and showed that both call types present a reliable vocal signature. Early vocal signature may allow the mother and other individuals in the group to identify the infant caller when visual contact is broken. Chimpanzee mothers may have developed abilities to cope with changing vocal signatures while their infant, still vulnerable, gains in independence in close habitat. Am. J. Primatol. 75:324–332, 2013. © 2012 Wiley Periodicals, Inc.

Key words: acoustic communication; vocal signature; wild infant chimpanzees; stability of vocal identity; pan troglodytes schweinfurthii

INTRODUCTION

Chimpanzees live in fission/fusion social organizations where individuals form temporary associations that can change in size and composition several times a day. Despite this apparent loose social structure, interactions between individuals are finely tuned, and the status of each chimpanzee is well defined in relation to all its potential congeners [de Waal, 1982; Duffy et al., 2007; Goodall, 1986; Newton-Fisher & Lee, 2011; Nishida & Hosaka, 1996]. Social interactions are upheld by acoustical and visual signals. In the tropical rainforest, sound signaling is a major communication channel allowing information to transfer through dense vegetation. Adult chimpanzees use a repertoire of calls, which have the potential to code information related to individual identity and status, motivational state, and emission context [Crockford & Boesch, 2003; Kojima et al., 2003; Slocombe & Zuberbühler, 2005a, 2005b, 2007; Slocombe et al., 2009; Townsend et al., 2011]. Vocalization variants serve different communicative functions relative to social and ecological circumstances. Recipients get cues about an ongoing event from calls only [Notman & Rendall, 2005; Slocombe & Zuberbühler, 2007; Slocombe et al., 2009]. Previous studies have confirmed individual vocal signatures in the structure of pant hoot [Goodall, 1968; Kojima et al., 2003; Marler & Hobbett, 1975; Mitani et al., 1996], the loud vocalization typically used by adult chimpanzees to communicate over long distances [Goodall, 1986; Mitani & Nishida, 1993; Wilson et al., 2001]. In contrast to adult vocalizations, vocal communication in infant apes has received little emphasis and information encoded in infant calls had been hardly studied despite decades of monitoring chimpanzee communities. Early knowledge comes from developmental studies with a

*Correspondence to: Florence Levréro, University of Lyon/Saint-Etienne, Equipe de Neuro-Ethologie Sensorielle, ENES/CNPS CNRS UMR 8195, 23 rue Michelon Saint-Etienne Cedex 2, France. E-mail: florence.levreiro@univ-st-etienne.fr

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sive vocalizations. In this study, we focused on one specific case in which a mother-directed distress call was recorded in wild chimpanzees (Pan troglodytes schweinfurthii) from the Kanyanchu community (Kibale National Park, Uganda; N 00°26'212" E 030°23'706") from mid-April to mid-July 2009. This community has been habituated for ecotourism since 1991 and has never been provisioned [Johns, 1996]. In total, 17 infants were individually identified of 76 animals. The average observation time for a mother–offspring pair was 5 hr and 20 min (range: 32 min–12 hr), but infant calls were detected during less than 1% of this time (mean call sequences = 2 min; range: 4 sec–16 min). We focused on seven infants aged approximately 3-year old for whom the identity of the caller and the context of the utterance were totally reliable. Their age was known thanks to the long-term monitoring of the community conducted by Uganda Wildlife Authority, which fitted with their morphological and behavioral features. At 3-year old, infant chimpanzees are still dependent on their mother for feeding and travelling but leave her to explore and interact with other congeners, thus enhancing the potential role of acoustics in mediating mother/offspring contact [Yerkes & Tomilin, 1935]. We focused here on mother-directed calls. Calls ranged from calm begging to get food or any maternal assistance (vocal begging could be associated with begging gesture) to screams produced in frustrating situation when infant does not get what is wanted or fearful situations while infants were not close and/or without visual contact with their mother. Three individuals were recorded when facing a stressful situation (separation from their mothers, first context: “distress”), while the other four individuals were recorded while begging to their mothers (second context: “begging”). Although highly challenging, recording infants in the wild is essential to evaluate the great range of environmental and social constraints known to modulate vocal communication [Baker & Smuts, 1994; Laporte & Zuberbühler, 2010]. Our research has been approved by the Uganda Wildlife Authority and Uganda
National Council for Science and Technology and adhered to the American Society of Primatologists principles for the ethical treatment of primates.

**Recordings and Analyses**

Recordings were performed from 6:30 a.m. to 16:30 p.m. at a distance of 8 to 35 m (Sennheiser MKH70 microphone, Wedemark, Germany; Marantz PMD670 digital recorder, D&M France SAS, Asnières sur Seine, France; sampling rate: 44.1 kHz). We analyzed all calls produced by infants in begging and distress contexts directed to the mother. The sound analysis was conducted using Avisoft-SASLab Pro version 4.39 (Avisoft Bioacoustics, Berlin, Germany) and Praat version 4.4.10 (Praat, Amsterdam, Netherlands). Infant chimpanzee calls are complex sounds that have a fundamental frequency associated with several harmonics (Fig. 1, Sound S1 in Supporting information). They are modulated in frequency and amplitude. To assess which of the spectral, amplitude, and temporal cues could support individual identity coding and thus vocal recognition by the mothers, we defined a set of 12 parameters describing the acoustic structure of the calls. To describe the frequency modulation of the call, we measured the following parameters from the spectrogram (window size: 512): the frequency value of the fundamental frequency at the start of the call ($F_{\text{start}}$), the maximum value of the fundamental frequency across the call ($F_{\text{max}}$) and the frequency value of the fundamental frequency at the end of the call ($F_{\text{end}}$). We calculated the slope of the ascending (Slope 1) and descending frequency modulation (Slope 2). We noted the total duration of the call ($D_t$) and the silence duration between the offset of the considered call and the onset of the following one (Interv). To describe the distribution of energy among the frequency spectrum, the following spectral parameters were measured from the average power spectrum, calculated from the total length of the call: the frequency value at the upper limit of the first quartile of energy (Q1), of the second...
quartile of energy (Q2), of the third quartile of energy (Q3), the frequency at the highest peak of amplitude (P_{pic}), and the mean value of the fundamental frequency across the call (F_0). All the frequency values are in Hertz, time in milliseconds and slopes in Hertz per milliseconds (Table I).

### Statistical Analysis of Individual Signatures

We computed a potential of individual coding (PIC) for each parameter that measured the relative variability of the acoustic parameter within (CV_i) and between individuals (CV_b) [Sokal & Rohlf, 1995; Vignal et al., 2004]. The coefficient of variation was calculated according to the following formula (CV = 100 × (SD/X_{mean}) × (1 + (1/n)), SD, standard deviation; X_{mean}, mean of the sample; n, sample size), and we assessed their PIC by calculating the ratio CV_b/CV_{mean} (CV_{i,mean}, mean value of the CV_i of all the individuals).

To quantify the reliability of the individual signature, we then followed a multivariate approach using a cross-validated discriminant function analysis (DFA). In the first step of the DFA, a training data set (two-thirds of the sounds from each individual) was used to generate a set of linear discriminant functions. In the second step, these discriminant functions were used to classify the remaining one-third of the sounds. This cross-validation step gives a measure of the effect size (the percentage of correctly classified sounds). We ran 100 iterations of these two-steps DFAs with both training and validation data sets chosen at random. The mean effect size (mean percentage of correctly classified sounds) was obtained by calculating the average of the percentages of correctly classified sounds obtained with each of the 100 validation data sets.

Besides those cross-validated DFAs performed on original data sets, we looked for getting the statistical significance of the mean effect size. In this aim, new data sets were created where the identity of sounds was randomly permuted between individuals (permuted DFA, [Mathevon et al., 2010; Mundry & Sommer, 2007]). From these randomized sets, the same steps, fitting and validation, were consecutively performed. After 1,000 iterations, we calculated the proportion of randomized validation data sets revealing a number of correctly classified calls being at least as large as the effect size obtained with the nonrandomized validation data set. This proportion gives the significance of the discrimination level and is equivalent to a P-value [Dentressangle et al., 2012; Mathevon et al., 2010; Mundry & Sommer, 2007].

Finally, because each infant was not recorded in both behavioral contexts, we tested whether the individual differences assessed by the cross-validated DFA could be due to differences between contexts. We thus compared the distances between DFA

### TABLE I. Statistical Analysis of the Acoustic Parameters of Infant Chimpanzee Calls

<table>
<thead>
<tr>
<th>Variables</th>
<th>Inf1 (55)</th>
<th>Inf2 (175)</th>
<th>Inf3 (42)</th>
<th>Inf4 (30)</th>
<th>Inf5 (91)</th>
<th>Inf6 (91)</th>
<th>Inf7 (154)</th>
<th>Inf8 (101)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fstart (Hz)</td>
<td>410 ± 190</td>
<td>419 ± 130</td>
<td>403 ± 119</td>
<td>390 ± 135</td>
<td>373 ± 201</td>
<td>394 ± 208</td>
<td>467 ± 208</td>
<td>480 ± 206</td>
</tr>
<tr>
<td>Fmax (Hz)</td>
<td>728 ± 85</td>
<td>687 ± 95</td>
<td>653 ± 95</td>
<td>699 ± 102</td>
<td>641 ± 110</td>
<td>654 ± 113</td>
<td>783 ± 113</td>
<td>732 ± 100</td>
</tr>
<tr>
<td>Fend (Hz)</td>
<td>512 ± 119</td>
<td>522 ± 115</td>
<td>515 ± 113</td>
<td>497 ± 111</td>
<td>482 ± 110</td>
<td>489 ± 110</td>
<td>588 ± 111</td>
<td>572 ± 109</td>
</tr>
<tr>
<td>Dur (msec)</td>
<td>1423 ± 142</td>
<td>1202 ± 118</td>
<td>1342 ± 119</td>
<td>1375 ± 120</td>
<td>1380 ± 120</td>
<td>1413 ± 121</td>
<td>1513 ± 122</td>
<td>1430 ± 121</td>
</tr>
<tr>
<td>Std (Hz)</td>
<td>190 ± 85</td>
<td>170 ± 90</td>
<td>165 ± 90</td>
<td>180 ± 100</td>
<td>180 ± 100</td>
<td>175 ± 100</td>
<td>200 ± 100</td>
<td>195 ± 100</td>
</tr>
<tr>
<td>Mean CV</td>
<td>100.8 ± 5.4</td>
<td>100.8 ± 5.4</td>
<td>100.8 ± 5.4</td>
<td>100.8 ± 5.4</td>
<td>100.8 ± 5.4</td>
<td>100.8 ± 5.4</td>
<td>100.8 ± 5.4</td>
<td>100.8 ± 5.4</td>
</tr>
<tr>
<td>PIC</td>
<td>1.34 ± 1.0</td>
<td>1.34 ± 1.0</td>
<td>1.34 ± 1.0</td>
<td>1.34 ± 1.0</td>
<td>1.34 ± 1.0</td>
<td>1.34 ± 1.0</td>
<td>1.34 ± 1.0</td>
<td>1.34 ± 1.0</td>
</tr>
</tbody>
</table>

**P**-values calculated using a cross-validated discriminant function analysis (DFA). In the first step of the DFA, a training data set (two-thirds of the sounds from each individual) was used to generate a set of linear discriminant functions. In the second step, these discriminant functions were used to classify the remaining one-third of the sounds. This cross-validation step gives a measure of the effect size (the percentage of correctly classified sounds). We ran 100 iterations of these two-steps DFAs with both training and validation data sets chosen at random. The mean effect size (mean percentage of correctly classified sounds) was obtained by calculating the average of the percentages of correctly classified sounds obtained with each of the 100 validation data sets.

**Statistical analyses:**

- **ANOVA** for mean CV and PIC values calculated using a cross-validated discriminant function analysis (DFA).
- **Kruskal-Wallis ANOVA** for mean CV and PIC values calculated using a cross-validated discriminant function analysis (DFA).

Finally, because each infant was not recorded in both behavioral contexts, we tested whether the individual differences assessed by the cross-validated DFA could be due to differences between contexts. We thus compared the distances between DFA
centroids of individuals recorded in the begging context with the distances between these centroids and those of the individuals recorded in the distress context. If the comparison between distances showed no significant difference, it would support the vocal signatures found are due to individual differences, eliminating the potential confounding effect of recording contexts.

Assessment of the Reliability of Individual Signatures in Whimpers and Screams

The acoustic structure of the calls recorded from the same individual can strongly vary, especially the slopes of frequency modulation (see Results). To assess the reliability of the signature across the calls of an individual, we did again the DFA procedure on two subsets of recordings. These two subsets were defined arbitrarily on the basis of the characteristics of the frequency modulations (almost non-modulated calls = “whimpers”; strongly modulated calls = “screams”), and to obtain a balanced number of calls between each subset. The first subset includes calls with the slope of either the ascending or the descending frequency modulation equal to zero and the other slope less than 8 Hz/msec (“whimpers,” N = 17–74 calls/individual, only five individuals considered). In total, 51% of “whimpers” were produced in begging context (N = 127/249; five individuals). In the second subset, calls were characterized by frequency modulation slopes up to 25 Hz/msec (“screams,” N = 25–102 calls/individual, only five individuals considered). Among the calls classified as “screams,” 55.4% were recorded in distress context (N = 148/267; five individuals). Whimpers and screams significantly differed for all the acoustic variables measured (Paired sample Wilcoxon test, P < 0.001; Table II). The DFA procedure was processed again separately for each subset.

RESULTS

Vocal Signature and Acoustic Cues Supporting the Individual Identity Coding

In total, 625 infant calls were recorded and analyzed with a mean of 89 calls per infant (range: 42–175 calls). The univariate approach showed that infant calls support a well-defined individual vocal signature (Table I). Among the 12 acoustic variables, the main individualized parameters (i.e. those with greatest PIC values) were the frequency value of the fundamental frequency at the start of the call, the maximum value of the fundamental frequency across the call, and the frequency values at the upper limit of the first and third quartiles of the energy spectrum (PIC values > 1.5). The multivariate analysis showed that the classification success rate across individuals was significantly greater than chance (mean = 56%, min–max = 33–71%, chance = 14%, P < 0.001,
Fig. 2. Information coding in infant calls. (A) Position of individuals’ centroids as a function of the first two discriminant variables that maximize individual separation (green dots: four individuals (1, 5, 6 and 7) recorded in the “begging” context; red dots: three individuals (2, 3 and 4) recorded in the “distress” context). The plotted ovals around the centroids show one standard error of the mean. (B and C) Call series from two distinct individuals recorded in a begging context. (D) Call series from a third individual recorded in a distress context. In both social contexts, weak and strong frequency modulations are successively observed in the same call series (to hear the sounds: see Sound S2 in Supporting information). The figure in color is online.

Fig. 2, Sound S2 in Supporting information). This classification is clearly due to differences in individual voices and not to recording contexts: the distance between DFA centroids of individuals recorded in the begging context were not closer to each other than to the centroids of the individuals recorded in the distress context (comparison between the distances separating centroids of “begging context” calls, and the distances separating centroids of “begging context” calls and centroids of “distress context” calls: two-sample Wilcoxon test, $N_1 = 12, N_2 = 6, W = 36, P = 1$). The maximum value of the frequency fundamental across the call and its value at the start of the call were the two main factors that separated individuals in the first discriminant function of the DFA (Table III). The second function relies mainly on the frequency value of the fundamental at the start and at the end of the call. Both multivariate and univariate approaches thus underline the importance of the frequency features to the individual signature.

**TABLE III. Factor Loadings of the Measured Acoustic Parameters on the First Three Discriminant Functions (LD1, LD2 and LD3, Representing 56%, 22%, and 11% of the Total Variance, Respectively)**

<table>
<thead>
<tr>
<th>Acoustic variables</th>
<th>LD1</th>
<th>LD2</th>
<th>LD3</th>
</tr>
</thead>
<tbody>
<tr>
<td>$F_{\text{max}}$ (Hz)</td>
<td>−162.40</td>
<td>17.76</td>
<td>−9.36</td>
</tr>
<tr>
<td>$F_{\text{start}}$ (Hz)</td>
<td>124.69</td>
<td>29.13</td>
<td>−10.35</td>
</tr>
<tr>
<td>$Q_2$ (Hz)</td>
<td>84.11</td>
<td>−5.54</td>
<td>1.74</td>
</tr>
<tr>
<td>$F_0$ (Hz)</td>
<td>66.89</td>
<td>−9.84</td>
<td>6.08</td>
</tr>
<tr>
<td>$F_{\text{end}}$ (Hz)</td>
<td>44.21</td>
<td>−34.36</td>
<td>9.62</td>
</tr>
<tr>
<td>$Q_3$ (Hz)</td>
<td>−35.64</td>
<td>−5.89</td>
<td>−0.93</td>
</tr>
<tr>
<td>$D_t$ (msec)</td>
<td>−22.82</td>
<td>1.19</td>
<td>2.07</td>
</tr>
<tr>
<td>Slope 1 (Hz)</td>
<td>20.76</td>
<td>−1.95</td>
<td>3.42</td>
</tr>
<tr>
<td>$Q_1$ (Hz)</td>
<td>10.57</td>
<td>10.87</td>
<td>−3.59</td>
</tr>
<tr>
<td>$F_{\text{pic}}$ (Hz)</td>
<td>8.69</td>
<td>−9.95</td>
<td>4.46</td>
</tr>
<tr>
<td>Slope 2 (Hz)</td>
<td>3.15</td>
<td>9.54</td>
<td>0.36</td>
</tr>
<tr>
<td>Interv (msec)</td>
<td>−2.68</td>
<td>4.02</td>
<td>−0.31</td>
</tr>
</tbody>
</table>

Legends of the acoustic parameters are given in the Table I.
Strength of Individual Vocal Signature across the Calls

Focusing on whimpers, the percentage of correct classification among these calls was significantly greater than chance (mean = 62.8%, min–max = 56.8–66.7%, chance = 20%, P < 0.001). Screams were also well classified by cross-validated DFA (mean of correct classification = 76.7%, min–max = 34.8–80.1%, chance = 20%, P < 0.001).

DISCUSSION

By analyzing recordings from animals behaving freely in their natural habitat, we showed that the calls of infant chimpanzees represent an individual signature that may allow the mother and other individuals in the group to identify the caller. Mammalian vocalizations result from sound vibrations of the vocal folds (sound source) producing a fundamental frequency that is subsequently filtered by the vocal tract, which determines the distribution of energy within the frequency spectrum. As in other mammals [Briefer & McElligott, 2011], the vocal signature of infant chimpanzees is supported by a combination of source- and filter-related parameters that are probably unique to each individual.

During their first year of life, infant chimpanzees are in close physical contacts with their mother and thus their communication is largely multimodal [Goodall, 1968]. During this period, the mothers likely learn passively to recognize the voice of their offspring. Then, when infants gain in independence and make more and more exploratory trips away from their mother, the audio channel plays a bigger role in mother–offspring communication. Although mother–offspring recognition still remains to be tested by playback experiments in chimpanzees, it has been shown in many mammal species [e.g. goats: Briefer & McElligott, 2011; fur seals: Charrier et al., 2001; vervets: Cheney & Seyfarth, 1980]. Reports of long-lasting period of observation indicate that chimpanzee mothers recognize the screams of their own offspring and respond rushing to him to give their defense [Goodall, 1986].

It is notable that neither the slope of the ascending frequency modulation, nor the slope of the descending frequency modulation bears strong information concerning individual identity; the intradividual variability of both these parameters is as high as the interindividual variability. The temporal dynamics of the frequency value of the fundamental are thus highly variable within the calls of an individual, and might bear information concerning the emitter’s emotional state. Interestingly, whimpers and screams have been recorded both in distress and begging contexts. Most of the recorded call series show various structures of calls (Fig. 2, Sound S2 in Supporting information). This various acoustics structure may express the course of the infant’s emotional arousal state such as frustration following unsuccessful begging or distress caused by physical and visual separation from the mother.

Interestingly, whereas we report that 3-year old infant chimpanzee calls directed to the mother code for the emitter’s identity, they seem unlikely to convey clear information concerning the context eliciting the calling behavior. The way that emotions influence vocal parameters is still poorly investigated contrary to the effect of motivation on animal vocalizations. However both may be tightly connected in the sense that “vocal correlates of motivation imply an underlying emotion” [see review Briefer, 2012]. Changes in vocal parameters in response to emotional states are expected in mammals [Coss et al., 2007; Scheiner & Fisher, 2011; Scherer & Kappas, 1988] in line with the motivational–structural rules of acoustic signals [August & Anderson, 1987; Manser, 2010; Morton, 1977]. Adult chimpanzee screams indeed varied acoustically reflecting the motivational state of the caller [Siebert & Parr, 2003]. Although the number of individuals in the recordings requires caution when evaluating the calls, these results suggest that mothers might rely on emotional cues to assess the degree of emergency and decide if they have to interfere.

Our results show that vocal signature does exist in whimpers and screams, underlying that infant chimpanzees can be individually recognized by their mothers whatever the way they call. However and obviously, the mother response may not be driven by sound signaling alone: other cues may help her to assess the urgency of responding to her young infant [Yerkes & Tomilin, 1935]. The social context such as the identities of other individuals at proximity and their activities are likely to guide the mothers’ responses. That is likely to change when offspring grow up since screams in older individuals are produced in a context-specific manner, namely depending on the aggressor or victim role they play in conflicts [Slocombe & Zuberbühler, 2005a]. The importance of the vocal signature, however, exceeds the simple mother–infant relationship. Within the fission/fusion system of chimpanzee communities, individuals have to cope with numerous, various, and changing social congeners, which promotes the development of effective abilities to reliably discriminate between them. Infant chimpanzee can produce other types of calls such as pant grunts but contrary to the calls presently studied, their pant grunting behavior is not part of mother–infant communication. It has a social function reflecting an infant’s efforts to interact with other group members and needs social learning. Interestingly, their pant-grunts convey information such as the social context experienced by the caller [Laporte & Zuberbuhler, 2011]. Social grunting must have evolved under selection forces to convey fine information in direction to the group.
members, which may be higher than those on calls exclusively exchanged among the tight bond mother–infant. Inversely, a mother will rush to her offspring to rescue him in response to any of their screams aiming at not risking her offspring’s life. Besides the fact that a newborn must be gradually integrated into such a complex social network, the capacity of chimpanzees to possess sophisticated understanding of third-party relationships might enhance the importance of being individually distinguished sooner in the community [Slocombe & Zuberbühler, 2007; Tomasello & Call, 1997]. As individual recognition may rely on familiarity, investigations should be performed to assess the ontogeny of vocal signature in chimpanzees in various call types.

To conclude, an interesting parallel with humans can be done since it is known that baby cries bear an individual signature allowing parental recognition [Green & Gustafson, 1983]. Acoustic analysis shows that this signature is also multiparametric, with temporal and frequency parameters involved in the coding information [Gustafson et al., 1984]. Information redundancy is probably important in strengthening vocal signature, for example, information appears resistant to propagation and allows the individual identification by adults at distances up to 30 m [Gustafson et al., 1994]. In line with what we found in infant chimpanzees, human infant cries are graded signals, coding for pain or frustration intensity more than for stimulus cause [Bellieni et al., 2004]. Cries of chimpanzee and human infants thus appear structurally and functionally similar, and may have evolved under similar selection forces.

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