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Communication gestuelle et multimodale chez les mangabeys à collier (*Cercocebus torquatus*)

Juliette Aychet

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Par

Juliette AYCHET

**Communication gestuelle et multimodale chez les mangabeys à collier
(*Cercocebus torquatus*)**

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« Sans vos gestes, j'ignorerais tout du secret lumineux de votre âme. »

José Ortega y Gasset

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Sommaire

Chapitre I – Introduction.....13

1. Aux origines du langage.....15

1.1. Le langage, un système de communication propre à l'humain.....15

1.2. Approche comparative pour l'étude des origines évolutives du langage.....15

1.3. Théories sur l'origine du langage.....17

2. Décrire la communication gestuelle et multimodale chez les primates non-humains.....21

2.1. Qu'est-ce qu'un signal communicatif ?.....22

2.2. Gestes communicatifs.....22

2.3. Expressions faciales.....24

2.4. Communication multimodale.....24

3. Propriétés cognitives « langagières » dans la communication gestuelle des primates non-humains.....25

3.1. Intentionnalité.....26

3.2. Latéralité.....31

3.3. Flexibilité.....37

4. Problématiques de la thèse.....43

4.1. Questions de recherche.....43

4.2. Espèce étudiée.....44

4.3. Objectifs de la thèse.....46

Chapitre II – Méthodologie générale.....49

1. Sujets d'étude.....51

1.1. Présentation de l'espèce.....51

1.2. Population captive étudiée.....54

2. Approche observationnelle.....56

2.1. Collecte de données.....56

2.2. Description des gestes et des expressions faciales.....	56
2.3. Analyse de l'intentionnalité des signaux.....	57
2.4. Analyse de la latéralité gestuelle.....	58
2.5. Description des combinaisons de signaux.....	58
2.6. Analyses du contexte et des facteurs sociodémographiques.....	60
3. Approche expérimentale.....	61
3.1. Paradigme de quémante alimentaire.....	61
3.2. Principe et mise au point du dispositif expérimental.....	62
4. Complémentarité des approches observationnelles et expérimentales.....	64
Chapitre III – Intentionnalité des signaux visuels spontanés.....	67
Article 1 : Intentional gesturing in red-capped mangabeys (<i>Cercocebus torquatus</i>).....	69
Article 2 : Facial displays in red-capped mangabeys (<i>Cercocebus torquatus</i>): repertoire, social context, and potential intentionality.....	105
Chapitre IV – Latéralité gestuelle.....	141
Article 3 : Multifactorial analysis of gestural laterality in captive red-capped mangabeys (<i>Cercocebus torquatus</i>).....	143
Chapitre V – Communication multimodale et multicomposante.....	167
Article 4 : Using sequential and network analyses to describe multimodal and multicomponent communication in captive red-capped mangabeys.....	169
Analyses complémentaires.....	215
Chapitre VI – Intentionnalité et multimodalité des gestes : approche expérimentale.....	221
Article 5 : Red-capped mangabeys (<i>Cercocebus torquatus</i>) adapt their interspecific gestural communication to the recipient's behaviour.....	223

Chapitre VII – Discussion générale.....241

1. Principaux résultats.....	243
2. Intentionnalité de la communication visuelle chez les cercopithécidés.....	244
2.1. Communication gestuelle intentionnelle chez des non-hominoïdes.....	244
2.2. Intentionnalité des expressions faciales des cercopithécidés : des gestes pas comme les autres ?.....	248
2.3. Perspectives méthodologiques pour l'étude de l'intentionnalité des signaux visuels.....	249
3. Facteurs déterminant la latéralité gestuelle	251
3.1. La communication gestuelle des mangabeys à collier est-elle latéralisée ?.....	251
3.2. Des facteurs contextuels influencent la latéralité gestuelle	252
4. Combinaison flexible de différents types et modalités de signaux communicatifs.....	255
4.1. Quelles causes et fonctions de la multimodalité de la communication ?.....	255
4.2. Développement d'une méthodologie descriptive pour l'étude de la multimodalité.....	258
5. Principales perspectives.....	259
6. Conclusion.....	260

Chapitre VIII – Bibliographie.....263**Chapitre IX – Annexes.....295**

Annexe 1 : Liste des publications.....	297
Annexe 2 : Communication dans des colloques nationaux et internationaux.....	299
Annexe 3 : Activités de vulgarisation scientifique.....	303
Annexe 4 : Activités d'enseignement et d'encadrement de projets scientifiques.....	305
Annexe 5 : Formations suivies et bourses.....	307



Chapitre I

Introduction





1. Aux origines du langage

Ce travail de thèse s'inscrit dans l'étude des origines évolutives du langage, abordée à travers la caractérisation de la communication des primates non-humains. Nous présenterons ici les approches comparatives adoptées dans le cadre de la recherche des origines du langage, ainsi que les principales théories dont ces approches ont découlé.

1.1. Le langage, un système de communication propre à l'humain

Le langage est un système de communication spécifique à l'humain (*Homo sapiens*), par lequel un individu encode et transmet intentionnellement des informations sur ses propres pensées et émotions, des indications sur des éléments extérieurs de l'environnement, ou demande une action de la part d'un autre individu (e.g. Hewes *et al.* 1973; Vauclair et Cochet 2013; Fitch 2017). Il n'existe pas actuellement de définition unique et universellement acceptée du langage, mais il a souvent été caractérisé selon un ensemble de critères permettant de le distinguer des autres systèmes de communication animaux (e.g. Hockett et Hockett 1960; Wacewicz et Żywicznyński 2015). De manière générale, le langage peut être défini selon deux perspectives. D'une part, le langage est une **faculté cognitive et sociale**, puisqu'il consiste en la production intentionnelle de signaux en direction d'autres individus, dans un but social informatif ou impératif, et dans le respect de règles socialement établies (Liebal *et al.* 2014). D'autre part, le langage peut être considéré comme un **système structuré de signaux** (vocaux, gestuels, écrits), répondant à des règles d'organisation précises sous-tendant leurs significations (e.g. Hockett et Hockett 1960; Liebal *et al.* 2014).

1.2. Approche comparative pour l'étude des origines évolutives du langage

Bien qu'il soit admis que le langage humain est un trait unique dans le monde animal, son histoire évolutive est encore sujet à grands débats, plusieurs scénarios évolutifs ayant été proposés pour expliquer son émergence dans l'espèce humaine (e.g. Corballis 2003; Arbib 2005; Seyfarth *et al.* 2005; Arbib *et al.* 2008; Masataka 2008b; Meguerditchian et Vauclair 2008; Prieur *et al.* 2019a). Une première approche est celle du « ponctualisme », posant le langage comme un trait qualitativement différent des autres systèmes de communication animaux, qui aurait émergé de capacités cognitives elles-mêmes propres au genre *Homo* (Chomsky 1981; Pallaud 2001). Cette hypothèse s'appuie notamment sur le caractère unique de certaines propriétés du langage, comme la récursivité (Hauser *et al.* 2002). Une autre suggestion est que le langage résulte de « préadaptations » à différents niveaux évolutifs (e.g. Hurford 2003). Le langage pouvant être défini comme un ensemble de propriétés sociocognitives et structurelles, il peut être fait l'hypothèse que certaines soient des traits nouveaux et que d'autres se soient développées à partir de systèmes de communication préexistants (Hauser *et al.* 2002; Fitch 2017).

L'approche comparative est ainsi la plus pertinente pour examiner cette hypothèse, à la recherche d'éventuelles homologues entre le langage humain et la communication d'autres animaux, des propriétés « langagières » pouvant avoir été héritées d'ancêtres communs. Selon la définition donnée au langage, ces propriétés dont les précurseurs sont recherchés chez les animaux correspondent : soit à des **capacités sociocognitives** mobilisées pour la communication, comme la capacité à diriger ses signaux dans un but social précis (intentionnalité), à utiliser des signaux de manière flexible dans différents contextes, ou à acquérir des compétences communicatives au contact de ses congénères ; soit à des **propriétés structurelles de la communication**, comme l'utilisation de signaux pour référer à un sens spécifique (sémantique), ou la combinaison de signaux selon des règles précises pour former de nouveaux sens (syntaxe) (Liebal *et al.* 2014).

De nombreux parallèles ont ainsi été dressés entre le langage et la communication vocale des oiseaux et des cétacés, chez qui un apprentissage social peut par exemple être nécessaire pour acquérir l'ensemble du répertoire de vocalisations (chez les oiseaux chanteurs : Baptista et Gaunt 1997 ; les orques, *Orcinus orca* : Foote *et al.* 2006 ; les grands dauphins, *Tursiops truncatus* : McCowan et Reiss 1997). Comme chez l'humain, les liens sociaux façonnent leur communication vocale, pouvant faire émerger des similarités dans le répertoire d'individus affiliés, voire des phénomènes de convergence vocale (e.g. chez les étourneaux, *Sturnus vulgaris* : Hausberger 1995 ; les Cassicans flûteurs, *Gymnorhina tibicen* : Brown *et al.* 1988 ; les grands dauphins : Janik 1997 ; et l'humain : Gallois *et al.* 2005). On observe même un évitement actif de superpositions de signaux chez certains oiseaux comme les étourneaux (Henry *et al.* 2015), ce qui pourrait être le reflet d'un respect de tours de parole. Une proto-sémantique a été mise en évidence dans les vocalisations de différents oiseaux, encodant des informations sur l'identité du signaleur (e.g. chez les hirondelles à front blanc, *Hirundo pyrrhonota* : Stoddard et Beecher 1983) ou sur l'environnement extérieur (e.g. chez les séricornes à sourcils blancs, *Sericornis frontalis* : Platzen et Magrath 2005 ; chez les poules domestiques, *Gallus gallus domesticus* : Evans et Evans 1999). Des signaux visuels semblent également pouvoir être référentiels chez les corvidés (grands corbeaux, *Corvus corax* : Pika et Bugnyar 2011). De plus, les oiseaux combinent plusieurs unités vocales dans leurs chants, et de récents travaux montrent que cette organisation peut être proto-syntaxique (e.g. chez les mésanges de Chine, *Parus minor*, et les cratérope bicolores, *Turdoides bicolor* : Suzuki 2016; Engesser *et al.* 2016). Du fait de l'éloignement phylogénétique entre ces espèces et le genre *Homo* (Kumar et Hedges 1998), il est probable que les similarités observées entre le langage et ces systèmes de communication ne soient pas sous-tendues par des mécanismes homologues, mais soient plutôt le fruit de *convergences évolutives*. Ainsi, étudier ces propriétés dans la communication d'espèces distantes permet de conjecturer sur les contraintes sociales et environnementales ayant conduit à leur émergence (Henry *et al.* 2015).

Pour rechercher des propriétés homologues à celles du langage dans la communication d'animaux non-humains, il est en revanche plus pertinent de s'intéresser aux espèces qui nous sont les plus proches,

c'est-à-dire aux primates (Steiper et Young 2006; Chatterjee *et al.* 2009; Springer *et al.* 2012). Une première approche, pour étudier les origines du langage, fut historiquement de se questionner sur la capacité des grands singes à apprendre ce moyen de communication. Bien que les tentatives d'apprendre le langage parlé à des chimpanzés (*Pan troglodytes*) se soient toujours soldées par des échecs (e.g. Kellogg et Kellogg 1933; Hayes et Hayes 1951), plusieurs grands singes furent capables d'apprendre la langue des signes (e.g. la chimpanzé Washoe et la gorille Koko, *Gorilla gorilla* : Gardner et Gardner 1969; Patterson et Cohn 1990) ou à communiquer grâce à des lexigrammes (e.g. le bonobo Kanzi, *Pan paniscus*, et le chimpanzé Nim : Savage-Rumbaugh *et al.* 1985), utilisant aussi bien des mots seuls qu'en combinaisons. Ces résultats suggéraient ainsi la capacité des grands singes à utiliser des signaux arbitraires pour faire référence à des objets ou des concepts (sémantique), et à combiner plusieurs signes pour former de nouveaux sens (syntaxe). La deuxième approche, actuellement privilégiée, est celle de l'étude de la communication spontanée des primates non-humains, aussi bien en captivité qu'à l'état sauvage. La communication vocale, gestuelle et faciale de différentes espèces est ainsi caractérisée, dans une perspective comparative (e.g. Call et Tomasello 2007; Arbib *et al.* 2008; Lemasson et Barbu 2011; Slocombe *et al.* 2011; Ghazanfar *et al.* 2012; Liebal *et al.* 2014; Meguerditchian 2014; Bouchet *et al.* 2016; Tomasello et Call 2018).

1.3. Théories sur l'origine du langage

La caractérisation de la communication spontanée des primates non-humains a mené à l'identification de propriétés « langagières » sous-tendant leurs vocalisations, leurs expressions faciales ou leurs gestes. Plusieurs théories ont alors été formulées, proposant différentes modalités de communication comme précurseur du langage.

1.3.1. Origine vocale du langage

Une première théorie est celle d'une origine vocale du langage (e.g. Masataka 2003; Seyfarth *et al.* 2005; Zuberbühler *et al.* 2009; Lemasson et Barbu 2011). Le premier argument en faveur de cette théorie est la nature référentielle de certaines vocalisations des primates non-humains, pouvant être qualifiées de **proto-sémantiques**. Des vocalisations spécifiques peuvent ainsi faire référence à des éléments extérieurs comme un type de prédateur (e.g. chez les vervets, *Chlorocebus pygerythrus*, et les mones de Campbell, *Cercopithecus campbelli* : Seyfarth *et al.* 1980; Seyfarth et Cheney 2003; Ouattara *et al.* 2009) ou un type d'aliment (e.g. chez les chimpanzés : Slocombe et Zuberbühler 2005). Les vocalisations peuvent également véhiculer des informations sur le signaleur, comme son rang hiérarchique ou son état émotionnel (e.g. chez les cercopithèques : Fischer *et al.* 2004; Lemasson *et al.* 2012). De plus, une **proto-syntaxe** a été mise en évidence dans la communication vocale de plusieurs espèces de catarrhiniens, plusieurs unités vocales pouvant être combinées de manière non-aléatoire pour

encoder un sens précis (e.g. Arnold et Zuberbühler 2006, 2012; Clarke *et al.* 2006; Ouattara *et al.* 2009; Schel *et al.* 2010; Collier *et al.* 2014; Coye *et al.* 2015, 2016, 2018).

Un autre argument majeur en faveur de l'hypothèse d'une origine vocale du langage est la flexibilité de production des vocalisations en fonction de facteurs sociaux. Des **règles conversationnelles** peuvent être identifiées dans les échanges vocaux de plusieurs espèces de singes platyrrhiniens et catarrhiniens, avec notamment un respect de tours de parole, un évitement du recouvrement des cris et un choix d'interlocuteurs dépendant de caractéristiques individuelles et de relations de dominance (e.g. Snowdon et Cleveland 1984; Sugiura et Masataka 1995; Lemasson et Hausberger 2004; Lemasson *et al.* 2010, 2018; Arlet *et al.* 2015; Bouchet *et al.* 2017; Levréro *et al.* 2019; Pougnauld *et al.* 2020a, b). Un **apprentissage social** pourrait être nécessaire pour apprendre ces règles sociales ou produire des vocalisations dans un contexte approprié (e.g. Seyfarth et Cheney 1997; chez les mones de Campbell : Lemasson *et al.* 2011a; les macaques japonais, *Macaca fuscata* : Bouchet *et al.* 2017; les gorilles : Pougnauld *et al.* 2020b). Chez des singes platyrrhiniens et catarrhiniens, des phénomènes de **convergence vocale** peuvent émerger entre individus selon leurs affiliations (e.g. Snowdon et Elowson 1999; Lemasson *et al.* 2011b; Candiotti *et al.* 2012; Watson *et al.* 2015; Marco *et al.* 2019), ou leurs relations hiérarchiques (Lemasson *et al.* 2016; Marco *et al.* 2019), signifiant une influence sociale sur la plasticité vocale des primates. Enfin, la production de vocalisations peut être dépendante de la présence d'une audience et de sa composition (e.g. chez les tamarins à crête blanche, *Saguinus oedipus* : Roush et Snowdon 2000; les chimpanzés : Slocombe et Zuberbühler 2007; les bonobos : Clay et Zuberbühler 2012; Clay *et al.* 2015), voire du niveau de connaissance des receveurs sur l'environnement extérieur (e.g. chez les semnopithèques de Thomas, *Presbytis thomasi* : Wich et de Vries 2006; les chimpanzés : Crockford *et al.* 2012; Schel *et al.* 2013), suggérant une possible **intentionnalité** (voir partie 3.1.).

1.3.2. *Origine labiale de la parole*

Une autre théorie propose que le langage parlé ait émergé de la capacité des primates à articuler **rythmiquement** les lèvres et la langue dans leur communication vocale et faciale (e.g. Ghazanfar *et al.* 2012; Bergman 2013; Ghazanfar et Takahashi 2014). Lorsque les humains parlent, les mouvements de fermeture et d'ouverture de la bouche suivent un rythme typique de 2 à 7 Hz (Chandrasekaran *et al.* 2009), et les signaux acoustiques sont émis sur une rythmicité allant de 3 à 8 Hz (Ghazanfar et Takahashi 2014). Cette même temporalité est retrouvée dans les vocalisations de plusieurs primates (e.g. Ghazanfar et Takahashi 2014 ; chez les babouins gelada, *Theropithecus gelada* : Gustison et Bergman 2017 ; les orang-outans, *Pongo pygmaeus* : Lameira *et al.* 2015 ; les macaques Rhésus et à face rouge, *Macaca mulatta* et *M. articoides* : Cohen *et al.* 2007; Toyoda *et al.* 2017). De plus, le rythme d'articulation des lèvres, de la langue et de l'os hyoïde est similaire dans la production d'expressions faciales comme le « lipsmacking », produite en contexte affiliatif (e.g. chez les babouins gelada : Bergman 2013 ; les

macaques Rhésus : Ghazanfar *et al.* 2010, 2012 ; les chimpanzés : Pereira *et al.* 2020), ou le « teeth-chattering » (e.g. chez les macaques à face rouge : Toyoda *et al.* 2017). Enfin, chez les macaques, le développement de la rythmicité du lipsmacking est semblable à l'ontogénie de la parole chez l'humain (Morrill *et al.* 2012), renforçant cette hypothèse de précurseurs du langage parlé dans la communication oro-faciale des primates.

1.3.3. *Origine gestuelle du langage*

La théorie d'une origine gestuelle du langage a également été formulée, en raison des mécanismes cognitifs et cérébraux sous-tendant la communication gestuelle des primates non-humains (e.g. Hewes *et al.* 1973; Corballis 2003, 2010; Gentilucci et Corballis 2006; Arbib *et al.* 2008; Meguerditchian et Vauclair 2008, 2014; McNeill 2012). L'un des principaux arguments en faveur d'une origine gestuelle du langage est en effet l'utilisation **flexible** et probablement **intentionnelle** des gestes par les primates non-humains, en particulier les grands singes (e.g. Call et Tomasello 2007; Meguerditchian et Vauclair 2008; Hobaiter et Byrne 2013b; Tomasello et Call 2018). Un même geste peut être utilisé de manière flexible dans différents contextes, et un même contexte éliciter différents gestes (e.g. chez les chimpanzés : Tomasello *et al.* 1994), ce qui peut être significatif d'une utilisation stratégique des signaux pour atteindre un but social précis (« means-ends dissociation », Bruner 1981. Voir partie 3.3.2.). A cette notion de flexibilité est liée une taille importante des répertoires de gestes en comparaison aux répertoires de vocalisations (e.g. Call et Tomasello 2007; répertoire de gestes des siamangs, *Symphalangus syndactylus* : Liebal *et al.* 2004c; des bonobos : Pika *et al.* 2005b; Graham *et al.* 2017; des chimpanzés : Hobaiter et Byrne 2011b; Roberts *et al.* 2014a; des gorilles : Genty *et al.* 2009; des macaques de Barbarie et des macaques à bonnet, *Macaca sylvanus* et *M. radiata* : Hesler et Fischer 2007; Gupta et Sinha 2019; des babouins olive, *Papio anubis* : Molesti *et al.* 2019;). De plus, la communication gestuelle spontanée des grands singes est associée à des marqueurs comportementaux d'intentionnalité (revues de littérature : Leavens *et al.* 2005; Liebal *et al.* 2014; Byrne *et al.* 2017; Tomasello et Call 2018, voir partie 3.1.3.). Cette communication gestuelle est également flexible en termes d'**apprentissage**, les individus les plus âgés ayant un répertoire plus restreint que les juvéniles et une utilisation des gestes plus efficace (e.g. chez les grands singes : Tomasello *et al.* 1985, 1994; Pika *et al.* 2005a; Call et Tomasello 2007; Hobaiter et Byrne 2011a). Les gestes des primates non-humains peuvent aussi présenter des propriétés **référentielles**, et notamment être *déictiques*, c'est-à-dire produits pour orienter l'attention du receveur vers un objet extérieur, comme dans le cas des gestes de pointage (e.g. Blaschke et Ettliger 1987; Call et Tomasello 1994; Genty et Zuberbühler 2014; Krause *et al.* 2018). Chez les bonobos, les gestes d'invitation (« beckoning gestures ») sont également un cas de gestes référentiels *iconiques*, c'est-à-dire représentant physiquement l'action à laquelle ils font référence (Genty et Zuberbühler 2014).

Outre ces propriétés sociocognitives, la théorie d'une origine gestuelle du langage s'appuie en grande partie sur la **latéralité** comportementale et neuro-anatomique mise en évidence dans la communication gestuelle des primates humains et non-humains (e.g. Meguerditchian et Vauclair 2014; Prieur *et al.* 2018, 2019a, b. Voir partie 3.2.). La communication verbale et non-verbale humaine est en effet latéralisée en faveur du côté droit, en raison d'une spécialisation de l'hémisphère gauche pour les fonctions langagières, en particulier au niveau des aires de Broca et de Wernicke (e.g. Broca 1865; Wernicke 1874; Kimura 1973; Grossi *et al.* 1996; Lieberman 2002; Cooper 2006; Meguerditchian *et al.* 2013b). Similairement, plusieurs primates non-humains présentent une latéralité gestuelle à droite à échelle populationnelle, dissociée d'une latéralité manuelle pour des actions non-communicatives (e.g. les chimpanzés : Meguerditchian *et al.* 2010; Hobaiter et Byrne 2013a; Prieur *et al.* 2016a ; les gorilles : Prieur *et al.* 2016b ; les babouins olives : Meguerditchian et Vauclair 2006, 2009; Meguerditchian *et al.* 2011b; Meunier *et al.* 2013c ; les mones de Campbell et les mangabeys à collier, *Cercocebus torquatus* : Maille *et al.* 2013). Chez les grands singes, cette latéralité gestuelle est associée à des asymétries anatomiques voire fonctionnelles au niveau des régions cérébrales homologues aux aires de Broca et de Wernicke (e.g. Gannon *et al.* 1998; Cantalupo et Hopkins 2001; Hopkins et Cantalupo 2004; Tagliatalata *et al.* 2006, 2008). Ces constatations ont mené à l'hypothèse que la spécialisation de l'hémisphère gauche pour le langage humain soit héritée d'une spécialisation de certaines régions cérébrales pour la communication gestuelle intentionnelle.

1.3.4. *Origine multimodale et multicausale du langage*

Des propriétés langagières étant retrouvées aussi bien dans la communication vocale, faciale et gestuelle des primates non-humains, l'hypothèse d'une *origine multimodale* du langage a été formulée, proposant que le langage résulte au moins en partie d'une coévolution de ces différents systèmes de communication (e.g. Arbib *et al.* 2008; Masataka 2008a; Tagliatalata *et al.* 2011; Slocombe *et al.* 2011; Meguerditchian *et al.* 2013a; Gillespie-Lynch *et al.* 2014; Liebal *et al.* 2014; Meguerditchian et Vauclair 2014; Levinson et Holler 2014; Fröhlich *et al.* 2019; Prieur *et al.* 2019a). Il a par exemple été suggéré que les propriétés langagières liées à la *perception* du langage aient émergé de caractéristiques de la communication vocale des primates (e.g. référentialité), et que les précurseurs de caractéristiques liées à la *production* du langage (e.g. intentionnalité) soient quant à eux retrouvés dans leur communication gestuelle (Meguerditchian et Vauclair 2008, 2010). La théorie d'une origine multimodale du langage est basée en particulier sur le constat de la **nature multimodale de la communication des primates** humains (e.g. Ekman 1979, 2004; Iverson et Goldin-Meadow 1998; Goldin-Meadow 1999; Vigliocco *et al.* 2014) et non-humains (e.g. Jones et Van Cantfort 2007; Pollick et De Waal 2007; Micheletta *et al.* 2013; Tagliatalata *et al.* 2015; Wilke *et al.* 2017; Hobaiter *et al.* 2017; Genty 2019). Les primates intègrent plusieurs types de signaux dans leur communication (vocalisations, gestes, expressions faciales, regards), pouvant être perçus via différentes modalités sensorielles (Liebal *et al.* 2014, voir

partie 2.4.), ces différentes modalités ayant supposément des **fonctions complémentaires** pour transmettre efficacement de l'information (e.g. Fröhlich et van Schaik 2018). La théorie d'une origine multimodale du langage s'appuie également sur des données collectées chez l'humain, suggérant l'existence d'un **système bimodal** contrôlant la communication vocale et gestuelle dans l'hémisphère gauche (e.g. Gentilucci et Corballis 2006; Bernardis *et al.* 2008; Gentilucci et Volta 2008), ainsi qu'un rôle important de la communication gestuelle dans le développement du langage vocal (revues de littérature : Meguerditchian *et al.* 2013a; Vauclair et Cochet 2013, 2016). Plusieurs scénarii évolutifs ont été proposés, suggérant une coévolution des systèmes gestuels et vocaux, et l'émergence de propriétés langagières à partir de l'un ou l'autre de ces systèmes à différents niveaux phylogénétiques (e.g. Meguerditchian *et al.* 2013a; Levinson et Holler 2014; Fröhlich *et al.* 2019).

Ces propriétés sont susceptibles de s'être développées sous la contrainte de changements écologiques et sociaux chez les ancêtres communs aux humains et aux autres primates actuels, nous menant à considérer une *origine multicausale* du langage (Prieur *et al.* 2019a). Ces changements peuvent notamment être un passage d'habitats arboricoles à terrestres, avec d'avantage de visibilité et un changement de postures de locomotion (e.g. Gentilucci et Corballis 2006; McNeill 2012), ou des changements de socialité impliquant différents niveaux de coopération, de compétition, de transmission culturelle (e.g. Dunbar 1996, 2003, 2009; Kaplan *et al.* 2009; Nowak et Highfield 2011; Burkart *et al.* 2018). En outre, différents facteurs peuvent impacter la communication des primates humains et non-humains, une balance coût-bénéfice de la production d'un signal s'établissant en fonction : des caractéristiques de l'espèce (comme l'écologie, la socialité, l'anatomie), des individus (comme des caractéristiques sociodémographiques, de personnalité, de génétique), du contexte interactionnel (comme le type de contexte social, la valence émotionnelle, la présence et la composition d'une audience ...), ou des signaux communicatifs eux-mêmes (comme leur modalité sensorielle, leurs composants, leur structuration en séquence, leur signification) (Prieur *et al.* 2018, 2019a). Ainsi, dans la perspective d'étudier les origines du langage, la communication des primates non-humains est de plus en plus considérée via une **approche multimodale** (intégrant différents types et modalités de signaux), mais aussi **multifactorielle** (en prenant en compte les facteurs ultimes et proximaux à l'origine de la production des signaux) (e.g. Waller *et al.* 2013; Liebal *et al.* 2014; Fröhlich et van Schaik 2018; Fröhlich *et al.* 2019; Prieur *et al.* 2019a).

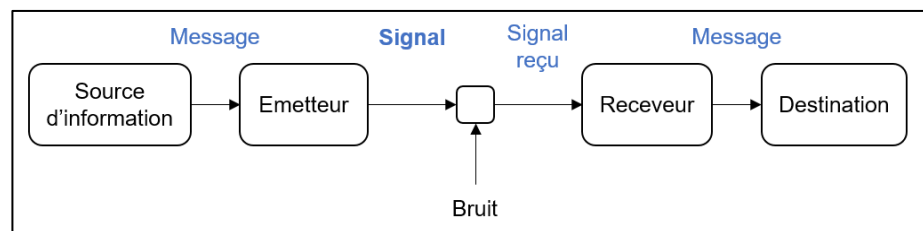
2. Décrire la communication gestuelle et multimodale chez les primates non-humains

Avant d'aborder plus en détail les propriétés langagières pouvant être caractérisées dans la communication gestuelle et multimodale des primates non-humains, et auxquelles nous nous intéresserons dans ce travail, nous présenterons ici la manière dont nous pouvons définir ces signaux.

2.1. Qu'est-ce qu'un signal communicatif ?

La communication est un processus par lequel une information est transmise d'un signaleur vers un receveur, impactant le comportement de celui-ci de manière indirecte (Altmann 1967; Deputte 1981; Zuberbühler 2012; Liebal *et al.* 2014b; Beauchaud 2019). Plus précisément, cette information est encodée dans une certaine modalité sensorielle, sous forme de signal, pour être perçue puis décodée par le receveur (Ruxton et Schaefer 2011; Zuberbühler 2012; Higham et Hebets 2013). Des perturbations indépendantes de l'émetteur, ou « bruits » de l'environnement, peuvent parfois affecter le signal (voir le modèle de communication proposé par Shannon et Weaver 1948, 1949. **Figure 1**). Un **signal communicatif** est ainsi un comportement, ayant été sélectionné pour la fonction de transmission d'une information, et provoquant un changement de comportement chez le receveur (Ruxton et Schaefer 2011; Laidre et Johnstone 2013). Un signal communicatif est à distinguer d'un **indice**, correspondant à un élément informatif secondaire, pouvant être perçu par le receveur mais véhiculé par l'émetteur de façon incontrôlée, par sa seule présence ou par ses caractéristiques (Deputte 1981; Smith et Harper 1995; Maynard-Smith *et al.* 2003; Tomasello 2008; Ruxton et Schaefer 2011).

Figure 1. Modèle de communication de Shannon et Weaver (1948, 1949).



2.2. Gestes communicatifs

Les gestes occupent une place significative dans la communication des primates, qui s'appuie grandement sur la modalité visuelle (e.g. Redican 1975; Cartmill *et al.* 2012; Liebal et Call 2012; Pika et Liebal 2012; Gillespie-Lynch *et al.* 2014; Liebal *et al.* 2014; Byrne *et al.* 2017; Tomasello et Call 2018; Liebal et Oña 2018). Chez l'humain, la communication gestuelle se développe en amont du langage articulé, notamment à travers la production de gestes de pointage, et constitue une étape clé dans l'ontogénèse de la communication verbale (e.g. Bretherton et Bates 1979; Butterworth 2003; Vauclair et Cochet 2016). Ainsi, les définitions de gestes communicatifs chez les primates non-humains se sont principalement construites à partir des nombreuses études de psychologie du développement s'intéressant aux gestes des enfants préverbaux (Liebal *et al.* 2014).

Bien que certains critères de définition diffèrent selon les auteurs, tous s'accordent sur la **nature communicative** du geste (revues de littérature : Scott et Pika 2012; Hobaiter et Byrne 2017; Bourjade *et al.* 2020). Pour différencier les gestes d'actions non-communicatives, ceux-ci doivent d'une part être produits **socialement**, c'est-à-dire en direction d'un receveur (e.g. Tomasello *et al.* 1985, 1994; Leavens

et Hopkins 1998; Leavens *et al.* 2004a; Liebal *et al.* 2004c; Pika *et al.* 2005b; Pollick et De Waal 2007; Genty et Zuberbühler 2014), ou a minima en présence d'une audience susceptible de percevoir ce signal (e.g. Call et Tomasello 2007; Genty *et al.* 2009). D'autre part, le geste, en tant que signal communicatif, doit pouvoir induire un **changement de comportement** chez le receveur (e.g. Liebal *et al.* 2004a, c, 2006; Pika 2008; Roberts *et al.* 2014a; Hobaiter *et al.* 2017; Gupta et Sinha 2019), et ce de manière indirecte. En ce sens, la plupart des auteurs définissent les gestes comme des mouvements **non-locomoteurs et « mécaniquement inefficaces »** (e.g. Pika *et al.* 2005b; Call et Tomasello 2007; Cartmill et Byrne 2007; Pollick et De Waal 2007; Hobaiter et Byrne 2011b, 2017; Scott et Pika 2012; Liebal et Call 2012; Bard *et al.* 2014; Fröhlich *et al.* 2017; Tomasello et Call 2018; Liebal et Oña 2018). Ce critère n'exclue pas cependant les gestes impliquant un contact avec un objet ou un receveur, tant que le mouvement n'est pas manipulateur et ne suffit pas de lui-même à induire un changement chez le receveur (e.g. Pollick et De Waal 2007b; Pollick *et al.* 2008; Gupta et Sinha 2019). Ainsi, un geste pourra être perçu via d'autres **modalités sensorielles** que la modalité visuelle, selon qu'il implique un contact physique avec le receveur (modalité tactile) ou qu'il implique la production d'un son (modalité acoustique) (e.g. Pika *et al.* 2003; Liebal *et al.* 2004a, 2014; Pika 2008; Fröhlich *et al.* 2016).

Dans certaines études, les gestes communicatifs ne sont considérés comme tels que s'ils sont supposément **intentionnels**, c'est-à-dire produits volontairement et stratégiquement par le signaleur pour atteindre un but social (e.g. Tomasello *et al.* 1985; Tanner et Byrne 1996; Pika *et al.* 2005; Liebal *et al.* 2006; Tomasello 2008; Genty *et al.* 2009; Hobaiter et Byrne 2011b; Cochet 2012; Roberts *et al.* 2012b; Fröhlich *et al.* 2016. Voir partie 3.1.1.). Pour remplir ce critère, en plus d'être dirigé vers un ou des receveurs, le geste devra être accompagné de marqueurs comportementaux suggérant qu'il est produit dans un but précis (voir partie 3.1.2.). L'un des principaux points de divergence dans la définition des gestes réside dans la forme physique de ce signal, concernant plus précisément les parties du corps mobilisées. Certaines définitions réduisent la notion de geste aux mouvements **brachio-manuels** (e.g. Leavens et Hopkins 1998; Pollick et De Waal 2007; Leavens *et al.* 2010; Roberts *et al.* 2012b, 2014a), voire aux mouvements brachio-manuels dits « libres », n'impliquant aucun contact avec un substrat ou le receveur (e.g. Pollick et De Waal 2007; Roberts *et al.* 2012b, 2014a). Selon cette définition stricte, il a été supposé par certains auteurs que les singes non-hominoïdes n'utilisaient pas de gestes brachio-manuels dans leur communication spontanée intraspécifique (Call et Tomasello 2007; Pollick et De Waal 2007; Cartmill *et al.* 2012; Roberts *et al.* 2012b, 2014a). A l'inverse, d'autres auteurs considèrent comme gestes des **mouvements de la tête et du tronc**, ainsi que des **postures** (e.g. Tanner et Byrne 1996; Pika *et al.* 2005; Call et Tomasello 2007; Pika et Liebal 2012). Enfin, certaines études s'intéressent à la communication gestuelle au sens large, incluant dans cette définition les **expressions faciales** (e.g. Maestriperi 1996, 1997; Liebal *et al.* 2006; Cartmill et Byrne 2007, 2010; Hesler et Fischer 2007).

2.3. Expressions faciales

Les primates ont une musculature faciale particulièrement complexe (Hill 1974; Burrows 2008; Diogo *et al.* 2009), leur permettant de produire une grande diversité de mouvements. Les expressions faciales correspondent ainsi à des mouvements **communicatifs** de la bouche, des lèvres, des paupières, des sourcils, et/ ou des oreilles dans le cas des primates non-humains (e.g. Van Hooff 1967; Waller et Micheletta 2013; Müri 2016). Ces mouvements peuvent être d'amplitudes différentes et donc être **graduels**, possiblement en conséquence de différents niveaux de motivation de la part du signaleur (e.g. Preuschoft et van Hooff 1996; Parr *et al.* 2005; Waller et Micheletta 2013).

La description et l'étude des expressions faciales des primates s'est classiquement basée sur les **émotions** qui leur sont associées (e.g. Liebal *et al.* 2014; Waller *et al.* 2016a). Dans « L'expression des émotions chez l'homme et les animaux », Darwin (1872) qualifie les expressions faciales de « contrepartie inévitable des émotions ressenties » par le sujet. Bien que le lien entre émotion et expression faciale soit confirmé (e.g. Levenson *et al.* 1990; Porter *et al.* 2012), l'aspect « inévitable » de ces expressions évoqué par Darwin est aujourd'hui remis en question par les données neuro-anatomiques émanant d'études sur les humains et les primates catarrhiniens. En effet, leurs expressions faciales sont à la fois contrôlées par des aires corticales permettant *l'expression d'émotions*, via des innervations des muscles faciaux reliées au système limbique, au niveau du gyrus cingulaire, et permettant des *mouvements volontaires*, au niveau d'aires du cortex moteur différentes de celles contrôlant les mouvements des membres (Sherwood *et al.* 2004, 2005; Cattaneo et Pavesi 2014; Müri 2016; Sliwa *et al.* 2018). Etudier les expressions faciales par le seul prisme des émotions du signaleur ne permet pas d'appréhender pleinement la **fonction communicative** de ces mouvements faciaux, au sens de *signaux* et non d'*indices* informant de l'état émotionnel du sujet (voir partie 2.1.). Ainsi, dans la perspective de l'étude comparative de la communication des primates, les expressions faciales sont plutôt considérées du point de vue de leur fonction sociale (e.g. « the Behavioural Ecology View », Fridlund 2002) et peuvent être définies, comme pour les gestes, comme des signaux dirigés vers un ou des receveurs et induisant un changement de comportement chez ces derniers. En ce sens, la description des expressions faciales selon leur **morphologie** est privilégiée, avec une volonté grandissante de gain en objectivité (Waller *et al.* 2016a).

2.4. Communication multimodale

Comme évoqué précédemment (voir partie 1.3.4.), la communication des primates non-humains est de plus en plus étudiée sous l'angle de la multimodalité. Les termes de « communication multimodale » couvrent cependant des sens différents, selon que l'on s'intéresse à la modalité de *perception* ou de *production* des signaux. La multimodalité peut ainsi faire référence à des signaux pouvant être perçus sur plusieurs **canaux sensoriels** (par exemple, acoustique et visuel. Partan et Marler 1999, 2005), ou à

des combinaisons de plusieurs **types de signaux** communicatifs (par exemple, des gestes combinés à des vocalisations. Pollick et De Waal 2007; Genty *et al.* 2014; Tagliabue *et al.* 2015), ou bien inclure ces deux possibilités (Liebal *et al.* 2014). Higham et Hebets (2013) proposent des définitions permettant de discriminer ces deux aspects, en distinguant la « **communication multimodale** », impliquant différentes modalités sensorielles, de la « **communication multicomposante** » impliquant différents types de signaux, perçus ou non sur la même modalité sensorielle. Chez les primates non-humains, la communication multimodale est principalement étudiée à travers les modalités visuelle, acoustique et tactile, les études multimodales portant principalement sur des combinaisons de gestes, de vocalisations et d'expressions faciales (e.g. Leavens *et al.* 2004b; Jones et Van Cantfort 2007; Pollick et De Waal 2007; Micheletta *et al.* 2013; Genty *et al.* 2014; Hobaiter *et al.* 2017). Il est à noter que la communication des primates peut inclure des signaux délivrés sur d'autres modalités, notamment olfactive, dont la mesure est toutefois limitée par des contraintes méthodologiques (Heymann 2006; Liebal *et al.* 2014).

Pour décrire la communication multimodale des primates, il est important de définir enfin si l'on étudie les combinaisons « **fixes** » ou « **libres** » de modalités (Higham et Hebets 2013). Certains signaux communicatifs peuvent en effet être intrinsèquement multimodaux (multimodalité « fixe », Partan et Marler 2005), puisque perceptible sur différents canaux sensoriels. C'est en particulier le cas des vocalisations, qui, même si elles sont perçues sur la modalité acoustique, sont nécessairement associées à des mouvements faciaux spécifiques. Ces mouvements constituent une composante visuelle du signal, perceptible voire identifiable par les receveurs (e.g. Ghazanfar et Logothetis 2003; Izumi et Kojima 2004; Ghazanfar *et al.* 2005). La multimodalité pourra aussi résider dans des combinaisons « libres » de signaux (Partan et Marler 2005; Fröhlich et van Schaik 2018), pouvant aussi bien être associés ou produits indépendamment les uns des autres. C'est le cas par exemple des combinaisons de gestes et de vocalisations utilisés dans des contextes spécifiques (e.g. Wilke *et al.* 2017; Genty 2019), et qui peuvent être significatifs d'une utilisation flexible des signaux par les primates (voir partie 3.3.3.).

3. Propriétés cognitives « langagières » dans la communication gestuelle des primates non-humains

Voyons à présent plus en détail les propriétés sociocognitives potentiellement impliquées dans la communication des primates. Nous nous intéresserons en particulier à la communication gestuelle (au sens large, i.e. impliquant des gestes brachio-manuels, des postures et mouvements du corps) et aux expressions faciales des primates, en termes d'intentionnalité, c'est-à-dire d'utilisation stratégique des signaux pour atteindre un but social précis, et de latéralité. La latéralité de cette communication gestuelle intentionnelle est d'un intérêt particulier concernant l'étude de l'émergence du langage, car elle pourrait avoir la même origine que la spécialisation de l'hémisphère gauche pour le contrôle des fonctions langagières chez l'humain. Nous aborderons enfin la question de la flexibilité de la communication

gestuelle et multimodale, qui peut être le reflet d'une utilisation stratégique de signaux dans le cas d'une communication intentionnelle.

3.1. Intentionnalité

3.1.1. Définir l'intentionnalité de la communication

L'étude de l'intentionnalité de la communication humaine et non-humaine actuelle est en majorité basée sur le concept théorisé par le philosophe et linguiste Paul Grice. Selon le point de vue **Gricéen**, un individu produisant un signal intentionnel communique *quelque chose* au receveur, et agit non seulement avec l'intention de modifier le comportement ou l'état mental de l'individu auquel il s'adresse, mais fait en sorte que le receveur lui-même reconnaisse cette intention pour y répondre (Grice 1957, 1969). Dans cette communication dite « ostensive », le signaleur et le receveur comprennent mutuellement les intentions et pensées de l'autre (Tomasello 2008; Scott-Phillips 2015; Townsend *et al.* 2017), et cette intentionnalité partagée est une capacité cognitive et sociale clé pour l'émergence du langage (Malle *et al.* 2001; Tomasello et Carpenter 2007; Tomasello et Rakoczy 2007; Tomasello 2008; Call 2009). Cette définition théorique, imputable à la communication linguistique, pose ainsi un cadre pour la formulation de définitions opérationnelles, plus applicables pour l'étude de la communication des animaux non-humains. Dans la continuité de la pensée « Gricéenne », Dennett (1983) propose de distinguer différents **niveaux d'intentionnalité** dans la communication animale. Pour illustrer cette classification, il donne l'exemple d'un singe vervet, Tom, produisant un cri d'alarme en présence d'un autre individu, Sam :

- Intentionnalité d'ordre zéro : Le signaleur n'a aucune intention de communication, et produit le signal « automatiquement » en réponse à un stimulus extérieur spécifique. Exemple : *Tom produit un cri d'alarme en réaction à l'excitation provoquée par un danger.*
- Intentionnalité de premier ordre : Le signaleur agit dans le but de changer le comportement du receveur. Exemple : *Tom produit un cri d'alarme pour que Sam fuie.*
- Intentionnalité de second ordre : Le signaleur agit dans le but de changer l'état mental du receveur. Ce degré d'intentionnalité implique une « attribution d'un état mental » au receveur de la part du signaleur. Exemple : *Tom produit un cri d'alarme pour que Sam pense qu'il y a un danger.*

- Intentionnalité de troisième ordre : Le signaleur agit avec l'intention de changer l'état mental du receveur, pour que celui-ci reconnaisse son intention de changer son comportement. Exemple : *Tom produit un cri d'alarme pour que Sam pense que Tom veut qu'il fuie.*
- Intentionnalité de quatrième ordre : Le signaleur agit avec l'intention de changer l'état mental du receveur et que celui-ci reconnaisse cette intention. Exemple : *Tom produit un cri d'alarme pour que Sam sache que Tom veut qu'il pense qu'il y a un danger.*

L'intentionnalité de la communication chez les animaux non-humains est principalement basée sur le **premier niveau d'intentionnalité**. Certains auteurs défendent toutefois l'intentionnalité de second ordre comme plus pertinente à étudier dans une perspective de recherche des précurseurs du langage (e.g. Graham *et al.* 2019), ce niveau d'intentionnalité étant considéré comme plus représentatif d'une communication linguistique (Grice 1957). Sa mesure est cependant moins accessible méthodologiquement, et d'autres auteurs avancent que rechercher directement cette « attribution d'un état mental » risquerait de nous faire passer à côté de certaines caractéristiques de la communication des animaux non-humains, pour qui cette capacité n'est pas vérifiée (e.g. Townsend *et al.* 2017). L'objectif d'étudier l'intentionnalité de la communication des primates n'est pas de tester chez eux l'existence d'une communication linguistique, mais de comprendre l'évolution de cette propriété langagière en recherchant les précurseurs (voir partie 1.2.). Ainsi, s'intéresser à l'intentionnalité de premier ordre dans leur communication constitue un premier pas pour la compréhension des origines de cette capacité (Townsend *et al.* 2017; Graham *et al.* 2019).

En ce sens, un signal sera considéré comme intentionnel s'il est volontairement produit par un signaleur *en direction d'un receveur* et dans le *but* de provoquer un *changement de comportement* chez ce dernier, le signaleur ayant recours à différentes stratégies communicatives pour atteindre ce but (Bretherton et Bates 1979; Tomasello *et al.* 1985; Bard 1992; Roeder et Gosset 2001; Hobaiter et Byrne 2013b). Différents **marqueurs comportementaux** sont alors recherchés dans la communication des primates non-humains, la plupart étant hérités d'études de psychologie du développement chez l'enfant, afin d'évaluer si le signaleur se comporte *comme si* son signal était intentionnel (e.g. Bretherton et Bates 1979; revues de littérature : Leavens *et al.* 2005; Liebal *et al.* 2014; Byrne *et al.* 2017).

3.1.2. Des marqueurs comportementaux pour mesurer l'intentionnalité

Récemment, Townsend *et al.* (2017) ont proposé une méthodologie basée sur trois grands **critères** à valider pour définir un signal communicatif comme intentionnel, vérifiant par différents marqueurs comportementaux que le signal : (i) est produit dans un but social précis ; (ii) est dirigé vers un receveur pour atteindre ce but ; (iii) produit un changement de comportement chez ce receveur, cohérent avec l'intention supposée du signaleur.

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- (i) Le premier critère d'intentionnalité, i.e. le fait que le signal soit produit dans un but précis (« goal-directedness »), peut être vérifié lorsque le signaleur **stoppe la production du signal** une fois ce but présumé atteint (e.g. Leavens *et al.* 2005). Lorsque le receveur ne répond pas favorablement à un signal intentionnel, il est attendu que le signaleur agisse stratégiquement pour que son but soit satisfait, en particulier en répétant le signal (**persistance**), en modifiant la forme du signal ou en en produisant de nouveaux (**élaboration**) (e.g. Liebal *et al.* 2004c; Leavens *et al.* 2005; Cartmill et Byrne 2007, 2010; Hobaiter et Byrne 2011b; Roberts *et al.* 2013; Graham *et al.* 2017; Gupta et Sinha 2019). De plus, si le signaleur maintient son regard en direction du receveur après avoir produit son signal, cela peut être significatif d'une **attente de réponse** du receveur (e.g. Tomasello *et al.* 1985, 1994; Pika *et al.* 2003; Liebal *et al.* 2004c; Call et Tomasello 2007; Cartmill et Byrne 2010; Hobaiter et Byrne 2011b; Roberts *et al.* 2012b, 2014a; Graham *et al.* 2017; Molesti *et al.* 2019).
- (ii) Le deuxième critère d'intentionnalité, i.e. le fait que le signal soit dirigé vers un receveur pour atteindre le but social (« social-directedness »), peut-être vérifié par différents indicateurs. D'une part, le signal doit être produit en présence d'un autre individu (« **social use** »), et être **physiquement dirigé** vers le receveur, via l'orientation du corps ou du regard du signaleur, ou s'il y a un contact physique entre le signaleur et le receveur (e.g. Tomasello *et al.* 1985, 1994; Leavens *et al.* 1996, 2004; Leavens et Hopkins 1998; Liebal *et al.* 2004c, 2014; Call et Tomasello 2007). Dans certains contextes, le signaleur pourra **alterner son regard** entre un objet extérieur et le receveur, indiquant à la fois une directionnalité sociale et une possible communication référentielle (e.g. Franco et Butterworth 1996; Gómez 2007). La **sensibilité à l'état attentionnel du receveur** est également un marqueur clé de ce second critère d'intentionnalité, qui sera vérifié si le signaleur produit préférentiellement des signaux visuels face à un receveur attentif (i.e. regardant en sa direction), ou adapte la modalité du signal à son état d'attention (e.g. Leavens *et al.* 2004; Liebal *et al.* 2004c; Poss *et al.* 2006; Call et Tomasello 2007; Maille *et al.* 2012; Bourjade *et al.* 2013b; Meunier *et al.* 2013c; Demuru *et al.* 2015). Ainsi, il pourra être noté si le signaleur vérifie l'état attentionnel de son receveur avant de produire un signal visuel (« **audience checking** ». Genty *et al.* 2009; Hobaiter et Byrne 2011b; Graham *et al.* 2017), et s'il cherche à attirer le regard de celui-ci en utilisant des signaux tactiles ou audibles (« **attention-getters** », e.g. Tomasello *et al.* 1994; Tomasello 2008).
- (iii) Le dernier critère, i.e. le fait que le signal provoque un **changement de comportement** chez le receveur, est en lien avec la nature communicative du signal (e.g. Marler 1967; Altmann

1968; Green 1975. Voir partie 2.1.), et permet de vérifier la nature du but social recherché par le signaleur. Ce changement de comportement doit être répétable et cohérent avec l'intention supposée du signaleur, le but social étant atteint ou « refusé » par le receveur (e.g. Liebal *et al.* 2004c, 2006; Roberts *et al.* 2012b, 2014a; Townsend *et al.* 2017).

Pour valider chacun des critères d'intentionnalité, un maximum de ces marqueurs doivent être observés (Schel *et al.* 2013), et les trois critères devront être vérifiés pour que le signal soit considéré comme intentionnel (Townsend *et al.* 2017). Cette méthodologie a l'avantage d'être applicable à différentes espèces et pour étudier différents types de communication (gestuelle, faciale, vocale). Elle présente cependant certaines limites, car les marqueurs d'intentionnalité présentés ci-dessus, pris indépendamment les uns des autres, peuvent être vérifiés dans le cas d'une communication non intentionnelle (Graham *et al.* 2019). Par exemple, si un signal est produit automatiquement en réponse à un stimulus extérieur (intentionnalité d'ordre zéro), il est probable que ce signal soit répété jusqu'à ce que le stimulus disparaisse, ce qui pourrait pourtant être interprété comme de la persistance. Un même stimulus pourrait aussi induire différents types de signaux, ce qui pourrait être interprété comme de l'élaboration. De plus, beaucoup de marqueurs comportementaux reposent sur la présence de regards du signaleur en direction du receveur, ce qui peut être observé dans des contextes élicitant davantage d'attention sociale. Enfin, un signal qui résulterait uniquement d'un changement d'état interne du signaleur pourrait être favorisé par le regard ou la simple présence d'autres individus, ces facteurs constituant des stimuli émotionnels (e.g. Zajonc 1965; Emery 2000). Dans ce cas, les signaux seraient préférentiellement produits en présence d'autres individus (« social use ») et en fonction de leur état attentionnel (Graham *et al.* 2019). Pour pallier à l'incertitude liée à l'interprétation de ces marqueurs, il est ainsi recommandé de s'appuyer sur un maximum d'indices comportementaux différents. En effet, plusieurs indices convergents sont plus susceptibles d'être expliqués par un seul mécanisme cognitif (intentionnalité) plutôt que par une série d'autres explications (e.g. Byrne et Bates 2006; Liebal *et al.* 2014c; Townsend *et al.* 2017), bien que chaque mécanisme cognitif possible doive être envisagé.

3.1.3. *La communication visuelle des primates non-humains est-elle intentionnelle ?*

Le fait que les gestes des primates soient produits dans un but précis fût d'abord étudié chez des jeunes chimpanzés captifs, à partir des marqueurs comportementaux développés dans les études de développement de l'enfant (Tomasello *et al.* 1985, 1989, 1994). Par la suite, se basant sur la définition de Bretherton et Bates (1979), Bard (1992) distingua la *communication* intentionnelle et les *autres comportements* intentionnels chez les orang-outans, se basant sur la directionnalité sociale des gestes. S'en suivirent de nombreuses études en captivité et à l'état sauvage mettant en évidence des marqueurs d'intentionnalité accompagnant les gestes des chimpanzés (e.g. Leavens et Hopkins 1998; Hostetter *et al.* 2001; Leavens *et al.* 2004b, 2005; Liebal *et al.* 2004b; Kaminski *et al.* 2004; Hobaiter et Byrne

2011a, b; Roberts *et al.* 2013, 2014a, b; Fröhlich *et al.* 2016; Graham *et al.* 2018), des bonobos (e.g. Pika *et al.* 2005; Halina *et al.* 2013; Demuru *et al.* 2015; Graham *et al.* 2018), des gorilles (e.g. Genty *et al.* 2009; Genty et Byrne 2010; Botting et Bastian 2019), des orang-outans (*P.pygmaeus* et *abelii*, e.g. Liebal *et al.* 2006; Cartmill et Byrne 2007, 2010; Russon et Andrews 2011; Tempelmann et Liebal 2012), et des siamangs (e.g. Liebal *et al.* 2004c). Il est ainsi admis que la communication gestuelle des grands singes est intentionnelle (Call et Tomasello 2007; Hobaiter et Byrne 2013b; Liebal *et al.* 2014; Byrne *et al.* 2017; Tomasello et Call 2018).

Les gestes des singes non-hominoïdes ont suscité moins d'attention (Slocombe *et al.* 2011). De premières descriptions de communication gestuelle intraspécifiques ont été faites chez les macaques Rhésus, les macaques à queue de cochon, et les macaques à face rouge (*M. mulatta*, *nemenstrina* et *articoïdes* : Maestriperieri 1996, 1997, 2005; Maestriperieri et Wallen 1997), mais sans s'intéresser aux marqueurs comportementaux d'intentionnalité comme étudié chez les grands singes. De nombreuses études expérimentales ont par la suite été réalisées en contexte interspécifique, impliquant des gestes de pointage ou de quémande appris et dirigés vers un expérimentateur humain pour obtenir une récompense. Chez plusieurs espèces de singes catarrhiniens et platyrrhiniens, une sensibilité à l'état attentionnel du receveur a été mise en évidence pour la production de ces gestes interspécifiques, avec souvent des alternances de regard entre le receveur et la récompense (e.g. chez les babouins olives : Bourjade *et al.* 2013a, b; Meunier *et al.* 2013c; Lamaury *et al.* 2017 ; les macaques de Tonkean, les macaques Rhésus et les macaques à bonnet, *M. tonkeana*, *M. mulatta* et *M. radiata* : Canteloup *et al.* 2015a, b ; Deshpande *et al.* 2018 ; les mangabeys à collier : Maille *et al.* 2012 ; les capucins, *Sapajus apella* : Hattori *et al.* 2007, 2010 ; et les singes écureuils, *Saimiri sciureus* : Anderson *et al.* 2007, 2010). Cela suggère une possible aptitude à communiquer intentionnellement chez ces espèces, mais ces expériences ne s'intéressant qu'à un nombre restreint de marqueurs d'intentionnalité, tous les critères n'en sont pas vérifiés (voir partie 3.1.2.). Récemment, deux études observationnelles ont mis en évidence des marqueurs d'intentionnalité accompagnant les gestes spontanés intraspécifiques des babouins olives (i.e. directionnalité, sensibilité et adaptation à l'état attentionnel du receveur, attente d'une réponse du receveur : Molesti *et al.* 2019) et des macaques à bonnet (i.e. directionnalité, sensibilité à l'état attentionnel du receveur, signal stoppé quand le but supposé est atteint, persistance ou élaboration dans le cas contraire, changement de comportement chez le receveur : Gupta et Sinha 2019). Ce sont, à notre connaissance, les seules études à s'être portées sur l'intentionnalité des gestes intraspécifiques de singes non-hominoïdes.

De plus, la potentielle intentionnalité de premier ordre de leurs expressions faciales n'a jamais été explorée. Des données neuro-anatomiques suggèrent un double contrôle volontaire et émotionnel des mouvements faciaux chez les primates catarrhiniens (e.g. Sherwood *et al.* 2004, 2005; Sliwa *et al.* 2018), et quelques données émanant d'observations des grands singes suggèrent un contrôle volontaire des expressions faciales (e.g. Hopkins *et al.* 2011b). Une implicite dichotomie oppose parfois la nature

émotionnelle et intentionnelle des signaux communicatifs dans la littérature, mais ces mécanismes peuvent au contraire agir en parallèle et être complémentaires (e.g. Liebal *et al.* 2014; Cattaneo et Pavesi 2014; Müri 2016). En effet, un signal peut être contrôlé et produit intentionnellement pour communiquer, et à la fois être associé voire motivé par un état émotionnel spécifique du signaleur. Chez les bonobos, les expressions faciales de jeu, associées à des émotions positives et une forte excitation, sont préférentiellement produites en contexte social et face à un receveur attentif (Demuru *et al.* 2015). Les mêmes résultats ont été obtenus chez les orang-outans, dont les expressions faciales de jeu impliquent davantage de mouvements faciaux lorsque le receveur regarde en direction du signaleur (Waller *et al.* 2015), et chez cinq espèces de gibbons, chez qui les expressions faciales sont de durée plus importante lorsque le signaleur et le receveur se font face (chez des siamangs, *S. syndactylus*, des gibbons à bonnet, *Hylobates pileatus*, des gibbons à mains blanches, *Hylobates lar*, des gibbons à joues jaunes, *Nomascus gabriellae*, et des gibbons à joues blanches, *Nomascus siki* : Scheider *et al.* 2016). Ces expressions faciales ne semblent donc pas être produites automatiquement pendant le jeu, mais d'autres mécanismes que l'intentionnalité pourraient expliquer ces résultats, comme une excitation plus importante face à un receveur visuellement attentif (voir partie 3.1.2.). Quelques études ont montré que les expressions faciales, au même titre que les gestes, pouvaient être accompagnées de certains marqueurs comportementaux d'intentionnalité chez les siamangs (Liebal *et al.* 2004c), les orang-outans (Cartmill et Byrne 2010) et les babouins olives (Molesti *et al.* 2019). Ces recherches restent jusqu'alors anecdotiques, et cette question de l'intentionnalité des expressions faciales, à notre connaissance, n'a jamais été abordée chez d'autres primates catarrhiniens. Ainsi, d'avantage de données sont nécessaires pour déterminer si les primates non-humains peuvent produire des expressions faciales intentionnellement pour communiquer (e.g. Arbib *et al.* 2008; Slocombe *et al.* 2011; Graham *et al.* 2019).

3.2. Latéralité

3.2.1. Spécialisation hémisphérique cérébrale pour la communication humaine

On observe chez l'humain une spécialisation de l'hémisphère gauche pour les fonctions langagières, avec en particulier une implication de l'aire de Broca (gyrus frontal inférieur gauche, aires de Broadmann 44-45) dans la production de la parole, et de l'aire de Wernicke (gyrus temporal supérieur gauche, aire 22) pour la compréhension du langage (e.g. Broca 1865; Wernicke 1874; Lieberman 2002; Cooper 2006). Cette spécialisation hémisphérique dans le contrôle du langage est associée à une asymétrie anatomique du *planum temporale*, plus développé du côté gauche (Lieberman 2002). Conjointement, la main droite est préférentiellement utilisée pour les gestes communicatifs, bien que certains individus puissent utiliser majoritairement le côté gauche pour communiquer (Vauclair 2004). A l'échelle populationnelle, on observe une préférence de la main droite pour les gestes accompagnant la parole (Kimura 1973; Vauclair 2004; Meguerditchian *et al.* 2013a), et pour les gestes communicatifs

utilisés dans la langue des signes (Grossi *et al.* 1996). De plus, la latéralité manuelle mesurée pour les gestes communicatifs est plus prononcée que celle observée pour des actions non-communicatives chez les enfants (e.g. Cochet et Vauclair 2010; Esseily *et al.* 2011), suggérant qu'ils ne soient pas contrôlés par les mêmes régions cérébrales que les autres mouvements manuels (Meguerditchian *et al.* 2013a). En effet, des données comportementales, neuro-anatomiques et fonctionnelles suggèrent que la production et la perception des gestes communicatifs soient sous-tendues par les mêmes régions cérébrales que le langage parlé, au niveau de l'hémisphère gauche (e.g. Gentilucci et Volta 2008; Xu *et al.* 2009; Meguerditchian *et al.* 2013a).

3.2.2. Latéralité gestuelle chez les primates non-humains

Chez les grands singes, une latéralité gestuelle en faveur du côté droit est également observée à échelle populationnelle, pour des gestes dirigés vers un expérimentateur humain (e.g. chez les chimpanzés, gorilles, bonobos et orang-outans : Hopkins *et al.* 2012 ; Hopkins et Leavens 1998; Hopkins *et al.* 2005), mais aussi pour des gestes intraspécifiques (e.g. chez les chimpanzés : Meguerditchian *et al.* 2010; Hobaiter et Byrne 2013a; Prieur *et al.* 2016a; les gorilles : Prieur *et al.* 2016b, 2017a, b). La même observation a été faite chez les babouins olives, qui produisent des gestes de menace "hand-slapping" préférentiellement avec la main droite, en contexte inter- ou intraspécifique (Meguerditchian et Vauclair 2006; Meguerditchian *et al.* 2011b). De plus, cette latéralité est stable dans le temps au niveau individuel chez les babouins et les chimpanzés (Meguerditchian *et al.* 2011b, 2012). Cette latéralité gestuelle intraspécifique est dissociée d'une éventuelle préférence manuelle pour des actions non-communicatives, qu'elles soient manipulatoires ou autodirigées (e.g. chez les chimpanzés : Prieur *et al.* 2016a ; chez les babouins olives : Meguerditchian et Vauclair 2009). Des approches expérimentales ont également permis de mettre en évidence chez d'autres cercopithécidés que la latéralité observée pour les gestes communicatifs interspécifiques (comme des gestes de pointage) et pour les actions manuelles non-communicatives (comme des actions de saisie) n'étaient pas corrélées, suggérant un contrôle cérébral différent (e.g. chez les macaques de Tonkean : Meunier *et al.* 2013b ; les mones de Campbell et les mangabeys à collier : Maille *et al.* 2013). De plus, les préférences manuelles démontrées pour les gestes de pointage sont moins dépendantes de la position de l'objet référent que dans le cas d'actions de saisie (e.g. chez les babouins olives : Meunier *et al.* 2012; Bourjade *et al.* 2013c ; les macaques de Tonkean : Meunier *et al.* 2013b ; les mones de Campbell et les mangabeys à collier : Maille *et al.* 2013). L'ensemble de ces résultats suggèrent, comme chez l'humain, une dominance de l'hémisphère gauche dans le contrôle cérébral de la communication intentionnelle chez ces espèces. De plus, une expérience comparative sur la latéralité gestuelle a montré une divergence entre les résultats obtenus chez des capucins (singes platyrrhiniens, Perelman *et al.* 2011), en comparaison à des enfants humains, des babouins olives et des macaques de Tonkéan (singes catarrhiniens, Meunier *et al.* 2013b). Il a ainsi été émis l'hypothèse que la spécialisation de l'hémisphère gauche pour le langage humain soit

héritée d'une latéralisation cérébrale pour le contrôle de la communication gestuelle chez l'ancêtre commun aux catarrhiniens actuels (e.g. Meguerditchian et Vauclair 2014; Prieur *et al.* 2018, 2019a, b; Meunier *et al.* 2013a).

Cette hypothèse est appuyée par des données neuro-anatomiques et fonctionnelles, en particulier chez les grands singes, montrant un lien entre les aires cérébrales homologues à celles du langage et la production de gestes communicatifs (revues de littérature : Meguerditchian et Vauclair 2014; Prieur *et al.* 2018). En effet, une asymétrie est observable en IRM (Imagerie par Résonance Magnétique) entre les deux hémisphères cérébraux des grands singes (chimpanzés, bonobos et gorilles), au niveau des aires homologues à l'aire de Broca qui sont plus développées du côté gauche (Cantalupo et Hopkins 2001). Cette asymétrie est d'autant plus marquée pour les chimpanzés les plus latéralisés à droite dans leur communication gestuelle (Tagliabata *et al.* 2006). De plus, des méthodes d'imagerie fonctionnelle (TEP-IRM) ont montré chez les chimpanzés que ces régions étaient activées lors de la production de gestes communicatifs (Tagliabata *et al.* 2008). Plus récemment, et pour la première fois chez une espèce non-hominoïde, il a été montré que les babouins olives présentaient une asymétrie du *planum temporale*, plus développé à gauche (Marie *et al.* 2018), comme mis en évidence chez les chimpanzés (e.g. Gannon *et al.* 1998). Ces résultats renforcent l'hypothèse d'une origine évolutive commune de ces structures cérébrales chez les singes catarrhiniens avec les substrats neuronaux de la production langagière chez l'humain.

3.2.3. *Quels facteurs ultimes et proximaux affectent la latéralité gestuelle ?*

Ainsi, l'étude de la latéralité gestuelle des primates non-humains est d'un intérêt certain pour explorer les origines du langage, et en particulier de la latéralité cérébrale et comportementale qui y est associée. Etudier la latéralité gestuelle via une approche comparative (e.g. Meguerditchian 2014) et/ou multifactorielle (e.g. Prieur *et al.* 2016a, 2017a) peut permettre de comprendre plus finement l'origine de ce trait, en s'intéressant aux facteurs ultimes et proximaux qui le déterminent. Différents facteurs peuvent en effet affecter la latéralité manuelle (e.g. Maille 2012), et nous présenterons ici ceux qui sont susceptibles d'impacter spécifiquement la latéralité en contexte de communication chez les primates.

3.2.3.1. Effet de l'espèce et de l'environnement

Tout d'abord, l'existence d'une latéralité gestuelle à échelle populationnelle et la force de cette latéralité peuvent dépendre de l'espèce étudiée (e.g. Prieur *et al.* 2017b), en raison notamment de leur socialité ou de leur écologie. La théorie d'une **origine sociale de la latéralité** des comportements propose qu'une latéralisation à échelle populationnelle favorise la coordination et la coopération entre les individus d'un même groupe (Ghirlanda et Vallortigara 2004; Vallortigara et Rogers 2005; MacNeilage *et al.* 2009). Suivant cette théorie, il est ainsi attendu qu'un plus haut niveau de coopération

au sein d'une espèce favorise une plus forte latéralité gestuelle à échelle populationnelle, et que celle-ci soit soumise à des contraintes sociales. Chez l'humain par exemple, de telles contraintes ont été mises en évidence dans le développement de la latéralité manuelle (Schaafsma *et al.* 2009). Des différences dans la latéralité gestuelle des chimpanzés et des gorilles ont ainsi été attribuées à des différences de structure et de dynamique sociale impactant leur communication (Prieur *et al.* 2017b). Les caractéristiques écologiques de l'espèce peuvent également affecter la latéralité gestuelle, notamment le type de locomotion. La théorie d'une **origine posturale de la latéralité** manuelle suggère que celle-ci résulte d'une spécialisation de la main droite pour réaliser des tâches complexes chez les espèces terrestres, en comparaison aux espèces arboricoles, l'utilisation d'une main ou de l'autre étant moins contrainte par les besoins de stabilité de leurs postures (MacNeilage *et al.* 1987; MacNeilage 2007; Hopkins *et al.* 2011). La direction de la latéralité manuelle chez les primates semble en effet dépendre de leur degré d'arboricolisme pour différentes tâches (Meguerditchian 2014). Dans le cas de la communication, nous pouvons ainsi faire l'hypothèse que les primates arboricoles soient moins latéralisés dans la production de leurs gestes que les espèces terrestres. L'**environnement captif ou naturel** dans lequel sont étudiés les primates pourrait impacter aussi leur latéralité gestuelle. Certains auteurs ont émis l'hypothèse que la latéralité manuelle mesurée chez plusieurs espèces de primates captifs était le résultat d'artefacts liés aux conditions expérimentales, notamment celles impliquant la présence d'un humain, ou liés directement au contexte de captivité (« artefactual hypothesis » : Warren 1980; McGrew et Marchant 1997, 2001). Aucun effet de la captivité ou de la présence humaine ne semble cependant être observé concernant spécifiquement la communication gestuelle chez les chimpanzés (Hopkins *et al.* 2005; Fletcher 2006). A l'inverse, certaines études chez les grands singes rendent compte d'une latéralité gestuelle à droite plus importante pour les gestes intraspécifiques que pour les gestes dirigés vers les humains, en contextes spontané ou expérimental (Hopkins *et al.* 2012; Prieur *et al.* 2017c).

3.2.3.2. Effet du contexte interactionnel

Le contexte interactionnel peut également impacter la latéralité gestuelle, et notamment la **valence émotionnelle** associée à ce contexte social (Prieur *et al.* 2016a, 2017a). Différentes hypothèses existent concernant une spécialisation hémisphérique cérébrale dans le traitement des émotions chez les vertébrés, associée à des asymétries comportementales (revue de littérature : Demaree *et al.* 2005). Une première théorie propose que la perception et l'expression des émotions soit gérées par l'hémisphère droit, quelle que soit la valence, positive ou négative, de ces émotions (« Right hemisphere theory » : Borod *et al.* 1983). Une deuxième théorie propose quant à elle que l'hémisphère droit soit responsable des émotions négatives, associées à des comportements de recul, et que l'hémisphère gauche contrôle les émotions positives, associées à des comportements d'approche (« Valence theory » ou « Approach / withdrawal theory » : Silberman et Weingartner 1986; Ehrlichman 1987). Il semble que selon l'une ou

l'autre de ces théories, des contextes sociaux négatifs devraient éliciter davantage de gestes avec la main gauche qu'avec la main droite. Pourtant, récemment, Prieur *et al.* (2016a, 2017a) ont démontré chez les chimpanzés et les gorilles une latéralité gestuelle à droite plus prononcée dans les contextes négatifs que dans les contextes positifs. Ces résultats s'expliquent probablement par une importante motivation d'approche dans les contextes négatifs étudiés, comme les agressions, qui serait donc associée à l'hémisphère gauche selon la théorie « Approach / withdrawal » (Rohlf et Ramirez 2006). Outre la valence du contexte interactionnel, les **positions relatives du signaleur et du receveur** peuvent influencer la main utilisée pour produire le geste (e.g. chez les chimpanzés et les gorilles : Prieur *et al.* 2016a, 2017b, c), en raison de la directionnalité du geste, ou d'asymétries dans les expressions faciales des émotions chez le receveur, pouvant éliciter la production d'un geste par le signaleur (e.g. Wallez *et al.* 2012; Prieur *et al.* 2016a). Les primates non-humains peuvent favoriser un côté ou l'autre pour approcher leurs congénères, et ce en fonction de paramètres sociaux comme le rang hiérarchique (e.g. chez les mangabeys à collier, *C. torquatus*, et les mangabeys à joues grises, *Lophocebus albigena* : Baraud *et al.* 2009). Ainsi, cette latéralité sociale pourrait avoir une influence sur leur communication gestuelle.

3.2.3.3. Effet des caractéristiques du signal

La latéralité gestuelle peut potentiellement être dépendante des caractéristiques des gestes eux-mêmes. En particulier, la latéralité peut dépendre du **type de geste** produit (e.g. chez les chimpanzés et les gorilles : Hopkins et Leavens 1998; Hopkins et Wesley 2002; Hobaiter et Byrne 2013a; Prieur *et al.* 2016a, 2017a, b). Par exemple, des gestes plus ou moins communs aux individus d'un même groupe pourraient être plus ou moins soumis à des pressions sociales modulant leur latéralité (Prieur *et al.* 2016a). La **modalité sensorielle** du geste peut également avoir un effet sur la main utilisée pour le produire. Par exemple, les chimpanzés utilisent préférentiellement la main ipsilatérale à la position du receveur pour produire des gestes tactiles ou visuels, supposément en raison de la directionnalité de ces gestes (Prieur *et al.* 2016a). La **posture du signaleur** pourrait aussi influencer la main utilisée pour communiquer, un effet postural ayant été mis en évidence sur la latéralité manuelle pour plusieurs tâches manipulatoires chez des cercopithécidés (e.g. chez les mangabeys à collier : Blois-Heulin *et al.* 2006 ; les mangabeys à joues grises : Blois-Heulin *et al.* 2007 ; les macaques Rhésus : Fagot *et al.* 1991). Cet effet est en lien avec la théorie d'une origine posturale de la latéralité (voir plus haut), et est d'autant plus marqué pour des tâches nécessitant des manipulations complexes (« task complexity hypothesis » : Fagot et Vauclair 1991). Dans le cas de la communication, certaines postures pourraient contraindre l'utilisation d'une main ou d'une autre pour produire un geste.

3.2.3.4. Effet des caractéristiques sociodémographiques du signaleur et du receveur

La **relation de dominance** entre les sujets peut induire une préférence manuelle, comme c'est le cas chez les chimpanzés qui sont plus latéralisés à droite pour des gestes dirigés vers des individus dominants (Prieur *et al.* 2016a). Aucun effet de la **parenté** entre signaleur et receveur n'a été mis en évidence dans la communication gestuelle des chimpanzés et des gorilles (Hopkins *et al.* 2005; Prieur *et al.* 2016a, 2017a), mais le potentiel effet de ce paramètre sur la latéralité gestuelle n'a, à notre connaissance, jamais été testé chez d'autres espèces. Un effet de l'**âge** et du **sexe** des individus sur la latéralité gestuelle a été mis en évidence chez plusieurs primates. Chez les chimpanzés, les gorilles et les babouins olives, certaines études montrent une préférence pour le côté droit plus marquée chez les individus adultes que chez les juvéniles (Hopkins et Leavens 1998; Meguerditchian et Vauclair 2006; Hobaiter et Byrne 2013a; Prieur *et al.* 2016a, 2017a). Ces résultats pourraient être le reflet d'une maturation de l'implication de l'hémisphère gauche dans la communication intentionnelle (Meguerditchian et Vauclair 2006), ou être l'effet d'un apprentissage, les gestes communicatifs des adultes étant susceptibles d'avoir été davantage façonnés par des expériences sociales (Call et Tomasello 2007). Prieur *et al.* (2016a) ont également observé un possible effet de senescence sur la latéralité gestuelle des chimpanzés, les vieux individus étant moins latéralisés que les jeunes adultes, peut-être en raison de limitations physiques. Il est toutefois à noter que d'autres études n'ont pas montré d'effet significatif de l'âge sur la latéralité gestuelle chez les chimpanzés et les babouins olives (Hopkins *et al.* 2005; Meguerditchian *et al.* 2011b). Enfin, plusieurs études ne montrent pas d'effet du sexe du signaleur sur la latéralité gestuelle chez les chimpanzés et les babouins (e.g. Hopkins *et al.* 2005; Meguerditchian et Vauclair 2006, 2009; Meguerditchian *et al.* 2011b), mais d'autres mettent en évidence des effets significatifs de ce facteur chez les grands singes. Notamment, des études montrent que les mâles bonobos sont plus latéralisés à droite que les femelles (Hopkins et de Waal 1995), que les femelles gorilles sont plus latéralisées à droite que les mâles et que ceux-ci utilisent d'avantage leur main droite pour communiquer avec d'autres mâles que lorsqu'ils communiquent avec des femelles (Prieur *et al.* 2017a), et une étude suggère une tendance des femelles chimpanzés à être plus latéralisées à droite que les mâles (Hopkins et Leavens 1998). Il peut être fait l'hypothèse que ces résultats soient liés aux liens de dominance qui existent entre les deux sexes chez ces espèces. Dans l'ensemble, l'effet des caractéristiques sociodémographiques des individus sur la latéralité gestuelle est encore peu étudié, et reste à élucider chez de nombreuses espèces.

Prieur *et al.* (2016a, 2017a, b) ont récemment et pour la première fois exploré l'effet conjoint de ces différents paramètres sur la latéralité gestuelle grâce à des analyses multifactorielles, chez les chimpanzés et les gorilles. Cette approche n'a encore jamais été adoptée pour caractériser la latéralité gestuelle intraspécifique d'autres espèces, mais pourrait être un moyen de comprendre le lien entre

latéralité comportementale et contrôle cérébral de la communication gestuelle chez les primates, dans la perspective d'une étude multicausale des origines du langage.

3.3. Flexibilité

3.3.1. Qu'est-ce qu'une communication flexible ?

Les mécanismes cognitifs impliqués dans la communication des primates peuvent être inférés par la caractérisation de leurs signaux en termes de flexibilité. En effet, la communication peut être considérée comme flexible lorsque la production des signaux n'est pas le résultat d'une simple association stimulus-réponse, suggérant ainsi qu'un ou des mécanismes cognitifs complexes la sous-tendent (e.g. Liebal *et al.* 2014). Dans la littérature relative à la communication des primates, le terme de flexibilité peut par exemple correspondre à :

- La capacité d'un individu à **acquérir de nouveaux signaux** communicatifs ou à apprendre à moduler leur structure en fonction du contexte (e.g. Meguerditchian *et al.* 2011a; Hobaiter et Byrne 2013b; Bouchet *et al.* 2016), son répertoire étant plastique face à des variations environnementales et sociales. En lien avec cette capacité, l'apprentissage social et les différences inter-groupes de répertoires sont des indicateurs de flexibilité de la communication (e.g. Pollick et De Waal 2007; Bouchet *et al.* 2016).
- L'**effet d'audience** sur la communication, c'est-à-dire l'effet que peut avoir la présence, l'identité, le comportement ou le niveau de connaissance des individus pouvant percevoir le signal (e.g. Zuberbühler 2008, 2012). Cet effet d'audience peut être considéré comme un marqueur d'intentionnalité (voir partie 3.1.2. Liebal *et al.* 2014).
- La capacité d'un signaleur à **persister** dans sa communication ou à **élaborer**, dans le cas d'une communication intentionnelle (voir partie 3.1.2. Cartmill et Byrne 2007).
- L'utilisation des signaux de manière indépendante du contexte, ou « **means-ends dissociation** » (voir partie 3.3.2. Bruner 1981; Pollick et De Waal 2007; Meguerditchian *et al.* 2011a). Ce trait permet de distinguer l'utilisation flexible des signaux en fonction de différentes motivations, d'une simple production de signal en réponse à un stimulus spécifique.

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- La capacité d'un individu à combiner plusieurs signaux simultanément ou en séquence, en adéquation avec le contexte ou l'intention du signaleur (voir partie 3.3.3. Call et Tomasello 2007; Pollick et De Waal 2007; Zuberbühler 2012; Liebal *et al.* 2014).

Nous nous intéresserons ici en particulier à la flexibilité d'utilisation des gestes en indépendance du contexte, et à l'utilisation combinée voire multimodale de signaux communicatifs, ces deux aspects pouvant refléter une utilisation stratégique des signaux pour communiquer efficacement.

3.3.2. « Means-ends dissociation » des signaux gestuels

La production de gestes communicatifs en indépendance du contexte est un signe de flexibilité, appelé « means-ends dissociation » (Bruner 1981), qui se manifeste par l'utilisation de différents signaux du répertoire dans un même contexte et l'utilisation d'un même signal dans différents contextes. Pour être représentatif d'un mécanisme cognitif complexe, ce trait de flexibilité devra être observé à échelle individuelle et pas seulement du groupe, c'est-à-dire qu'un même signal sera considéré comme « utilisé dans différents contextes » si cela a été observé pour un même individu (Liebal *et al.* 2014). Cette utilisation flexible des gestes communicatifs a été mise en lumière chez les grands singes (e.g. chez les chimpanzés : Tomasello *et al.* 1997; Call et Tomasello 2007; Hobaiter et Byrne 2011b, 2014 ; les bonobos : Pika *et al.* 2005 ; les gorilles : Pika *et al.* 2003; Genty *et al.* 2009 ; les orang-outans : Liebal *et al.* 2006 ; les siamangs : Liebal *et al.* 2004c). Quelques études montrent également cette flexibilité d'utilisation des gestes chez des non-hominoïdes, comme chez les macaques de Barbarie et les macaques à bonnet (Hesler et Fischer 2007; Gupta et Sinha 2019), et les babouins olives (Molesti *et al.* 2019).

Pollick et de Waal ont proposé l'hypothèse selon laquelle les gestes des primates seraient utilisés de manière plus flexible que les signaux faciaux ou vocaux, car moins associés à un contexte ou une émotion spécifique et plus adaptables à différentes situations sociales (« gestural flexibility hypothesis », Pollick et De Waal 2007). Selon cette hypothèse, un geste aurait ainsi différentes significations possibles, qui seraient discriminées par le receveur selon le contexte d'émission du geste ou sa combinaison avec des vocalisations ou expressions faciales, plus contexte-spécifiques (Moore 2014; Byrne *et al.* 2017). Cette hypothèse peut cependant être nuancée, les expressions faciales et les vocalisations des primates pouvant elles-mêmes être associées à différents contextes (e.g. les expressions faciales des siamangs : Liebal *et al.* 2004c).

3.3.3. Combinaisons de signaux et multimodalité

La flexibilité d'utilisation des signaux peut être reflétée non seulement par leur indépendance vis-à-vis du contexte, mais également par la production de signaux seuls ou en combinaisons, pour servir différentes fonctions communicatives (Call et Tomasello 2007; Pollick et De Waal 2007; Zuberbühler 2012; Liebal *et al.* 2014). La communication des primates peut ainsi être flexible en termes de

multimodalité « libre » (voir partie 2.4.) et être multicomposante, différentes modalités (tactile, audible, visuelle) et types de signaux (gestes, vocalisations, expressions faciales) pouvant être combinés (Jones et Van Cantfort 2007; Pollick et De Waal 2007; Micheletta *et al.* 2013; Wilke *et al.* 2017; Genty 2019). La lumière n'est pas encore faite, cependant, sur les causes proximales et ultimes d'une telle complexité de communication (Partan 2013; Liebal et Oña 2018; Fröhlich et van Schaik 2018).

3.3.3.1. Fonctions des combinaisons de signaux

L'utilisation de plusieurs signaux en combinaisons plutôt qu'un seul a un coût énergétique pour les individus, et peut mobiliser des parties du corps qui deviennent donc indisponibles pour d'autres fonctions (Partan et Marler 2005). Différentes hypothèses ont été formulées quant aux bénéfices que peut avoir, en contrepartie, la communication multimodale ou multicomposante. Partan et Marler (1999, 2005) ont proposé une classification des signaux multimodaux des animaux en fonction de la réponse du receveur (**Tableau 1**), à partir de laquelle la fonction des combinaisons de signaux peut être inférée (e.g. Micheletta *et al.* 2013; Wilke *et al.* 2017; Hobaiter *et al.* 2017). Cette classification distingue les combinaisons de signaux ayant a priori la même signification (redondance), des combinaisons de signaux ayant des significations différentes. La redondance pourrait notamment permettre d'augmenter la perceptibilité des signaux, et donc transmettre une information malgré des bruits environnementaux (Johnstone 1996). Combiner des signaux non redondants peut permettre d'obtenir des réponses différentes de la part du receveur, ou communiquer d'avantage d'informations par unité de temps (Moller et Pomiankowski 1993; Partan et Marler 1999. **Tableau 1**).

Tableau 1. Classification des combinaisons multimodales de signaux d'après la réponse du receveur (adapté de Partan et Marler 1999).

	Signaux produits indépendamment		Combinaison multimodale de signaux		Catégorie
	Signaux	Réponses	Signaux	Réponses	
Redondance	a	→ x	a + b	→ x	Equivalence
	b	→ x	a + b	→ X	Amplification
Pas de redondance	a	→ x	a + b	→ x + y	Indépendance
			a + b	→ x	Dominance
	b	→ y	a + b	→ X ou x	Modulation
			a + b	→ z	Emergence

Plus récemment, un nouveau cadre théorique a été proposé, en continuité de celui de Partan et Marler (1999), pour classer les hypothèses formulées sur les fonctions des différentes catégories de combinaisons de signaux. Les hypothèses basées sur la **signification** des signaux combinés sont distinguées des hypothèses portant sur l'**efficacité** de transmission de la communication multimodale (Hebets et Papaj 2005; Fröhlich et van Schaik 2018), bien qu'elles ne soient pas incompatibles les unes

avec les autres. Cette distinction est fondée sur l'idée selon laquelle l'évolution des signaux communicatifs dépend de deux grands types de contraintes, liées à la stratégie ou à l'efficacité de la communication (Guilford et Dawkins 1991). Enfin, certaines hypothèses concernent de possibles **interactions entre les signaux** produits simultanément ou en séquence par un même signaleur, en termes aussi bien de modulation du message que d'amélioration de la détection des signaux. La classification de Hebets et Papaj (2005) distingue les possibles facteurs sociaux et environnementaux contraignant l'utilisation de différentes modalités sensorielles. En effet, il est fait l'hypothèse que la communication multimodale soit plus appropriée pour des interactions à courte distance, dans lesquelles le receveur peut percevoir simultanément des signaux sur différentes modalités (Partan et Marler 2005; Fröhlich et van Schaik 2018). La densité de l'environnement physique des primates pourrait favoriser une modalité de communication ou une autre, des habitats moins denses facilitant la perception de signaux visuels, et les vocalisations étant plus adaptées à une communication à distance et un environnement visuellement dense (e.g. Marler 1965; Gautier 2001; de la Torre et Snowdon 2002; Partan et Marler 2005). Par exemple, les primates forestiers terrestres semblent utiliser davantage de signaux visuels que les espèces arboricoles (Lemasson et Barbu 2011).

La première catégorie d'hypothèses concerne les facteurs impactant le message sous-tendu par les signaux, sur une base de redondance ou non-redondance comme défini par Partan et Marler (« **content-based hypotheses** » : Hebets et Papaj 2005; Fröhlich et van Schaik 2018). Dans le cas de significations **redondantes** (Moller et Pomiankowski 1993; Partan et Marler 1999), la combinaison de signaux peut augmenter les chances que le receveur interprète correctement le message, et augmente la probabilité de pertinence de sa réponse. L'hypothèse de cette fonction de la communication multimodale et/ou multicomposante a été émise en se basant sur la description de signaux multimodaux chez des espèces autres que les primates, comme chez des oiseaux, des poissons ou des insectes (revue de littérature : Fröhlich et van Schaik 2018). Dans le cas de la communication des primates non-humains, cela peut être mis en évidence dans la persistance ou l'élaboration de la communication pour atteindre un but social (voir partie 3.1.2. Leavens *et al.* 2005; Cartmill et Byrne 2007). Par exemple, en cas d'échec d'un premier signal vocal, les chimpanzés peuvent élaborer leur communication en utilisant des combinaisons de signaux vocaux et gestuels (Hobaiter *et al.* 2017). Dans le cas de combinaisons de signaux non-redondants, les significations de chacun des signaux peuvent se superposer, la communication multimodale ou multicomposante permettant alors de convier différents messages à la fois (« **multiple message hypothesis** » ou « **complementary hypothesis** » : Moller et Pomiankowski 1993; Johnstone 1996; Partan et Marler 1999, 2005; Fröhlich et van Schaik 2018).

La deuxième catégorie d'hypothèses relatives à la fonction des combinaisons de signaux concerne l'efficacité de transmission du signal, en prenant en compte l'environnement à travers lequel ces signaux vont être diffusés (« **efficacy-based hypotheses** » : Hebets et Papaj 2005; Fröhlich et van Schaik 2018). Il est fait l'hypothèse que certains signaux redondants pourraient être combinés pour assurer un

« **backup** », c'est-à-dire pour garantir une perception des signaux communicatifs de la part du receveur, en particulier dans des environnements contraignants (manque de visibilité, bruit ambiant, etc.). Selon cette hypothèse, la communication multimodale serait un moyen d'augmenter la probabilité de recevoir une réponse aux signaux (Hebets et Papaj 2005). Cette hypothèse a été vérifiée concernant la communication multimodale de plusieurs animaux (e.g. chez les araignées-loups, *Schizocosa retrorsa* : Hebets *et al.* 1996; Hebets et Uetz 1999), mais n'a jamais été démontrée chez les primates, pour lesquels il est méthodologiquement difficile de tester séparément les effets de l'interaction sociale et de l'environnement physique (Fröhlich et van Schaik 2018).

Enfin, il pourrait exister des **interactions entre les signaux**, comme l'hypothèse d'une amélioration de la détection et de la discrimination des signaux (« **increased detection and discrimination hypothesis** » : Hebets et Papaj 2005; Fröhlich et van Schaik 2018). Selon cette hypothèse, la présence d'un signal peut aussi bien augmenter la probabilité qu'un second signal soit perçu (amélioration de la détection) ou correctement compris par le receveur (amélioration de la discrimination). Ainsi, les combinaisons multimodales ou multicomposantes de signaux pourraient être un moyen d'augmenter la probabilité d'obtenir une réponse de la part du receveur, ou de la recevoir plus vite (e.g. Liebal *et al.* 2004c; Pollick et De Waal 2007; Genty et Byrne 2010; Leavens *et al.* 2010; Genty *et al.* 2014; Wilke *et al.* 2017). Par exemple, chez les macaques Rhésus et les macaques à crête (*Macaca nigra* et *M. mulatta*), les « lipsmacks » multicomposants ont plus de chance d'être suivis de contacts affiliatifs que les « lipsmacks » unicomposants (Partan 2002; Micheletta *et al.* 2013). Les combinaisons de signaux, et en particulier multimodales et/ou multicomposantes, pourraient aussi être un moyen d'affiner la signification d'un signal ou d'en changer le sens (« **refinement** », Fröhlich et van Schaik 2018). Chez les humains, la combinaison de la parole avec des gestes est un moyen de moduler la signification du discours (e.g. Goldin-Meadow 1999), et la compréhension du discours va être perçue via l'intégration de signaux perçus sur différentes modalités, vocale ou visuelle (Vigliocco *et al.* 2014). Chez les grands singes, les combinaisons multicomposantes voire multimodales semblent également être un moyen d'affiner le message convié, notamment en levant l'ambiguïté de signification d'un signal associé à différents contextes (e.g. Holle et Gunter 2007; Moore 2014; Genty *et al.* 2015; Byrne *et al.* 2017; Wilke *et al.* 2017; Fröhlich et van Schaik 2018). Chez les jeunes bonobos par exemple, la signification des vocalisations « **contest hoots** », produites aussi bien en contexte d'agression que de jeu, semble élucidée par sa combinaison ou non avec des gestes spécifiques (Genty *et al.* 2014). Il est également fait l'hypothèse que la combinaison de gestes entre eux permette de créer de nouvelles significations (Liebal *et al.* 2004a).

3.3.3.2. Etude de la communication multimodale et multicomposante chez les primates

La communication multimodale est étudiée chez de nombreux animaux, comme des araignées, des oiseaux, des insectes ou des petits mammifères (e.g. Hutchison *et al.* 1997; Uetz et Roberts 2002; Cooper

et Goller 2004; Elias *et al.* 2005; Partan *et al.* 2010). Chez les primates, l'étude de la communication multimodale et multicomposante reste assez rare (Slocombe *et al.* 2011), mais suscite de plus en plus d'intérêt, en particulier dans la perspective d'étudier les origines évolutives du langage (Waller *et al.* 2013; Liebal *et al.* 2014; Fröhlich *et al.* 2019). Pour comprendre les déterminants de cette potentielle flexibilité dans la communication des primates (voir partie 3.3.3.1.), qui peut être significative de mécanismes cognitifs complexes, il est nécessaire de décrire de manière systématique les circonstances dans lesquelles des combinaisons multimodales et multicomposantes peuvent être observées, chez différentes espèces et dans différents environnements (Fröhlich et van Schaik 2018).

Actuellement, à notre connaissance, la plupart des descriptions de communication multimodale et/ou multicomposante chez les primates non-humains sont centrées sur un type précis de combinaisons de signaux (par exemple, sur les combinaisons gestes-vocalisations, e.g. Pollick et De Waal 2007; Genty 2019), ou sur différentes utilisations d'un même signal, seul ou en combinaison à d'autres (par exemple, le « lipsmack » chez les macaques : Micheletta *et al.* 2013 ; ou les vocalisations « pout-moan » et « contest hoot » chez les bonobos : Genty *et al.* 2014; Genty 2019), ces approches permettant de tester spécifiquement certaines hypothèses concernant la fonction des combinaisons de signaux. En revanche, pour pouvoir adopter une approche comparative fiable concernant les contextes élicitant une communication multimodale et/ou multicomposante chez différentes espèces, des descriptions plus exhaustives des combinaisons de signaux sont nécessaires, comme celle réalisée récemment par Wilke *et al.* (2017) chez les chimpanzés sauvages. De plus, afin de permettre des comparaisons entre différentes espèces et différents environnements, ces descriptions doivent être basées sur des méthodologies similaires. Les comparaisons entre études « multimodales » sont actuellement contraintes par des différences importantes dans la définition temporelle des combinaisons de signaux. Certains auteurs considèrent que des signaux produits par un même individu sont combinés seulement s'ils se superposent (e.g. Wilke *et al.* 2017), d'autres s'ils se superposent ou sont séparés par un « silence » d'une durée inférieure à une valeur arbitraire (e.g. 1 seconde : Genty et Byrne 2010; Hobaiter et Byrne 2011b; Genty *et al.* 2015; Hobaiter *et al.* 2017; Genty 2019; Knox *et al.* 2019 ; 2 secondes : Taglialatela *et al.*, 2015; 5 secondes : Liebal *et al.*, 2004a, 2006; Tempelmann et Liebal, 2012), d'autres encore si l'initiation des signaux est séparée par une latence d'une valeur également arbitraire (e.g. 10 secondes : Pollick et De Waal 2007). Enfin, le degré de précision dans la description des répertoires de combinaisons de signaux est important à prendre en compte. La description systématique des combinaisons de signaux, chez une espèce ou dans une population, peut mener à l'identification d'une grande diversité d'associations différentes, dont une grande partie est susceptible d'être unique. Pour décrire les contextes de production de ces différentes combinaisons de signaux, il est pourtant nécessaire de les comparer entre elles et grouper celles qui sont les plus similaires, tout en rendant compte de leur diversité (Baraud *et al.* 2016). Ainsi, la caractérisation de la communication multimodale et multicomposante chez les primates non-humains, dans une perspective d'étude multimodale et

multicausale des origines évolutives du langage, nécessite des descriptions chez une grande diversité d'espèces et d'environnement, mais aussi une certaine unité dans les méthodologies de description utilisées.

4. Problématiques de la thèse

4.1. Questions de recherche

Nous nous intéressons dans le présent travail aux **précurseurs du langage pouvant être retrouvés dans la communication gestuelle des singes cercopithécidés**, en termes d'intentionnalité, de latéralité et de flexibilité, **et dans leur communication multimodale et multicomposante**, en termes d'utilisation flexible des signaux. La littérature scientifique actuelle sur la communication gestuelle des primates non-humains est principalement centrée sur l'étude des grands singes (Slocombe *et al.* 2011), et en particulier des chimpanzés (Lameira et Call 2020). Certaines propriétés de la communication gestuelle des singes non-hominoïdes ne sont encore que peu ou pas étudiées, malgré l'intérêt significatif qu'aurait leur caractérisation pour la compréhension des origines évolutives du langage humain. Nous avons donc abordé les questions suivantes :

- **La communication visuelle des cercopithécidés est-elle intentionnelle ?**

L'intentionnalité des gestes et des expressions faciales des singes non-hominoïdes est encore peu claire en contexte spontané intraspécifique. Deux récentes études ont mis en évidence des marqueurs d'intentionnalité dans la production de gestes des macaques à bonnet (Gupta et Sinha 2019) et des gestes et expressions faciales des babouins olives (Molesti *et al.* 2019), suggérant que des singes cercopithécidés puissent communiquer intentionnellement par leurs signaux visuels. Tous les marqueurs d'intentionnalité observés dans la communication gestuelle des grands singes (voir partie 3.1.2.) n'ont cependant pas été investigués dans ces études, et des analyses de la communication gestuelle d'autres espèces sont nécessaires pour potentiellement généraliser ces résultats à la sous-famille des cercopithécidés. De plus, l'existence de gestes brachio-manuels « libres » et intentionnels, d'une importance particulière pour l'étude des origines évolutives du langage, reste à ce jour questionnée chez les non-hominoïdes.

- **Quels sont les déterminants ultimes et proximaux de la latéralité gestuelle chez les cercopithécidés ?**

Elucider quelles contraintes ultimes et proximales façonnent la latéralité gestuelle chez les primates non-humains est un moyen de déterminer les facteurs ayant contribué à l'émergence d'une spécialisation hémisphérique dans le contrôle du langage. La latéralité

gestuelle à droite, partagée par les catarrhiniens d'après des données expérimentales, n'a jusqu'à aujourd'hui été étudiée en contexte intraspécifique que chez une seule espèce non-hominoïde, les babouins olives.

- **Les cercopithécidés peuvent-ils utiliser leurs signaux communicatifs de manière flexible et multimodale en fonction du contexte ?**

Il est encore débattu que les non-hominoïdes puissent produire leurs gestes de manière flexible, en termes d'indépendance vis-à-vis du contexte mais également en termes de combinaisons à d'autres signaux. De manière générale, la communication multimodale et multicomposante des primates non-humains est encore sous-étudiée. Afin d'en comprendre la fonction, un développement méthodologique est nécessaire pour décrire systématiquement les circonstances dans lesquelles les primates combinent des signaux, dans une perspective d'étude multimodale et multicausale des origines évolutives du langage.

4.2. Espèce étudiée

Pour tenter de répondre à ces questions, nous nous sommes intéressés à la communication d'une population captive de non-hominoïdes encore peu étudiés, les mangabeys à collier (*Cercocebus torquatus*). Les mangabeys sont des cercopithecinés du clade des *Papionini* (**Figure 2**), comme les macaques et les babouins, chez qui la communication gestuelle est suggérée comme intentionnelle et flexible (voir parties 3.1.3. et 3.3.3.), et dont certaines espèces présentent une latéralité gestuelle à droite à échelle populationnelle (voir partie 3.2.2.). L'ancêtre commun des mangabeys à collier et des autres *Papionini* date d'il y a environ 12 millions d'années, et leur ancêtre commun avec les hominoïdes, dont *Homo sapiens*, date d'il y a environ 29 millions d'années (Chatterjee *et al.* 2009; Springer *et al.* 2012).

Les mangabeys à collier sont originaires des forêts humides d'Afrique de l'Ouest (Jones et Sabater-Pi 1968; Gautier-Hion *et al.* 1999; Oates *et al.* 2008; Cooke 2012; Orimaye *et al.* 2016; Orimaye 2017), et occupent les strates les plus basses de la forêt, leur locomotion étant considérée « semi-terrestre à tendance terrestre » (Jones and Sabater-Pi 1968; Cooke 2012; Mitani *et al.* 2012). Ces caractéristiques écologiques suggèrent ainsi que la communication des mangabeys puisse reposer sur une utilisation riche de signaux visuels et multimodaux, adaptée aux contraintes environnementales (voir partie 3.3.3.1.). Les mangabeys vivent dans de grands groupes multi-mâles, multi-femelles, organisés selon une hiérarchie linéaire, et dont la dynamique de dominance pourrait être qualifiée de « semi-tolérante » (Jones et Sabater-Pi 1968; Gautier-Hion *et al.* 1999; Thierry 2007; Dolado et Beltran 2011, 2012). Cette complexité sociale, impliquant une grande diversité de contextes sociaux et des interactions entre individus de sexe, d'âge et de rangs hiérarchiques différents, pourrait ainsi être associée à une communication complexe, intentionnelle et flexible (e.g. Dunbar 2009; Freeberg *et al.* 2012).

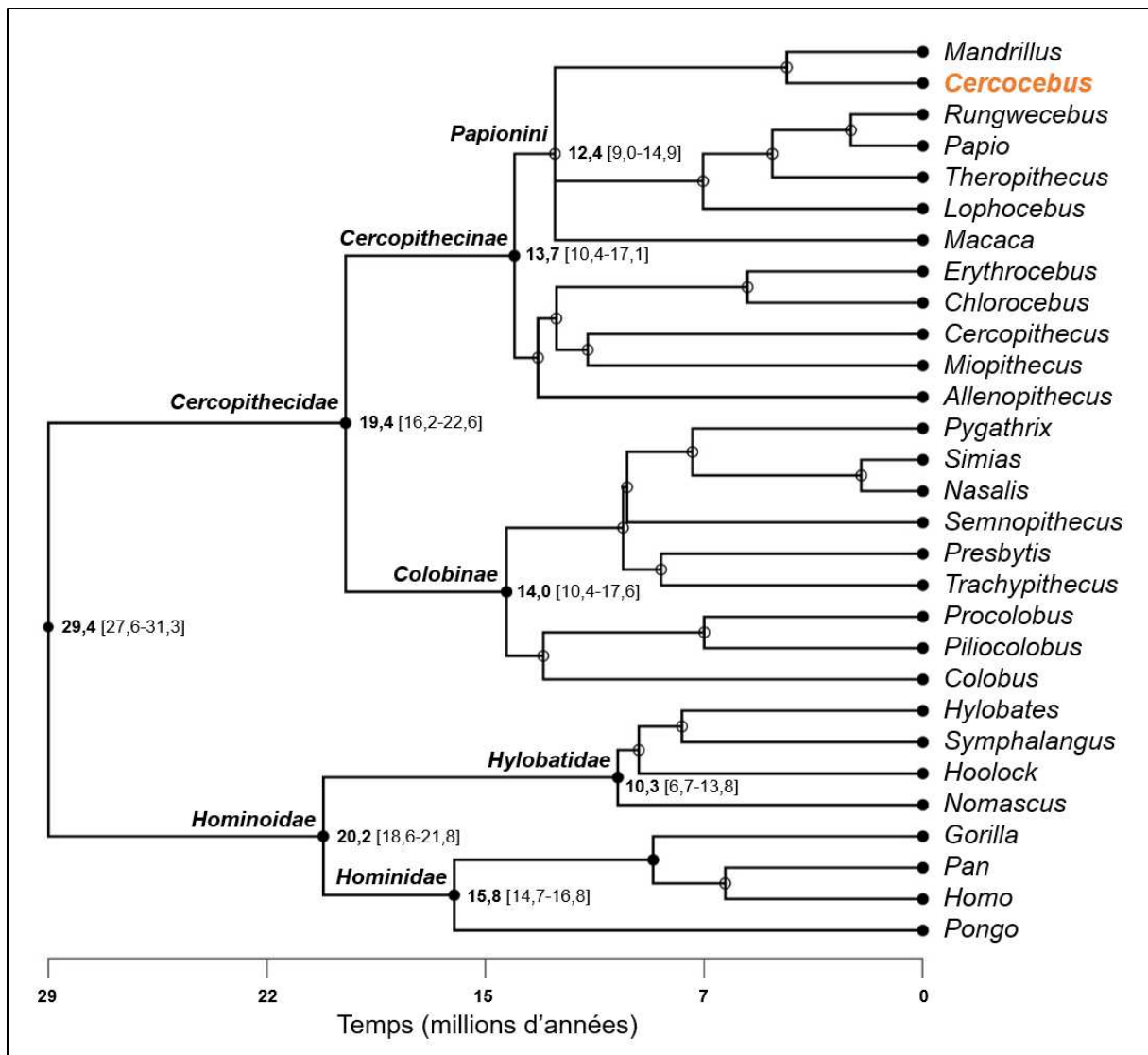


Figure 2. Arbre phylogénétique des singes catarrhiniens. Les catarrhiniens sont les primates haplorrhiniens d'Afrique et d'Asie. Les dates de divergence des familles et sous-familles sont renseignées en millions d'années, avec l'intervalle de confiance à 95% entre crochets (source : TimeTree, Kumar *et al.* 2017).

Le répertoire vocal des mangabeys à collier est connu en captivité (Bouchet *et al.* 2010) mais leurs autres signaux spontanés n'ont pas encore été décrits, bien que de premières études présagent d'une riche communication visuelle et multimodale chez cette espèce. Notamment, une étude expérimentale a mis en évidence une capacité des mangabeys à adapter la production de gestes de quémante appris en fonction de l'état attentionnel d'un receveur humain (Maille *et al.* 2012), suggérant une *possible capacité à communiquer intentionnellement* par les gestes. De plus, une autre expérience, impliquant la production de gestes de pointage, a mis en lumière une latéralité gestuelle à droite plus marquée pour les individus ayant les meilleures capacités de communication référentielle (Maille *et al.* 2013), cette latéralité n'étant pas corrélée à celle observée pour des gestes non-communicatifs (voir partie 3.2.2.). Ces résultats sont prometteurs quant à une *possible latéralité gestuelle à échelle populationnelle* dans

leur communication intraspécifique. De plus, d'après les résultats d'études portant sur leur latéralité manuelle ou sociale chez cette espèce, il peut être hypothétisé un effet de la posture et du contexte social sur leur latéralité gestuelle (voir partie 3.2.3. Nedellec-Bienvenue et Blois-Heulin 2005; Blois-Heulin *et al.* 2006; Baraud *et al.* 2009). Enfin, une première étude a été réalisée pour décrire certaines interactions multimodales chez les mangabeys à collier captifs, et suggère chez eux une capacité d'*utilisation flexible de différentes modalités* de communication en fonction du contexte (Baraud *et al.* 2016).

4.3. Objectifs de la thèse

Pour répondre aux questions précédemment posées (voir partie 4.1.), l'objectif de ce travail de thèse était ainsi de **caractériser la communication gestuelle et multimodale des mangabeys à collier en captivité**, en termes d'intentionnalité, de latéralité gestuelle et de flexibilité, et à cette occasion de compléter la description de leur répertoire de signaux communicatifs.

- Nous avons d'abord cherché à savoir si la communication visuelle (gestes et expressions faciales) des mangabeys à collier pouvait présenter des marqueurs comportementaux d'intentionnalité, semblables à ceux utilisés pour analyser l'intentionnalité des gestes des grands singes (**Articles 1, 2 et 5**). Nous avons également testé l'existence de gestes brachio-manuels « libres » intentionnels dans leur communication spontanée (**Article 1**).
- Nous avons ensuite testé si les mangabeys étaient latéralisés pour la production de leurs gestes intraspécifiques, et avons cherché à déterminer les facteurs affectant leur latéralité gestuelle, relatifs au contexte interactionnel, aux caractéristiques du signal ou aux caractéristiques sociodémographiques des sujets (**Article 3**).
- Enfin, nous nous sommes interrogés sur la capacité de mangabeys à utiliser leurs gestes de manière flexible en termes d'indépendance vis-à-vis du contexte (**Article 1**) et de multimodalité (**Articles 4 et 5**). Plus généralement, nous avons cherché à décrire la communication multimodale et multicomposante intraspécifique des mangabeys à collier, avec la perspective d'en étudier la fonction. Pour cela, nous avons cherché une méthodologie permettant une description la plus objective possible des combinaisons de signaux (**Article 4**).

Nous avons adopté une double approche observationnelle et expérimentale, pour à la fois décrire la communication spontanée intraspécifique des mangabeys à collier, et tester en conditions plus contrôlées les mécanismes cognitifs sous-tendant cette communication.



Chapitre II

Méthodologie générale





1. Sujets d'étude

1.1. Présentation de l'espèce

1.1.1. Morphologie et histoire de vie

Les mangabeys à collier ont un pelage très contrasté, allant du gris foncé sur le dos et les membres à blanc sur le ventre et le bout de la queue. Leur visage est entouré d'un pelage blanc, et couronné de poils roux, dont ils tirent leur nom en anglais : « red-capped mangabey » ou « cherry-crowned mangabey ». Les paupières blanches des mangabeys se démarquent du noir de leur visage, ce qui a probablement une fonction dans leur communication faciale, accentuant la visibilité des mouvements de sourcils (**Figure 1**, Hill 1974; Redican 1975; Gautier-Hion *et al.* 1999). Un dimorphisme sexuel est à noter chez cette espèce, les mâles adultes pesant environ 10 kg pour une taille de 60 cm, et les femelles adultes pesant environ 6 kg pour une taille de 50 cm (dimorphisme mâle / femelle $\approx 1,8$. Gautier-Hion *et al.* 1999; Swedell 2010). De plus, les mâles adultes présentent de très grandes canines supérieures, qui se développent avec la maturité sexuelle (**Figure 2**, Hill 1974; Deputte 1986; O'higgins et Jones 1998). D'après des descriptions du développement des traits sexuels secondaires chez une espèce proche, les mangabeys à joues grises (*Lophocebus albigena*), cette maturité est atteinte au cours de la 4^{ème} année chez les femelles, et entre 5 et 7 ans chez les mâles (Chalmers 1968; Gautier-Hion et Gautier 1976; Deputte 1992). Une saisonnalité de la reproduction est observée chez les cercocèbes : la majorité des naissances en captivité ont ainsi lieu en automne, résultant de reproductions au printemps (Gautier-Hion et Gautier 1976). Enfin, la longévité médiane des mangabeys en captivité est de 15 ans (durée de vie moyenne \pm E.S. = 16,0 \pm 2,1 ans, d'après les données démographiques de la Station Biologique de Paimpont).

1.1.2. Ecologie

Les populations sauvages de mangabeys à collier sont distribuées dans les régions côtières d'Afrique de l'Ouest, le long du Golfe de Guinée (au Nigeria, Cameroun, Guinée-Equatoriale, et Gabon. **Figure 3**). Les mangabeys sont retrouvés dans des habitats forestiers variés, principalement en futaies (hautes forêts) mais également dans des mangroves et forêts alluviales, et parfois autour d'aires cultivées (Jones et Sabater-Pi 1968; Gautier-Hion *et al.* 1999; Oates *et al.* 2008; Cooke 2012; Orimaye *et al.* 2016; Orimaye 2017). Ils se déplacent aussi bien de manière terrestre qu'arboricole, et peuvent donc être qualifiés de « semi-terrestres à tendance terrestres » (Jones et Sabater-Pi 1968; Cooke 2012; Mitani *et al.* 2012). Les mangabeys occupent ainsi les strates les plus basses de la forêt et passent beaucoup de temps au sol, mais fourragent et se nourrissent dans la canopée (Jones et Sabater-Pi 1968; Mitani 1989; Gautier-Hion *et al.* 1999). Principalement végétariens, ils se nourrissent de graines et de fruits, et

peuvent occasionnellement consommer des invertébrés et certains champignons (Jones et Sabater-Pi 1968; Mitani 1989; Cooke 2012; McGraw *et al.* 2014).

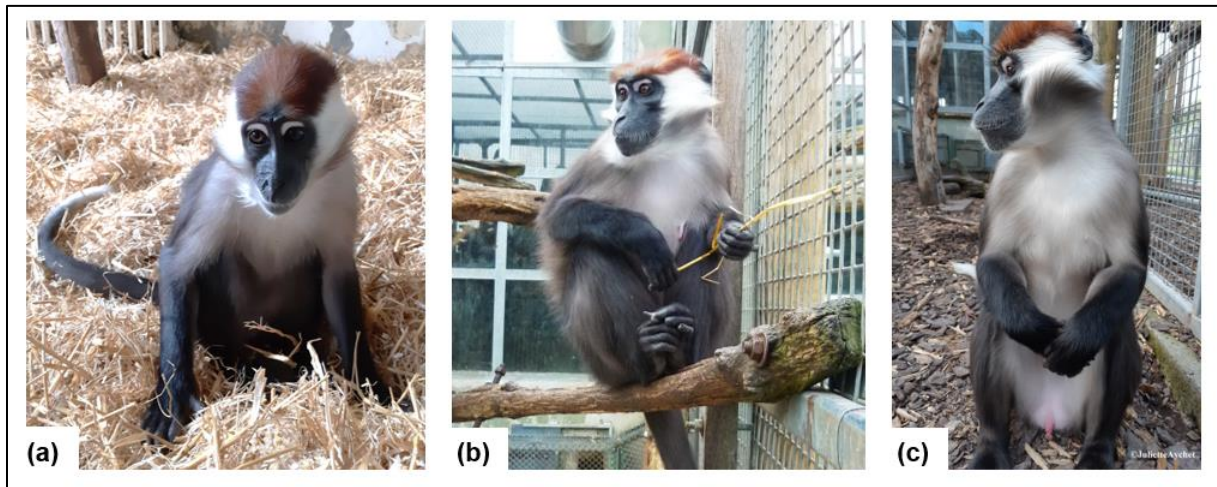


Figure 1. Photographies de mangabeys à collier. (a) Mâle juvénile de 3,5 ans ; (b) femelle adulte de 11 ans ; (c) mâle adulte de 10 ans. Crédit photographique : J. Aychet.

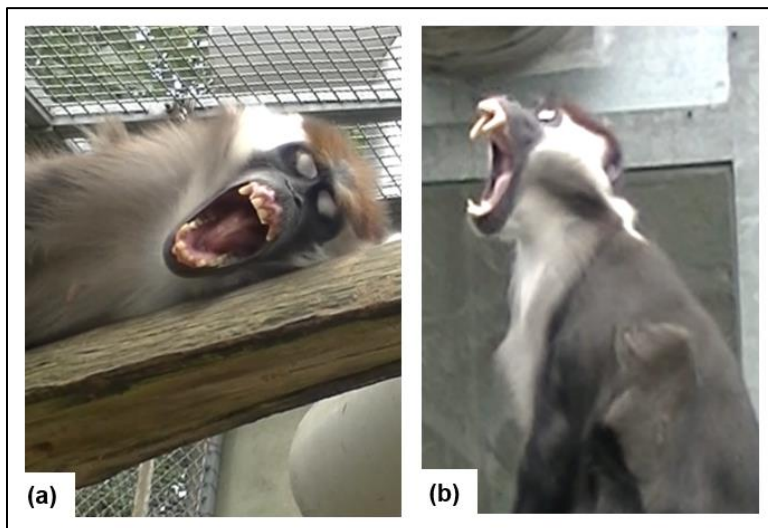


Figure 2. Dimorphisme sexuel pour la taille des canines, mis en évidence par les bâillements d'une femelle (a) et d'un mâle (b) adultes. Crédit photographique : J. Aychet.

Figure 3. Distribution géographique des populations sauvages de mangabeys à collier en Afrique centrale (Source : IUCN Red List of Threatened Species, Oates *et al.* 2008)



1.1.3. Organisation sociale

Les mangabeys à collier vivent naturellement dans de larges groupes multi-mâles, multi-femelles, allant de 10 à 25 individus, et pouvant exceptionnellement atteindre jusqu'à 60 individus (Jones et Sabater-Pi 1968; Gautier-Hion *et al.* 1999). Ces groupes peuvent se disperser en sous-ensembles, en particulier lors des déplacements et des activités de fourragement (Jones et Sabater-Pi 1968; Mitani 1989). Il existe jusqu'alors peu d'études sur la cohésion temporelle et spatiale des groupes de mangabeys à collier, mais de récentes données suggèrent que la présence de fruits dans l'environnement impacte la taille des groupes, qui varie de manière saisonnière (Dolado *et al.* 2016). Cependant, on ne retrouve pas chez les mangabeys à collier de dynamique de fission-fusion journalière comme chez les chimpanzés (*Pan troglodytes*, van Lawick-Goodall 1968), et bien qu'une variabilité saisonnière soit observée dans la taille des groupes, leur composition reste stable en termes de ratio âge-sexe (Dolado *et al.* 2016). Le ratio mâles : femelles : juvéniles au sein des groupes est de 1 : 1,25 : 1,86 (Mitani 1989). Comme chez la plupart des espèces de cercopithécins, les femelles sont philopatriques, tandis que les mâles émigrent au moment de la puberté et peuvent changer de groupe plusieurs fois au cours de leur vie (Pusey 1992; Range et Noë 2002; Range *et al.* 2007; Mitani *et al.* 2012). Ainsi, des mâles solitaires peuvent être observés en périphérie des groupes de mangabeys (Mitani 1989).

En captivité, les mangabeys sont organisés socialement selon une hiérarchie linéaire, avec une forte uni-directionnalité des agressions (Dolado et Beltran 2011, 2012), comme chez les sociétés de macaques dites « despotiques » (Thierry 2007). En revanche, certains aspects de la socialité des mangabeys captifs sont semblables à ce qui est observé chez des espèces dites « tolérantes » : les comportements agressifs sont très fréquents mais de faible intensité ; les individus dominants se tiennent en périphérie du groupe ; une forte proximité est observée entre les individus et l'épouillage est réciproque au sein des dyades (Dolado et Beltran 2012). D'après l'étude de groupes de mangabeys enfumés (*Cercocebus atys*), une espèce phylogénétiquement proche des mangabeys à collier et un temps considérée comme une sous-espèce de *C. torquatus* (Liedigk *et al.* 2014), la hiérarchie en captivité ne dépend des lignées maternelles que dans les 3 premières années de vie (Gust et Gordon 1994). En revanche, l'influence du rang hiérarchique des mères est durable dans les groupes sauvages (Range 2006). Les individus apparentés interagissent plus fréquemment (Mielke *et al.* 2020a). De plus, l'âge et le sexe des individus sont déterminants dans la fréquence des interactions au sein du groupe. Par exemple, les mâles adultes vivant au sein de groupes multi-mâles, multi-femelles, n'ont que de rares interactions affiliatives avec leurs juvéniles (Gust *et al.* 1998), et ne s'épouillent pas ou peu entre eux (Mielke *et al.* 2018) ; les individus sub-adultes sont fortement affiliés entre eux, en particulier pour les individus de même sexe (Mielke *et al.* 2020b) ; enfin, les femelles juvéniles épouillent préférentiellement des juvéniles de même rang hiérarchique et des femelles adultes (Range 2006). D'une manière générale, les mâles tiennent un rôle de protection du groupe ou sous-groupe (vigilance, alarme, défense du groupe), et les femelles sont

davantage impliquées dans les interactions sociales intra-groupes (Chalmers 1968; Gust et Gordon 1994; Range *et al.* 2007).

1.2. Population captive étudiée

Les présents travaux ont été réalisés sur des mangabeys à collier vivant en captivité à la Station Biologique de Paimpont (Université de Rennes 1, 35380 Paimpont, France). L'animalerie est agréée comme établissement utilisateur d'animaux à des fins scientifiques (n° d'agrément D 35-211-18 du 30/05/2017 délivré par la Direction Départementale de la Cohésion Sociale et de la Protection des Populations). Vingt-cinq individus ont été étudiés ici, dont 10 femelles et 15 mâles, et trois classes d'âges ont été distinguées : « juvéniles » pour les mâles de moins de 7 ans et la femelle de moins de 4 ans, « adultes » pour les autres individus de moins de 15 ans (longévité médiane), « vieux adultes » pour les individus de plus de 15 ans (**Tableau 1**). Tous les sujets sont nés en captivité, à la Station de Paimpont ou au zoo de Münster (Allwetterzoo Münster, Dutschland), et tous les liens de parentés au sein de la colonie sont connus.



Figure 4. Enclos extérieurs (a, b) et intérieurs (c) des mangabeys à collier à la Station Biologique de Paimpont. Crédit photographique : J. Aychet

Tableau 1. Caractéristiques des sujets d'étude et de leurs groupes sociaux. Tous les individus ont été inclus dans les études observationnelles. *: individus inclus dans l'étude expérimentale.

Groupe social	Ratio ♂ : ♀ : juvéniles	Sujet	Sexe	Date de naissance	Catégorie d'âge	Parents ♂ x ♀
I.	1 : 9 : 3	Bell*	Femelle	31/03/2002	Vieil adulte	Karlo x Zunie
		Chipie*	Femelle	28/06/1992	Vieil adulte	Boss x Sarah
		Gofrette*	Femelle	08/11/1996	Vieil adulte	Karlo x Zunie
		Joly*	Femelle	22/10/2000	Vieil adulte	Karlo x Zunie
		Zunie*	Femelle	03/07/1987	Vieil adulte	Zouzou x Nice
		Chipse*	Femelle	03/01/2006	Adulte	Pirate x Chipie
		Julie*	Femelle	08/05/2004	Adulte	Pirate x Chipie
		Maillette*	Femelle	29/12/2009	Adulte	Pirate x Gofrette
		Many*	Femelle	14/08/2008	Adulte	Pirate x Chipie
		Triskelle*	Femelle	21/04/2015	Juvénile	Kargi x Bell
		Kargi*	Mâle	19/05/2005	Adulte	<i>Zoo de Münster</i>
		Litchi*	Mâle	20/04/2015	Juvénile	Lupa x Julie
		Pouët	Mâle	14/03/2015	Juvénile	Lupa x Gofrette
II.	2 : 0 : 0	Kamel	Mâle	07/09/2010	Adulte	Isba x Bell
		Roby*	Mâle	18/11/2010	Adulte	Isba x Joly
III.	3 : 0 : 0	Bandit	Mâle	15/06/1991	Vieil adulte	Boss x Nancy
		Coët*	Mâle	31/08/2011	Adulte	Pirate x Gofrette
		Tips*	Mâle	10/07/2011	Adulte	Pirate x Chipse
IV.	4 : 0 : 0	Pirate	Mâle	17/10/1992	Vieil adulte	Boss x Nancy
		Carillon	Mâle	02/04/2007	Adulte	Pirate x Chipie
		Elky	Mâle	06/11/2009	Adulte	Pirate x Chipie
		George	Mâle	05/06/2006	Adulte	Pirate x Gofrette
V.	3 : 0 : 0	Marti	Mâle	16/10/1998	Vieil adulte	Karlo x Zunie
		Isba	Mâle	20/04/2004	Adulte	Karlo x Zunie
		Lenni	Mâle	07/10/2006	Adulte	Karlo x Zunie

Les groupes sont hébergés dans des enclos intérieurs et extérieurs de tailles variables (de 8 à 26,4 m² en intérieur, et de 14,7 à 37,2 m² en extérieur), dont la hauteur va de 2,5 à 4,4 m. Ces enclos sont reliés entre eux par des tunnels, permettant aux singes d'entrer et de sortir à volonté. La température intérieure est maintenue à 22 ± 2°C. Le sol des enclos intérieurs est couvert de paille et de copeaux de bois, et celui des enclos extérieurs est cimenté ou couvert d'écorce (**Figure 4**). Des perchoirs en bois ou métal sont fixés dans chacun des enclos, auxquels peuvent être accrochés des chaînes ou rubans. Les singes sont nourris deux fois par jour, avec des fruits et légumes frais le matin, et des granulés industriels l'après-midi. Des enrichissements alimentaires sont parfois distribués en supplément, comme des insectes (criquets), des œufs de caille, du feuillage ou des pommes de pin. L'eau est accessible *ad libitum* depuis les enclos intérieurs, grâce à des robinets actionnables.

2. Approche observationnelle

Afin de caractériser la communication gestuelle et multimodale des mangabeys à collier, en particulier en termes d'intentionnalité, de latéralité et de flexibilité, nous nous sommes d'abord intéressés à leur communication spontanée, en contexte dyadique intraspécifique. Est présenté ici le principe général des méthodes d'observation et d'analyse utilisées. Ces méthodes seront ensuite plus détaillées dans les **articles 1, 2, 3 et 4**.

2.1. Collecte des données

Les observations ont été réalisées selon la méthode d'échantillonnage en focal (Altmann 1974), via des enregistrements de vidéos par sessions de 15 minutes. Les individus ont été observés à toutes heures de la journée entre 9 h et 18h, et à toutes périodes de nourrissage (avant et pendant le premier nourrissage ; entre deux nourrissages ; pendant ou après le deuxième nourrissage). Les données comportementales ont ensuite été extraites des vidéos grâce à des logiciels de codage, Salomon Coder v.15.1.13.0 (**Article 1**) et BORIS v.6.0.6 (**Articles 2, 3 et 4**. Friard et Gamba 2016).

Une première période d'échantillonnage a eu lieu en amont de cette thèse, réalisé par Axelle Bono (étudiante de Master) de Janvier à Avril 2015, pour un total de 136 sessions d'observations de 17 individus (soit 34 heures). Les données issues de ces observations ont été analysées au cours de la présente thèse dans le cadre d'une collaboration internationale avec le docteur Anne Schel de l'université d'Utrecht (Pays-Bas), et ont permis une première description des gestes des mangabeys et de l'intentionnalité de ces gestes (**Article 1**). J'ai à mon tour réalisé des observations de Janvier à Juin 2018 sur 25 individus, suivant la même méthode d'échantillonnage et correspondant à 200 sessions d'observations (soit environ 52 heures). Ces données ont permis de décrire le répertoire d'expressions faciales des mangabeys et d'en étudier l'intentionnalité dans le cadre d'une deuxième collaboration internationale avec le professeur Elisabetta Palagi de l'université de Pise (Italie) (**Article 2**), de compléter le répertoire de gestes et d'en caractériser la latéralité (**Article 3**), et de décrire l'utilisation flexible de signaux en combinaisons, notamment multimodales et multicomposantes (**Article 4**).

2.2. Description des gestes et des expressions faciales

Les gestes ont été définis ici comme tous mouvements du corps, mécaniquement inefficaces et dirigés vers un receveur (d'après l'orientation du corps, du regard, et/ou un contact physique entre le signaleur et le receveur). Ainsi, pour décrire le répertoire de signaux visuels des mangabeys à collier, les gestes ont été définis au sens large et incluaient aussi bien des mouvements brachio-manuels que des postures et mouvements du corps ou de la tête (e.g. Call et Tomasello 2007; Pika et Liebal 2012; Liebal *et al.* 2014). Les expressions faciales ont quant à elles été définies comme tous mouvements de la

bouche, des lèvres, des sourcils ou des oreilles, qui pouvaient être produits seuls ou en combinaisons, au cours d'interactions sociales ou non (van Hooff 1967; Waller et Micheletta 2013; Liebal *et al.* 2014).

La description du répertoire de signaux visuels des mangabeys s'est ainsi réalisée en deux temps. Suite à une première description (**Article 1**, basée sur les sessions d'observation 1 à 136), le répertoire a été complété par la description d'autres gestes et la description des expressions faciales (sessions 137 à 337). Pour déterminer si le répertoire était exhaustif, nous avons tracé une courbe du nombre cumulé de signaux visuels décrits au cours des sessions d'observations (**Figure 5**), l'atteinte d'une asymptote indiquant que la totalité du répertoire de la population est décrit (e.g. Pika *et al.* 2005a; Molesti *et al.* 2019). Une asymptote semblait avoir été atteinte à la 284^{ème} session d'observation pour le répertoire de gestes, mais un nouveau geste décrit à la dernière session suggère que quelques autres gestes pourraient être décrits à l'avenir. En revanche, le répertoire d'expressions faciales semble être complet, la taille maximale du répertoire ayant été atteinte en 31 sessions d'observation sur 200 (**Article 2**).

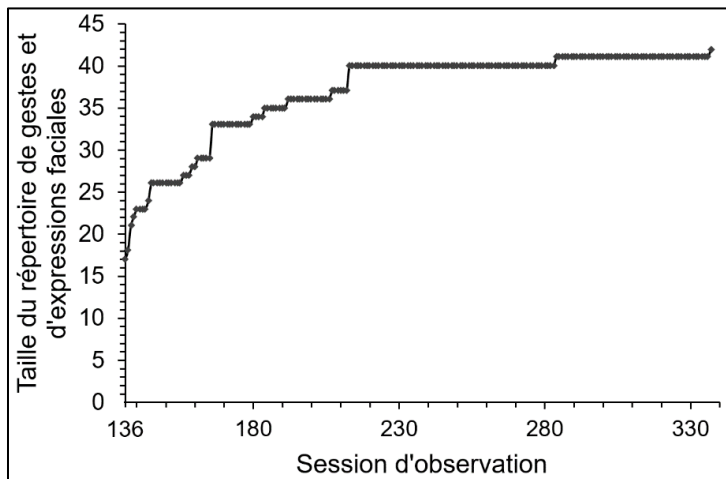


Figure 5. Evolution de la taille du répertoire de signaux visuels décrits chez les mangabeys au cours de la seconde période d'échantillonnage (sessions 137 à 337).

2.3. Analyse de l'intentionnalité des signaux

L'intentionnalité des signaux visuels des mangabeys à collier a été évaluée, d'une part pour les gestes (**Article 1**) et d'autre part pour les expressions faciales (**Article 2**). Nous nous sommes intéressés ici à la communication intentionnelle de « niveau 1 » (Dennett 1983), dans laquelle un individu (le signaleur) produit volontairement un signal en direction d'un receveur, dans le but de modifier le comportement de celui-ci (voir Chapitre I, partie 3.1.1.). Nous basant sur la méthodologie classiquement utilisée pour étudier l'intentionnalité de la communication chez les primates, en particulier la communication gestuelle (Leavens *et al.* 2005; Liebal *et al.* 2014; Byrne *et al.* 2017; Townsend *et al.* 2017), nous avons testé la présence de **marqueurs comportementaux d'intentionnalité** accompagnant les signaux des mangabeys (détaillés dans le Chapitre I, partie 3.1.2.). Ces marqueurs peuvent être regroupés en trois grands critères (Townsend *et al.* 2017), indiquant que le signal est (i) dirigé vers un receveur, (ii) produit dans un but précis et (iii) provoque une réponse du receveur, cohérente avec

l'intention supposée du signaleur. Pour qu'un signal soit considéré comme intentionnel, ces trois grands critères doivent être vérifiés. Nous avons ainsi décrit la présence ou absence de ces marqueurs au moment de la production des gestes et expressions faciales des mangabeys, puis utilisé des **statistiques non paramétriques** pour tester si ces marqueurs étaient associés avec les signaux visuels de manière non aléatoire.

2.4. Analyse de la latéralité gestuelle

Nous avons cherché ensuite à évaluer la latéralité gestuelle des mangabeys à collier, en s'intéressant spécifiquement à leurs gestes brachio-manuels (**Article 3**). Ces analyses ont été réalisées dans le cadre d'un stage de Master 1 (co-encadrement de l'étudiante Noémie Monchy).

Dans un premier temps, nous avons testé l'existence d'une latéralisation aux niveaux individuel et populationnel. Un individu est considéré comme latéralisé s'il utilise préférentiellement un côté pour effectuer un geste (McGrew et Marchant 1997). La latéralité gestuelle a ainsi été analysée au niveau individuel à l'aide de **tests Binomiaux**, comparant la proportion de gestes effectués avec la main droite ou la main gauche à une proportion théorique de 0,5. Nous avons ensuite calculé pour chacun un indice de latéralité **HI** (« Handedness Index »), couramment utilisé pour étudier la latéralité chez les primates non-humains et indiquant la direction d'une éventuelle latéralisation pour une tâche donnée (e.g. Hamilton et Vermeire 1988). La valeur absolue de cet indice, **ABSHI**, permet quant à elle d'estimer la force de la latéralité. La latéralité à échelle populationnelle correspond à un cas de population dans laquelle la majorité des individus présente une préférence manuelle (e.g. Rogers 2009; Chapelain *et al.* 2011), voire une préférence pour la même main (e.g. Fagot *et al.* 1991). Elle a ainsi été estimée en se basant sur le nombre d'individus latéralisés, et sur la comparaison du nombre de gestes produits avec la main droite ou la main gauche dans la population.

Dans un deuxième temps, nous avons testé l'effet de différents facteurs (contextuels, relatifs au geste et sociodémographiques) sur une éventuelle préférence manuelle dans la production de gestes intraspécifiques. Pour cela, nous avons choisi d'adopter une approche multifactorielle, en analysant l'effet de ces facteurs à l'aide d'un modèle mixte linéaire généralisé (**GLMM**). Cette approche, précédemment adoptée par Prieur *et al.* (2016a, 2017a) pour caractériser la latéralité gestuelle des chimpanzés et gorilles, permet de tester l'effet de chaque facteur tout en prenant en compte l'effet des autres facteurs « fixes », et des effets individuels, facteurs « aléatoires ».

2.5. Description des combinaisons de signaux

Nous nous sommes ensuite intéressés au potentiel usage flexible des signaux communicatifs par les mangabeys, en termes de combinaisons de signaux (**Article 4**). Nous avons cherché en particulier à décrire et quantifier les combinaisons de différents types et modalités de signaux. Nos observations nous

ayant permis de décrire les signaux gestuels et faciaux des mangabeys (**Articles 1, 2 et 4**), et leur répertoire vocal ayant été précédemment établi (**Figure 6**, Bouchet *et al.* 2010), nous avons pu prendre en compte ces trois types de signaux communicatifs dans nos analyses. Nous avons également distingué trois types de modalités sensorielles : visuelle, audible et tactile. Les signaux ont été définis comme « visuels » s’il s’agissait de gestes ou mouvements faciaux silencieux et distants, comme « tactiles » s’ils impliquaient un contact physique avec le receveur et comme « audibles » s’ils impliquaient la production d’un son vocal ou non-vocal (e.g. Pika *et al.* 2003; Liebal *et al.* 2004a; Pika 2008; Fröhlich *et al.* 2016).

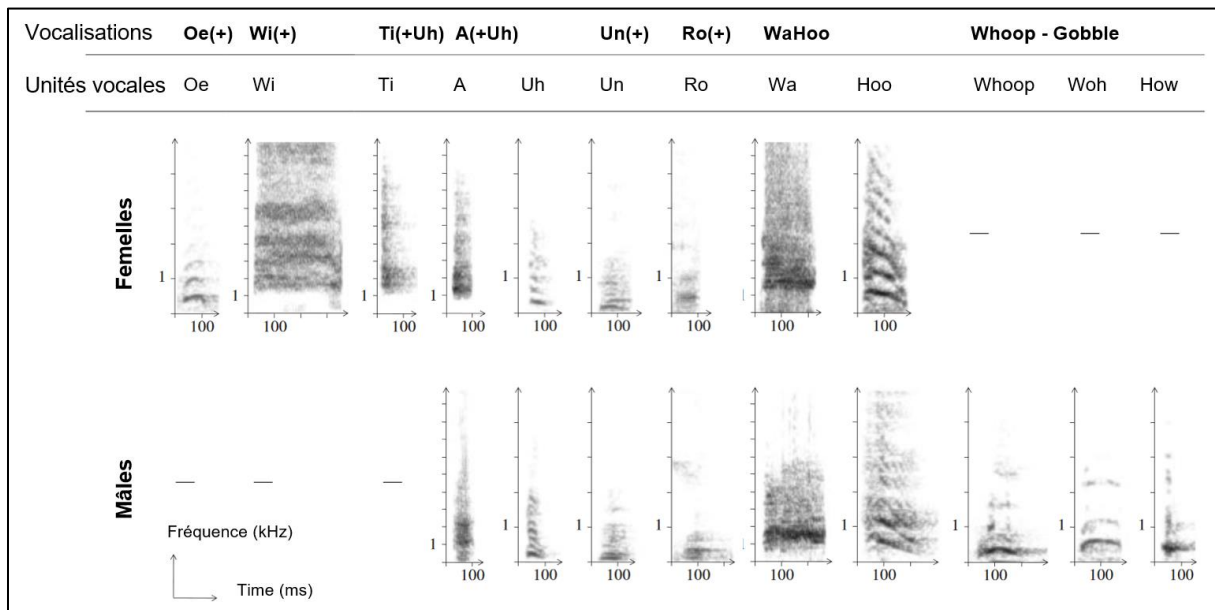


Figure 6. Répertoire vocal des mangabeys à collier (d’après Bouchet *et al.* 2010). Les vocalisations sont nommées d’après les unités vocales qui les composent. (+) indique une éventuelle répétition de l’unité vocale, (Uh) indique l’éventuelle présence d’une unité Uh terminant la vocalisation.

La **définition temporelle** des combinaisons de signaux diffère grandement d’une étude à l’autre. Certains auteurs considèrent des signaux comme combinés uniquement s’ils se superposent (e.g. Wilke *et al.* 2017), d’autres s’ils se superposent ou sont séparés par une pause d’une durée inférieure à une valeur arbitraire, par exemple 1 seconde (e.g. Genty et Byrne 2010; Hobaiter et Byrne 2011a; Genty *et al.* 2015; Hobaiter *et al.* 2017; Genty 2019; Knox *et al.* 2019), 2 secondes (e.g. Tagliatela *et al.* 2015) ou 5 secondes (e.g. Liebal *et al.* 2004a, 2006; Tempelmann et Liebal 2012). Enfin, certains auteurs considèrent des signaux comme combinés s’ils sont initiés à moins de 10 secondes les uns des autres (Pollick et De Waal 2007). Cherchant ici à utiliser un critère de définition moins arbitraire et qui soit le plus pertinent possible au regard de l’espèce étudiée, nous avons basé la définition des combinaisons de signaux sur les latences *observées* séparant généralement l’initiation de deux signaux communicatifs chez les mangabeys à collier. Nous avons pour cela utilisé la même méthode graphique que dans les études portant sur les échanges vocaux des primates (Lemasson *et al.* 2010, 2018a; Levréro *et al.* 2019),

nous permettant d'identifier une latence seuil X. Les signaux étaient alors considérés comme combinés s'ils étaient produits au sein d'une même « séquence communicative », définie comme une série de signaux produits par un même signaleur vers un même receveur, et initiés à moins de X secondes les uns des autres (ces signaux pouvant ainsi se superposer ou non).

Une fois les séquences communicatives extraites du jeu de données grâce à cette définition, nous avons cherché à identifier les « séquences types » produites par les mangabeys à collier. Nous avons pour cela appliqué une méthode d'**analyse séquentielle**, grâce à TraMineR, un outil d'analyse sur R (R Core Team 2018) initialement développé pour des études de sciences sociales (Gabadinho *et al.* 2011). Des distances ont été calculées entre chaque dyade de séquences, selon la méthode de l'« optimal matching » (Levenshtein 1966; Needleman et Wunsch 1970; Abbott et Forrest 1986; Studer et Ritschard 2016), le calcul étant basé sur le nombre de modifications qu'il faudrait appliquer à une séquence pour la transformer en une autre. Cette méthode nous a permis de grouper les séquences similaires entre elles, et donc d'identifier les principaux types de séquences communicatives produites par les mangabeys, pour tester alors l'effet de différents facteurs contextuels et sociodémographiques sur leur production. Pour décrire plus précisément les combinaisons de signaux au sein des séquences, différentes méthodes ont ensuite été envisagées. La première approche imaginée fut d'analyser les séquences de signaux communicatifs comme des chaînes de Markov, et ainsi de décrire les probabilités de transitions d'un signal à un autre, comme cela a été souvent fait pour les séquences vocales chez différents animaux (Kershenbaum *et al.* 2014), ou même pour des séquences de gestes chez les grands singes (Genty et Byrne 2010). Cependant, souhaitant décrire particulièrement les dyades de signaux fréquemment combinés par les mangabeys, et évaluer l'implication de chaque type et modalité de signal dans ces combinaisons, nous ne cherchions pas spécifiquement à décrire l'ordre de production des signaux communicatifs. Cet aspect pourra être plus détaillé dans de futures études. Nous nous sommes finalement tournés vers une autre méthode, et avons analysé les combinaisons de signaux comme un **réseau d'associations**. Cette approche nous a permis de représenter de façon claire les combinaisons de signaux, ainsi que de quantifier et comparer l'importance de chaque type et modalité de signal grâce aux **indices de réseaux** (Whitehead 2008; Sosa *et al.* 2020). Nous avons utilisé le logiciel SOCPROG v.2.9 (Whitehead 2009), développé pour l'analyse de réseaux sociaux, afin de calculer les indices d'association de chaque dyade de signaux (Ginsberg et Young 1992), et des indices de réseaux (degré, force, affinité, et coefficient d'agrégation). Un diagramme a ensuite été tracé pour représenter le réseau de combinaisons de signaux, grâce au logiciel GEPHI 0.9.2 (Bastian *et al.* 2009).

2.6. Analyses du contexte et des facteurs sociodémographiques

Nous avons testé le potentiel effet de facteurs contextuels et sociodémographiques sur la production des signaux visuels (**Articles 1 et 2**), sur la latéralité gestuelle (**Article 3**) et sur la production de signaux en combinaisons (**Article 4**). Le **contexte** dans lequel ont été produits les signaux communicatifs des

mangabeys a été catégorisé selon les comportements observés chez le signaleur et le receveur dans les 5 secondes précédant et suivant le signal communicatif. Huit contextes ont été distingués : affiliation, épouillage, alarme, agression, soumission, jeu social, socio-sexuel et non-social (Baraud 2007; Bouchet *et al.* 2010; Baraud *et al.* 2016). Les caractéristiques sociodémographiques du signaleur et du receveur ont toujours été définies via des variables catégorielles, permettant d'analyser leurs effets conjointement à d'autres facteurs grâce à des modèles mixtes. Outre l'**âge** et le **sexe** des sujets, nous nous sommes intéressés à la relation entre le signaleur et le receveur. Nous avons ainsi déterminé la relation de **dominance** pour chaque dyade d'individus, identifiant pour chacune d'elle l'individu dominant et dominé, en nous basant sur les comportements d'évitement (voir comportements de « rupture de contact », Baraud 2007). La connaissance des liens de **parenté** entre les différents sujets nous a permis d'identifier les dyades d'individus dits « apparentés » (parents et enfants, frères ou sœurs) ou « non-apparentés » (dont le lien est plus éloigné). Nous n'avons pas pu prendre en compte ici l'affiliation entre les individus, car une catégorisation basée sur une valeur d'indice d'affiliation (e.g. ratio de comportements affiliatifs et agonistiques : Weaver et De Waal 2002 ; Indice Composite de Socialité : Silk *et al.* 2006, 2013 ; Indice d'Affiliation Dyadique : Prieur 2015; Prieur *et al.* 2016a), n'aurait pu être utilisée de manière fiable ici en raison de l'inégalité de composition des différents groupes sociaux étudiés.

3. Approche expérimentale

Afin de tester l'intentionnalité de la communication gestuelle des mangabeys en conditions contrôlées, ainsi que leur capacité à utiliser différentes modalités sensorielles de manière flexible, nous avons mis en place une expérience impliquant une communication avec un expérimentateur humain. Cette expérience a été réalisée dans le cadre d'un stage de Master 2 (co-encadrement de l'étudiant Pablo Pezzino). Quinze mangabeys à collier ont été testés (**Tableau 1**), entre Janvier et Avril 2019. Nous présentons ici le principe de l'approche expérimentale adoptée, dont le détail sera explicité dans l'**article 5**.

3.1. Paradigme de quémante alimentaire

La sensibilité à l'état attentionnel du receveur, et la capacité à attirer son attention, sont des marqueurs clés de communication intentionnelle (voir Chapitre I, partie 3.1.2). Pour tester cette aptitude cognitive chez les primates non-humains, en particulier dans leur communication gestuelle, des expériences impliquant la **production de gestes de quémante envers un humain** sont classiquement mises en place (e.g. chez les grands singes, *Pan troglodytes*, *P. paniscus*, *Gorilla gorilla*, *Pongo pygmaeus* : Call et Tomasello 1994; Povinelli *et al.* 2003; Leavens *et al.* 2004a; Liebal *et al.* 2004b; Poss *et al.* 2006; Cartmill et Byrne 2007; Roberts *et al.* 2014b ; les babouins olives, *Papio anubis* :

Bourjade *et al.* 2013a; Meunier *et al.* 2013c ; les macaques Rhésus et à bonnet, *Macaca mulatta* et *radiata* : Canteloup *et al.* 2015a; Deshpande *et al.* 2018 ; les singes écureuils, *Saimiri sciureus* : Anderson *et al.* 2007, 2010 ; les singes capucins, *Cebus apella* : Defolie *et al.* 2015). Cette approche permet de modéliser une communication dyadique en plaçant l'expérimentateur comme *receveur*, et ainsi de tester l'effet du comportement de celui-ci sur la communication, en contrôlant notamment sa posture et donc son état d'attention visuelle (potentiellement perçu par la direction des yeux, l'orientation de la tête, du corps : Emery 2000). En plus de standardiser les conditions dans lesquelles les sujets vont communiquer, l'utilisation de ce paradigme expérimental permet de tester l'intentionnalité de la communication chez plusieurs espèces avec la même approche, autorisant des comparaisons plus directes entre les études.

Cette approche expérimentale nécessite généralement un **entraînement** préalable des singes pour la production de gestes de quémade, absents du répertoire comportemental des sujets étudiés (e.g. Anderson *et al.* 2007, 2010; Maille *et al.* 2012; Bourjade *et al.* 2013a; Meunier *et al.* 2013c; Canteloup *et al.* 2015a; Defolie *et al.* 2015). Ainsi les potentielles capacités des singes à communiquer de manière intentionnelle sont étudiées au travers d'un geste dont l'ontogénèse est connue. Le geste de quémade est une extension du bras en direction d'un receveur pour obtenir une récompense alimentaire, la main ouverte. Ce geste peut être acquis selon un processus de ritualisation ontogénétique, à partir d'une action de saisie de la récompense alimentaire dans les mains de l'expérimentateur, progressivement positionné hors d'atteinte (Bourjade *et al.* 2013a; Meunier *et al.* 2013c; Canteloup *et al.* 2015a). C'est selon ce protocole que nous avons entraîné les mangabeys à collier à produire des gestes de quémade, préalablement aux sessions expérimentales.

3.2. Principe et mise au point du dispositif expérimental

Une précédente étude avait mis en évidence la sensibilité des mangabeys à l'état attentionnel de leur receveur, grâce au paradigme de quémade alimentaire (Maille *et al.* 2012). Ces résultats montraient que la production et la fréquence des gestes dépendaient de la posture de l'expérimentateur, en particulier de l'orientation de sa tête et de son corps. Notre objectif ici était d'approfondir cette question, relative à la capacité des mangabeys à utiliser un geste communicatif intentionnellement et de manière flexible. L'expérience impliquait sept conditions expérimentales différentes, pour :

- (i) Vérifier que les gestes de quémade appris avaient bien une valeur communicative, et étaient donc dépendants de la **présence d'un potentiel receveur**. Pour cela, nous avons comparé des conditions dans lesquelles l'expérimentateur était présent ou absent, hypothétisant que les gestes ne seraient produits qu'en présence de l'humain et accompagnés d'alternances de regards.

- (ii) Evaluer l'effet de l'**état attentionnel du receveur** sur la production des gestes, et en particulier sur la stratégie potentiellement mise en place face à un receveur visuellement non attentif. Différentes conditions impliquaient différentes postures de l'expérimentateur, faisant varier la direction de sa tête et de son corps. Nous avons alors utilisé un dispositif original, permettant aux singes de se déplacer autour de l'expérimentateur, et/ou d'utiliser différentes modalités de gestes pour communiquer, visuelle ou audible. Nous avons ainsi fait l'hypothèse que les singes produiraient moins de gestes de quémade face à un receveur inattentif, et dans le cas où celui-ci leur tournerait le dos, se déplaceraient pour se placer face à lui ou attireraient son attention avec des signaux acoustiques.

- (iii) Evaluer l'effet de la **réponse du receveur** aux gestes communicatifs, en particulier pour tester la capacité des mangabeys à persister et/ou élaborer leur communication en cas d'échec d'un premier signal. Pour tester cela, différentes conditions ont été mises en place, dans lesquelles l'expérimentateur mettait plus de temps à répondre que dans la condition contrôle (« pas de réponse ») ou répondait de manière incongrue (« mauvaise réponse »). Nous avons alors fait l'hypothèse qu'en l'absence d'une réponse satisfaisante de la part du receveur, les mangabeys répèteraient leurs gestes et/ou élaboreraient de manière visuelle (en modulant leurs gestes de quémade ou en produisant d'autres signaux) ou de manière audible (en produisant des gestes audibles ou des vocalisations).

Nous avons utilisé un dispositif mis au point et fabriqué spécialement pour cette expérience de quémade alimentaire. Il s'agissait d'une cage cubique de 1,70 m de côté, dont deux faces étaient équipées de « trous de quémade », à travers lesquels les mangabeys pouvaient passer leurs bras pour quémader une récompense à l'expérimentateur placé au centre (**Figure 7**). Au-dessus de l'un des « trous de quémade » étaient disposées des clochettes. Ainsi, produire un geste de quémade à travers ce trou permettait aux mangabeys de produire un signal audible plutôt qu'uniquement visuel, sans en changer la forme.



Figure 7. Dispositif expérimental conçu pour tester l'intentionnalité des gestes interspécifiques. Une cage cubique de 1,70 m de côté a été fabriquée (a), dont deux faces étaient pourvues de trous permettant aux singes de passer leurs bras pour communiquer, de manière sonore ou silencieuse (b). L'expérimentateur se trouvait au centre de la cage, permettant aux singes de se déplacer autour de lui (c). Crédit photographique : J. Aychet.

4. Complémentarité des approches observationnelles et expérimentales

En premier lieu, il est à noter que la communication spontanée et intraspécifique des individus captifs peut différer de la communication observée à l'état sauvage. En effet, la composition des groupes sociaux diffère de celle des groupes naturels (au niveau de la taille et des paramètres démographiques), ce qui peut avoir un impact significatif sur le type d'interactions au sein des groupes (voir partie 1.1.3.). La proximité spatiale des individus au sein d'un groupe peut également impacter les relations sociales, et la proximité des cages favoriser les interactions inter-groupes. Certains contextes existants dans un environnement naturel seront absents ici, comme des déplacements de groupe ou des contextes de prédation. Inversement, certains paramètres sont inhérents à l'environnement captif des individus, comme les nourrissages, pouvant impliquer des périodes d'anticipation alimentaire (Waitt et Buchanan-Smith 2001). Ces facteurs sociaux et contextuels sont donc susceptibles d'affecter la composition du répertoire de signaux communicatifs, et leurs fréquences d'utilisation. Enfin, l'environnement visuel en captivité est moins encombré que l'environnement naturel des mangabeys (voir partie 1.1.2.), ce qui peut avoir un effet sur les modalités sensorielles impliquées dans la communication (Hebets et Papaj

2005; Fröhlich et van Schaik 2018). Bien que ces facteurs soient susceptibles d'impacter le répertoire de signaux communicatifs, étudier des populations captives permet d'explorer les caractéristiques cognitives sous-tendant la communication via une double approche, observationnelle et expérimentale.

L'observation permet d'étudier les propriétés de la communication dans un contexte intraspécifique spontané, donc cohérent avec la biologie de l'espèce, et en particulier avec sa socialité. Les données d'observation en contexte intraspécifique nous ont permis ici de caractériser la communication gestuelle et multimodale des mangabeys, en évaluant l'effet de différents facteurs, liés aux contextes des interactions ou aux caractéristiques sociodémographiques du signaleur et du receveur. L'observation ne permet pas en revanche de tester l'effet de certains paramètres de manière isolée, comme le comportement du receveur. Une approche expérimentale nous a ainsi permis de contrôler certains aspects de la communication gestuelle dyadique pour évaluer l'intentionnalité et la flexibilité des gestes des mangabeys, en complément des résultats de nos observations. Comme évoqué précédemment, l'approche expérimentale a également l'avantage de faciliter la comparaison des résultats avec ceux obtenus chez d'autres espèces dans des conditions similaires. Cette approche présente cependant des limites dans l'interprétation à donner aux résultats, car l'expression de certains marqueurs comportementaux d'intentionnalité pourrait être favorisée dans ce contexte (Liebal *et al.* 2014). Un meilleur contrôle du contexte de communication, permis par l'approche expérimentale en comparaison à l'approche observationnelle, offre davantage d'occasions de détecter des marqueurs d'intentionnalité dans la communication des sujets. Cependant, l'entraînement à produire des gestes, et l'interaction avec l'humain, pourraient également être à l'origine de l'expression de ces comportements. Il a par exemple été montré chez les babouins olives que les expériences individuelles d'entraînement à produire des gestes de quémade peuvent avoir un effet sur la sensibilité des singes à certains indices d'état attentionnel de l'humain, ou sur la manière dont ils alternent le regard conjointement à leurs gestes (Bourjade *et al.* 2015, 2019). Le contexte de quémade alimentaire avec un humain est également une situation très différente d'un contexte intraspécifique, puisqu'il implique une interaction avec un individu partageant de la nourriture, sans aucun contact physique possible, ce qui peut conduire au développement de stratégies de communication différentes de celles habituellement utilisées face à des congénères (Liebal *et al.* 2014).

Ainsi, les résultats issus de l'approche expérimentale ne reflèteront pas forcément des stratégies de communication que les singes adoptent en contexte intraspécifique, mais permettront d'évaluer s'ils sont *capables* de les mettre en place. L'approche observationnelle, quant à elle, permet de s'affranchir des biais liés à l'interaction avec l'humain, pour s'intéresser à l'effet de facteurs spécifiques aux interactions entre congénères. C'est la raison pour laquelle ces deux approches ont été adoptées ici, afin de caractériser la communication gestuelle et multimodale des mangabeys à coller en termes d'intentionnalité, de latéralité et de flexibilité.



Chapitre III

Intentionnalité des signaux visuels spontanés



Article 1

Intentional gesturing in red-capped mangabeys (*Cercocebus torquatus*)

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SYNTHESE DE L'ARTICLE 1

Contexte

Les recherches menées ces trente dernières années sur la communication gestuelle des grands singes mettent en évidence la capacité de ces derniers à communiquer de manière intentionnelle, suggérant que cette propriété clé du langage soit héritée de l'ancêtre commun aux hominoïdes actuels. Peu d'études se sont cependant intéressées à la communication gestuelle des autres singes en contexte intraspécifique. Le caractère intentionnel des gestes des cercopithécidés est encore débattu, tout comme l'existence de gestes manuels visuels dans leurs répertoires communicatifs.

Méthode

Nous avons analysé la communication gestuelle intraspécifique de 17 mangabeys à collier en captivité, cherchant à savoir si leurs gestes (mouvements des membres, de la tête, du tronc) étaient associés à des marqueurs comportementaux d'intentionnalité. Pour cela, les mangabeys ont été observés selon la méthode d'échantillonnage en focal, et une première description de leur répertoire de gestes a été réalisée.

Résultats

Nous avons montré que la majeure partie des gestes communicatifs produits par les mangabeys à collier présentaient des marques d'intentionnalité. Les mangabeys produisaient préférentiellement leurs gestes visuels face à un receveur attentif, et utilisaient d'autres modalités (tactile, audible) lorsqu'il ne l'était pas. Ils regardaient en direction du receveur avant de produire leurs gestes (« audience checking »), et maintenaient ensuite leurs regards vers le receveur en l'attente d'une réponse. Lorsque le receveur ne répondait pas, les mangabeys persistaient dans leur communication, répétant leurs signaux. Enfin, parmi les 20 gestes associés à ces marqueurs d'intentionnalité, quatre étaient des gestes brachio-manuels visuels.

Conclusion

Ainsi, il semble que les mangabeys à collier communiquent intentionnellement avec leurs congénères grâce à leurs gestes, notamment brachio-manuels. Conjointement aux récentes descriptions de la communication gestuelle spontanée des babouins olives et des macaques à bonnet, ces résultats suggèrent que la communication intentionnelle n'est pas seulement un trait commun aux hominoïdes mais à l'ensemble des primates catarrhiniens.

Intentional gesturing in red-capped mangabeys (*Cercocebus torquatus*)

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Abstract

Apes, human's closest living relatives, are renowned for their intentional and highly flexible use of gestural signals. In stark contrast, evidence for intentional signalling in monkeys is scarce. Here, we investigated spontaneous gestural communication amongst red-capped mangabeys (*Cercocebus torquatus*) with a special focus on manual gestures and hallmarks of intentionality. We applied established methods used in ape gesture research to analyse the communicative behaviour of a total of 17 individuals living in three different groups in captivity. Results showed that signallers showed hallmarks of intentionality during the production of 20 out of a total of 21 different body signal types, with four of these being strictly manual gesture types. During the production of these socially-directed signals, the monkeys showed sensitivity to the attentional states of recipients, adjustment of signal modality, audience checking before signal production, and response waiting. Moreover, in case of communication failure, the monkeys showed goal persistence. We discuss our results in light of several scientific directions that have been taken with regards to the comparative approach towards human language evolution and propose the red-capped mangabey as a model species to investigate these questions further. We further challenge the view that precursors to flexible intentional communicative strategies emerged in hominoids around 18 MYR ago. Instead, our results show that the origins of flexible and intentional communicative strategies are evolutionary older, *i.e.* already appearing in the primate lineage around 30 MYR ago.

Keywords: Gestural communication, Intentionality, Flexibility, Primates, gesture, manual

Introduction

Human language is a unique communication system in the animal kingdom, which crucially depends on a complex interplay of several sensory-motor, cognitive and computational capacities (Hauser et al. 2002). Trying to unravel its evolutionary roots has been a primary interest of researchers studying non-human animal communication and human language evolution in past decades (e.g. Hewes, 1973; Snowdon et al. 1982; Seyfarth, 2005; Arbib et al., 2008; Tomasello 2010; Petkov & Jarvis 2012; Lemasson et al. 2013; Fitch 2017). In this context, past comparative research revealed that precursors or pre-adaptations for several cognitive abilities needed for human language can be found in non-human animal communication systems (Hockett 1959; Fitch 2010; Hauser et al. 2002). One of these is the ability to communicate intentionally, which requires from individuals involved in the communicative act a certain degree of intentionality. In cognitive sciences, intentionality has been described as the capacity of mental states (e.g. knowing, believing and desiring) to be ‘about’ particular objects or situations: this assumes a certain form of rationality from the creature to which intentional states are attributed (Dennett, 1983). In animals, this may range from an individual having one’s own beliefs about a particular situation to having beliefs about the beliefs that other individuals have about that situation (e.g. Dennett, 1983; Cheney & Seyfarth, 1990; Hurford, 2007; Townsend et al., 2016; Sievers et al., 2017; Krupenye et al., 2017).

Animal studies investigating the intentionality of communication typically build onto the ‘intentional stance’ (Dennett, 1983), which explicitly assumes that animals are capable of having mental states. Following this view, several orders of cognitive complexity required for different levels of intentional communication can be differentiated. The simplest form is communication with ‘zero-order intentionality’, in which signallers produce their communicative signals reflexively. For this, they neither need to have a mental state of their own, nor to recognize the consequences of their signalling behaviour on the behaviour or mental state of others. In first order intentional communication, a signaller has a mental state of its own and recognizes the effects of its signalling behaviour on the behaviour of others, but he does not have mental states about mental states of others. In this case, a signaller may thus intend to signal to produce a desired behaviour change in the recipient, but not a mental one. Communication with second order intentionality occurs when a signaller is able to recognize both its own *and* the recipient’s mental state and intends to signal to change the latter. In this case, a signaller may for instance intend to signal about an external event that he is knowledgeable about, but the recipient is ignorant about (e.g. the presence of a predator). Third- and higher-order forms of intentional communication require ‘mutual mind-reading’, in which both signaller *and* recipient recognize each other’s mental states/ intentions and act accordingly (Dennett 1983; Scott-Philips 2015; Sievers et al., 2017). This latter type, also termed ‘overtly intentional’ or ‘ostensive’ communication (Sperber & Wilson 1995; Scott-

Philips 2015), has traditionally been regarded as ‘true communication’ and is common in human language (Grice 1957).

Currently, there is no consensus on whether or not non-human animals have, and actually need, the cognitive capacity for (mutual) mind-reading during their communicative exchanges (Scott-Philips 2015; Fischer & Price 2016; Moore 2016; Fitch 2016). Instead, it has been proposed that most animals possess a fully functional and adequate communication system *without* these higher forms of intentionality (Fischer & Price 2016; Townsend et al., 2016; Moore, 2016). In line with this, past studies on intentional non-human animal communication have mainly been focusing on the question whether or not first-order intentionality is used from the signallers’ perspective, without further implying anything about their capacity for mental state attribution or recipients recognizing their intentions (reviewed in Liebal et al. 2013; Sievers et al., 2017; but see Engh 2006; Crockford et al. 2017).

The majority of such studies have concentrated on the gestural signalling behaviour of apes. Gestures are generally defined as socially directed, mechanically ineffective body signals that result in a voluntary response from the recipient (*e.g.* Bates 1975; Plooij 1978; Tomasello et al. 1985; Pika 2008). In many studies, the described body signals include body postures, body movements and movements of hands, feet, limbs and head (reviewed in Call & Tomasello 2007; Pika & Liebal 2012; Liebal et al. 2013). Some studies include facial expressions too, resulting in a broader definition of the term gesture (*e.g.* Liebal et al. 2004; Gupta & Sinha, 2019; Molesti et al. 2020: but see Byrne et al. 2017 for argumentation to classify facial expressions and gestures as independent systems), whereas other studies only consider strictly manual gestures, *i.e.* free movements of the hands, feet and/or limbs that do not involve interaction with a substrate or object, as gestures (de Waal 2003; Pollick & de Waal 2007; Roberts et al. 2012, 2014), leading to a more restrictive definition. Moreover, more recent studies often only consider body signals produced during episodes of intentional communication as gestures (see *e.g.* Fröhlich & Hobaiter, 2018). For this, it is essential to be able to determine whether such signals are produced intentionally.

Determining whether or not body signals are produced intentionally has typically been done by applying methodologies originally developed to measure intentionality in preverbal human infant communication (*e.g.* Bates et al. 1975; Tomasello et al. 1994; Leavens et al. 2005). This method aims at identifying whether subjects make use of the behavioural ‘markers of intentionality’ (**Table 1**) during their signal production (see Townsend et al., 2016 for a recently re-evaluated theoretical framework concerning this topic), and whether they show flexibility in gesture use, *e.g.* in terms of ‘means-ends dissociation’ (Bruner 1981; Tomasello & Call, 1997). Using these methods, it has become clear from a large number of studies in captive and wild settings that all ape species make flexible use of intentionally produced gestures during their communicative interactions (*e.g.* Tomasello et al. 1985, 1994; Bard, 1992; Leavens et al. 1996, 2005; Liebal et al. 2004, 2006; Pika et al. 2003; 2007; Poss et al. 2006;

Cartmill & Byrne 2007, 2010; Genty et al. 2009; Hobaiter & Byrne 2011; Graham et al. 2016; Knox et al., 2019). In addition, these studies showed that within- and between-species differences of gesture use exist, which may for example reflect differences between species' socio-ecologies, differences in group composition (*e.g.* age-sex ratios), and associated sociocognitive abilities (*e.g.* Maestriperieri 1997; Liebal et al, 2006; Fröhlich & Hobaiter, 2018).

Table 1. Description of the behavioural markers used to identify whether or not body signals are produced with first order intentionality (cf. ape gesture studies, *e.g.* Tomasello et al. 1985, 1994; Call & Tomasello 2007; Pika 2008; Cartmill & Byrne 2007, 2010; Genty et al. 2009; Hobaiter & Byrne 2011; Hopkins & Leavens 1998; Hostetter et al. 2001; Leavens et al. 1996, 2004, 2005; Leavens & Hopkins 1998; Liebal et al. 2004, 2006; Pika et al. 2003; Poss et al. 2006; Roberts et al. 2012; Fröhlich et al. 2016).

Marker	Description
(0.) Social use (prerequisite to be considered 'communicative')	The signal is produced in the presence of individuals at close proximity and directed at one of them
(i.) Sensitivity to- and manipulation of attentional state of recipient	Signaller adjusts its signalling behaviour to the attentional state of the recipient, <i>i.e.</i> it takes into account whether the recipient can visually perceive its signals. If the signaller is not in the visual field of the recipient, the signaller produces tactile or audible signals or moves into the visual field of the recipient before signalling.
(ii.) Audience checking	Signaller monitors its audience before signalling and may visually orient to the recipient the signal is directed at.
(iii.) Gaze alternation	Signaller alternates its gaze between the recipient and an external object/event or individual of interest.
(iv.) Response waiting	After signalling, signaller pauses signalling for at least one second, during which he maintains visual contact, apparently monitoring the recipient's behaviour.
(v.) Goal persistence (persistence and elaboration)	Signaller repeats the same signal (persistence) or enhances its original signal by elaborating on it with an additional component (elaboration) when (apparently) unsatisfied* with a recipient's response.
	*Signaller satisfaction is identified by the signaller stopping its signalling behaviour after a specific (<i>intended and requested</i>) behaviour change from the recipient.

Whether or not primates other than apes also communicate with flexibly produced intentional gestures remains more controversial. Although the intentional use of body signals was already reported for macaques in the 1990's (*e.g.* *Macaca mulatta*; *M. nemestrina*, *M. arctoides*: Maestriperieri 1996, 1997, 1999), these studies did not apply the same and thus comparable methodology as used in ape gesture studies; *i.e.* systematically assessing the use of markers of intentionality during signal

production. Although more recent studies *did* use this methodology, there are several limitations. First of all, most of these studies exclusively focused on human-trained manual gesture use (e.g. manual pointing or begging signals) during monkeys' communicative interactions with human experimenters. One potential issue with this is that in these cases intensive training experience may affect the animals' behaviour (e.g. Bourjade et al., 2015; Leavens et al. 2019), resulting in possible misinterpretations of these species' natural capacities for intraspecific intentional gestural communication. Secondly, these studies often only tested the use of one or a restricted subset of the markers of intentionality during signal production, despite the fact that lower level explanations exist for the isolated use of every marker of intentionality (Liebal et al., 2013; Graham et al., 2019), and a more powerful approach into the study of communicative intentions would be to investigate whether or not subjects use *all* markers of intentionality simultaneously during their gestural communication (Liebal et al. 2013; Scott-Philips, 2015; Townsend et al. 2016; Graham et al 2019). Despite these issues, however, these previous studies found that monkeys can adjust their (trained) signals to the attentional states of human recipients, with some of them providing evidence for the additional use of one other marker of intentionality during signal production, such as gaze alternation or elaboration (e.g. *Cebus apella*: Hattori et al. 2007; 2010; Defolie et al. 2015; *Saimiri sciureus*: Anderson et al. 2010; *Cercocebus torquatus*: Maille et al. 2012; Aychet et al. 2020; *Papio anubis*: Meunier et al. 2013; Bourjade et al. 2014; ; *Macaca tonkeana*: Canteloup et al. 2015a; *Macaca mulatta*: Canteloup et al. 2015b). As mentioned, whether or not monkeys use species-specific body signals to intentionally communicate with conspecifics has received less research attention, with currently only two studies providing evidence that wild bonnet macaques (*Macaca radiata*: Gupta & Sinha, 2019) and captive olive baboons (*Papio anubis*; Molesti et al. 2020) use a particular subset of markers of intentionality when communicating with conspecifics.

In addition to this, naturally occurring intentional 'free manual gestures', i.e. gestures produced with the hands, feet and/or limbs that do not involve physical contact with a substrate or partner (Pollick & de Waal, 2007; Roberts et al., 2012), have been claimed to be virtually non-existent in monkeys (Call & Tomasello 2007; de Waal 2003; Pollick & de Waal 2007; Cartmill & Maestripietri, 2012; Roberts et al. 2012, 2014; de Waal 2016). In contrast, they are frequent communicative means in the gestural repertoires of apes (e.g. Hobaiter & Byrne, 2011; Liebal, 2007; Genty et al., 2009; Roberts et al. 2014; Graham et al., 2016; Knox et al., 2019). Manual gesture production has been identified as particularly relevant for theories on human language evolution (e.g. Call & Tomasello 2007; Cartmill & Maestripietri 2012; de Waal 2003, 2016; Pollick & de Waal 2007; Roberts et al. 2012, 2014), because the behavioural lateralization in their production may reveal more about the evolutionary roots of hemispheric asymmetry and specialization found in humans, which has been linked to the unique emergence of human language (e.g. Meguerditchian et al. 2010; 2013; Hopkins et al., 2012; Maille et al., 2013; Prieur et al., 2018; Fagot et al. 2019). Yet, keeping in mind the relative scarcity of systematic studies investigating whether primates other than the apes produce intentional gestures at all during their natural

intraspecific communicative exchanges, the necessary comparative work to support this view on manual gesture use is currently also lacking.

Therefore, the aim of this study was twofold. First, we systematically analysed whether captive red-capped mangabeys (*Cercocebus torquatus*), a monkey species of the *cercopithecoïd* superfamily of catarrhine primates, showed hallmarks of intentionality during their spontaneous intraspecific communicative exchanges involving body signals. For this, we determined which types of body signals were produced by the signallers and whether the animals adhered to *all* behavioural markers of intentionality during their production, which would classify them as (intentional) gestures. To be able to directly compare our results with similar studies done in apes we used methodology traditionally used in ape gesture studies (see **Table 1**). Secondly, we assessed whether these monkeys are capable of *free manual* gesture production. For this, from the subset of intentionally produced gesture types, we determined which ones were produced by making movements of the hands, feet and/or limbs only, without making physical contact with a substrate or partner (de Waal 2003; Roberts et al. 2012, 2014). Given the fact that in previous studies red-capped mangabeys were found to use human-trained (manual) gestures in intentional ways towards human experimenters (Maille et al. 2012; Aychet et al. 2020), we expected the monkeys to be able to use their body signals produced amongst conspecifics in intentional ways as well.

Methods

Study site and subjects

From January – April 2015, we collected focal video footage from a total of 17 adult and subadult captive red-capped mangabeys living in three social groups (*Cercocebus torquatus*) at the Station Biologique de Paimpont, France (**Table 2**). Red-capped mangabeys are medium sized (7.5-10 kg) diurnal and predominantly terrestrial primates that live in multimale-multifemale groups naturally occurring in Atlantic forest coastal areas ranging from Western Nigeria to Gabon, Africa (Gautier-Hion et al. 1999; Jones & Sabater-Pi 1968; Cooke 2012; Orimaye 2017). Reported group sizes in the wild range from 10 to 25 individuals (Jones & Sabater Pi 1968). Individual females and males are classified as adults when they are > 4 and 7 years of age, respectively, and as subadults when they are between 3 and 4 (females) or 7 (males) years of age, based on demographic data on a closely related species, *i.e.* grey-cheeked mangabeys (*Lophocebus albigena*; Chalmers 1968; Gautier-Hion and Gautier 1976; Deputte 1992). In this study, we considered individuals as ‘old’ adults if they were more than 15 years of age, corresponding to the median lifespan of mangabeys in captivity (based on 45 years data from our breeding facility on grey-cheeked and red-capped mangabeys).

Each individual had access to one outdoor enclosure and one indoor enclosure with different sizes (ranging from 15.3 to 29 m²), which were connected by tunnels. The different enclosures for the groups were subdivided into several sub-enclosures separated by gratings. The monkeys could move freely between the inside and outside enclosures, except during keepers' cleaning activities. The floor of the indoor enclosures was covered by straw and sawdust, whereas the floor of the outdoor enclosures was covered by bark or cement. Enrichment consisted of beams, ropes, chains, and tires. In the indoor enclosures, the temperature was stabilized at 22 ± 2 ° C. The monkeys were fed twice daily with fresh vegetables and fruits in the morning and monkey chow in the afternoon. Fresh water was available *ad libitum*.

Table 2. Social composition and individual details of the mangabeys in the study groups.

Group	Individual	Sex	Age at study (yrs)	Year of birth	Age category
I.	Chipie	Female	23	1992	Old
	Many	Female	7	2008	Young
	Chipse	Female	9	2006	Young
	Tips	Male	4	2011	Young
	Julie	Female	11	2004	Young
	Gofrette	Female	19	1996	Old
	Coet	Male	4	2011	Young
	Maillette	Female	6	2009	Young
II.	Bell	Female	13	2002	Young
	Kamel	Male	5	2010	Young
	Zunie	Female	28	1987	Old
	Joly	Female	15	2000	Old
	Roby	Male	5	2010	Young
III.	Pirate	Male	23	1992	Old
	George	Male	9	2006	Young
	Carillon	Male	8	2007	Young
	Elky	Male	6	2009	Young

Data collection & analyses

Daily observations took place between 9 a.m. and 5 p.m., with the monkeys being observed for a total of 4-6h per day. 15 min continuous focal-animal sampling (Altmann 1974) was used to video record the interactions of 17 adult and subadult focal individuals (the signallers) with their group members (the recipients) using a Panasonic HC-X920 digital video camera. Focal animals were selected following a preset randomized order. Usually, the focus was on individuals from one group in the morning and another in the afternoon, and the next day this order was alternated. If a focal subject moved outside the range of vision, the recording was stopped, but the recorded focal time was added to the total sampling time for that individual if it had lasted at least one minute. If a focal subject did not return within one minute after moving out of sight, the next session with a new focal animal was started. Each

of the focal individuals was sampled for a total of 120 minutes. When necessary, comments were given on the focal individuals' general behaviour, identity and sex of the potential recipient, the recipient's response, and identities of other animals present within the same area of the enclosure. We aimed to capture both the signaller and recipient in the same video frame. The video recordings were transferred to a PC and then loaded into Solomon Coder 15.1.13.0 for further video analyses.

Identifying body signals

During video analyses, we first identified all instances of expressive and mechanically ineffective body signals produced by a focal individual (the signaller), which were directed at a particular recipient (indicated via body orientation, eye gaze, or physical contact). In this study, we used the term 'body signals' in the broad sense, such that it comprised all brachio-manual movements, body postures, and body movements, including those where (nonmechanically effective) physical contact with any other individual or a substrate was made.

Identifying intentionality of body signals

After extracting all socially directed body signals produced by the focal individuals, we assessed for each signal separately whether they qualified as intentionally produced gestures. Because we aimed to compare our results with previous ape studies using similar methodology, we scored for all socially directed body signals whether they were accompanied by any of the behavioural markers of intentionality (**Table 1**). The marker 'gaze alternation' was omitted from these analyses as a preliminary inspection of our results revealed that none of the produced body signals appeared to concern an external object or third party and testing this experimentally did not fall within the aim of this study. Moreover, in order to assess whether the signaller exhibited goal persistence depending on the type of recipient's response, it was first of all scored whether the recipient responded with a 'positive' or 'negative' response after receiving a body signal that was directed at it. A positive response was scored when one of the two following situations applied: (1.) the recipient stopped its current activity within a particular behavioural context and changed this to one within a different behavioural context, or (2.) within one behavioural context the recipient changed its focus from self-directed behaviour or interacting with another individual than the signaller to interacting with the signaller. Behavioural contexts identified were: grooming (including *e.g.* start/stop grooming, change of grooming position), agonistic (including aggression and submission), affiliative (social positive behaviours other than grooming), sexual (*e.g.* copulation, inspect or touch genitals), and playing. A negative response was scored when a recipient did not show a behaviour change after receiving a signal that was directed at it. Important to note here is that because the occurrence of goal persistence is likely to depend on whether the signaller received a 'satisfactory (*intended*) response' (see **Table 1**) from the recipient as a reply to its initial signal, it can occur both after receiving a positive (but unsatisfactory) or a negative (and therefore unsatisfactory)

response from the recipient, *or* it may not occur at all, e.g. after receiving a satisfactory positive response. Therefore, goal persistence is expected to not always be present in all intentional communicative events, yet, at the same time it is considered a strong indicator that communication is intentional (Liebal et al. 2013).

Identification of whether or not the monkeys' signal production was influenced or accompanied by the above-mentioned markers (**Table 1**) was determined using the following operational criteria:

(i.) Sensitivity to- and manipulation of the attentional state of the recipient: recipient was either (a) *attending*: within the 5 sec prior to signal production, the recipient was directly looking into the direction of the signaller, or the signaller was stationary within the field of vision of the recipient who had its head oriented at most 45° either side from its looking direction straight ahead towards the signaller (cf. Genty et al. 2009; Pika et al. 2003), or (b) *not attending*: during the entire 5 sec prior to signal production, the recipient's head was turned away from the signaller and its attention was never directed towards the signaller, but distracted by other social partners or incidents in its environment (cf. Liebal et al. 2006). In the case of a nonattending recipient, we assessed whether the signaller used a tactile or audible signal instead of a visual only signal (see below; Call & Tomasello 2007); ***(ii.) Audience checking:*** within the 5 sec. prior to signal production, the signaller was directly looking at the recipient, or the recipient was within the field of vision of the signaller who had its head oriented at most 45° either side from its looking direction straight ahead towards the recipient (cf. Genty 2009; Hobaiter & Byrne 2011), ***(iii.) Response waiting:*** following the end of signal production the signaller paused signalling for at least 1s and kept monitoring the recipient's behaviour during this period by maintaining visual contact (cf. Pika et al. 2003; Liebal et al. 2004; Cartmill & Byrne 2010; Hobaiter & Byrne 2011; Roberts et al. 2014; Fröhlich et al 2016; Graham et al. 2017), ***(iv.) Goal persistence:*** following response waiting, it was scored for every signal whether the signaller either **a.** stopped further signalling, **b.** produced the same signal (*i.e.* '**persistence**': cf. Leavens et al. 2005; Cartmill & Byrne 2007; Cartmill & Byrne 2010; Genty & Byrne 2010; Hobaiter & Byrne 2011; Fröhlich et al 2016), **c.** enhanced its original signal by elaborating on it (*i.e.* '**elaboration**'; cf. Leavens et al. 2005; Cartmill & Byrne 2007; Cartmill & Byrne 2010), or **d.** produced a new signal altogether. In case of any further signalling behaviour, we started the process of assessing whether the markers of intentionality accompanied it over again.

Identifying (manual) gesture types

To identify which gesture types were produced by the signallers, every intentionally produced body signal was classified as a particular gesture type, which was further categorized within one of the following signal categories (cf. Pika et al. 2003): (i) visual only gestures: distant signals representing movements of hands, body parts, or body postures, (ii) tactile gestures: visual signals that involve

physical contact between the interacting animals, and (iii) audible gestures: visual signals that simultaneously produce a sound during their performance (see **Table 3**). Using this classification, it was determined whether the mangabeys made use of strictly manual gesture types, by checking which gestures were produced by making movements of the arms and/or hands only, without making physical contact with a substrate or partner (de Waal 2003; Roberts et al. 2012, 2014).

Production details

To examine whether the mangabeys showed contextual and individual variation in gesture production similar to that found in apes (*e.g.* Call & Tomasello 1997), we investigated the production details of the signal types and -categories in terms of production context, determined by the general behavioural situation in which the gesture occurred and the observed behavioural change from the recipient, and prevalence across specific age-sex classes, based on the individual details provided in **Table 2**.

Inter-observer reliability

Inter-observer reliability coding of the occurrence of all criteria during production of each signal was performed by a second observer for 25% of all recipient-directed bodily actions. ‘Substantial’ levels of inter-observer agreement ($0.846 > \kappa > 0.643$; McHugh, 2012) were found for all measured criteria (gesture form, attentional state, audience checking, response waiting, change of recipient behaviour, persistence, elaboration).

Statistics

We used R. 3.5.0 software (R Core Team 2018) to run all statistical tests. Because of our relatively small sample size ($N = 17$ individuals), we mainly used descriptive statistics and nonparametric statistical tests. All tests were two-tailed and the alpha-level was set at 0.05. The presence of intentionality markers associated to the production of body signals was studied both at the level of body signal occurrences (lumping all instances together), using tests for proportion comparisons (binomial and Fisher exact tests), and at the individual level, using Wilcoxon signed ranks tests.

Regarding the first marker of intentionality, *i.e.* ‘sensitivity and manipulation of recipient’s attentional state’, we first tested whether or not body signals were preferentially produced in the presence of a visually attending or non-attending recipient. Moreover, we compared the proportion of each signal category (visual only or non-visual only, *i.e.* audible or tactile) depending on recipient’s attentional state. In order to run this analysis at the individual level, we only kept the data of individuals that produced body signals both in the presence of attending and non-attending recipients ($N = 7$). Then, we tested whether or not instances of body signals were associated with the second and third intentionality

markers: ‘audience checking’ and ‘response waiting’. Regarding the supplementary intentionality marker ‘goal persistence’, we first determined whether the proportion of body signalling instances that was followed by further signal production depended on the type of response by the recipient (positive or negative). In order to run this test at the individual level, we only kept the data of signal producers that were confronted with both positive *and* negative responses from their recipients (N = 15). Then, we determined whether the proportion of persistence or elaboration when the signaller produced further signals after its initial signal depended on whether or not it had received a positive or negative response by the recipient. For this analysis at the individual level, we only kept data of individuals that produced further body signals after receiving a positive or negative response from the recipient (N = 13).

Using Wilcoxon-Mann-Whitney tests, we analysed the effect of individual characteristics on the production of body signals. Particularly, we compared the frequency of body signals and the total number of signal types between age and sex categories, considering all signals and each signal category (visual, tactile, audible) separately. Due to uneven distributions of males and females among age categories, and vice versa, we could only test the effect of the signallers’ sex amongst young individuals, and the effect of age only amongst females.

Results

From the 34 hours of focal observations (N = 17 individuals, 120 minutes per individual), we extracted a total of 297 instances of mechanically ineffective, recipient-directed body signals (range = 1 – 40 per individual; median=16, N = 17 individuals) that were produced across focal individuals (see **Table 4**). These were further used to assess the intentionality of signal use.

Intentionality of signal use

(i) Sensitivity to- and manipulation of the attentional state of the recipient

For 2 out of the 297 recorded body signals the attentional state of the recipients could not be determined due to insufficient recording conditions. From the 295 signals for which the recipients’ attentional state could be determined, the majority (280; 95%) were produced by the signallers when recipients were visually attending (Binomial test: N = 295, $P_{\text{exp}} = 0.50$, $P_{\text{obs}} = 0.95$, $p < 0.001$). This was also significant at the individual level, with mangabeys generally producing more body signals in front of visually attending compared to non-attending recipients (Wilcoxon signed rank test: N = 17, V = 136, $p < 0.001$).

From the 280 signals produced to visually attending recipients, 234 (84%) were visual only signals, 42 (15%) were tactile signals and 4 (1%) were audible signals. From the 15 signals that were produced when recipients were not visually attending, 6 (40%) were visual only signals, 8 (53%) were

tactile signals and 1 (7%) was an audible signal. Thus, the majority of signals produced in front of visually attending recipients were visual only (Binomial test: $N = 280$, $P_{exp} = 0.50$, $P_{obs} = 0.84$, $p < 0.001$), and there was no significant difference in the amount of visual only compared to non-visual only (*i.e.* tactile or audible) signals produced in front of non-attending recipients (Binomial test: $N = 15$, $P_{exp} = 0.50$, $P_{obs} = 0.40$, $p = 0.607$). Correspondingly, at the individual level, we found that the mangabeys preferentially produced visual only signals when recipients were visually attending (Figure 1, Wilcoxon signed rank test: $N = 7$, $V = 0$, $p = 0.036$), and both visual only and non-visual only signals (*i.e.* tactile or audible) in similar proportions when recipients were not attending (Wilcoxon signed rank test: $N = 7$, $V = 12$, $p = 0.829$). When combined, however, these results revealed that signallers who produced signals in both situations (*i.e.* to attending and non-attending recipients: $N=7$) used higher proportions of non-visual signals (*i.e.* tactile or audible signals) when recipients were not attending compared to when recipients were attending, and vice versa (Fisher exact test for visual only vs. non visual only signals when recipients attending vs. not attending: exact $p = 0.004$).

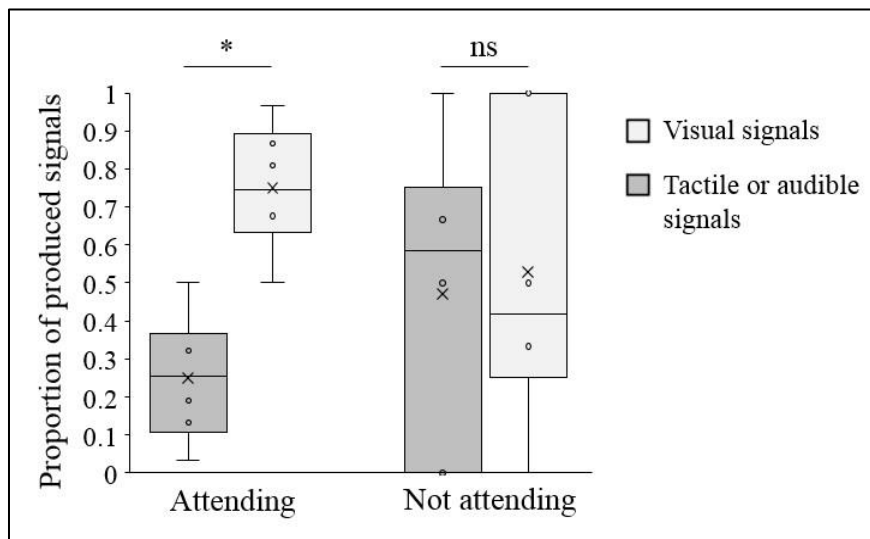


Figure 1. Individual proportions of signalling instances falling within the visual only or nonvisual only signal categories in relation to the attentional state of the recipients. Wilcoxon signed rank tests: $N = 7$ individuals; *: $p \leq 0.050$; ns: $p > 0.050$.

(ii.) Audience checking

From the total of 297 body signalling instances, the majority (293; 99%) was preceded by audience checking (Binomial test: $N = 297$, $P_{exp} = 0.50$, $P_{obs} = 0.99$, $p < 0.001$). This effect was also significant at the individual level, with the mangabeys visually orienting to their audience before signalling in the majority of cases (Wilcoxon signed rank test: $N = 17$, $V = 153$, $p < 0.001$).

(iii.) Response waiting

From the total of 297 body signalling instances, the majority (285; 96%) was followed by response waiting (Binomial test: $N = 297$, $P_{\text{exp}} = 0.50$, $P_{\text{obs}} = 0.96$, $p < 0.001$). This effect was also significant at the individual level, with the mangabeys monitoring a recipient's behaviour after producing body signals in the majority of cases (Wilcoxon signed rank test: $N = 17$, $V = 153$, $p < 0.001$).

Goal persistence

A total of 104 (35%) out of all 297 instances of body signal production resulted in a negative response from the recipients (*i.e.* no behaviour change at all). From these 104 instances, signallers stopped signalling in 50 (48%) cases and continued signalling in 54 (52%) cases after response waiting (Binomial test: $N = 104$, $P_{\text{exp}} = 0.50$, $P_{\text{obs}} = 0.52$, $p = 0.769$). Correspondingly, at the individual level, signallers were equally likely to stop signalling *or* produce further signals after receiving a negative response to their signals (**Figure 2A**, Wilcoxon signed rank test: $N = 15$, $V = 44.5$, $p = 0.972$). In contrast, from the 193 (65%) of all 297 body signals leading to a positive response (*i.e.* a behaviour change) in the recipient, the signallers were more likely to stop signalling (127 instances; 66%) than to continue signalling (Binomial test: $N = 193$, $P_{\text{exp}} = 0.50$, $P_{\text{obs}} = 0.66$, $p < 0.001$), and this was also significant at the individual level (**Figure 2A**, Wilcoxon signed rank test: $N = 15$, $V = 75.5$, $p = 0.039$). When combined, these results revealed that the monkeys showed higher proportions of further signalling behaviour after they had received a negative response to their initial signal compared to when having received a positive response (Fisher exact test for further signalling vs. no further signalling after positive response vs. negative response from the recipients: exact $p = 0.004$).

A further in-depth analysis of the details of the continuation of signalling behaviour after receiving either a positive, yet apparently unsatisfactory, response ($N = 66$) or a negative response ($N = 54$) to the initial signal in terms of persistence and elaboration revealed that the monkeys elaborated on (38 instances; 58%) *or* persisted with (28 instances; 42%) their initial signalling behaviour after receiving a positive response from their recipients (Binomial test: $N = 66$, $P_{\text{exp}} = 0.50$, $P_{\text{obs}} = 0.42$, $p = 0.267$), whereas they preferentially persisted with their initial signalling behaviour when they had received a negative response to their initial signal (39 instances; 72%; Binomial test: $N=54$, $P_{\text{exp}} = 0.50$, $P_{\text{obs}} = 0.72$, $p = 0.001$). This effect was significant at the individual level as well (**Figure 2B**, Wilcoxon signed rank test: persistence after positive response: $N = 13$, $V = 24$, $p = 0.438$; persistence after negative response : $N = 13$, $V = 10$, $p = 0.041$). Combined, these results thus showed that the monkeys were more likely to persist with the same signal when confronted with a negative response (*i.e.* no behaviour change) compared to when confronted with a positive, but unsatisfactory, response: in the latter case they also often chose to elaborate on their initial signal (Fisher exact test for persistence vs. elaboration when further signalling after positive vs. negative response from recipients: exact $p = 0.002$).

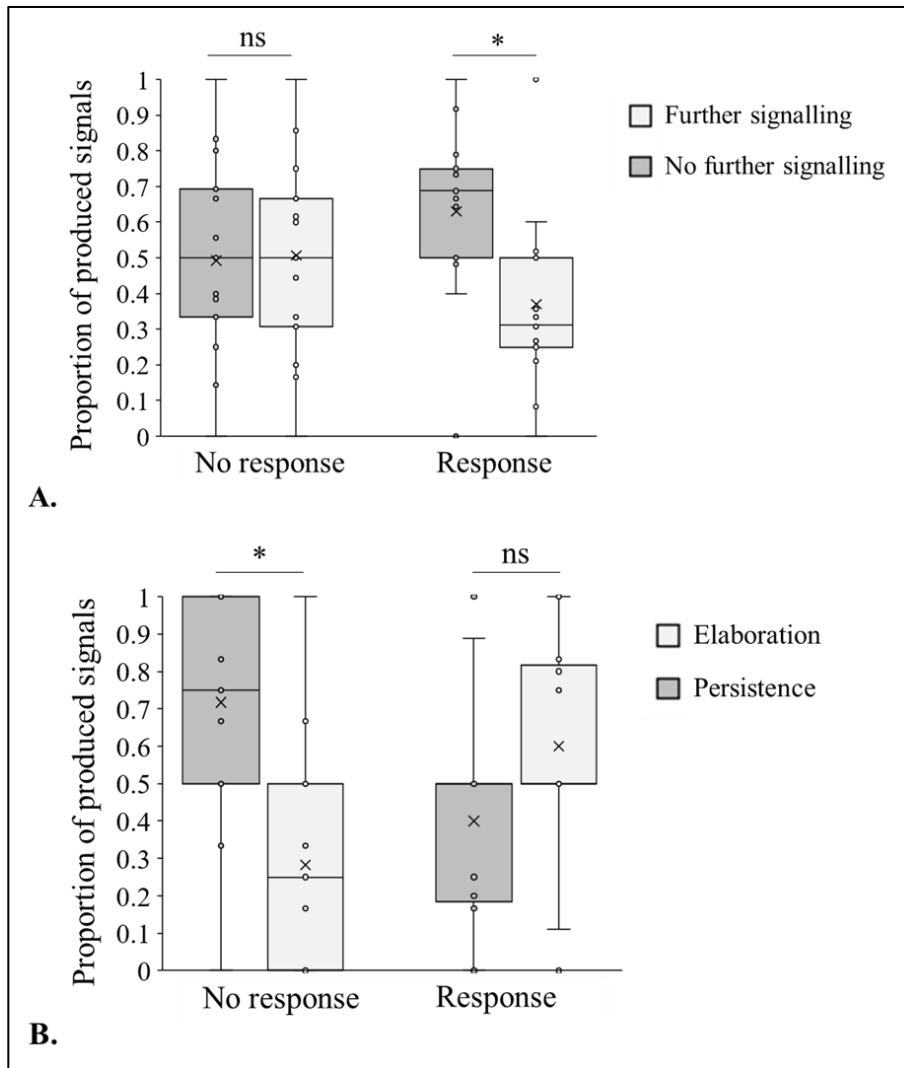


Figure 2. A. Individual proportions of further signalling behaviour by the signaller after receiving either a negative or a positive response (i.e. behavioural change) to its initial signal. N = 15. B. Individual proportions of elaboration and persistence as further signalling behaviour by the signaller in relation to receiving a negative or positive response to its initial signal. N = 13. Wilcoxon signed rank tests: *: $p \leq 0.050$; ns: $p > 0.050$.

In sum, for a total of 295 body signal instances it was possible to determine whether their production was accompanied by the abovementioned three markers of intentionality, *i.e.* in addition to the prerequisite marker social use and in potential combination with goal persistence in case of a seemingly unsatisfactory response. This was the case for 275 (93%) of body signal instances. The remaining body signal instances were all accompanied or influenced by 2 markers of intentionality, *i.e.* in addition to social use and in potential combination with goal-directedness.

Description of gesture types

From the total number of 297 body signals produced by the red-capped mangabeys, we identified 21 different types of body signals (**Table 3**), of which 20 were produced intentionally (*i.e.* accompanied by *all* three markers of intentionality in addition to social use and, potentially, goal persistence) and were therefore considered as gestures: the only signal type that was not accompanied by all these markers in the focal individuals was ‘shake object’ (see **Table 4**). Four of the 20 gesture types were categorised as ‘tactile’ gestures, two were categorised as ‘audible’ gestures, and 14 were categorised as ‘visual only’ gestures. Of the 14 visual only gesture types, four were strictly manual (gesture types 6, 7, 12 and 14 in **Table 3**), *i.e.* produced by making movements of the arms and/or hands only, without making physical contact with a substrate or partner (de Waal 2003; Roberts et al. 2012, 2014).

Table 3. Overview and description of the different gesture types produced by red-capped mangabeys during this study. Gesture types are further specified per signal category (visual only, tactile, or audible signals). Manual gestures are indicated with *.

Gesture name	Description
<i>Visual gestures</i>	
1. Crouch	Subject is in crouching position on the ground in front of the other, belly touching the ground, on four legs.
2. Head bob	Subject makes short forward movement of the head, ‘lunging’ its head towards the other, while staring at him intently.
3. Head shake	Subject moves head in quick, jerky movements in front of the other, horizontally and/or vertically.
4. Hop	Subject jumps/ hops in the air with both feet leaving the ground, either in one position or moving around in front of the other.
5. Lie down wiggling	Subject is lying down on its belly in front of the other, wiggling its body at the same time. This can also occur with one arm extended towards the other, with body and arm wiggling at the same time.
6. Make grabbing movement towards*	Subject throws arm towards the other with hand closing at the end of the movement.
7. Move arm in front*	Subject puts its arm with elbow flexed in 90° in front of its face or its body.
8. Present body part	Subject exposes one particular body part to the other, by orienting its body appropriately. Subject can present different body parts (including back, belly, rear, neck, penis, head, side) using different postures. This occurs in three main positions: while seated, standing, or lying down rigidly (subject is lying down on the belly or on the back in front of the other, not moving, exposing body part). At least 25 different varieties of this signal were recorded (<i>e.g.</i> present back seated arms relaxed, present back seated one arm up, present back seated two arms up, present back lying on belly, etc.).
9. Roll on ground	Subject rolls on the ground in front of the other.

10. Somersault	Subject jumps and makes a forwards or backwards salto/ flip.
11. Swing body	Subject moves its body in quick movements in front of other: swinging its body from side to side, seated, arms relaxed.
12. Throw arm towards*	Subject extends and throws arm (arm extended) with hand open, palm facing down, towards the other in a brief, quick movement.
13. Throw body towards	Subject throws its upper body in direction of other, with two hands and arms stiff, thereby hitting the ground or support.
14. Throw hand towards (hand fling)*	Subject ‘throws’ one hand towards the other in a brief movement, with hand open, palm facing down, no movement of arm.
<i>Tactile gestures</i>	
15. Embrace	Subject puts one arm or both arms around the body of the other, dorsally (by the back) or ventrally (by the front).
16. Grab body part	Subject grabs a body part of the other with its hand or feet, without pulling body part. The subject can hold the body part briefly (<1s) or longer (>1s). Body parts include: top of the head, arm, hand, penis, tail, hips.
17. Hit/ slap body part	Subject hits a body part of the other with a flat hand, in a quick movement (<1s). Body parts include: top of the head, limb, back, hand, tail.
18. Put body part on other	Subject places its hands or feet gently on a body part of other (>1s). Body parts of others include tail, arm, top of the head, back.
<i>Audible gestures</i>	
19. Kick object	Subject jumps in the air and stamps once on an object (<i>e.g.</i> cage) with two feet.
20. Shake object	Subject holds and shakes an object or other support (cage) with its hands or with its hand and feet.
21. Slap object	Subject hits/slaps the ground or an object (<i>e.g.</i> cage) with one or two hands.

Production details

We explored the production details of gesture types and signal categories (visual, tactile and audible) in relation to signaller characteristics (age and sex; see **Table 2**) and production context. We found that males had a tendency to produce more different signal types compared to females (Median $\pm IQR$ (interquartile range) males vs females = 7 ± 7 vs 2 ± 3 , respectively: Wilcoxon-Mann-Whitney test: $N_{\text{males}} = 7$, $N_{\text{females}} = 5$, $Z = -1.802$, $p = 0.0715$), and in particular that they produced more tactile signal types compared to the females (Median $\pm IQR$ males vs females = 3 ± 2 and 1 ± 1 , respectively: Wilcoxon-Mann-Whitney test: $Z = -2.277$, $p = 0.043$). Correspondingly, the males made more frequent use of tactile body signals compared to females (Median $\pm IQR$ males vs females = $4 \pm 8 / 120$ min vs $1 \pm 1 / 120$ min, respectively: Wilcoxon-Mann-Whitney test: $Z = -2.655$, $p = 0.008$), although their *overall* frequency of signalling was comparable to that of females (Median $\pm IQR$ males vs females = $24 \pm 23 / 120$ min vs $7 \pm 23 / 120$ min, respectively: Wilcoxon-Mann-Whitney test: $Z = -0.976$, $p = 0.329$). These effects

were not found for the other two categories, *i.e.* the use of visual only and audible body signals was similar across sexes (frequency of visual signals: Median $\pm IQR$ males vs females = 18 $\pm 21/120$ min vs 6 $\pm 22/120$ min, respectively: Wilcoxon-Mann-Whitney test: $Z = -0.570$, $p = 0.568$; frequency of audible signals: Median $\pm IQR$ males vs females = 0 $\pm 0/120$ min vs 0 $\pm 1/120$ min, respectively: Wilcoxon-Mann-Whitney test: $Z = 0.748$, $p = 0.454$). Regarding the effect of signaller's age on signal production, we found that the frequency of signalling and total number of different signal types used did not differ between age categories (WilcoxonMann-Whitney tests: $N_{\text{young}} = 5$, $N_{\text{old}} = 4$, Frequency of signalling: Median $\pm IQR$ young vs old = 7 $\pm 23/120$ min vs 14 $\pm 21/120$ min, respectively: $Z = 0.861$, $p = 0.389$; number of different signal types: Median $\pm IQR$ young vs old = 2 ± 3 vs 2 ± 3 , respectively: $Z = 0.135$, $p = 0.893$).

Whether or not there was variation in production context per gesture type could only be reliably determined for eight of the total of 20 intentionally produced gesture types: the other 12 gesture types were produced fewer than five times across different individuals, not providing enough statistical power to determine the (potential) diversity of contexts in which these gestures may be produced. Inspection of the eight intentional gesture types for which this could be determined revealed that two manual gesture types ('throw arm towards' and 'throw hand towards') and four non-manual gesture types ('grab body part', 'hit body part', 'put body part on other' and 'present body part') were produced flexibly, *i.e.* in both the play context and at least one additional behavioural context (*i.e.* agonism or grooming, with 'present body part' being produced in two contexts additional to play, *i.e.* groom and sexual).

Table 4. Signal instances per individual. All signal instances were accompanied by a minimum 2 markers of intentionality. x/y means that the signallers’ production of x instances (of the total of y) of a particular signal type was (i.) preceded by audience checking, (ii.) followed by response waiting, *and* (iii.) was adjusted to the attentional state of the recipients, in addition to (prerequisite) use of marker ‘social use’ and potential use of marker goal-directedness in cases of communicative failure (see text for details). ID: individual; F: female; M: male; Y: young individual; O: old individual, *: manual gesture type.

ID	Sex	Age category	Signal types																			Total number of signals per ID	Total number of intentional signal types (gesture types) per ID			
			Visual											Tactile				Audible								
			Crouch	Head bob	Head shake	Hop	Lie down wiggling	Make grabbing move. towards*	Move arm in front*	Present body part	Roll on ground	Salto	Swing body	Throw arm towards*	Throw body towards	Throw hand towards (<i>hand fling</i>)*	Embrace	Grab body part	Hit/ slap body part	Put body part on other	Kick object			Shake object	Slap object	
Chipie	F	O					1/1			29/31															30/32	2/2
Many	F	Y								31/33				1/1											32/35	2/3
Chipse	F	Y		1/1						7/8				2/2	2/2			1/1			1/1				14/15	6/6
Tips	M	Y					1/1			4/5			5/5				1/1	3/3	1/1						15/16	6/6
Julie	F	Y								2/2															2/2	1/1
Gofrette	F	O						2/2		5/5															7/7	2/2
Coet	M	Y			1/1		1/1			9/10				6/6		1/1	2/2			2/3					22/24	7/7
Maillette	F	Y								6/6							0/1								6/7	1/2
Belle	F	Y								1/2										1/1					2/3	2/2
Kamel	M	Y				1/1	2/2	1/1		4/4				10/10	0/1	3/4	1/1	4/5	1/2						27/31	9/10
Zunie	F	Y				1/1		1/1		11/11				2/3	2/2			1/1							18/19	6/6
Joly	F	O								7/7							1/1								8/8	2/2
Roby	M	Y				3/3		1/1	1/1	20/20	1/1	1/1						1/1							28/28	7/7
Pirate	M	O						1/1		13/13				6/6	1/1										21/21	4/4
George	M	Y								2/4									2/3				1/1		5/8	3/3
Carillon	M	Y																1/1							1/1	1/1
Elky	M	Y	2/2		1/1	5/5	1/1	0/1		6/6			1/1	7/8			3/3	2/2	5/7		1/1		2/2		36/40	12/13
Total nb			2/2	1/1	2/2	10/10	4/4	6/7	3/3	157/167	1/1	1/1	1/1	39/41	1/1	4/5	8/8	8/9	15/18	8/10	2/2	0/1	3/3		275/297	
Total ID			1/1	1/1	2/2	4/4	3/3	6/7	2/2	16/16	1/1	1/1	1/1	8/8	1/1	2/3	3/3	5/6	6/6	5/5	2/2	0/1	2/2			

Discussion

In this study, we investigated whether the intra-specific body signals of a group of captive redcapped mangabeys qualified as intentional gestures, and whether these monkeys used free manual gestures during their communication as well. The mangabeys produced a total of 21 body signal types that were socially directed at particular recipients, mechanically ineffective, and led to a voluntary response in the recipients. Of these, 20 were classified as intentionally produced gesture types (**Table 3**) as in the majority of cases these fulfilled the following hallmarks of intentionality: they were (i.) adjusted to the attentional state of the recipient, (ii.) preceded by audience checking, (iii.) followed by response waiting, and (iv.) followed by signs of persistence and elaboration in cases of communicative failure (see **Table 4**). In particular, in terms of attentional state adjustment, the mangabeys used tactile or audible gestures more frequently than visual gestures in situations with inattentive recipients compared to attentive recipients, and in terms of goal persistence they repeated their initial signal if this had been followed by a negative response from the recipient (i.e. no behaviour change at all), whereas they elaborated *or* repeated their initial signal if this had been followed by a positive, yet unsatisfactory, response from the recipient (i.e. a non-intended behaviour change). The monkeys thus appeared to communicate in a goal-directed manner, and, together, our results provide convergent evidence that red-capped mangabeys are proficient at intentional gestural communication and use this to communicate with conspecifics. As such, our results strengthen the findings of two recent studies that brought to light intra-specific intentional gesture use in two other catarrhine monkey species, wild bonnet macaques (Gupta & Sinha, 2019) and captive olive baboons (Molesti et al., 2020). The study on bonnet macaques found evidence for ‘response waiting’ and ‘goal persistence’ (see **Table 1** for definitions) during the gestural communication between already attentive communicative partners, and the study on olive baboons found evidence for ‘audience checking’, ‘attentional state adjustment’, and ‘response waiting’ (see **Table 1**). However, neither of these studies investigated the combined use of the markers ‘social use’, ‘adjustment to recipient’s attentional state’ and ‘goal persistence’ in their study species: these have recently been argued to be the three markers that (at least) need to be used simultaneously by one animal species if one is to invoke first order intentional communication in this species (Liebal et al., 2013; Townsend et al. 2016; Graham et al., 2019). Our study provides such evidence and therefore clearly shows that, indeed, the evolutionary roots of intentional communicative strategies can be dated back to approximately 30 My ago (cf. Gupta & Sinha, 2019; Molesti et al., 2020).

Whether or not this conclusion is strengthened by the fact that in our study we do not only provide evidence for the combined use of the markers social use, attentional state adjustment, and goal persistence, but also for audience checking and response waiting during the communicative interactions, remains debated. Like any of the markers of intentionality, audience checking and response waiting may carry little weight as markers of intentionality on their own, but in combination with all other markers they certainly contribute to the evidence that these animals communicate intentionally (Liebal et al.

2013; Townsend et al., 2016; Graham et al. 2019). The only marker that we did not find any evidence for in the current study was the use of gaze alternation. This is not surprising, because this marker is by definition only found in triadic communicative contexts (see **Table 1**), and the majority of communicative interactions across adult primates occur as non-triadic communicative events (Hurford, 2007; Liebal et al. 2013). Consequently, in gesture studies the capacity for gaze alternation is often studied experimentally in trained ‘food requesting’ paradigms between primate subjects and human experimenters (e.g. Leavens et al., 2004). This experimental setup has recently also been used in the red-capped mangabeys, who were found to alternate their gaze between a preferred food item and the experimenter whilst producing their (trained) requesting gestures (Aychet et al. 2020). Although this shows that these animals are capable of gaze alternation in such experimental situations, it is possible that the display of gaze alternation may have been affected by experimental training in this study (see e.g. olive baboons: Bourjade et al., 2015), and studying this in more naturally occurring intraspecific communicative interactions will reveal more about these primates’ natural capacity for this behaviour. A more natural communicative context in which gaze alternation has been reported to occur in concordance with naturally occurring *vocal* signalling in this same study population concerned the emission of the Un (+ Hu) vocalisation in the ‘recruiting for help’ context during agonistic encounters with conspecifics (Bouchet et al. 2010). Signallers directed these vocalisations at a particular group member, whilst alternatively glancing back and forth between this individual and their opponent (Bouchet et al., 2010), but unfortunately it was not investigated whether the other markers of intentionality applied to this signal as well. Whether or not these monkeys also accompany their intentionally produced gestures by gaze alternation in the presence of an external entity with the possible aim of directing a conspecific recipients’ attention to it, is not yet answered and should be further investigated. Such studies could reveal more about this primate’s capacity for intentional triadic communication, which has been related to human’s complex communicative capacity of informing others about external objects or events in their environment (Hurford, 2007). One possible candidate for such a study would be the ‘tail arched over back’ posture, a body signal that we did not observe during our study but which has been reported to occur during predator encounters and/or other major disturbances in an earlier study on the red-capped magabeys (Bouchet et al., 2010) and in two subspecies of the closely related sooty mangabey (*Cercocebus atys lunulatus*: S. Waasdrorp, pers. comm; *Cercocebus atys atys*: A. Mielke, pers. comm., pers. obs.). Whether or not this body posture is produced intentionally and is accompanied by gaze alternation is not yet clear, but could be easily investigated further.

But even when these monkeys show gaze alternation as the final marker of intentionality, which would provide the rigorous proof of intentional (gestural) communication in one single monkey species that is needed (Liebal et al. 2013; Townsend et al., 2016; Graham et al. 2019), more recently the validity of checking for the use of markers of intentionality as evidence for intentionality of communication has

actually been questioned as a whole, i.e. in particular when put in the context of studying human language evolution (Graham et al., 2019). A first issue revolves around the validity of each single marker of intentionality and the unsystematic use of these across gesture studies. To counter this, it has been suggested that studies on intentionality of communication should at least consistently use one uniform methodology, ideally including multiple, and preferably *all*, markers when assessing intentionality of signal use, and applying these to *all* signal instances: this is what we did in the current study. A second, more fundamental, concern is about the cognitive mechanisms underlying first order intentional communication as indicated by a species' use of the markers of intentionality during communication: even when a species uses all markers simultaneously during its communicative attempts, the mere fact that by using this method several hallmarks of intentional communication have now been found in animals as distantly related as, for example, fish (Vail et al. 2013) casts doubts on the relevance of this methodology in light of the comparative approach towards human language evolution (Graham et al. 2019). Instead, it has been proposed to focus studies on intentional communication in relation to human language evolution on second-order intentionality during communicative interactions, as second order intentionality would, a priori, imply first order intentionality and second order intentional communication lies at the heart of our own ostensive communicative strategy (cf. Graham et al. 2019). For this, it would be necessary to show mental state attribution in signalling individuals. Studying this in (semi-) natural conditions is not a trivial task, however, and the only systematic studies so far that have explicitly studied mental state attribution during intraspecific communication focused on the vocal communication of wild chimpanzees (Crockford et al. 2012; 2017) and two macaque species in captivity (Cheney & Seyfarth, 1990), with results tentatively pointing to evidence for this capacity in the chimpanzees but not the macaques.

However, taking these findings to conclude that 'apes' are capable of second order intentional communication and 'monkeys' are not is still overly simplistic, as several studies have suggested that the presence of communicative and cognitive complexity in an animal species may be linked to its sociality and related socio-cognitive capacities (e.g. McComb & Semple, 2005; Freeberg et al. 2012; Fröhlich & Hobaiter, 2018; Peckre et al. 2019), leading to large differences between species. For example, compared to species living in relatively small and stable groups, species living in complex social societies show larger repertoire sizes (e.g. Maestriperi 1999; McComb & Semple, 2005; Freeberg et al. 2012; Pollard & Blumstein, 2012; Krams et al. 2012; Pika, 2017; Roberts et al., 2019), more variation and flexibility in the communicative domain (Call & Tomasello, 1996; Cartmill & Maestriperi, 2012; Bouchet et al., 2013; Roberts et al. 2019; Rebut et al., 2020), and may use more advanced cognitive capacities during their communication, *e.g.* those also needed to deal with complex social group life, such as perspective taking or ToM (Humphrey 1976; Crockford et al., 2012, 2017). We therefore argue that studying this in a broader range of primate species with different socioecological backgrounds is needed for a balanced comparative view on this topic. In mangabeys, who live in a

relatively complex social environment based on a fission-fusion organisation (Bouchet et al. 2013; Aureli et al. 2008), one could for example focus on the aforementioned ‘tail arched over back’ posture produced during predator encounters and assess whether or not a complex audience effect applies to this behaviour, e.g. only adopting or prolonging the duration of this behaviour in the presence of ignorant others or others for whom the snake is out of their viewing range.

As mentioned, an additional direction that has been taken in the comparative approach towards human language evolution is to study manual gesture use and its laterality (reviewed in Prieur et al., 2018; Fagot et al., 2019). Although debated (see for example Fitch & Braccini, 2013), this idea is based on the premise that studies on both humans and non-human primates found evidence for a right-hand preference during manual gesture production, in combination with strong size asymmetry and neuronal firing activity during the production of such gestures in particular neuroanatomical areas of the left cerebral hemisphere that have been linked to speech production and perception in humans (Broca’s & Wernicke’s areas) and in anatomically homologous areas in non-human primates (e.g. Meguerditchian et al., 2010; Hopkins et al., 2012; Prieur et al., 2017; 2018; Fagot et al., 2019). The ground slapping gesture by olive baboons is one particularly well investigated example supporting this idea (Meguerditchian & Vauclair, 2006; Marie et al., 2018). Whether or not the production of naturally occurring ‘free’ manual gestures (i.e. species-specific manual gestures that do not involve physical interaction with a substrate or partner) is also governed by such left hemispheric dominance in monkeys is not yet clear, possibly as a result of the fact that free manual gestures have so far been rarely documented in monkeys (but see Molesti et al. 2020 for one example in olive baboons). In our study we found evidence for the intentional production of four free manual gesture types in the natural communication amongst red-capped mangabeys, with these gesture types being used in variable frequencies by 11 of the 17 focal individuals (see **Table 4** for details). A preliminary inspection revealed that there did not appear to be any hand preference during their production, but it should be noted here that we did not observe enough instances per gesture type and individual to formally analyse individuals’ hand preferences during the production of these gestures (for example by calculating the HI index cf. Hobaiter & Byrne, 2013) and adding more data may tell a different story. In fact, in a systematic study on manual laterality during an experimental fruit requesting paradigm between these same focal individuals and human experimenters (Maille et al., 2013), these monkeys showed a right-hand preference for the use of their trained pointing gestures (Maille et al., 2013). Whether or not these (preliminary) contrasting results are attributable to the relatively few focal observation hours of the current study and the fact that we did not systematically determine hand use, by the potential effect of human training on behaviour during experimental tests (Bourjade et al., 2015; Leavens et al. 2019), or by the recent idea that laterality of hand use may differ across behavioural contexts (Roberts et al., 2019) is not yet clear and could be further investigated in this species. This could contribute valuable data to further the debate on this topic in particular and human language evolution more broadly.

Moreover, the fact that such free manual gestures are produced highly flexible in terms of means-ends dissociation (Bruner, 1981) by some ape species, has been taken to suggest that such flexibly produced free manual gestures formed the ‘starting point’ of human language evolution (e.g. Pollick & de Waal, 2007; Cartmill & Maestripieri, 2012). This would imply that this capacity for *flexible* manual gesture production appeared somewhere in the hominoid lineage (~ 17 Mya), but the comparative work on more distantly related monkey species to support this idea has been lacking. In the current study we found evidence for the flexible use of two of the four free manual gesture types and four tactile gesture types: these signals were produced in both the play context and at least one additional behavioural context. Yet, because a remarkable diversity of behavioural patterns from a variety of contexts is a characteristic of play behaviour in several different primate species (Yanagi & Berman 2014; reviewed in Byrne 2016), this finding may not be so surprising, and more data on the flexibility of use of all other gesture types are needed. One finding of the present study that actually may be clarified with these preliminary findings on flexibility of use is the relatively high proportion of tactile gesture use towards attentive recipients: in such situations visual gestures would theoretically suffice and may be a more conservative option, i.e. especially in aggressive agonistic contexts. As described above, tactile gesture types were commonly produced in both the play context and another, more ‘formal’, context (agonism or grooming). The only other tactile gesture type that was found in this species so far (‘embrace’) occurred only in the play context, and was also mostly produced to attentive recipients. When initiating play, it is highly relevant for a signaller that a recipient understands that its gesture is produced in a playing context rather than in the more ‘formal’ context in which it is also commonly produced (e.g. agonism). In several other primate species in which gestures to initiate play also take the form of tactile gesture types that are also used in other contexts (e.g. rhesus macaques: Symons, 1974; bonobos and chimpanzees: Palagi, 2006; Barbary macaques: Hesler & Fischer, 2007; siamangs: Liebal, 2004; gorillas: Genty & Byrne, 2010), this is often achieved by producing additional signals such as a ‘play face’ (van Hooff, 1972). In addition, in species where particular play signals accompanying tactile gestures produced in the play context are not part of a species’ communicative repertoire, other subtle signals may reveal to a recipient that the signaller ‘is only playing’. This for example includes the absence of aggressive vocalisations and/or of piloerection that would normally accompany an aggressive gesture in its more ‘formal’ context, producing the signals at a slower tempo and in more inhibited form during play (Symons, 1974), or (non-intentionally) producing the signal with the left hand as opposed to the right hand that may be used in the more ‘formal’ or ‘evolutionary urgent’ communicative interactions concerning this gesture (e.g. Roberts et al., 2019). In most of these cases, being visible to a recipient and thus producing gestures to attentive recipients, is paramount. Whether or not red-capped mangabeys have particular play signals such as the play face, or show inhibition and/or lateralisation during the production of signals produced in particular contexts is not yet clear, and is another interesting topic for further studies in this species on the flexibility of (manual) gesture use and its laterality.

Finally, with respect to the communicative repertoire of these animals, we can currently again only provide a preliminary picture. The two hours of focal observations per individual were, of course, by no means sufficient to describe a species' entire repertoire (see e.g. Hobaiter & Byrne who described that for the full description of the chimpanzee gestural repertoire a minimum of 15 hours of active gesture time per individual were needed), and several gesture types in this study also did not fulfil the often used requirement of having to have been used for an overall minimum of three times by at least two individuals to be included in the repertoire (e.g. Liebal et al., 2004; Hobaiter & Byrne, 2011; Graham et al., 2016: see **Table 4**). In addition, the animals lived in relatively small subgroups compared to their wild counterparts, which may have impacted on their communicative behaviour, as this meant they had a less complex social environment than their wild counterparts (Roberts et al., 2019). However, as the four free manual gesture types actually *were* produced three or more times by at least two individuals in our study and therefore can be considered part of these animals' repertoire, we feel that a brief comparative picture of manual gesture use in primates is in place here. Thus, the absolute number of four manual gesture types reported for the mangabeys falls in between that found for captive ape species, is relatively high when compared to other monkey species, but is low when compared to wild apes, in particular chimpanzees, bonobos and gorillas (**Figure 3**). Especially when taking into account the relatively few total observation hours of the present study (see **Figure 3** for comparison with other studies), it is likely that adding more video recordings of intra-specific interactions is going to reveal a larger number of gesture types in these monkeys, including manual ones. This idea is supported by video observations of several other intentionally produced signal types that were directed at focal individuals by other individuals of the social groups, a method often used in gesture studies describing species' repertoires (e.g. Liebal et al. 2004; Graham et al., 2016). These 'received' signals included 'hang' (*subject hangs with two arms on a support in front of the other*), 'jump towards' (*subject jumps/ lunges towards the other*), 'open arms' (*subject opens both arms while facing the other*), and 'mock-bite body part' (*subject grabs body part of the other and puts it in its mouth: teeth touch, but no biting*), which all adhered to all markers of intentionality. Adding these gesture types to the preliminary gestural repertoire found so far shows that (also) in terms of free manual gesture types the gesture repertoire of these red capped mangabeys is likely to be larger than currently reported here and may fall somewhere between that of the monkey species and apes that live in similarly complex social environments.

In sum, in this study we provide systematic evidence that these red-capped mangabeys use their naturally occurring body signal types in flexible and intentional communicative ways, by showing simultaneous adherence to at least five intentionality markers during their production, something that was not earlier described for any other monkey species. Their preliminary intentional gesture repertoire includes body postures, but also free movements of the hands and/ or arms. These monkeys appear to produce their gestures flexibly, both in terms of behaviour (e.g. elaboration during goal persistence) and context, and show potential for the use of gaze alternation during intraspecific gestural communication,

(intentional) triadic communication, and laterality of (manual) gesture use. Next to the fact that studies on the vocal communication of these monkeys have indicated this species' capacity for syntactic like semantic vocal communication: Bouchet et al., 2010), we argue that red-capped mangabeys are a highly interesting model species for further comparative studies in relation to human language evolution and to include in systematic Primate Cognitive Battery Testing (Hermann et al., 2007; Schmitt et al., 2012). The results of this study contradict claims that flexible and intentional communicative strategies appeared in the primate lineage after the split of the hominoids from the other primates, about 18 My ago (*e.g.* Pollick & de Waal 2007; Cartmill & Maestriperi, 2012; Chatterjee et al. 2009). In stark contrast, and in concordance with recent findings on macaque and baboon species (Gupta & Sinha 2019, Molesti et al. 2019), our results reveal that the origins of these precursors for language may date back to approximately 30 My ago, *i.e.* at the start of the catarrhine primate lineage.

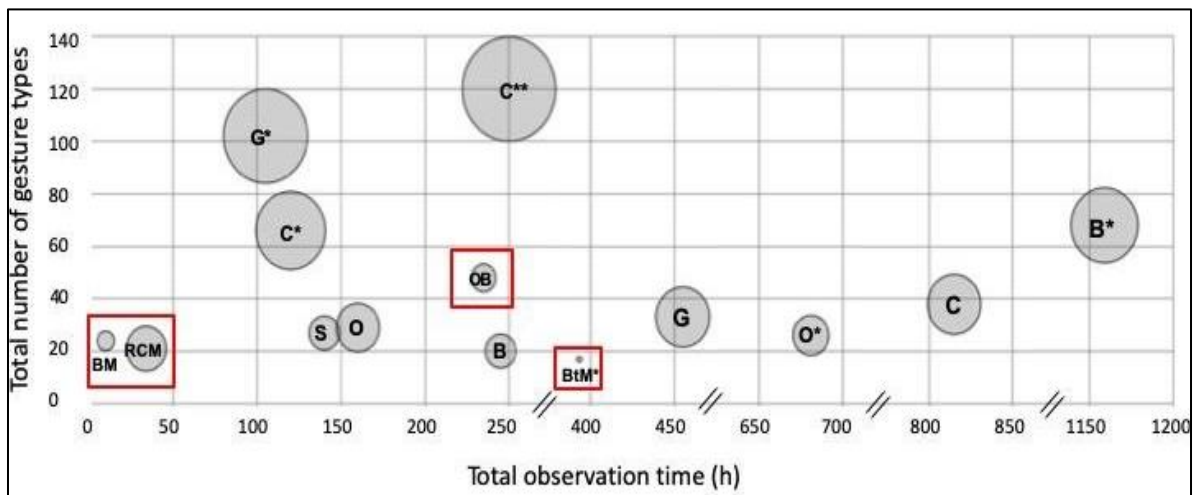


Figure 3. Bubble chart representing the number of gesture types (y-axis) in relation to total observation time (x-axis) found in several primate gesture studies. The size of the bubble represents the absolute number of manual gesture types found in the represented study. The bubbles within the boxes represent non-ape studies. */** indicates the study was done on (semi) wild subjects; all other studies were done in captivity. **B**: bonobos (Pika 2007); **B***: bonobos (Graham et al. 2016); **BM**: Barbary macaques (Hesler & Fischer 2007); **BtM**: Bonnet macaques (Gupta & Sinha, 2019); **C**: chimpanzees (Tomasello 2007); **C***: chimpanzees (Hobaiter & Byrne 2011); **C****: chimpanzees (Roberts et al. 2012); **G**: gorillas (Pika 2007); **G***: (semi-wild) gorillas (Genty et al. 2009); **O**: orangutans (Liebal 2007); **O***: orangutans (Knox et al. 2019); **OB**: Olive baboons (Molesti et al. 2020); **RCM**: red-capped mangabeys (this study); **S**: siamangs (Liebal et al., 2004).

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Article 2

Facial displays in red-capped mangabeys (*Cercocebus torquatus*): repertoire, social context, and potential intentionality

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SYNTHESE DE L'ARTICLE 2

Contexte

Des observations récentes menées sur les grands singes (gibbons, orang-outans, bonobos) ont montré que leurs expressions faciales pouvaient être accompagnées de marqueurs d'intentionnalité comme l'adaptation à l'état attentionnel d'un receveur, ou l'attente d'une réponse de la part de ce dernier. Les expressions faciales de nombreux singes non-hominoïdes ont été décrites, mais leur potentielle intentionnalité reste quant à elle en question. Les gestes intraspécifiques des mangabeys à collier semblant être intentionnellement produits, nous avons émis l'hypothèse que les expressions faciales faisaient partie de la communication visuelle intentionnelle chez cette espèce.

Méthode

Nous avons observé 25 mangabeys à collier captifs, selon la méthode d'échantillonnage en focal, afin de décrire leur répertoire d'expressions faciales. Nous avons ensuite cherché à savoir si ces expressions faciales étaient communicatives, c'est-à-dire dirigées vers d'autres individus, et si elles étaient intentionnelles. Nous avons alors décrit les contextes de production de ces expressions faciales, et avons testé la présence ou l'absence de marqueurs comportementaux d'intentionnalité, semblables à ceux utilisés pour l'étude de la communication gestuelle.

Résultats

Nous avons décrit 6 expressions faciales différentes chez les mangabeys à collier, correspondant à des mouvements de la bouche, des sourcils et des oreilles, produites seules ou en combinaisons. Toutes ces expressions étaient produites en contextes sociaux, mais certaines étaient également produites en contexte non-social, comme les « lipsmacks » et les bâillements. Toutes les expressions décrites, excepté les bâillements, pouvaient être produites conjointement à des marqueurs de communication intentionnelle (directionnalité, « audience checking », sensibilité à l'état attentionnel du receveur, attente d'une réponse, effet sur le comportement du receveur). Les expressions faciales de jeu « open mouth » étaient les plus fréquemment associées à ces marqueurs.

Conclusion

Cette étude souligne la nature communicative des expressions faciales des mangabeys. Corroborant des résultats obtenus chez les grands singes, les expressions de jeu sont fortement associées à des marqueurs d'intentionnalité. Les présents résultats ouvrent la voie à de futures études s'intéressant à d'autres indices comportementaux d'intentionnalité, comme la persistance ou l'élaboration de la communication.

Facial displays in red-capped mangabeys (*Cercocebus torquatus*): repertoire, social context, and potential intentionality

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Abstract

Primate communication relies strongly on the visual modality, notably through the production of a wide range of expressive facial signals. We investigated here the facial display repertoire of a relatively little-studied cercopithecoid species, red-capped mangabeys (*Cercocebus torquatus*), and questioned whether their facial displays were dependent on social contexts and accompanied by indices of intentionality. Although the dual intentional and emotional use of apes' facial expressions has recently been suggested, the question of whether monkeys produce facial expressions intentionally to communicate remains open. We described six facial displays produced by captive red-capped mangabeys in social contexts. They are based on movements of the mouth, eyebrows and ears, possibly graded in intensity and produced independently or in combination. We showed that most of the facial displays were produced preferentially in specific social contexts, and that repertoires varied with subjects' characteristics, highlighting the communicative function of these displays. Moreover, behavioral markers of intentionality commonly used in gestural studies were found to accompany the production of some of the facial signals observed. Particularly, playful "open mouth" appeared strongly associated with intentionality indices, as previously noticed in ape species. All other facial displays, except yawns, did not exhibit all defined intentional indices but were, at least, directed towards a recipient. Interestingly, yawns presented different variants of intensity associated presumably with different social functions. Altogether, these results emphasize the communicative function of red-capped mangabeys' facial displays, and provide a basis for further research on their intentional communication.

Keywords: Monkeys, Intentionality, Facial expression, Play face, Yawn

Introduction

Primate communication strongly relies on the visual modality (Redican 1975; Liebal et al., 2014a) through a variety of gestural and postural signals. Moreover, compared to other mammals, primates produce a wide range of expressive facial movements, due to their complex facial musculature (Burrows 2008; Diogo et al., 2009). Facial expressions can involve movements of the mouth and lips, eyelids and eyebrows, forehead and ears (van Hooff 1967; Waller and Micheletta 2013). Substantial variations are notable between primate genera and species regarding facial mobility (Santana et al., 2014) and facial expression repertoires (Marler 1965; van Hooff 1967). Thus, the understanding of visual communication in primate species needs precise descriptions of their facial expression repertoire and the context of production as their communicative signals. Some authors include facial displays in the gestural domain (e.g. Altmann 1962; Call and Tomasello 2007; Chalmers 1968a; Dube 2013; Hesler and Fischer 2007; Hinde and Rowell 1962; Hostetter et al., 2001; Maestripieri 1997, 2005; Poss et al., 2006; Wolfheim and Rowell 1972); whereas others consider facial displays as disentangled from gestures due to differences in the definitions of signal intentionality (e.g. Byrne et al., 2017; Graham et al., 2017; Genty et al., 2009; Hobaiter and Byrne 2011; Liebal et al., 2004b, 2006; Pollick and de Waal 2007; Roberts et al., 2014). Indeed, the intentional use of facial expressions in primates is still matter of debate (Arbib et al., 2008; Hopkins et al., 2011; Slocombe et al., 2011).

Non-human primates seem to have a voluntary control of their facial movements, which is required for the flexible use of facial expressions. Regarding neuroanatomical data from humans and great apes, facial expressions are controlled by both voluntary and emotional pathways acting in parallel within the facial motor system that differs from the motor system controlling limb movements (Cattaneo and Pavesi 2014; Müri 2016; Sliwa et al., 2018; Sherwood et al., 2004, 2005). Moreover, some facial expression asymmetries are associated with attention-getting calls in chimpanzees, suggesting voluntary control of these facial movements (Hopkins et al., 2011; Reynolds-Losin et al., 2008). This possible voluntary control may reveal that primates could use facial expressions intentionally as communication signals.

The distinction between intentional behaviors and intentional communication was previously addressed by Bretherton and Bates (1979) in their developmental studies in children, based on the implication of social agents within intentional sequences of behavior. Then, the philosophical stance of intentional communication as a goal-directed process was formulated by Dennett (1983), who defined different degrees of intentionality. The first degree, as studied in animal communication, supposes that an intentional signal would be controlled and produced voluntarily by a signaler and directed towards a recipient in order to trigger the appropriate response by the receiver (Hobaiter and Byrne 2013; Roeder and Gosset 2001). The goal-directedness discriminates intentional communicative signals from mere informative signals, which convey messages without being voluntarily emitted by the signaler (Poggi

and D'Errico 2012). One example of “informative signal” could be piloerection, which conveys information about the individual’s internal state (e.g. Benedek and Kaernbach 2011; Dettling et al., 1998) without appearing voluntarily emitted. Bard (1992) introduced Bates’ definition of intentional communication to the study of primate communication, distinguishing intentional communication from other intentional behaviors in orangutan mother-infant interactions. In the same line, several behavioral indices of intentional communication inherited from child developmental studies were then applied to non-human gestural studies to assess intentionality (see for reviews: Byrne et al., 2017; Leavens et al., 2005, Liebal et al., 2014c; Schel et al., under review; Townsend et al., 2017). Townsend et al. (2017) recently gathered these indices in a general framework implying three main criteria to attribute intentionality to communicative signals: the signal has to be directed towards a recipient, produced in order to reach a particular social goal, and has to be followed by a response from the recipient that is consistent with the goal that is deduced for the signaler. This last criterion, related to the communicative value of the signal (Altmann 1968; Green 1975; Marler 1967), would imply that the signal is followed by a consistent change in the recipient’s behavior, consistency with signaler’s intention corresponding to an acceptance or a refusal of signaler’s goal. Following this framework, appropriate behavioral markers have thus to accompany the production of the signal so that it could be associated with intentionality. These behavioral markers may have validity limitations to admit a signal’s intentionality, since each of them can also be explained by unintentional processes, such as learning or changes in signaler’s emotional state (Graham et al., 2019; Liebal et al., 2014b). It has been argued that the more indices observed, the more we get confidence that the criteria are fulfilled and so that the signal might be intentional (Schel et al., 2013), considering that several convergent indices are more likely to be explained by a single cognitive mechanism (intentionality) rather than a series of lower-level cognition explanations (Byrne and Bates 2006; Liebal et al., 2014b; Townsend et al., 2017). However, these markers have to be used cautiously when studying animal signals, with due consideration to all possible cognitive mechanisms underlying signal production.

A signal is considered as recipient-directed if it is produced in the presence of potential receivers (i.e. “socially used”), and physically directed to another individual (Call and Tomasello 2007; Leavens et al., 1996, 2004a; Leavens and Hopkins 1998; Liebal et al., 2004c, 2014b; Schel et al., under review; Tomasello et al., 1985, 1994). To discriminate socially-dependent signals from others, supplementary indicators should be taken into account, such as the fact that the signaler first checked the audience’s attentional state before producing the display (Genty et al., 2009; Graham et al., 2017; Hobaiter and Byrne 2011a; Schel et al., under review), at least in case of signals that have to be perceived on the visual channel. Furthermore, the sensitivity to the attentional state of the recipient, both regarding the rate or the modality of the signal, is often studied as an indicator of intentional use of gestures (e.g. Bourjade et al., 2013; Demuru et al., 2015; Leavens et al., 2004b; Liebal et al., 2004c; Maille et al., 2012; Meunier et al., 2013; Poss et al., 2006). The second dimension of intentional communication, i.e.

the goal-directedness of the signal, could be checked by monitoring response-waiting from the signaler after it produced the display (Call and Tomasello 2007; Cartmill and Byrne 2010; Graham et al., 2017; Hobaiter and Byrne 2011a; Liebal et al., 2004c; Molesti et al., 2019; Pika et al., 2003; Roberts et al., 2012, 2014; Schel et al., under review; Tomasello et al., 1985, 1994). Moreover, goal-directedness is recognized when the signaler stops producing the signal once the presumed goal has been reached, and repeats and/or elaborates the signals in case the goal has not been met yet (Cartmill and Byrne 2007, 2010; Genty et al., 2014; Graham et al., 2017; Gupta and Sinha 2019; Hobaiter and Byrne 2011b; Hostetter et al., 2001; Leavens et al., 2005; Liebal et al., 2004b, 2014b; Roberts et al., 2013).

Based on these indices, the intentionality of great apes' communication gestures has been admitted, notably from Tomasello et al. (1994)'s work on chimpanzee sensitivity to the receiver's attentional state when gesturing, followed by numerous field and lab studies on great apes (see reviews: Byrne et al. 2017; Call and Tomasello 2007; Liebal et al., 2014c). Intentional gestures have been explored recently in monkey species such as macaques (*Macaca mulatta*, *tonkeana*, and *radiata*, Canteloup et al., 2015a, b; Gupta and Sinha 2019; Deshpande et al., 2018), olive baboons (*Papio anubis*, Bourjade et al., 2013; Meunier et al., 2013; Molesti et al., 2019), red-capped mangabeys (*Cercocebus torquatus*, Aychet et al., under review; Maille et al., 2012 ; Schel et al., under review), squirrel monkeys (*Saimiri sciureus*, Anderson et al., 2010). However, studies of potential intentionality markers accompanying the production of primates' facial expressions are still rare.

Some observational studies seem to indicate the social-dependency of apes' facial expressions. The facial expressions of five gibbon species were shown to last longer when the signaler and the receiver were facing each other in social contexts (Scheider et al., 2016). This social directedness and sensitivity to receiver's attentional state were also observed in orangutans (*Pongo pygmaeus*) playful facial expressions as they produce more intense play faces when facing a visually-attentive play partner (Waller et al., 2015), and in bonobos (*Pan paniscus*), who display this facial expression more during social than solitary play, and more in the presence of a visually-attentive recipient (Demuru et al., 2015). Thus, the audience effect supports the communication function of the play faces in these species and their social-directedness may reveal both their emotional and intentional use. Moreover, four of siamangs' (*Symphalangus syndactylus*) facial expressions, mostly performed in combination with tactile or visual gestures, were found to be recipient-directed and accompanied by response waiting or persistence (Liebal et al., 2004c). Assumptions of intentional facial displays were also made for orangutans (*Pongo pygmaeus*), with the same recipient-directedness and goal-directedness indices found for both gestures and facial expressions (Cartmill and Byrne 2010).

Although observations of apes suggest the dual intentional and emotional use of facial expressions, the question whether monkeys produce facial expressions intentionally to communicate remains open. To our knowledge, even though the facial expressions of numerous catarrhine and

platyrrhine monkey species have been described (e.g. *Macaca* genus: Hesler and Fischer 2007, Hinde and Rowell 1962, Maestriperi 2005, Partan 2002, Thierry et al., 2000; grey-cheeked mangabeys: *Lophocebus albigena*, Chalmers 1968a; hamadryas baboons: *Papio hamadryas*, Dube 2013; Talapoin: *Miopithecus talapoin*, Wolfheim and Rowell 1972; capuchin monkeys: *Cebus apella*, De Marco and Visalberghi 2007, Visalberghi et al., 2006, Weigel 1979; and see comparative studies of Redican 1975; van Hooft 1967), there is no evidence that non-hominoid monkeys produce facial expressions in association with behavioral markers of intentional communication, as reported for gestures. The investigation of this topic is necessary to fill the gap in understanding both monkeys' facial signal functions and the evolutionary history of intentional communication, which is of prime interest in the study of language origin (Fröhlich et al., 2019, Hauser 1996; Hauser et al., 2002).

Here, we investigated the facial display repertoire of a relatively little-studied cercopithecoid species, red-capped mangabeys (*Cercocebus torquatus*), and questioned whether these facial displays were dependent of social contexts and accompanied by indices of intentionality. Red-capped mangabeys are semi-terrestrial primates (Mitani et al., 2012) that originate from West African rainforest coastal regions (Cooke 2012; Gautier-Hion et al., 1999; Jones and Sabater-Pi 1968;Orimaye 2017). They have colored hair and skin and white eyelids that contrast with their black face (**Figure 1**), presumably in accordance with a communication function of facial expressions (Gautier-Hion et al., 1999; Hill 1974; Redican 1975). Their gestural communication has been described recently (Schel et al., under review), and suggests, together with data on their multimodal interactions (Baraud et al., 2016), a wide use of visual signals for communication. Experimental studies highlighted the ability of red-capped mangabeys to use a learnt begging gesture intentionally, as a function of visual attentional state of a human receiver (Aychet et al., under review; Maille et al., 2012). Moreover, spontaneous intra-specific gestures produced by red-capped mangabeys were associated with key-markers of intentional communication (Schel et al., under review). Thus, we hypothesized that the intentional use of visual displays as communication signals by this species would encompass facial expressions. Our first aim was to describe the repertoire of facial displays produced by red-capped mangabeys in social situations, and test how this repertoire depends on individual characteristics. Moreover, in accordance with a presumed communication function, we expected that facial displays would be performed under particular social contexts, while their production in non-social contexts would connote a predominant emotional component underpinning the display. Then, we hypothesized that facial displays would be part of this species' intentional dyadic communication, and thus that they would be accompanied by behavioral markers of intentionality, similarly to gestures.



Figure 1. Contrasts in a red-capped mangabey's facial coloration

Methods

Subjects and housing conditions

Twenty-five red-capped mangabeys (*Cercocebus torquatus*), born in captivity and housed at the Station Biologique de Paimpont (University Rennes 1, France), were involved in the present study. Subjects were 10 females and 15 males living in social groups composed of two to 13 individuals (**Table 1**), whose compositions have been stable for at least 8 months. Individuals were classified as juveniles when they were less than 4 years old for females and less than 7 years old for males, based on demographic data on a closely related species, i.e. grey-cheeked mangabeys (*Lophocebus albigena*) (Chalmers 1968b; Deputte 1992; Gautier-Hion and Gautier 1976). Old adults were also differentiated from middle-aged adults (Bouchet et al., 2012) if they were more than 15 years old, corresponding to the median lifespan of mangabeys in captivity (based on 45 years data from our breeding facility on grey-cheeked and red-capped mangabeys). Kinship was known for every individual in this colony.

Social groups were housed in outdoor-indoor enclosures of different sizes (from 8 to 26.4 m² for indoor enclosures, 14.7 to 37.2 m² for outdoor enclosures, and height from 2.5 m to 4.4 m). Individuals were free to move in and out at all time, using connecting tunnels. Indoor enclosure

temperature was maintained at 22°C. Each enclosure was enriched with wood and metal perches, completed with chains or hessian ribbons. The floor of the indoor enclosures was covered with straw and sawdust, while the floor of the outdoor enclosures was covered with cement or bark. Mangabeys were fed twice a day with fresh fruits and vegetables in the morning and with monkey chows in the afternoon. Water was available ad libitum in their indoor enclosures.

Data collection and analyses

Observations

A total of 52.22 hours of observations, distributed from the end of January to the end of June 2018, was collected in order to describe facial displays produced by red-capped mangabeys. We applied the individual focal sampling method (Altmann 1974), recording focal videos of about 15 minutes per session (mean session duration \pm SE = 15.67 \pm 0.10 min) using a JVC Full HD GZ-RX615 camcorder. Each individual was observed during 8 sessions, for a total of more than 2 hours (125.33 \pm 0.75 min). These sessions were scheduled semi-randomly, so that all individuals were observed at all times of day (from 9 am to 6 pm) and at all feeding periods (before first feeding / between two feedings / after second feeding). The experimenter recorded her vocal comments during the video recordings notably to identify individuals interacting with the focal subject.

Videos were then extracted to a computer for further video analyses. Software BORIS v.6.0.6 (Friard and Gamba 2016) was used to play videos and to code each event of facial display and each social interaction involving the focal individual. Because monkeys were free to move, the focal individual was sometimes out of sight for few seconds on the camera field. Data were further analyzed taking into account the exact observation durations when the focal subject was visible.

Facial displays

All the events of facial display produced by the focal individuals were recorded. We defined as “facial displays” all facial movements (i.e. mouth and lips, eyebrows, ears) that could be produced either alone or combined with others, during social interactions or not (Liebal et al., 2014c; van Hooff 1967; Waller and Micheletta 2013). We included all the facial displays that were produced by at least two individuals, discarding idiosyncratic signals.

Table 1. Characteristics of the red-capped mangabeys

Social group	Subject	Sex	Date of birth	Age Category
I.	Bell	Female	31/03/2002	Old adult
	Chipie	Female	28/06/1992	Old adult
	Chipse	Female	03/01/2006	Middle-aged
	Gofrette	Female	08/11/1996	Old adult
	Joly	Female	22/10/2000	Old adult
	Julie	Female	08/05/2004	Middle-aged
	Kargi	Male	19/05/2005	Middle-aged
	Litchi	Male	20/04/2015	Juvenile
	Maillette	Female	29/12/2009	Middle-aged
	Many	Female	14/08/2008	Middle-aged
	Pouët	Male	14/03/2015	Juvenile
	Triskelle	Female	21/04/2015	Juvenile
	Zunie	Female	03/07/1987	Old adult
II.	Kamel	Male	07/09/2010	Middle-aged
	Roby	Male	18/11/2010	Middle-aged
III.	Bandit	Male	15/06/1991	Old adult
	Coët	Male	31/08/2011	Middle-aged
	Tips	Male	10/07/2011	Middle-aged
IV.	Carillon	Male	02/04/2007	Middle-aged
	Elky	Male	06/11/2009	Middle-aged
	George	Male	05/06/2006	Middle-aged
	Pirate	Male	17/10/1992	Old adult
V.	Isba	Male	20/04/2004	Middle-aged
	Lenni	Male	07/10/2006	Middle-aged
	Marti	Male	16/10/1998	Old adult

Contexts of facial displays production

The social contexts in which facial displays occurred were categorized according to the signaler’s and recipient’s behavior observed during the 5 seconds before and the 5 seconds after the signal was produced, using the same timeframe as defined for our analysis of behavioral markers of intentionality. The context was considered “non-social” when the signal was not physically directed towards another subject, or when the facial display was accompanied only by non-social behaviors. This yielded nine categories of social and non-social different contexts: affiliative, grooming, alarm, agonistic, submissive, play, sexual, unclear and non-social (**Table 2**). In order to assess the overall importance of each of these nine categories and to weight contextual data accordingly in our analyses, we also established a population-level time budget. To do so, we coded every 10 sec (scan sampling method, Altmann 1974) the social and non-social contexts in which the focal individual was involved, for one session per individual (totalizing 2250 scans for the population).

Table 2. Contexts of production of facial displays

Context	Associated behaviors
Affiliative	Physical proximity between subjects (at less than one arm length), calm approach of recipient or gentle physical contact
Grooming	Grooming, tactile examination
Alarm	Production of alarm calls by the signaler (i.e. so-called Whoop-gobble and WaHoo calls - Bouchet et al., 2010)
Agonistic	Physical aggression of recipient by signaler (biting, beating, rough manipulation), flight or avoidance of signaler by recipient, or intergroup conflict in which signaler and recipient were in different social groups
Submissive	Flight or avoidance of recipient by signaler
Social play	Play-fight, rough or gentle (involving manual fighting, biting, gentle or rough touching and grabbing), or locomotor-rotational play (play with few physical contacts, but involving pursuits, jumps, saltos)
Sexual	Touching, smelling, licking genital parts or mounting
Unclear	Behaviors accompanying the signal were not sufficient to classify the context, or the interaction could be classified in several categories.
Non-social	The signal was not physically directed towards another subject, or the facial display was accompanied only by non-social behaviors, directed towards the environment (foraging, manipulation, visual, olfactory or gustative exploration of the environment) or self-directed (self-grooming, feeding, peeing or defecation, sleep or rest, solitary play).

Dominance relationships

Dominance relationships between subjects were determined to evaluate their effect on the production of facial expressions. Dominance relationships were based on avoidance behaviors only (see “contact rupture behaviors”: Baraud 2007), as physical aggressions were too rare to be used systematically (Easley and Coelho 1991). All avoidance behaviors involving focal subjects were analyzed. Avoidance was defined as turning away from another individual, avoiding an individual by changing direction, avoiding contact with an individual by moving a body part away from the proximity of another individual, fleeing an individual by walking or running in the opposed direction. The total numbers of occurrences of these behaviors were adjusted for 120 minutes observation per focal

individual. When at least 3 occurrences were observed for a dyad, we computed the percentage of avoidance of subject A from subject B over the total number of avoidance behaviors between A and B (Zumpe and Michael 1986). When this percentage was above 50%, subject A was considered subordinate to subject B.

Behavioral markers of intentionality

Using the framework proposed by Townsend et al. (2017), we evaluated whether facial displays produced during dyadic interactions (see “prerequisite”) fulfilled the three intentionality criteria of being (i) directed towards a recipient (“recipient-directed”), (ii) produced to reach a particular goal (“goal-directed”), and (iii) if they produce a change in the recipient’s behavior (“followed by recipient’s response”). Behavioral markers corresponding to these criteria and commonly used in gestural studies were coded on a presence / absence basis for each occurrence of facial display (see details in **Table 3**). Then, intentionality criteria were analyzed at the facial display-level based on the proportion of occurrences accompanied by these behavioral markers (see the statistical analyses section). Some of the markers relative to goal-directedness of signals were yet not included in the present framework, i.e. persistence and elaboration (Cartmill and Byrne 2007; Leavens et al., 2005), because these markers suppose that the observer is knowledgeable about signaler’s intention and were so not consistent with this first study of red-capped mangabeys’ facial displays. In this line, changes in recipient’s behavior that were directed to signaler were considered as estimates of consistent recipient’s responses to the facial display.

Inter-observer reliability

To assess reliability of the video coding, two supplementary observers coded one random session per individual, corresponding to 12.4% of the total duration of observation and 14.5% of the total number of facial displays noted (77 occurrences). One observer coded the facial displays and the other coded the intentionality markers and contextual variables. Cohen’s Kappa coefficients were computed (Siegel and Castellan 1988), and good levels of agreement (Viera and Garrett 2005) were found for the recognition of the facial displays and their variants ($\kappa = 0.77$, $P < 0.001$), all intentionality markers (Directionality: $\kappa = 0.94$, $P < 0.001$; Audience checking: $\kappa = 0.73$, $P < 0.001$; Response waiting: $\kappa = 0.69$, $P < 0.001$; Attentive audience: $\kappa = 0.66$, $P < 0.001$; Response of receiver: $\kappa = 0.73$, $P < 0.001$) and context categories ($\kappa = 0.79$, $P < 0.001$).

Table 3. Behavioral markers used to assess intentionality of facial displays, based on criteria adapted from Townsend et al. (2017)

Criteria	Behavioral markers	Description	References from gestural studies
Prerequisite for the present framework	Presence of an audience and dyadic context	The facial display is produced in the presence of an audience, i.e. with other individuals in the same enclosure. Moreover, we took into account only occurrences for which the observer identified a unique putative recipient.	e.g. Leavens et al., 1996; for review: Liebal et al., 2014b
(i.) Recipient-directed signal	Directionality	At least one of the following postural or physical markers of directionality accompanied the facial display: head or body is oriented towards the recipient; a movement is produced in the direction of the recipient; the signaler is approaching the recipient; signaler and recipient are in physical contact.	e.g. Schel et al., under review; Tomasello et al., 1985, 1994; Leavens and Hopkins 1998; Leavens et al., 2004a; Liebal et al., 2004b, 2014b; Call and Tomasello 2007
	Audience checking	During the 5 seconds preceding the production of the facial display, the signaler looks in the direction of the recipient (recipient is more or less 45° in front of the signaler's face).	e.g. Schel et al., under review; Genty et al., 2009; Hobaiter and Byrne 2011
(ii.) Goal-directed signal	Response waiting	The signaler maintains a look in the direction of the recipient for at least 1 second after the facial display was produced (recipient is more or less 45° in front of signaler's face),	e.g. Schel et al., under review; Tomasello et al., 1985, 1994; Pika et al., 2003; Liebal et al., 2004c; Call and Tomasello 2007; Cartmill and Byrne 2010; Hobaiter and Byrne 2011; Roberts et al., 2012, 2014; Graham et al., 2017; Molesti et al., 2019
		while the recipient is visually attentive (signaler is more or less 45° in front of recipient's face).	e.g. Pika et al., 2003; Genty et al., 2009
(iii.) Signal followed by recipient's response	Recipient's behavioral change or signaling	Within the 5 seconds following the facial display, the receiver changes his/her behavior compared to before the signal, interacting socially with the signaler or producing a communication signal (vocalization, gesture or facial expression) directed towards the signaler.	e.g. Liebal et al., 2004a, b, 2006; Roberts et al., 2014; Schel et al., under review

Statistical analyses

Given our sample size, non-parametric statistics were used for data analyses. All tests were two-tailed and alpha-level was set at 0.05. We used R. 3.5.0 software (R Core Team 2018) to run all statistical tests. The number of statistical units for each test is stated in the result section using the letter “N”.

First, we tested the effects of individual characteristics on the repertoire of facial displays. We analyzed sex and age effects on the production of facial displays using non-parametrical model based on permutation ANOVA (using package {ImPerm} on R.3.5.0). Models included sex and age categories as fixed factors and were all run ten times, from which average p-values were computed for each fixed factor. When homoscedasticity of variances was not verified, as for the total number of facial displays, the number of “open mouth fully” and yawns of second and third types, age and sex effects were analyzed separately using non-parametrical univariate tests. Kruskal-Wallis one-way analyses of variance by ranks and post-hoc Mann-Whitney tests were used to compare numbers of facial displays produced between age categories and Mann-Whitney tests were used to compare numbers of facial displays produced between males and females.

Second, the social use of facial displays was evaluated based on the contexts in which signals were produced. The number of occurrences in each context was weighted based on the general time-budget (Nonsocial context typically representing 83.29% of total time; Affiliative: 2.40%; Agonistic: 0.53%; Alarm: 0.22%; Grooming: 5.82%; Play: 0.62%; Sexual: 0.09%; Submissive: 2.13%; Unclear: 4.89%). Thus, the weighted frequencies were compared between social and non-social contexts using Wilcoxon signed rank tests, and p-values were adjusted for multiple comparisons using “False Discovery Rate” (FDR) method, controlling the proportion of false significant p-values (Noble 2009). Then, the weighted frequencies of facial displays produced by subjects were compared between the different context categories using Friedman tests and post-hoc Wilcoxon signed rank tests, completed by FDR correction. The same tests were used to analyze the effects of other contextual factors corresponding to the relationship between the signaler and the recipient. We tested the effects of dominance, kinship and age differences on the numbers of facial expressions produced, except for “ears back” and “stick tongue out” for which the numbers of subjects producing them in dyadic interactions were not sufficient (N<5).

Finally, to assess the intentionality of each type of facial displays, we computed the proportion of occurrences observed in social contexts for which the criteria of intentionality were fulfilled. In order to verify that the markers were not randomly associated to the facial displays, we tested whether the distribution of the cumulative criteria of intentionality differed from a theoretical distribution using Fisher’s exact test for count data. Moreover, to complete this assessment of intentionality based on the presence / absence of behavioral markers, we also explored the social-dependency of facial signals by testing if they were more produced in front of attentive than inattentive recipients. We computed the

proportion of occurrences in a presence of a visually attentive audience, and compared it to a random distribution using exact binomial tests.

Results

Repertoire of facial displays

On a total of 531 occurrences of facial displays recorded, we described six different facial displays, that had all been produced by at least five different signalers (**Table 4**). These facial displays involved mouth, eyebrows or ear movements and were produced in combination or independently. Some were clearly categorized and stereotyped whereas two of them, “open mouth” and “yawn”, seemed graded in relation to their intensity. This potential gradation was reported as different variants of form in the repertoire. We assume that the present repertoire of red-capped mangabeys’ facial displays is complete at the population-level. Indeed, while the total number of hours of observation was quite low compared to what may be needed to describe the entire gestural repertoire of a group (e.g. above “15 hours of active gestures or 150 full days of observation”: Hobaiter and Byrne 2011), the cumulative number of described facial displays reached an asymptote (Molesti et al., 2019; Pika et al., 2005) at the 31st session of observation, as no new display was observed up to the final 200th session.

Individual characteristics affected facial display repertoires (**Table 5**). Sex had a significant effect on the size of repertoires and numbers of facial displays produced, males producing more facial displays than females (permutation model on repertoire size: $N_{\text{males}} = 15$, $N_{\text{females}} = 10$, $P = 0.022$; and Mann-Whitney test on number of facial displays produced: $Z = -2.33$, $P = 0.007$). Age had a tendency to affect repertoire size ($N_{\text{juveniles}} = 3$, $N_{\text{middle-aged}} = 14$, $N_{\text{old}} = 8$, $P = 0.053$), as the repertoire of old individuals was significantly smaller than the one of juveniles ($P = 0.021$) and middle-aged adults ($P = 0.033$). Moreover, old individuals also had a tendency to produce fewer facial displays than middle-aged adults (Mann-Whitney test: $Z = 2.18$, $P = 0.087$).

Analyses of data for each facial display separately showed that the numbers of occurrences varied with age and sex of the signaler (**Table 5**). Juveniles produced significantly more “open mouth” displays than middle-aged (Mann-Whitney test: $Z = 2.66$, $P = 0.012$) and old adults ($Z = 2.67$, $P = 0.012$). Furthermore, this age effect was found for both “open mouth fully” and “open mouth half” displays. Juveniles produced “open mouth half” more frequently than did middle-aged (permutation model: $P < 0.001$) and old adults ($P < 0.001$), and tended to produce “open mouth fully” more frequently (Mann-Whitney test, comparing juveniles to middle-aged: $Z = 2.20$, $P = 0.077$; juveniles to old adults: $Z = 1.95$, $P = 0.077$). However, numbers of “open mouth” did not differ significantly between sexes (open mouth fully: Mann-Whitney test, $Z = -1.07$, $P = 0.284$; open mouth half: permutation model, $P = 0.120$).

Table 4. Facial displays of red-capped mangabeys and sample size. Nb: Number of occurrences; N: Number of signalers.

Facial display	Variants	Description	Nb	N
Open mouth	Fully	Signaler opens his/her mouth completely, uncovering upper and lower teeth.	64	5
	Half	Signaler opens his/her mouth half or slightly, forming an oval shape with the lips, teeth covered or slightly visible.	74	11
Raise eyebrows	-	Signaler raises his/her eyebrows, enlarging the white part of eyelids.	28	13
Ears back	-	Signaler puts his/her ears backwards, stretching the upper part of his/her face.	12	7
Lipsmack	-	Signaler sticks out his/her tongue and moves it between the lips with rapid repeated movements.	112	23
Stick tongue out	-	Signaler sticks his/her tongue out and retracts it briefly (not repeated).	15	9
Yawn	Type 1	Signaler yawns by half opening mouth, forming an oval shape, teeth covered by lips.	55	15
	Type 2	Signaler yawns by half opening mouth, canines uncovered.	30	8
	Type 3	Signaler yawns by opening mouth fully and uncovering all teeth.	116	15
	<i>Non-visible</i>	Signaler yawns, but type of yawn is not visible by the observer.	25	5

We found no effect of age and sex on the production of yawns as a whole (permutation model, sex effect: $P = 0.132$; age effect: $P = 0.126$), but these individual characteristics affected differently the production of variants of yawns. Although yawns of the first type were not affected by age and sex of subjects (sex effect: $P = 0.727$; age effect: $P = 0.385$) (**Table 5**), males produced significantly more yawns of the second type than did females (Mann-Whitney test: $Z = -2.68$, $P = 0.007$). Moreover, subjects' age and sex had both an effect on the production of yawns of the third type, as middle-aged males produced this display more frequently than did other individuals (Mann-Whitney tests, comparing males to females: $Z = -3.039$, $P = 0.002$; middle-aged to juveniles: $Z = -2.12$, $P = 0.034$; old adults to juveniles: $Z = -1.42$, $P = 0.156$; middle-aged to old adults: $Z = 1.769$, $P = 0.077$).

Table 5. Facial displays produced depending on individual characteristics. *N*: Number of subjects; *n*: Number of subjects of each age and sex category, which produced the facial display; *: Kruskal-Wallis one-way analysis of variance by ranks and Mann-Whitney tests; others: non-parametrical mixed model based on permutation ANOVA. a and b indicate respectively significant age and sex effects ($P \leq 0.05$).

Sex and age groups	<i>N</i>	Reper- toire size (<i>a+b</i>)	Median numbers of facial display occurrences $\pm IQR$ (<i>n</i>)											
			Total* (<i>b</i>)	Open mouth – All* (<i>a</i>)	Open mouth fully* (<i>a</i>)	Open mouth half (<i>a</i>)	Raise eye- brows	Ears back	Lip- smack	Stick tongue out	Yawn - All	Yawn Type 1	Yawn Type 2* (<i>b</i>)	Yawn Type 3* (<i>a+b</i>)
Males	15	5 \pm 2	22.50 \pm 33.89	0.00 \pm 4.73 (6)	0.00 \pm 0.92 (4)	0.00 \pm 4.73 (6)	0.95 \pm 2.97 (8)	0.00 \pm 0.98 (6)	2.86 \pm 4.86 (14)	0.00 \pm 0.98 (6)	10.40 \pm 11.79 (14)	1.91 \pm 3.91 (10)	0.95 \pm 3.67 (8)	5.09 \pm 8.58 (13)
Females	10	3 \pm 4	10.04 \pm 10.86	0.48 \pm 2.48 (5)	0.00 \pm 0.00 (1)	0.48 \pm 1.98 (5)	0.48 \pm 1.23 (5)	0.00 \pm 0.00 (1)	4.84 \pm 3.57 (9)	0.00 \pm 0.97 (3)	0.97 \pm 5.30 (5)	0.97 \pm 4.35 (5)	0.00 \pm 0.00 (0)	0.00 \pm 0.76 (2)
Juveniles	3	4 \pm 4	43.52 \pm 62.24	38.58 \pm 58.04 (3)	13.85 \pm 40.92 (2)	24.13 \pm 17.72 (3)	1.05 \pm 2.97 (2)	0.00 \pm 0.00 (0)	0.00 \pm 1.98 (1)	0.00 \pm 2.10 (1)	0.00 \pm 1.05 (1)	0.00 \pm 1.05 (1)	0.00 \pm 0.00 (0)	0.00 \pm 0.00 (0)
Middle- aged	14	5 \pm 2	18.78 \pm 22.34	0.00 \pm 2.16 (6)	0.00 \pm 0.00 (2)	0.00 \pm 1.87 (6)	0.95 \pm 2.35 (8)	0.00 \pm 1.20 (5)	3.83 \pm 4.61 (14)	0.96 \pm 0.99 (8)	10.45 \pm 13.36 (13)	1.93 \pm 4.38 (10)	0.48 \pm 4.18 (7)	5.38 \pm 10.03 (11)
Old adults	8	3 \pm 3	8.38 \pm 9.74	0.00 \pm 0.74 (2)	0.00 \pm 0.00 (1)	0.00 \pm 0.74 (2)	0.00 \pm 1.74 (3)	0.00 \pm 0.73 (2)	4.94 \pm 4.76 (8)	0.00 \pm 0.00 (0)	3.98 \pm 5.75 (5)	0.96 \pm 3.44 (4)	0.00 \pm 0.00 (1)	0.48 \pm 4.58 (4)

Individual characteristics did not affect the production of the other facial displays, as age and sex had no significant effects on the numbers of “ears back” (permutation model: age effect: $P = 0.432$; sex effect: $P = 0.951$), “lipsmack” (age effect: $P = 0.278$; sex effect: $P = 0.820$), “raise eyebrows” (age effect: $P = 0.862$; sex effect: $P = 0.603$) or “stick tongue out” (age effect: $P = 0.284$; sex effect: $P = 0.959$) (Table 5).

Contexts of facial display production

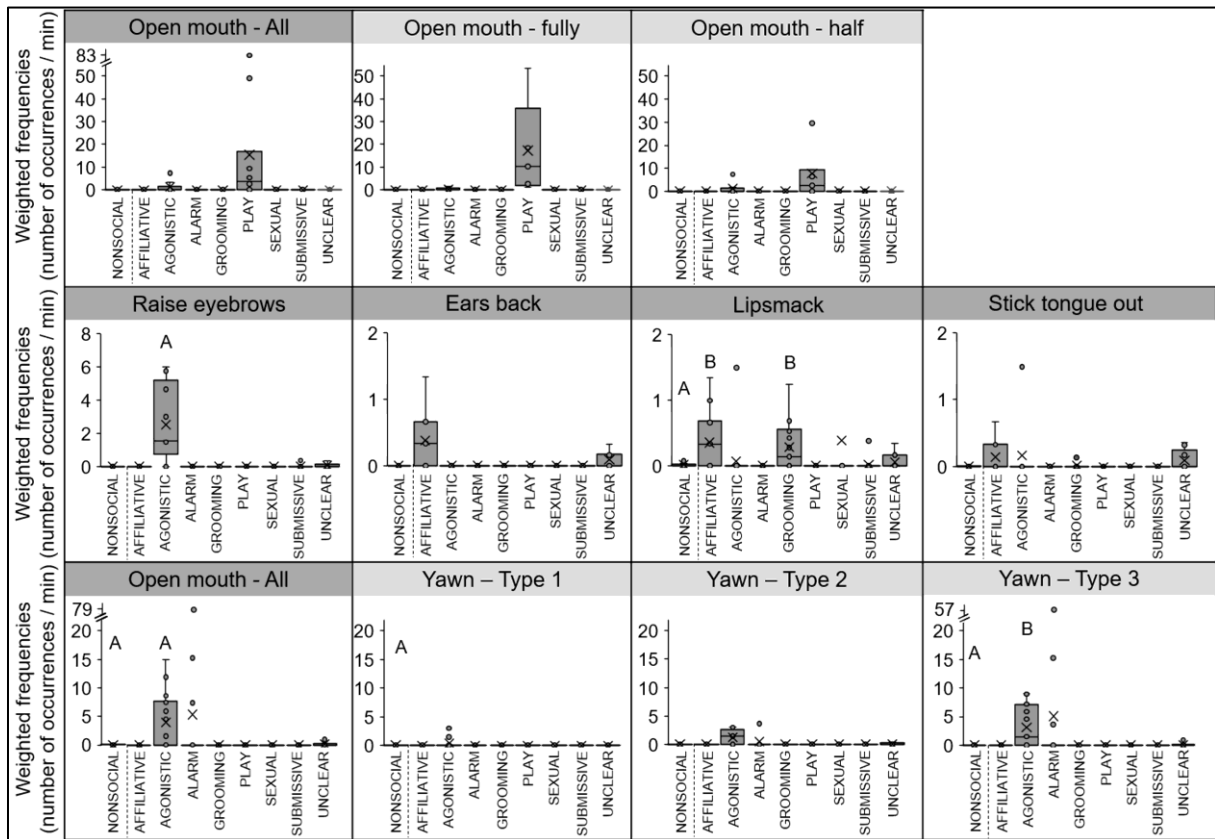


Figure 2. Facial displays produced by red-capped mangabeys in relation to non-social and social contexts. Post-hoc Wilcoxon signed rank tests: capital letters (A, B) indicate significant differences with other contextual categories ($P \leq 0.05$).

All facial displays were produced in social contexts, but lipsmacks, “stick tongue out” and yawns were also observed in non-social contexts. Lipsmacks were produced significantly more in social than non-social contexts (Wilcoxon signed rank test: $N = 23$, $V = 30.5$, $P = 0.003$), but this was not significant for “stick tongue out” ($N = 9$, $V = 7$, $P = 0.124$), and yawns of second ($N = 8$, $V = 18$, $P = 1.000$) and third types ($N = 15$, $V = 61$, $P = 0.978$). However, yawns of first type were produced significantly more in non-social than social contexts ($N = 15$, $V = 102.5$, $P = 0.002$). All other facial displays were produced exclusively in social contexts.

Moreover, the different facial displays were associated with particular social contexts (**Figure 2**) (Friedman tests: open mouth (all): $N = 11$, $X^2 = 38.59$, $P < 0.001$; open mouth fully: $N = 5$, $X^2 = 35.69$, $P < 0.001$; open mouth half: $N = 8$, $X^2 = 38.59$, $P < 0.001$; raise eyebrows: $N = 13$, $X^2 = 58.60$, $P < 0.001$; ears back: $N = 7$, $X^2 = 25.14$, $P = 0.001$; lipsmack: $N = 23$, $X^2 = 54.95$, $P < 0.001$; yawns (all): $N = 19$, $X^2 = 81.129$, $P < 0.001$; yawns of first type: $N = 15$, $X^2 = 84.58$, $P < 0.001$; yawns of second type: $N = 8$, $X^2 = 34.66$, $P < 0.001$; and yawns of third type: $N = 15$, $X^2 = 60.21$, $P < 0.001$), except for “stick tongue out” ($N = 9$, $X^2 = 13.61$, $P = 0.092$), for which contexts of production were unclear.

We also evaluated contextual effects of the relationships between signaler and recipient. We found that neither dominance relationship nor kinship affected the numbers of any of the facial expressions produced during dyadic interactions (Wilcoxon signed rank tests: Dominance relationship: $5 < N < 18$, $5 < V < 38$, $P = 1.000$; Kinship: $5 < N < 18$, $1 < V < 65$, $P > 0.375$). Age difference between individuals influenced the production of lipsmacking as it was emitted more frequently towards older individuals than towards same-age subjects ($N = 18$, $V = 12.5$, $P = 0.039$). Age difference between signaler and recipient had no significant effect on all the other types of facial expressions ($5 < N < 13$, $2 < V < 34$, $P > 0.11$).

Behavioral markers of intentionality

All the facial displays of our repertoire, except yawns, were in some cases associated with the behavioral markers of all criteria of intentionality. These markers were indices of social-directedness (i.e. physical directionality and/or audience checking), goal-directedness (i.e. response waiting towards an attentive recipient) and change in recipient’s behavior. However, distributions of these behavioral markers differed depending on the facial displays produced in social contexts (**Figure 3**). These distributions differed significantly from a random theoretical distribution for “open mouth” (all variants summed: $N = 138$, $P = 0.001$), “open mouth fully” ($N = 64$, $P < 0.001$), “open mouth half” ($N = 74$, $P < 0.001$), “lipsmack” (Fisher’s exact test: $N = 81$, $P < 0.001$), yawns (all types summed: $N = 98$, $P < 0.001$), as well as for the third type of yawns (type 1: $N = 5$, $P = 0.211$; type 2: $N = 14$, $P = 0.211$; type 3: $N = 63$, $P < 0.001$). The highest level of association with intentional cues was for “open mouth fully” and “half open” displays that were generally accompanied by markers of all criteria of intentionality (95/138 occurrences). The distribution of the cumulative behavioral markers did not differ from a random distribution for “raise eyebrows”, “ears back”, and “stick tongue out”. Lipsmacks and yawns were sparsely or never displayed in association with markers of goal-directedness (20/81 occurrences for lipsmacks, and 2/98 occurrences for yawns). However, lipsmacks were mainly produced in the direction of a recipient (71/81 occurrences), whereas all types of yawns seemed disentangled from dyadic interactions (85/98 occurrences non directed).

Finally, we found that “open mouth” and “raise eyebrows” were mainly displayed in the presence of a visually attentive recipient (Exact binomial tests: open mouth (all): $N = 134$, $P < 0.001$;

open mouth fully: $N = 64$, $P < 0.001$; open mouth half: $N = 70$, $P < 0.001$; raise eyebrows: $N = 19$, $P < 0.001$), and that yawns of second and third type were produced less in the presence of a visually attentive recipient (yawns (all): $N = 88$, $P < 0.001$; yawns of second type: $N = 12$, $P = 0.010$; and third type: $N = 59$, $P < 0.001$), and it was a tendency for yawns of first type ($N = 5$, $P = 0.063$) (**Figure 4**). We found no significant difference with a theoretical distribution for “ears back” ($N = 4$, $P = 0.188$), “lipsmack” ($N = 64$, $P = 1.000$), and “stick tongue out” ($N = 5$, $P = 1.000$).

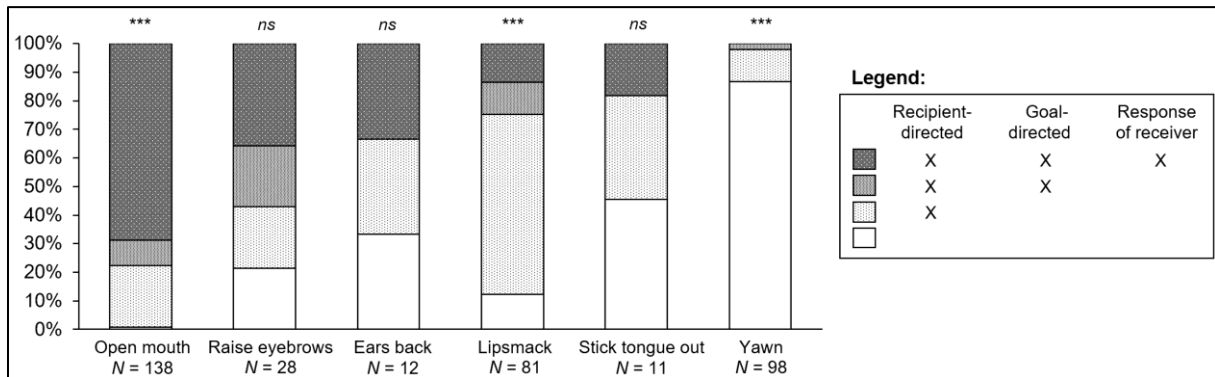


Figure 3. Distributions of the cumulative intentionality markers accompanying facial displays. Percentages are computed on total numbers of occurrences observed in social contexts (N). Comparisons with random theoretical distributions were computed using Fisher’s exact tests. ns: $P > 0.05$; *: $P \leq 0.05$; **: $P < 0.01$; ***: $P < 0.001$.

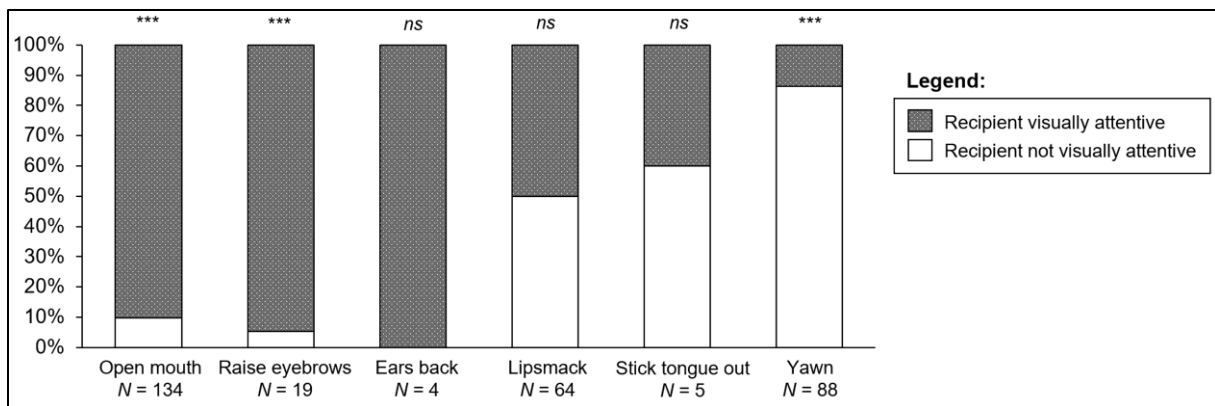


Figure 4. Proportion of occurrences in the presence of a visually attentive recipient. Percentages are computed on total numbers of occurrences observed in social contexts and only when recipient was visible (N). Comparisons with random theoretical distributions were computed using exact binomial tests. ns: $P > 0.05$; **: $P < 0.01$; ***: $P < 0.001$.

Discussion

This study explored the repertoire of six facial displays of a captive population of red-capped mangabeys, and tested whether these displays were produced socially and accompanied by indices of intentional communication. This preliminary assessment of first-order intentionality in mangabeys' facial displays was based on behavioral markers similar to those used in gestural studies, to evaluate whether signals were (i) directed towards a recipient, (ii) produced in order to reach a specific goal and (iii) led to a change in the recipient's behavior (Townsend et al., 2017). The social condition of mangabeys' facial displays, as well as the effects of individual characteristics on the repertoire, supports their communication function. The playful "open mouth" displays were produced exclusively in social contexts and in most cases in the direction of an attentive recipient, with all defined markers of intentional communication. We discuss below the significance of these results regarding the potential intentionality of these displays, given the current limitations of the behavioral method used to assess first-order intentionality in animal communication (Graham et al. 2019). Although other cognitive mechanisms may explain our observations, the present results constitute a first step to address the potential intentionality of red-capped mangabeys' facial displays, particularly the "open mouth". While not meeting criteria for goal-directed signals for all occurrences, other facial displays ("raise eyebrows", "ears back", lipsmacks and "stick tongue out") except yawns were at least recipient-directed in most cases. Finally, yawns seemed not associated with dyadic communication, and thus did not fulfill the defined criteria for intentional communication. Interestingly, these displays presented different variants of intensity, which were presumably associated with different functions.

We described six facial displays produced by red-capped mangabeys, which involve movements of the ears, eyebrows or mouth, and can be produced in combination or independently one from the other. One noticeable point of the present repertoire is the description of unitary ear displays used socially by red-capped mangabeys. While non-human primates' ear musculature is controlled by facial nerves (Müri 2016), few studies of facial displays describe ear movements (but see in rhesus and long-tailed macaques, *Macaca mulatta* and *fascicularis* : Chance et al., 1977; Hinde and Rowell 1962; Partan 2002). Although most facial displays of the repertoire are discrete, we distinguished variants for two of them, corresponding to different intensities of mouth displays. The repertoire size and this possible gradualness of the morphology of some facial displays suggest that red-capped mangabeys' communication relies strongly on complex visual cues (Dobson 2009; Freeberg et al., 2012).

Thus, the "open mouth" displays, highly related to play contexts, appeared graded. Some facial displays are indeed graded signals that can be associated with different motivations of the signaler (Marler 1965; Parr et al., 2005; Preuschoft and van Hooff 1996; Waller and Micheletta 2013). In primates, the variants "open mouth fully" and "half" have been largely described as playful facial displays (Chevalier-Skolnikoff 1994; van Hooff 1967). Moreover, subjects' age influenced the

production of “open mouth fully” and “half”, as younger subjects were involved in playful interactions more frequently and were possibly more emotionally involved in play than adults (Demuru et al., 2015). Although primate gestures are used in variable contexts (Byrne et al., 2017; Call and Tomasello 2007; Hobaiter and Byrne 2013; Liebal et al., 2014c), the fact that facial displays are more context-specific allows us to hypothesize that their function is to help elucidate the meaning of associated signals used in multimodal communication. These facial displays may act as “metacommunicative signals” (Altmann 1967; Bateson 1955), notably because play might involve agonistic-like gestures (Demuru et al., 2015; Palagi 2008; Waller and Cherry 2012).

Red-capped mangabeys generally produced “open mouth fully” and “open mouth half” in association with all previously defined behavioral markers of intentionality, and significantly more in situations when the receiver was visually attentive. Therefore, our results on red-capped mangabeys’ directed “open mouth” are consistent with previous observations of great apes. Bonobos’ (*Pan paniscus*: Demuru et al., 2015) and orangutans’ (*Pongo pygmaeus*: Waller et al., 2015) homologous facial displays were suggested to be dependent on audience attentional state, indicating that these facial expressions are not an automatic response to play.

However, we should be careful before drawing the conclusion that these “open mouth” displays are produced intentionally, given some alternative explanations to audience effect. For instance, the production of “open mouth” preferentially in front of an attentive recipient could be the result of a learnt discrimination. Individuals may be more likely to produce a facial display in these conditions because they have learnt that seeing the face of a recipient is necessary to obtain a response from their signal (Graham et al., 2019). Moreover, the social use of “open mouth” and the sensitivity to the recipient’s attentional state cannot rule out an emotional-based production of these displays. Eye gaze is an emotional stimulus in primates (Emery 2000), and arousal is prone to be higher in the presence of others compared to alone (Zajonc 1965). Thus, these factors could induce changes in the signaler’s emotional state, resulting in the production of the facial expressions. Besides, observations in apes suggest that the production of play faces has a strong emotional component. This expressions can be observed during bonobos’ (*Pan paniscus*) solitary play (Demuru et al., 2015), and the example of a female gorilla (*Gorilla gorilla*) hiding her play face (Tanner and Byrne 1993) suggests that she was not able to inhibit this facial display, as it is the case of humans experiencing intense emotions (Porter et al., 2012). We found concomitant markers of other criteria of intentional communication (i.e. waiting for a response from the signaler and recipient’s consistent behavioral response) accompanying red-capped mangabeys’ “open mouth”, but one particular limit of the present observations is that “response waiting” should be cautiously interpreted as a goal-directedness marker per se (Graham et al., 2019; Liebal et al., 2014b). As a first insight in the intentionality of facial displays in red-capped mangabeys, the present framework about “goal-direction” did not include markers related to goal-dependent cessation of communication or persistence and elaboration, because these aspects of signal’s “aboutness” require that the observer is

knowledgeable of the signal function and thus presumed signaler's intention displaying it. Thus, we must remain cautious when concluding about the possible intentionality of the signals studied, given that criteria of recipient-directedness and goal-directedness were both assessed based on markers related to visual attention only. Moreover, while analyzing intentionality at the signal-level, this study did not address yet the question of inter-individual variability in intentional communicative facial displays. In this sense, the present results will need to be supplemented by further investigations of the goal-directedness of "open mouth fully" and "half", which presumably corresponds to an invitation to play or to maintain a playful interaction. We believe that a multimodal approach would be beneficial in this regard, addressing goal-persistence by taking into account associated vocalizations and gestures.

Overall, there are current validity limitations in the behavioral method used to assess first-order intentionality in animal communication (see the above-mentioned examples of other cognitive processes possibly underlying the behaviors identified as intentionality markers). The framework proposed by Townsend et al. (2017) has the advantage to be widely applicable to diverse species and communication modalities, although it does not permit to conclude with certainty that signals are intentionally produced. Graham and colleagues (2019) suggested some perspectives in light of this methodological problem, such as experimentally address second-order intentionality (which implies mental-state attribution, see Dennett 1983), or complete observational studies with valid measures of arousal during signal production. Until such approaches are applicable, behavioral assessment of first-order intentionality still permits to gather meaningful information, such as the present results, which we believe constitute a first step in assessing the intentionality of red-capped mangabey facial displays, particularly for "open mouth".

Other facial displays "raise eyebrows", "ears back", lipsmacks and "stick tongue out" appeared only partially accompanied by defined behavioral markers of intentionality. However, these displays were at least recipient-directed in most of the cases, thus indicating their communicative function (Call and Tomasello 1994; Leavens et al., 1996). Eyebrow raising and ears back were exclusively produced in social contexts, i.e. agonistic and affiliative contexts respectively, and mostly directed to a visually attentive recipient. Lipsmacks were produced more in social than non-social contexts, particularly in affiliative and grooming situations, but not more in front of an attentive than an inattentive recipient, as found for "stick tongue out". While lipsmacks' production was not dependent on recipient's visual attention, we may hypothesize that this signal can also be acoustically perceived (as the "audible smacking sound" produced by macaques: Maestripiéri and Wallen 1997; Maestripiéri 2005), and therefore visual attention would not be necessary. We note that most of the above-cited facial displays described, except "stick tongue out", were preferentially or exclusively produced in social contexts. Lipsmacks were produced in affiliative and grooming contexts, as found for instance in olive baboons (*Papio anubis*: Easley and Coelho 1991), but also in non-social contexts, especially during auto-grooming. This enabled us to hypothesize that lipsmacking may be an automatic response to grooming

actions and, as for non-social production of yawns, might indicate a prominent emotional component driving the production of this facial display.

Yawns, as opposed to the other facial displays, seem to be disentangled from dyadic interactions, as even in social contexts we found almost no signs of recipient-directed use. The high frequency of yawns in non-social context is in agreement with the hypothesis that yawns are strongly linked to internal states of the signaler (Deputte 1994). Moreover, regarding their production in social conditions, yawns may have an informative function, for conspecifics, on the signaler's emotional state during agonistic and alarm contexts (Bolwig 1959; Deputte 1994). An interesting point concerning this particular display lies in the relationship between its form and function, as red-capped mangabeys produced different types of yawns, with regard to mouth opening and teeth uncovering, in different contexts. These variations are known and characterized for grey-cheeked mangabeys (*Lophocebus albigena*: Deputte 1994), as well as for macaque species (*Macaca fascicularis*: Deputte 1994; Zannella et al., 2017), geladas (*Theropithecus gelada*: Palagi et al., 2009) and chimpanzees (*Pan troglodytes*: Vick and Paukner 2010).

Yawns of the first type, with mouth less open, were used only in non-social contexts and might correspond to physiological regulators during transition between activity and resting or during feeding anticipation (Deputte 1978). Some yawns of the second and third types, with mouth more open and teeth more visible were associated with alarm calls, as described also for grey-cheeked mangabeys (*Lophocebus albigena*: Deputte 1994), apparently because of high arousal and social tension. Moreover, yawns of the third type were mainly produced in agonistic contexts, as visible canines are hypothesized to play the role of threat or pre-threat (Altmann 1967; Redican 1975). Yawns of the third type were produced more frequently by middle aged and old adult males, while individual characteristics did not affect the production of yawns of the first type. In our sample, the males were not equally distributed in the social groups, most of them living in all-male groups. However, as sex influenced some variants of yawns and not the others, we assume that male group membership did not bias the analysis of the effect of sex on facial display repertoire. These results on sex effects are consistent with the hypothesis of a threat value of the yawns with visible canines (Leone et al., 2014; Zannella et al., 2017), particularly because red-capped mangabeys exhibit an important sexual dimorphism in canine size that becomes evident with sexual maturity (Deputte 1986; Hill 1974). This hypothesis is supported by similar sexual differences of yawn production by macaque species (*Macaca fuscata* and *tonkeana*: Zannella et al., 2017), taken that this difference was not found for primate species such as lemurs (*Propithecus verreauxi* and *Lemur catta*: Zannella et al., 2015) or humans (*Homo sapiens*: Schino and Aureli 1989), with absent or slight sexual dimorphism in canine-size. Moreover, the age effect on yawn production may be associated with testosterone level changing with sexual maturity since testosterone was correlated with yawn production in rhesus macaques (*Macaca mulatta*: Phoenix and Chambers 1982; Robinson et al., 1975; Wallen and Goy 1977). The relationship between yawn morphological variability and function, highlighted by the contexts of production and by the effect of individual characteristics, is in agreement

with previous results for geladas (*Theropithecus gelada*: Leone et al., 2014). In macaques, this was associated with communication redundancy observed in species showing more tolerant social styles (Zannella et al., 2017) which also exhibit larger meaningful communicative repertoires (Dobson 2012).

Moreover, we found no dominance or kinship effects on any of the facial expressions displayed, presumably in relation with the sociality of red-capped mangabeys, which have been shown to adopt both despotic and egalitarian behaviors (Dolado and Beltran 2012). Despite a steep hierarchy within their groups, red-capped mangabeys have indeed relatively dynamic dominance relationships (Dolado and Beltran 2011) with some propensity to counter-attack, as do tolerant macaque species (de Waal and Luttrell 1989; Thierry 2007).

Conclusion

In sum, the repertoire of red-capped mangabeys' facial displays is composed by six different displays that could be graded in intensity. We characterized the social-dependent production of facial expressions by red-capped mangabeys, and brought to light behavioral indices of intentionality accompanying facial displays. Particularly, playful "open mouth" appeared strongly associated with some intentionality indices, as previously noticed in ape species. We believe that the present repertoire provides a basis for further research on function and intentionality of red-capped mangabeys' facial expressions. As the gestural, vocal and facial signals are now described in this species, we also believe that it will constitute a useful tool for a multimodal approach for the study of catarrhine monkeys' intentional communication, a key feature for evolutionary research on language origins.

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Chapitre IV

Latéralité gestuelle





Article 3

Multifactorial analysis of gestural laterality in captive red-capped mangabeys (*Cercocebus torquatus*)

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SYNTHESE DE L'ARTICLE 3

Contexte

La communication verbale et non-verbale humaine est latéralisée en faveur du côté droit du corps, en raison d'une spécialisation de l'hémisphère gauche pour le contrôle du langage. L'hypothèse d'une origine gestuelle du langage a été formulée au regard de l'utilisation préférentielle du côté droit pour produire des gestes chez plusieurs singes catarrhiniens. Ainsi, afin de comprendre les causes distales et proximales de la latéralisation du langage, nous nous intéressons à la latéralité gestuelle des primates non-humains, tentant de déterminer les facteurs dont elle dépend.

Méthode

Les gestes brachio-manuels intraspécifiques de 25 mangabeys à collier captifs ont été décrits, à partir d'observations en focal. Nous avons d'abord testé l'existence d'une latéralité gestuelle à échelle individuelle voire populationnelle pour la globalité des gestes étudiés. Nous avons ensuite analysé l'effet de différents facteurs sur la main utilisée par les mangabeys pour communiquer, en particulier des facteurs contextuels, sociodémographiques, et relatifs à la forme des gestes.

Résultats

Nous n'avons pas observé de latéralisation gestuelle significative à échelle individuelle ou populationnelle chez les mangabeys étudiés, possiblement en raison de la taille de notre échantillon. Cette étude préliminaire a en revanche permis de mettre en évidence un effet significatif du contexte interactionnel sur la main utilisée par les mangabeys pour communiquer. En particulier, les mangabeys utilisaient préférentiellement le côté droit pour communiquer en contextes sociaux négatifs (agressions). La position du receveur a également eu une influence significative sur la latéralité gestuelle, les mangabeys utilisant préférentiellement la main ipsilatérale, pour diriger leur geste. Les caractéristiques sociodémographiques des sujets, la modalité sensorielle des gestes et la posture du signaleur n'ont en revanche eu aucun effet significatif sur la main utilisée pour communiquer.

Conclusion

Cette première analyse de la latéralité gestuelle des mangabeys à collier souligne l'importance du contexte interactionnel sur ce trait, comme mis en évidence chez les chimpanzés et les gorilles. Ces résultats devront être complétés par un échantillon plus important, permettant notamment d'analyser plus finement la latéralité à échelle individuelle.

Multifactorial analysis of gestural laterality in captive red-capped mangabeys (*Cercocebus torquatus*)

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Abstract

Several catarrhine primates gesture preferentially with their right hand, which led to the hypothesis of a gestural origin of human left-hemispheric specialization for language. In order to test for this assumption and elucidate the proximate and ultimate causes of language lateralization, it is needed to characterize gestural communication in a higher diversity of primate species. Recently, studies showed that chimpanzees and gorillas' gestural laterality was modulated by factors related to social context and gesture characteristics as well as by socio-demographic factors. Although a right-handedness has been evidenced in the gestural communication of several non-hominoid species, factors influencing this laterality remain understudied, particularly in intra-specific contexts. We present here a preliminary investigation of intraspecific gestural laterality in catarrhine monkeys, red-capped mangabeys. We observed five social groups of captive subjects and described the spontaneous production of their brachio-manual intentional gestures. We did not evidence any significant gestural lateralization neither at the individual level nor at the population level. However, corroborating previous findings from ape studies, we found that mangabeys preferentially used their right hand to gesture in negative social contexts such as aggressions. They also adapted to the position of their receiver by preferentially using their ipsilateral hand to communicate. By contrast, factors related to gesture form and socio-demographic characteristics of signaler and receiver did not affect gestural laterality. To understand better the relationships between gestural laterality and brain lateralization from an evolutionary perspective, we suggest that the gestural communication of other monkey species should be examined with this multifactorial approach.

Keywords: Catarrhine monkeys, gestures, manual laterality, social laterality, language origins

Introduction

Humans exhibit a left-hemispheric specialization for language functions, particularly through Broca's and Wernicke's brain areas, which results in a right-biased lateralization for verbal and non-verbal communicative behaviors (e.g. Broca 1865; Wernicke 1874; Kimura 1973; Grossi et al. 1996; Lieberman 2002; Cooper 2006; Meguerditchian et al. 2013). Great apes also exhibit neuroanatomical asymmetries in favor of the left hemisphere in brain regions homologous to Broca's area (in chimpanzees, *Pan troglodytes*, bonobos, *Pan paniscus*, and gorillas, *Gorilla gorilla gorilla*: Cantalupo and Hopkins 2001), and functional association of these regions with gestural communication have been evidenced in chimpanzees (Tagliabue et al. 2006, 2008). Moreover, population-level right-handedness for the production of communicative gestures have been evidenced in several catarrhine primates (e.g. chimpanzees: Fletcher 2006; Meguerditchian et al. 2010; Hobaiter and Byrne 2013; Prieur et al. 2016a; gorillas: Hopkins et al. 2012; Prieur et al. 2016b, 2017a; Tonkean macaques, *Macaca tonkeana*: Meunier et al. 2013a, b; olive baboons, *Papio anubis*: Meguerditchian and Vauclair 2006; Meguerditchian et al. 2011; Meunier et al. 2013a). Gestural laterality is dissociated from hand preference observed in non-communicative actions in numerous species (e.g. chimpanzees: Prieur et al. 2016a; Campbell's mona monkeys, *Cercopithecus campbelli*, and red-capped mangabeys, *Cercocebus torquatus*: Maille et al. 2013; Tonkean macaques: Meunier et al. 2013b; and olive baboons: Meguerditchian and Vauclair 2009), which suggest different neuronal control for communicative and non-communicative gestures.

A communicative gesture can be defined as a non-locomotor and mechanically ineffective brachio-manual signal, that is directed to a recipient and lead to a voluntary response from the latter (e.g. Tomasello et al. 1985; Liebal et al. 2005; Cartmill and Byrne 2007; Pollick and De Waal 2007; Pika 2008; Call and Tomasello 2008; Hobaiter and Byrne 2011; Bard et al. 2014; Gupta and Sinha 2016; Fröhlich et al. 2016, 2017; Schel et al. under review), although it has to be noted that this operational definition may vary depending on the authors (Bourjade et al. 2020). The above-cited neuroanatomical and behavioral similarities between language lateralization and gesture production in several primate species, together with their phylogenetical proximity with *Homo sapiens* (Raaum et al. 2005; Chatterjee et al. 2009; Perelman et al. 2011), led to the hypothesis that the brain lateralization for language control is inherited from a left-hemispheric specialization for intentional gestures in the common ancestor of humans and other catarrhine primates (e.g. Hewes et al. 1973; Corballis 2003, 2010; Vauclair 2004; Meguerditchian et al. 2013; Prieur et al. 2019a, b). Thus, studying gestural laterality in primates seems particularly relevant to elucidate the proximate and ultimate causes of language lateralization.

Different hypotheses have been formulated concerning the emergence of manual laterality. Notably, the "postural origin theory" (MacNeilage et al. 1987; MacNeilage 2007) proposes that manual laterality results from adaptations of the right hand for complex tasks in terrestrial species, free from postural constraints implied by arboreal locomotion. Some authors also hypothesized that manual

laterality evidenced in captive non-human primates was the by-product of experimental biases and captivity (“artefactual hypothesis”: Warren 1980; McGrew and Marchant 1997, 2001). Moreover, the “task complexity hypothesis” suggests that manual laterality is stronger for tasks requiring high level of manipulation, i.e. involving multiple acts such as bimanual coordination (Fagot and Vauclair 1991). Looking specifically at communicative gestures, different factors might influence manual laterality in primates. Firstly, gestural laterality may depend on factors related to the interactional context, such as its emotional valence. Prieur and colleagues (2016a, 2017a, c) evidenced a preferential use of the right hand for gestures associated to negative emotions in chimpanzees and gorillas, whereas theories on brain asymmetries for emotion perception and expressions would predict left-lateralized behaviors in negative contexts (see “right hemisphere theory” and “valence theory”, reviewed by Demaree et al. 2005). The relative position of the signaler and receiver during the interaction can also affect gestural laterality, as shown in chimpanzees and gorillas (Prieur et al. 2016a, 2017b, c), presumably because of gesture directionality (which may imply a preferential use of the ipsilateral hand) and to asymmetrical emotional signals from recipient which could drive gesture production (e.g. Wallez et al. 2012; Prieur et al. 2016a). Secondly, gesture characteristics may affect hand preference, such as the type of gesture, as shown in chimpanzees and gorillas (Hopkins and Leavens 1998; Hopkins and Wesley 2002; Hobaiter and Byrne 2013; Prieur et al. 2016a, 2017b, c), or the sensory modality on which it is delivered (i.e. visual only, acoustic or tactile: Prieur et al. 2016a, 2017b). Moreover, in line with the “postural origin theory”, it can be hypothesized that the hand used to gesture depends on whether hands are engaged for signaler posture stability. This postural effect on laterality has notably been evidenced for manual tasks in red-capped mangabeys (Blois-Heulin et al. 2006) and grey-cheeked mangabeys (*Lophocebus albigena*, Blois-Heulin et al. 2007). Thirdly, sociodemographic characteristics of the signaler and receiver may affect gestural laterality. Although no or slight effects of dominance and kinship have been found in chimpanzees and gorillas (Hopkins et al. 2005; Prieur et al. 2016a, 2017c), the age of the signaler affects gestural laterality in several species, as right-handedness increases with age (e.g. in chimpanzees: Hopkins and Leavens 1998; Hobaiter and Byrne 2013; Prieur et al. 2016a; gorillas: Prieur et al. 2017a, c; olive baboons: Meguerditchian and Vauclair 2006).

To understand how all these factors may affect gestural laterality, it seems judicious to observe non-human primate gestures occurring in intraspecific contexts. Prieur and colleagues (2016a, 2017c) were the first to adopt a multifactorial approach to characterize intraspecific gestural laterality, in chimpanzees and gorillas. To our knowledge, such method has never been adopted to study catarrhine monkeys’ gestural communication. Yet, right-handedness for communicative gestures have been evidenced in cercopithecoid species (Tonkean macaques: Meunier et al. 2013a, b; Campbell’s mona monkeys and red-capped mangabeys: Maille et al. 2013), including for intraspecific gestures (olive baboons: Meguerditchian and Vauclair 2006; Meguerditchian et al. 2011), suggesting that it could be investigated beyond the great ape clade. Moreover, our understanding of the causes of gestural laterality,

and thus to a greater extent our understanding of language evolutionary origins, benefits from comparisons between primates with different social systems and ecologies (Meguerditchian 2014).

We present here a preliminary investigation of intraspecific gestural laterality in captive red-capped mangabeys, a semi-terrestrial monkey (Mitani et al. 2012) originating from West African rainforest coastal regions (Jones and Sabater-Pi 1968; Gautier-Hion et al. 1999; Cooke 2012; Orimaye 2017). They naturally live in multi-male, multi-female social groups from 10 to 25 individuals (Jones and Sabater-Pi 1968; Gautier-Hion et al. 1999), and exhibit linear hierarchy in captivity (Dolado and Beltran 2011), with aggression and affiliation patterns both observed in despotic and relaxed macaque societies (Dolado and Beltran 2012). Recent results evidenced that captive red-capped mangabeys produce intentional body signals as part of their intraspecific communication, and notably manual gestures (Schel et al., under review). Experimental assessment of manual laterality in human-directed communication brought to light lateralized individuals for pointing gestures, and a dissociation of hand preference for communicative compared to non-communicative manual acts (Maille et al. 2013). However, mangabeys' intraspecific gestural laterality has never been studied. Our first aim here was to test whether captive red-capped mangabeys are lateralized at the individual and population-level for their intraspecific gestures. Based on previous findings in catarrhine apes and monkeys (e.g. Meguerditchian and Vauclair 2006; Hobaiter and Byrne 2013; Prieur et al. 2016a, b), we expected to find a right-hand bias in mangabey manual gesturing. Secondly, we tested which proximate factors would affect hand preference in red-capped mangabey gestures, among which factors related to the gesture production and characteristics (sensory modality involved, signaler posture), to the interactional context (emotional valence of context, relative positions of signalers and receivers), and socio-demographic characteristics (age and sex of the signaler, relationship between signaler and receiver in terms of difference of age and sex, dominance and kinship).

Methods

Subjects and housing conditions

This study was purely observational and did not imply any modification of the living conditions of the captive mangabeys housed at the Station Biologique de Paimpont (University Rennes 1, France), where animal facilities and animal care procedures are regularly monitored by the responsible local authorities (Housing agreement for research D35-211-18, delivered by the “Direction Départementale de la Cohésion Sociale et de la Protection des Populations” (DDCSPP)).

Twenty-five captive red-capped mangabeys (*Cercocebus torquatus*) were observed in the present study, living in social groups from two to 13 individuals that have been stable from at least 8 months. The subjects were 10 females and 15 males, among which 3 were juveniles, 14 middle-aged

and 8 old adults (Aychet et al. in press, **Table 1**). They were housed in outdoor-indoor enclosures of different sizes (from 8 to 26.4 m² for indoor enclosures, 14.7 to 37.2 m² for outdoor enclosures, and height from 2.5 m to 4.4 m), and were free to move in and out at all time, using connecting tunnels. Indoor enclosure temperature was maintained at 22°C. Each enclosure was enriched with wood and metal perches, completed with chains or hessian ribbons. The floor of the indoor enclosures was covered with straw and sawdust, while the floor of the outdoor enclosures was covered with cement or bark. Mangabeys were fed twice a day with fresh fruits and vegetables in the morning and with monkey chows in the afternoon. Water was available ad libitum in their indoor enclosures.

Table 1. Characteristics of the red-capped mangabeys

Social group	Subject	Sex	Date of birth	Age Category
I.	Bell	Female	31/03/2002	Old adult
	Chipie	Female	28/06/1992	Old adult
	Gofrette	Female	08/11/1996	Old adult
	Joly	Female	22/10/2000	Old adult
	Zunie	Female	03/07/1987	Old adult
	Chipse	Female	03/01/2006	Middle-aged
	Julie	Female	08/05/2004	Middle-aged
	Maillette	Female	29/12/2009	Middle-aged
	Many	Female	14/08/2008	Middle-aged
	Triskelle	Female	21/04/2015	Juvenile
	Kargi	Male	19/05/2005	Middle-aged
	Litchi	Male	20/04/2015	Juvenile
	Pouët	Male	14/03/2015	Juvenile
	II.	Kamel	Male	07/09/2010
Roby		Male	18/11/2010	Middle-aged
III.	Bandit	Male	15/06/1991	Old adult
	Coët	Male	31/08/2011	Middle-aged
	Tips	Male	10/07/2011	Middle-aged
IV.	Pirate	Male	17/10/1992	Old adult
	Carillon	Male	02/04/2007	Middle-aged
	Elky	Male	06/11/2009	Middle-aged
	George	Male	05/06/2006	Middle-aged
V.	Marti	Male	16/10/1998	Old adult
	Isba	Male	20/04/2004	Middle-aged
	Lenni	Male	07/10/2006	Middle-aged

Data collection

Focal observations

Observations of captive mangabeys took place from the end of January to the end of June 2018. We applied the individual focal sampling method (Altmann 1974), recording focal videos of about 15 minutes per session (mean session duration \pm S.E. = 15.67 \pm 0.10 min) using a JVC Full HD GZ-RX615 camcorder. Each individual was observed during 8 sessions, for a total of more than 2 hours (125.33 \pm 0.75 min) per individual and 52.22 hours of observations overall. These sessions were scheduled randomly, and then balanced so that all individuals were observed at all times of day (from 9 am to 6 pm) and at all feeding periods (before or during the first feeding / between two feedings / after or during the second feeding). We then transferred videos to a computer for further analyses. Software BORIS v.6.0.6 (Friard and Gamba 2016) was used to code each event of manual gesture and each social interaction involving the focal individual. Because subjects were free to move, the focal individual was sometimes out of sight for few seconds on the camera field, hence data were analyzed taking into account the exact observation durations when the focal subject was visible.

Brachio-manual gestures

We recorded every instances of unimanual gestures produced by the focal individuals, in intraspecific dyadic context. A brachio-manual gesture was defined as any movement of one arm or hand that was: (i) nonlocomotor and “mechanically ineffective”, though not excluding gestures that implied contact with a substrate or the recipient (e.g. Pollick and De Waal 2007; Pollick et al. 2008; Gupta and Sinha 2019); (ii) physically directed to a receiver, as shown by the signaler’s head or body orientation and/or physical contact between the signaler and the receiver (e.g. Aychet et al. in press; Call and Tomasello 2007; Hopkins and Leavens 1998; Liebal et al. 2004; Pollick and De Waal 2007; Prieur et al. 2017; Schel et al. under review; Tomasello et al. 1985), and/or preceded by “audience checking” within the 5 seconds before the gesture (e.g. Aychet et al. in press; Hobaiter and Byrne 2011); (iii) adapted to the receiver attention, i.e. produced in front of a visually attentive recipient (the signaler being more or less 45° in front of the receiver’s face), except for tactile and audible gestures (e.g. Aychet et al. in press; Pika et al. 2003; Liebal et al. 2004; Pollick and De Waal 2007; Genty et al. 2009; Schel et al. under review); and (iv) followed by a voluntary response of the receiver within 5 sec (e.g. Aychet et al. in press; Liebal et al. 2004, 2006; Schel et al. under review; Roberts et al. 2014).

Emotional valence of context

The social contexts of gesture production were determined based on the signaler and receiver’s behavior within the 5 seconds before and after the signal (Aychet et al. in press). Six different contexts

were distinguished, and then categorized according to their assumed emotional valence (**Table 2**). Aggression and submission contexts were assumed to be “negative”, in contrast to affiliation, grooming, social play and socio-sexual contexts that were qualified as “positive or neutral”. We note that the latter contexts may involve ambiguous behaviors, falling within “positive” contexts while possibly eliciting negative emotions in interactants.

Table 2. Social contexts of gestures (adapted from Aychet et al. in press)

Valence	Context	Associated behaviors
Positive or neutral	Affiliation	Physical proximity between subjects (at less than one arm length), calm approach of recipient or gentle physical contact.
	Grooming	Grooming, tactile examination
	Social play	Play-fight, rough or gentle (involving manual fighting, biting, gentle or rough touching and grabbing), or locomotor-rotational play (play with few physical contacts, but involving pursuits, jumps, somersaults)
Negative	Socio-sexual	Touching, smelling, licking genital part or mounting
	Aggression	Physical aggression of the recipient by the signaler (biting, beating, rough manipulation), flight or avoidance of the signaler by the recipient, or intergroup conflict in which the signaler and recipient were in different social groups
	Submission	Flight or avoidance of recipient by signaler

Social laterality

For each gesture instance, we also recorded the relative positions of the signaler and the receiver in each other’s visual field (Prieur 2015; Prieur et al. 2016a, 2017a, b, c). The receiver position was coded as “front” if it was positioned more or less 60° in front of either signaler’s face (Baraud et al. 2009), and “right” or “left” depending on whether it was in the signaler’s right or left visual field. The position of the signaler was similarly coded from the receiver’s point of view.

Gesture characteristics and signaler posture

For each gesture occurrence, we noted the hand used (left or right), the type of gesture produced (Aychet et al. under review; Schel et al. under review) and the sensory modality on which it could be perceived. Gestures were classified as “visual” if they were silent and distant brachio-manual movements, “audible” if they provoked a sound and “tactile” if they involved a physical contact with the receiver (Aychet et al. under review; Fröhlich et al. 2016; Liebal et al. 2004b; Pika et al. 2003; Pika 2008; Schel et al. under review). According to the “postural” theory on gestural laterality origins (MacNeilage et al. 1987; MacNeilage 2007), signaler posture may constraint the availability of hands to gesture and so be a determining factor shaping gestural laterality. To test for this effect in red-capped mangabeys, we categorized the signaler posture when gesturing, depending on whether one hand was

“engaged” in posture as a support (subject walking or standing quadrupedally, standing bipedally with hand on substrate, climbing or hanging on cage) or hands were “free” (subject sitting, laying, jumping or standing bipedally without other support).

Signaler and receiver relationship

In order to assess the effect of social factors on the hand used to gesture, we characterized the relationship between the signaler and the receiver in terms of dominance and kinship. Dominance was deduced from avoidance behaviors (Easley and Coelho 1991), i.e. turning away from another individual, avoiding an individual by changing direction, avoiding contact by moving a body part away from the proximity of another individual, fleeing an individual by walking or running in opposed direction (Baraud 2007). All avoidance behaviors involving focal subjects were analyzed, and when at least 3 occurrences were observed for a dyad, we computed the percentage of avoidance of subject A from subject B over the total number of these behaviors between A and B (Zumpe and Michael 1986). Subject A was considered subordinate to subject B if this percentage was above 50%. Moreover, kinship was known for all individuals in the colony, and the signaler and the receiver were considered as “kin” if they were first-degree relatives (parents or siblings). Finally, we noted whether the signaler and the receiver were of same age or not (based on age categories: juveniles, middle aged and old adults) and of same sex or not.

Statistical analyses

We used R v.3.6.2 (R Core Team 2018) for all statistical analyses. All tests were two-tailed and alpha-level was set at 0.05.

We first tested the presence of an overall gestural laterality in our captive red-capped mangabeys. To assess gestural laterality at the individual level, and for each individual that produced at least 6 manual gestures, we performed binomial tests to compare the proportion of right and left hand gestures to a theoretical proportion of 0.5. For each of these subjects, a handedness index (HI) was also computed using the following formula: $HI = (R-L) / (R+L)$, where R corresponds to the number of gestures produced with the right hand and L with the left hand. This index, between -1 and 1, is commonly used to assess laterality (e.g. Hamilton and Vermeire 1988), as its sign reveals the potential bias direction: toward the right if it is positive, and the left if it is negative. We tested whether HI differed from null values using a Wilcoxon signed-rank test. The strength of individuals’ hand preference was estimated by the absolute value of HI (ABSHI). Gestural laterality was assessed at the population level based on the proportion of lateralized individuals in the population and the average ABSHI value. Moreover, we compared the number of gestures that mangabeys produced with the right or left hand using a Wilcoxon signed rank test.

Secondly, we tested which factors affected hand use in red-capped mangabey gestural communication, among contextual factors (valence of social context, signaler and receiver positions in each other’s visual field), gesture production characteristics (gesture sensory modality, signaler posture) and socio-demographic factors (dominance and kinship between the signaler and receiver, signaler age category and sex). To do so, we used a Generalized Linear Mixed Model (GLMM) of the binomial family to analyze the hand used to produce gestures (right or left) depending on the above-cited variables. The identity of the signaler was included as a random effect, and the model quality was verified by checking for the absence of data overdispersion.

Results

Manual gestures

We recorded 275 occurrences of unimanual gestures produced in intraspecific dyadic contexts by captive red-capped mangabeys. Twenty of the 25 captive mangabeys produced manual gestures, and 10 different gestures were observed (**Table 3**), of which 7 have been previously described as intentional gestures (Schel et al. under review).

Table 3. Manual gestures observed in captive red-capped mangabeys (adapted from Aychet et al., under review). *Nb*: number of instances; *N*: number of different signalers; *: previously described as intentional gesture, Schel et al. under review.

Gesture	Description	Sensory modality	Nb	N
Embrace*	Signaler puts one arm around the receiver’s body.	Tactile	13	7
Grab body part*	Signaler closes one hand on a receiver’s body part.	Tactile	144	17
Grabbing movement*	Signaler throws one arm in the receiver’s direction, with hand closing at the end of the movement.	Visual	9	4
Pull body part	Signaler hold and pulls a receiver’s body part.	Tactile	6	3
Push	Signaler push the receiver away.	Tactile	1	1
Slap object*	Signaler slaps cage element or ground with an open hand.	Audible	16	6
Slap receiver*	Signaler hits a receiver’s body part with an open hand.	Tactile	14	6
Slap self	Signaler hits itself with an open hand, in a unique or repeated movement.	Visual	2	1
Touch*	Signaler gently puts one open hand on receiver’s body.	Tactile	1	1
Throw arm*	Signaler throws one arm in the receiver’s direction.	Visual	69	18

Gestural laterality at the individual and population level

None of the red-capped mangabeys were significantly lateralized for their manual gestures (Binomial test, **Table 4**). Thus, there was no laterality bias at the population-level. The HI did not overall differ from null values (Wilcoxon signed rank test: $N = 11$, $V = 30$, $P = 0.823$), and the mean ABSHI value was low (ABSHI \pm S.E. = 0.24 ± 0.04), as mangabeys produced as much manual gestures with the right than with the left hand (Wilcoxon signed rank test: $N = 20$, $V = 98$, $P = 0.320$).

Table 4. Hand use in red-capped mangabey gestures. *Nb*: number of unimodal gestures; *Prop.R*: proportion of gestures produced with the right hand; *HI*: handedness index; *P*: binomial test p-values

Signaler	Sex	Age category	Nb	Prop.R.	HI	P
Bell	Female	Old adult	7	0.71	0.43	0.453
Chipie	Female	Old adult	2	-	-	-
Gofrette	Female	Old adult	7	0.71	0.43	0.453
Joly	Female	Old adult	5	1.00	-	-
Zunie	Female	Old adult	13	0.69	0.38	0.267
Chipse	Female	Middle-aged	4	0.25	-	-
Julie	Female	Middle-aged	11	0.45	-0.09	1
Maillette	Female	Middle-aged	1	-	-	-
Many	Female	Middle-aged	12	0.33	-0.33	0.388
Triskelle	Female	Juvenile	8	0.63	0.25	0.727
Pirate	Male	Old adult	4	0.50	-	-
Coët	Male	Middle-aged	17	0.59	0.18	0.629
Isba	Male	Middle-aged	5	0.60	-	-
Kamel	Male	Middle-aged	2	-	-	-
Kargi	Male	Middle-aged	21	0.57	0.14	0.664
Lenni	Male	Middle-aged	4	1.00	-	-
Roby	Male	Middle-aged	19	0.63	0.26	0.359
Tips	Male	Middle-aged	2	-	-	-
Litchi	Male	Juvenile	61	0.44	-0.11	0.443
Pouet	Male	Juvenile	70	0.47	-0.06	0.720

Factors affecting hand use in gestural communication

Although mangabeys were not lateralized in their overall production of manual gestures, contextual factors affected the hand they used to communicate (GLMM Binomial, detailed comparison results in **Table 5**). Particularly, we found a significant effect of the emotional valence of context in which the gestures were produced (GLMM Binomial, Type II Wald Chi-square test: $X^2_1 = 6.383$, $P = 0.011$) with more right-hand gestures in “negative” contexts than in others (**Figure 1**). Moreover, the relative receiver and signaler’s positions had a significant effect on the hand used to gesture (receiver position: $X^2_2 = 29.233$, $P < 0.001$; signaler position: $X^2_2 = 7.068$, $P = 0.029$). Signalers adapted the side used to communicate to the position of the receivers, using more the right hand when the receivers was

in their right visual field and conversely (**Figure 2a**). Moreover, they used less the right hand when they gestured in the right visual field of receivers than when they were in front of them (**Figure 2b**). Interestingly, we found no effect of the sensory modality of gestures on hand use ($X^2_2 = 3.148$, $P = 0.207$), nor of the signaler posture ($X^2_1 = 1.373$, $P = 0.241$) or socio-demographic factors (Dominance: $X^2_2 = 0.500$, $P = 0.779$; Kinship: $X^2_1 = 0.005$, $P = 0.941$; Age difference: $X^2_1 = 1.670$, $P = 0.196$; Sex difference: $X^2_1 = 0.065$, $P = 0.799$; Signaler's age: $X^2_2 = 0.718$, $P = 0.698$; Signaler's sex: $X^2_1 = 0.246$, $P = 0.620$).

Table 5. Fixed effects of the GLMM Binomial. The first factor cited for each comparison corresponds to the reference factor. Positive values of the estimate indicate that the reference factor drives higher proportion of right-hand gestures, and conversely.

Fixed effects	Comparison	Estimate	Standard error	z	P
Context valence	Negative VS Positive/neutral	1.111	0.440	2.526	0.012
Receiver position	Signaler's right VS left	2.945	0.549	5.363	< 0.001
	Signaler's right VS front	1.576	0.435	3.626	< 0.001
	Signaler's left VS front	-1.369	0.467	-2.931	0.003
Signaler position	Receiver's right VS left	-0.846	0.472	-1.792	0.073
	Receiver's right VS front	-1.117	0.423	-2.643	0.008
	Receiver's left VS front	-0.272	0.407	-0.667	0.505
Sensory modality	Audible VS Tactile	0.150	0.690	0.217	0.828
	Audible VS Visual	-0.523	0.693	-0.754	0.451
	Tactile VS Visual	-0.673	0.383	-1.754	0.079
Posture	“Engaged” hand VS “free”	-0.332	0.440	-1.172	0.241
Dominance of signaler	Dominant VS subordinate	0.112	0.328	0.342	0.732
	Dominant VS unclear	-0.303	0.582	-0.521	0.603
	Subordinate VS unclear	-0.415	0.596	-0.696	0.486
Kinship	Non-kin VS kin	0.029	0.395	0.073	0.941
Age difference	Different VS same	-0.681	0.527	-1.292	0.196
Sex difference	Different VS same	0.111	0.434	0.255	0.798
Signaler age category	Juvenile VS middle-aged	-0.153	0.366	-0.418	0.676
	Juvenile VS old adult	-0.580	0.685	-0.846	0.397
	Middle-aged VS old adult	-0.427	0.613	-0.696	0.486
Signaler sex	Female VS male	0.236	0.476	0.496	0.620

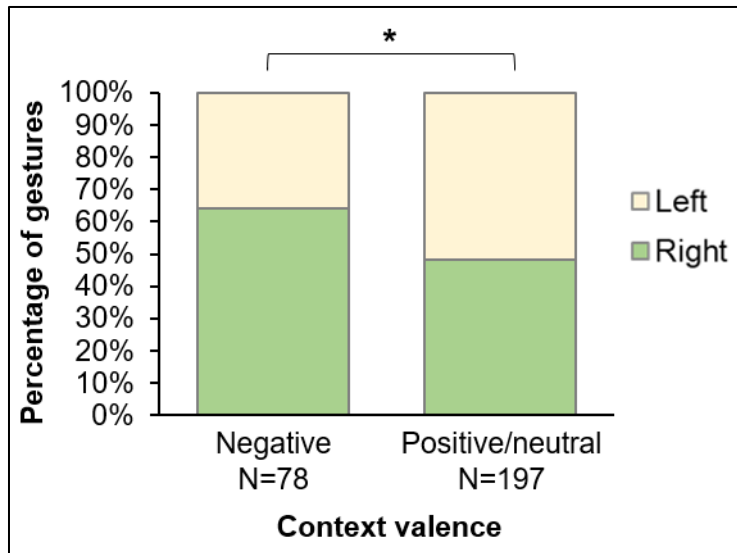


Figure 1. Percentage of gestures produced with the left or right hand depending on the emotional valence of context. “Negative” valence corresponds to aggression and submission contexts, and “positive/neutral” corresponds to affiliation, grooming, play and sexual contexts. GLMM Binomial: *: $P < 0.05$

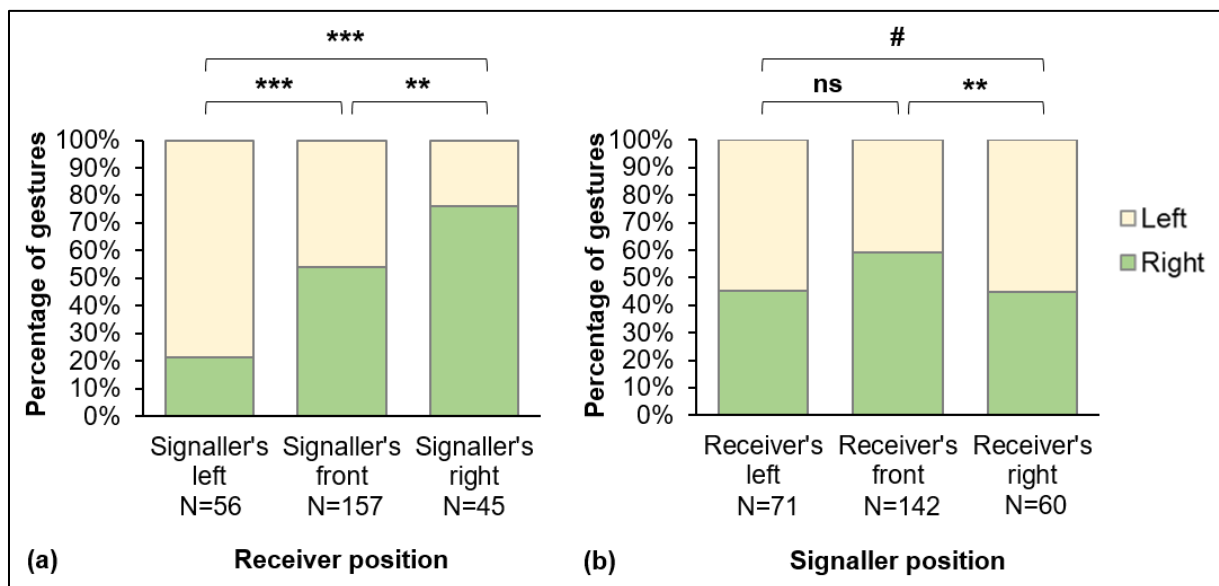


Figure 2. Percentage of gestures produced with the left or right hand depending on (a) receiver position in the signaller’s visual field; (b) signaller position in the receiver’s visual field. GLMM Binomial: *ns*: non-significant difference; #: $0.05 < P < 0.1$; **: $P < 0.01$; ***: $P < 0.001$.

Discussion

We present here a preliminary assessment of captive red-capped mangabey intraspecific gestural laterality. None of the individuals we observed were significantly lateralized for their communicative gestures, and thus no population-level bias was observed. Nevertheless, we found a significant effect of interactional context factors on the hand used by red-capped mangabeys to

communicate, corroborating previous findings from ape studies. On the contrary, factors related to gesture production and socio-demographic characteristics of the signaler and the receiver did not affect mangabey gestural laterality.

Looking at the production of brachio-manual gesture as a whole, we found no significant gestural lateralization at the individual nor population level in captive red-capped mangabeys. Given that population-level right handedness for communicative gesture was found in several catarrhine monkey species (Meguerditchian and Vaclair 2006, 2009; Meguerditchian et al. 2011; Meunier et al. 2013a, b), we hypothesize that the absence of gestural lateralization found here results from our sample size, which is the main limit on research on behavioral laterality (Chapelain 2010). On one hand, the small number of data points per subjects could hide existing individual biases (Hopkins et al. 2012). On the other hand, the number of subjects may be not sufficient to reveal a population-level bias (Hopkins and Cantalupo 2005; Hopkins 2006). A previous study evidenced right-handed mangabeys for human-directed pointing gestures, yet this was found only for the individuals with high referential communication abilities, suggesting substantial inter-individual variability for this trait (Maille et al. 2013). Present results should be completed by measures on an increased sample, to confirm or contradict this hypothesis. Moreover, it should permit to analyze independently the different types of gestures produced by mangabeys, as gesture type could affect the direction and strength of laterality (Hopkins and Leavens 1998; Hopkins and Wesley 2002; Hobaiter and Byrne 2013; Prieur et al. 2016a, 2017b, c).

We found that contextual factors affected the hand used by red-capped mangabeys to communicate with their conspecifics. As found in chimpanzees and gorillas (Prieur et al. 2016a, 2017a, c), mangabeys used more their right hand to gesture in contexts associated with negative emotional states (i.e. aggression and submission contexts). These findings seem to contradict theories on brain asymmetries for emotion processing (reviewed by Demaree et al. 2005). The “right hemisphere theory” proposes that the right hemisphere controls perception and expressions of emotions (Borod et al. 1983), and the “valence theory” or “approach/ withdrawal theory” suggests that the right and left hemispheres control negative and positive emotions respectively (Silberman and Weingartner 1986; Ehrlichman 1987), thus both would predict a left-hand preference for negative contexts. Prieur and colleagues hypothesized that the observed right-hand bias of apes in negative contexts originates from the same mechanisms that underlie left prefrontal brain region activation in humans during negative events, such as aggressions (Rohlf and Ramírez 2006). Taking the perspective that aggression contexts involve not only negative emotions (e.g. anger), but also motivation for “approaching” behaviors (Rohlf and Ramírez 2006), this seems actually in accordance with the “approach/withdrawal” theory on brain asymmetries, which could explain results on chimpanzees, gorillas and red-capped mangabey gestures. Aside from the effect of emotional context, we found that gestural laterality was significantly affected by the relative positions of the signaler and the receiver. Red-capped mangabeys preferentially used their ipsilateral hand to gesture toward conspecifics, probably to direct more efficiently their signal. This

is in accordance with observation of captive chimpanzees and gorillas (Prieur et al. 2016a, 2017b, c), who preferentially performed visual and tactile gestures with their right hand when their recipient was in their right visual field. These results highlight the importance of taking into account receiver position when studying intraspecific gestural laterality of primates, or to control this parameter in experimental conditions, given its substantial effect on hand use.

Factors related to the gesture production in itself did not affect gestural laterality, since we found no effect of the sensory modality involved (visual only, acoustic or tactile) nor of the signaler posture while signaling. Experimental studies brought to light an effect of red-capped mangabeys' postures for manual tasks, and this was particularly true for complex tasks (Blois-Heulin et al. 2006). We can hypothesize that this postural effect is not found for communicative gestures because they are less demanding in terms of movement precision, compared for instance to bimanual manipulation tasks ("task complexity hypothesis": Fagot and Vauclair 1991). Interestingly, socio-demographic characteristics of the signaler and the receiver had no effect on gestural laterality. The signaler's sex did not affect the hand used to gesture, as found in apes and olive baboons (Hopkins et al. 2005; Meguerditchian and Vauclair 2006, 2009; Meguerditchian et al. 2011; Prieur et al. 2016b). Although right-hand preference has been found to increase with age in apes and olive baboons (Hopkins and Leavens 1998; Meguerditchian and Vauclair 2006; Hobaiter and Byrne 2013; Prieur et al. 2016a, 2017a, c), we did not find this effect in red-capped mangabeys. This is not surprising regarding the absence of lateralized individuals in our population, but these aspects should be further investigated with an increased sample size. Finally, the absence of dominance or kinship effect on mangabey gestural laterality was in accordance with the results obtained from ape studies (Hopkins et al. 2005; Prieur et al. 2017c). One study showed an effect of social hierarchy on gestural laterality of primates, describing more right-handedness in subordinate captive chimpanzees than in other individuals (Prieur et al. 2016a). This was hypothesized to result from the higher level of psychological stress in these individuals, in line with the effect of negative context on right-handedness.

Conclusion

This first investigation of captive red-capped mangabey gestural laterality did not highlight any bias at individual or population level, possibly because of the sample size. However, our results corroborate previous findings from ape gesture studies, particularly regarding the effect of interactional context on hand use, which suggests that social factors shape manual preference in non-human primate gestural communication. These promising results should be completed with further observational studies of mangabey gestures, and by similar investigations in other monkey genera, with the view to understand the evolutionary roots of modern human language and handedness.

Conflict of interests: The authors declare that they have no conflict of interest.

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Chapitre V

Communication multimodale et multicomposante





Article 4

Using sequential and network analyses to describe multimodal and multicomponent communication in captive red-capped mangabeys

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SYNTHESE DE L'ARTICLE 4

Contexte

L'étude de la communication des primates non-humains s'est jusqu'alors principalement portée sur un système communicatif à la fois (gestuel, facial, ou vocal), bien qu'une approche « multimodale » semble plus pertinente, notamment dans la perspective d'étudier les racines évolutives du langage humain. La compréhension des fonctions ultimes de la communication multimodale (impliquant différentes modalités sensorielles) et multicomposante (impliquant différents types de signaux) nécessite une description plus systématique des combinaisons de signaux et de leurs contextes de production dans la communication spontanée des primates.

Méthode

A partir d'observations en focal de 25 mangabeys à collier en captivité, nous avons cherché à décrire les combinaisons de signaux produites par cette espèce, en nous intéressant en particulier à leur communication multimodale et multicomposante. Nous avons alors décrit les vocalisations, gestes et expressions faciales produits par les mangabeys dans différentes modalités (audible, visuelle, tactile), complétant la description du répertoire communicatif de cette espèce. Nous avons utilisé une analyse originale, adaptant des méthodes d'analyses de séquences et de réseaux d'association pour décrire et quantifier la production de combinaisons de signaux. Nous avons ensuite testé l'effet du contexte social et des caractéristiques sociodémographiques des sujets sur cette communication.

Résultats

Nous avons montré que les mangabeys à collier combinent fréquemment différents types et modalités de signaux de manière flexible, et ce en fonction du contexte social, de l'âge et du sexe du signaleur et du receveur, ainsi que de leur relation de dominance et leur apparentement. En particulier, les contextes de jeu social et d'agression élicitent une communication plus complexe, avec davantage de combinaisons multimodales et multicomposantes. Nous avons pu représenter les combinaisons de signaux les plus fréquentes grâce à un diagramme de réseau, et avons montré que tous les types et modalités de signaux étudiés y étaient intégrés de manière égale.

Conclusion

Complétant les descriptions « unimodales » de la communication intraspécifique des mangabeys à collier, nos résultats soulignent l'importance de l'approche « multimodale » pour comprendre la complexité de la communication des primates. Nos résultats permettront par la suite de s'intéresser à la fonction des combinaisons de signaux. Enfin, nous suggérons que la méthodologie utilisée ici puisse servir à décrire la communication d'autres espèces, dans une perspective comparative.

Using sequential and network analyses to describe multimodal and multicomponent communication in captive red-capped mangabeys

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Highlights

- We used sequence and network analyses to describe signal combinations in mangabeys.
- Captive red-capped mangabeys flexibly combine signal types and sensory modalities.
- Their communication complexity depends on context and socio-demographic factors.
- Play and aggression contexts elicit more multimodal and multicomponent signalling.

Abstract

Although studies on primate communication have mainly focused on single communication systems (gestural, facial or vocal), there is an increasing claim for a multimodal approach to describe the communication of our closest relatives, particularly from the perspective to investigate the evolutionary roots of human language. The understanding of the ultimate functions of multimodal communication (involving different sensory modalities) and multicomponentiality (combination of different signal types) needs more systematic description of signal combinations in primate species, with details on the circumstances leading to such complex signalling. In the present study, we describe the multimodal and multicomponent use of communicative signals in a captive population of catarrhine monkeys, the red-capped mangabeys (*Cercocebus torquatus*). We applied existing analysis methods from other disciplines to define, systematically describe and quantify the production of communicative combinations. We notably used sequence analysis tools (based on dissimilarity measures) to identify the typical signal sequences produced by mangabeys, and network analysis to describe signal combinations among these sequences. The focal observation of five social groups of mangabeys allowed us to identify 479 communicative sequences, which could be grouped in ten main categories, and whose complexity, multimodality and multicomponentiality, were depending on contextual and socio-demographic factors. Overall, captive mangabeys frequently combined communication signals of all types (body, facial and vocal signals) and modalities (visual, audible and tactile), in a flexible way. Our results complete previous findings arising from “unimodal” studies, and highlight the need for a multimodal and multicomponent approach to understand the complexity of primate communication. Moreover, we propose the method we used as a way to enhance primate communication analysis, in the frame of comparative research.

Keywords

Gestures, Facial expressions, Flexibility, Monkeys, Network analysis, Sequence analysis, Signal combination, Vocalizations

Introduction

Language is an intrinsically multimodal communication system, both regarding the production and perception of signals (Levinson & Holler, 2014; Vigliocco et al., 2014). Humans (*Homo sapiens*) frequently combine gestures, body movements and facial expressions with speech (Ekman, 1979, 2004; Goldin-Meadow, 1999; Iverson & Goldin-Meadow, 1998; Levinson & Holler, 2014; Özyürek & Woll, 2019). Co-speech gestures occur even in the absence of learning (Iverson & Goldin-Meadow, 1998), and pre-verbal children communicate with combinations of sounds, gestures and facial expressions (Tronick et al., 1978). Co-speech signals are presumably a way to enhance communication (Wu & Coulson, 2007): for instance, gestures might permit to disambiguate speech (Holle & Gunter, 2007), as receivers rely on both visual and vocal modalities to interpret the message conveyed (Cassell et al., 1999; Goldin-Meadow et al., 1992; Thompson & Massaro, 1986). Thus, there is an increasing claim that research on language evolutionary origins, which is commonly based on comparisons between human and non-human animal communication systems (e.g. Arbib et al., 2008; Liebal et al., 2014a; Pika, 2008; Pollick & De Waal, 2007; Prieur et al., 2018, 2019; Scott-Phillips, 2015; Sievers & Gruber, 2020; Vauclair, 2013; Zuberbühler, 2005), should account for this multimodal characteristic of language, especially by adopting a multimodal approach to study the communication of our closest relatives, non-human primates (Fröhlich et al., 2019; Fröhlich & van Schaik, 2018; Liebal et al., 2014a; Waller et al., 2013). As a matter of fact, non-human primate communication can also be multimodal (e.g. in chimpanzees, *Pan troglodytes*: Hobaiter et al., 2017; Pollick & De Waal, 2007; Taglialatela et al., 2015; Wilke et al., 2017; bonobos, *Pan paniscus*: Genty, 2019; Genty et al., 2014; Pollick & De Waal, 2007; howler monkey, *Alouatta palliata*: Jones & van Cantfort, 2007; crested macaques, *Macaca nigra*: Micheletta et al., 2013), but communication modalities are generally investigated separately, gestural communication being mainly studied in great apes, and vocal and facial communication in other species (Slocombe et al., 2011). This “unimodal” approach is sometimes inherent to the research question, given that different types of signalling (for instance gestures and facial expressions), may have different underlying cognitive processes (Waller et al., 2013), or it can be constrained by methodological limitations (Liebal et al., 2014a). However, it is more and more acknowledged that focusing on a unique modality of signal production prevents researchers from apprehending the whole complexity of primate communication (Liebal et al., 2014a; Waller et al., 2013).

In the animal communication literature, “multimodal communication” sometimes refers to the use of signals simultaneously perceived through more than one sensory modality (for instance, auditory and visual: Partan & Marler, 1999; Partan & Marler, 2005), but can also be defined as the combined use of signals from different production channels (for instance, gestures combined with facial expressions or vocalisations: e.g. Genty et al., 2014; Liebal et al., 2014a; Pollick & De Waal, 2007; Taglialatela et al., 2015). Following Higham & Hebets (2013), we differentiate here “multicomponent communication” from “multimodal communication”. “Multicomponent communication” refers to

communication that implies combinations of different production types of signals (notably gestures or body postures, facial expressions, vocalisations) delivered on one or more sensory channels, while “multimodal communication” refers to signal combinations perceived on more than one sensory channel (notably visual, acoustic or tactile). We note that some signals can be perceived on different sensory channels in their inherent form, in a way that one modality is inevitably associated to the other (“fixed” multimodality, Partan & Marler, 2005). For instance, some vocal signals, even though they are perceived on the acoustic modality, are necessarily associated to specific facial movements that are perceived on the visual channel (Ghazanfar et al., 2005; Ghazanfar & Logothetis, 2003; Izumi & Kojima, 2004). In contrast, we will focus here on “free” multimodality (Fröhlich & van Schaik, 2018; Higham & Hebets, 2013; Partan & Marler, 2005), which implies signal modalities that are not obligatory associated, and whose combinations may be then meaningful of a flexible use of communication signals, depending on social and environmental factors (Fröhlich & van Schaik, 2018). The “free” combination of signal types and modalities have been mainly investigated in animals other than primates (e.g. in the courtship displays of jumping spiders, *Habonattus dossenus*, and wolf spiders, *Schizocosa* genus: Elias et al., 2005; Uetz & Roberts, 2002; in birds such as brown-headed cowbirds, *Molothrus ater*, and Barbary dove, *Streptopelia risoria*: Cooper & Goller, 2004; Hutchison et al., 1997; in the alarm behaviour of Eastern gray squirrels, *Sciurus carolinensis*: Partan et al., 2010), yet reports of multimodal and multicomponent communication in primates are still rare and concern few species (i.e., captive and wild chimpanzees: Hobaiter et al., 2017; Leavens et al., 2004, 2010; Pollick & De Waal, 2007; Tagliabata et al., 2015; Wilke et al., 2017; bonobos: Genty, 2019; Genty et al., 2014, 2015; Pollick & De Waal, 2007; orangutans: Knox et al., 2019; siamangs, *Symphalangus syndactylus*: Liebal et al., 2004; crested and Rhesus macaques, *M. nigra* and *mulatta*: Micheletta et al., 2013; Partan, 2002; howler monkeys: Briseño-Jaramillo et al., 2015; Jones & van Cantfort, 2007).

Different hypotheses have been formulated on the ultimate functions of combining signals of different types and modalities, based on selection pressures which could act at the content-level or efficacy-level of signal production (Guilford & Dawkins, 1991; Hebets & Papaj, 2005; Partan & Marler, 2005; reviewed in Fröhlich & van Schaik, 2018). Regarding the content-level, different combined signals could notably convey the same information, and be associated to increase the accuracy of receiver response (“redundant signal hypothesis”, Moller & Pomiankowski, 1993; Partan & Marler, 1999). In primate species, numerous evidence of communication persistence or elaboration in case of first-attempt failure are in accordance with this hypothesis (e.g. in apes: Byrne et al., 2017; Cartmill & Byrne, 2007; Genty & Byrne, 2010; Leavens et al., 2005; Liebal et al., 2004; Tomasello & Call, 2018). In contrast, combined signals could convey different information that complement each-others (“multiple messages hypothesis” or “complementarity hypothesis”, Fröhlich & van Schaik, 2018; Johnstone, 1996; Moller & Pomiankowski, 1993; Partan & Marler, 1999). This is the case in human multimodal communication, in which meaning can arise from the integration of signals produced on

different channels (Vigliocco et al., 2014). Moreover, hypotheses have been formulated regarding the efficacy of multimodal communication. The “efficacy-backup hypothesis” states that producing multimodal signals instead of unimodal single signals permits to increase the probability of being perceived (and so to receive a response) under the presence of environmental constraints, such as lack of visibility or ambient noise (Fröhlich & van Schaik, 2018; Hebets & Papaj, 2005). This has been suggested in non-primate species, for instance in wolf spiders (*Schizocosa retrorsa*), whose multimodal visual and vibratory courtship signalling permits a detection both in light and dark environments (Hebets & Uetz, 1999; Hebets et al., 1996). Finally, the “increased detection and discrimination hypothesis” (Fröhlich & van Schaik, 2018; Hebets & Papaj, 2005) proposes that one signal increases either the probability of a second signal to be perceived or to be accurately understood (“refinement”, Fröhlich & van Schaik, 2018). Several primate studies support the latter assumption, either showing that multimodal and multicomponent signalling is more likely to receive a response than single signals (e.g. multicomponent lipsmacks in crested and rhesus macaques: Micheletta et al., 2013; Partan, 2002; facial and gestural signal combinations in siamangs: Liebal et al., 2004; vocal-gesture combinations in chimpanzees and bonobos: Genty et al., 2014; Pollick & De Waal, 2007; Wilke et al., 2017), or suggesting that some signals are used to disambiguate another signal meaning (e.g. vocal-gesture combinations in wild chimpanzees: Wilke et al., 2017; and bonobos: Genty et al., 2014).

To our knowledge, the description of multimodal and multicomponent communication in primates is generally centred on one specific type of combination (e.g. vocal-gestural combinations: Genty, 2019; Pollick & De Waal, 2007) or on different uses of one specific signal (e.g. lipsmacks in crested macaques: Micheletta et al., 2013; “pout-moan” and “contest hoot” calls in bonobos: Genty, 2019; Genty et al., 2014), but rarely addresses the entire repertoire of signal combinations (but see the description of multimodal signals in chimpanzees by Wilke et al., 2017). However, to test for all the above-cited hypotheses and understand the evolution constraints that shaped primate multimodal and multicomponent communication (including human language), more systematic descriptions of signal type and modality combinations are needed (Fröhlich & van Schaik, 2018; Liebal et al., 2014a; Waller et al., 2013), with reports on the circumstances leading to such complex communication (social contexts, physical environment, developmental stage, etc.). Moreover, in order to draw distinctions between the effect of sociality and environment on the production of multimodal and multicomponent communication, this has to be investigated in a sufficient diversity of species, both in captive and wild environments (Fröhlich & van Schaik, 2018). In order to permit comparisons between species and environmental conditions, primate multimodal communication studies have to be based on similar methodologies, notably regarding their working definitions of multimodality and multicomponentality. The differential use of the word “multimodal” explained above could be easily identified and is not a major obstacle while comparing study results. However, one constraining methodological inconsistency is the temporal definition used to identify signal combinations. Some studies consider combinations

only if the signals produced by a same individual overlap (e.g. Wilke et al., 2017), while some others will consider both overlapping and sequences of signals, i.e. signals separated by a pause up to an arbitrary value (e.g. 1 sec: Genty, 2019; Genty et al., 2015; Hobaiter et al., 2017; Knox et al., 2019; 2 sec: Tagliatalata et al., 2015; and in gestural studies 1 sec: Genty & Byrne, 2010; Hobaiter & Byrne, 2011; 5 sec: Liebal et al., 2004, 2006; Tempelmann & Liebal, 2012), or signals which initiations are separated by an arbitrary latency (e.g. 10 sec: Pollick & De Waal, 2007). This may lead to identify more or less instances of multimodal or multicomponent signal use, which prevent reliable comparisons on their frequencies in different species and under different conditions. Despite this consistency issue, one methodological problem that can arise when describing multimodal and/or multicomponent communication in a population is whether we should account for slight variations in sequential signal production. The less frequent signal combinations could either be random variations of more frequent ones, or could be biologically relevant by themselves, hence it is important to analyse them in their integrity without transformation (Baraud et al., 2016). One approach to acknowledge this variability in signal combinations' production, without missing their similarities, can be to focus on one unique signal and report all possible use, with all possible combinations and their contexts (for instance, see the description of "pout-call" use in young bonobos: Genty, 2019). However, this approach needs a preliminary selection of one signal of interest, and is likely to be time-consuming if applied to the entire communication repertoire of a species. Thus, another method is to use sequence analysis tools to describe the structure of such signal use (Baraud et al., 2016), taking into account signals of all types and modalities, and all slight variations observed in the population.

In the present study, we used a new approach to define and systematically describe the multimodal and multicomponent use of communicative signals in a captive population of catarrhine monkeys, the red-capped mangabeys (*Cercocebus torquatus*). Red-capped mangabeys are semi-terrestrial monkeys (Mitani et al., 2012) originating from West African rainforest coastal regions (Cooke, 2012; Gautier-Hion et al., 1999; Jones & Sabater-Pi, 1968; Orimaye, 2017), and naturally living in large multi-male, multi-female groups from 10 to 25 individuals (Gautier-Hion et al., 1999; Jones & Sabater-Pi, 1968). In captivity, they are organised in steep linear hierarchy (Ruth Dolado & Beltran, 2011) and exhibit aggression and affiliation patterns both observed in despotic and more relaxed macaque societies (Dolado & Beltran, 2012; e.g. unidirectionality of aggressions, high rate of aggressions, low aggression intensity, reciprocal grooming behaviour. Thierry, 2007; Thierry et al., 2000). Communicative signals of captive red-capped mangabeys have been previously described, bringing to light a rich set of innate gestures and body signals (produced either on the visual, audible or tactile channel, Schel et al., under review), as well as facial (Aychet et al. 2020) and vocal signals (Bouchet et al., 2010). Moreover, a first description of their multimodal interactions, centred on their use of vocal signals, suggest flexible multimodal and multicomponent signalling in this species (Baraud et al., 2016).

Our objective here was threefold. First, we attempted to complete the communicative repertoire of captive red-capped mangabeys, by describing the typical sequences of signals they spontaneously produce in their intraspecific dyadic interactions. Second, our aim was to quantify multimodality and multicomponentiality in mangabeys' communicative sequences, and assess the effect of social context and socio-demographic factors on the production of complex signalling. In order to address the above-cited methodological issues, we applied methods that we propose as a way to enhance future comparisons between descriptions of primate species multimodal and multicomponent communication. We notably propose to base the temporal definition of signal sequence on a less-arbitrary criterion, but also adapted to the study species. Based on the method used in vocal exchange studies (Alban Lemasson et al., 2010, 2018; Levréro et al., 2019), we established the sequence definition time-window on the distribution of latencies between two signals that was actually observed in the studied population. Additionally, we used a sequence analysis methodology (Gabadinho et al., 2011) to describe red-capped mangabey sequences of signals, and network analysis (Whitehead, 2008) to describe signal combinations among these communicative sequences, and particularly investigate how signal types (body, facial, vocal signals) and modalities (visual, audible, tactile) were integrated in complex communication events.

Methods

Ethical note

This purely observational study was conducted without modifying the living conditions of the captive mangabeys housed at the Station Biologique de Paimpont (University Rennes 1, France), where animal facilities and animal care procedures are regularly monitored by the responsible local authorities (Housing agreement for research D35-211-18, delivered by the “Direction Départementale de la Cohésion Sociale et de la Protection des Populations” (DDCSPP)).

Subjects

We studied twenty-five captive red-capped mangabeys (*Cercocebus torquatus*), housed at the Station Biologique de Paimpont (University Rennes 1, France) and living in social groups composed of two to 13 individuals (**Table 1**), whose compositions have been stable for at least 8 months. Individuals were considered as juveniles when they were less than 4 years old for females and less than 7 years old for males, based on demographic data on a closely related species, grey-cheeked mangabeys (*Lophocebus albigena*) (Chalmers, 1968; Deputte, 1992; Gautier-Hion & Gautier, 1976). Old adults were differentiated from middle-aged adults if they were more than 15 years old, corresponding to the median lifespan of mangabeys in captivity (based on 45 years data from our breeding facility on grey-cheeked and red-capped mangabeys).

Mangabeys were housed in outdoor-indoor enclosures of different sizes (from 8 to 26.4 m² for indoor enclosures, 14.7 to 37.2 m² for outdoor enclosures, and height from 2.5 m to 4.4 m). Individuals were free to move in and out at all time, using connecting tunnels. Indoor enclosure temperature was maintained at 22°C. Each enclosure was enriched with wood and metal perches, completed with chains or hessian ribbons. The floor of the indoor enclosures was covered with straw and sawdust, while the outdoor enclosure floor was covered with cement or bark. Mangabeys were fed twice a day with fresh fruits and vegetables in the morning and with monkey chows in the afternoon. Water was available *ad libitum* in their indoor enclosures.

Table 1. Characteristics of the red-capped mangabeys

Social group	Subject	Sex	Date of birth	Age Category
I.	Triskelle	Female	21/04/2015	Juvenile
	Chipse	Female	03/01/2006	Middle-aged
	Julie	Female	08/05/2004	Middle-aged
	Maillette	Female	29/12/2009	Middle-aged
	Many	Female	14/08/2008	Middle-aged
	Bell	Female	31/03/2002	Old adult
	Chipie	Female	28/06/1992	Old adult
	Gofrette	Female	08/11/1996	Old adult
	Joly	Female	22/10/2000	Old adult
	Zunie	Female	03/07/1987	Old adult
	Litchi	Male	20/04/2015	Juvenile
	Pouët	Male	14/03/2015	Juvenile
	Kargi	Male	19/05/2005	Middle-aged
	II.	Kamel	Male	07/09/2010
Roby		Male	18/11/2010	Middle-aged
III.	Coët	Male	31/08/2011	Middle-aged
	Tips	Male	10/07/2011	Middle-aged
	Bandit	Male	15/06/1991	Old adult
IV.	Carillon	Male	02/04/2007	Middle-aged
	Elky	Male	06/11/2009	Middle-aged
	George	Male	05/06/2006	Middle-aged
	Pirate	Male	17/10/1992	Old adult
V.	Isba	Male	20/04/2004	Middle-aged
	Lenni	Male	07/10/2006	Middle-aged
	Marti	Male	16/10/1998	Old adult

Data collection

Observations

We collected 52.22 hours of observations, from the end of January to the end of June 2018. Applying the individual focal sampling method (Altmann 1974), we recorded focal videos of about 15

minutes per session (mean session duration \pm SE = 15.67 \pm 0.10 min) using a JVC Full HD GZ-RX615 camcorder. Each subject was observed during 8 sessions, for a total of more than 2 hours (125.33 \pm 0.75 min). These sessions were scheduled semi-randomly, so that all individuals were observed at all times (from 9 am to 6 pm) and all periods of day (before or during first feeding / between two feedings / after or during second feeding). We transferred the videos to a computer for further video analyses. Software BORIS v.6.0.6 (Friard and Gamba 2016) was used to play videos and to code each event of communicative act and each social interaction involving the focal individual.

Communicative signals

We recorded and identified every occurrence of body, facial or vocal signal produced by or in the direction of the focal individual. Communicative signals were considered as such, only if the signaller physically directed it toward a receiver, i.e., if at least one of the following markers of directionality was observed during signal production: signaller's head or body was oriented towards the receiver; the signal was a movement produced in the direction of the receiver; the signaller was approaching the receiver; the signaller and the receiver were in physical contact (Aychet et al., in press; Call & Tomasello, 2007; Leavens & Hopkins, 1998; Liebal et al., 2004; Tomasello et al., 1985, 1994; Schel et al., under review). We identified 48 different signals, categorized in three types (**Table 2**): “body signals”, including brachio-manual gestures, body movements and postures (Schel et al., under review); “facial signals”, including facial displays (Aychet et al., in press) and actions such as biting; and “vocal signals” (Bouchet et al., 2010). The modality on which these signals could be perceived by the receiver were classified as: “visual” if they were silent distant movements of the face or the body; “tactile” if they included physical contact between the signaller and the receiver; “audible” if they included vocal or nonvocal sound production (Fröhlich et al., 2016; Liebal, Call, et al., 2004; Pika, 2008; Pika et al., 2003; Schel et al., under review)

Table 2. Répertoire of communicative signals observed in captive red-capped mangabeys. Modality: main modality on which the signal could be perceived; **Nb:** total number of occurrences observed, with number of occurrences recorded within communicative sequences (as opposed to single occurrences) indicated within brackets; **N:** number of signallers.

Type	Subtype	Signal	Description	Modality	Nb	N	
Body signals ¹	Head movements	Mouth-to-mouth	Signaller approaches his/her nose close to the receiver's face (few centimetres or less).	Visual	108 (64)	21	
		Shake head	Signaller moves his/her head with quick repeated movements, horizontally or vertically.	Visual	12 (11)	5	
		Throw head	Signaller produces a brief head movement toward the receiver.	Visual	50 (34)	13	
	Brachio-manual movements	Embrace	Embrace	Signaller puts one or two arms around the receiver's body.	Tactile	35 (28)	9
			Open arm	Signaller opens one or two arms in the direction of the receiver, like before embracing, without contact.	Visual	4 (1)	4
		Grab object	Signaller takes an object that the receiver is already manipulating.	Visual	2 (2)	2	
		Grab body part	Grab body part	Signaller closes one or two hands or feet on a receiver's body part.	Tactile	412 (372)	21
			Grabbing movement	Signaller throws one or two arms in the receiver's direction, with hands closing at the end of the movement.	Visual	30 (28)	10
		Kick	Signaller hits the receiver with one or two feet.	Tactile	4 (2)	3	
		Pull body part	Signaller holds and pulls a receiver's body part.	Tactile	16 (16)	7	
		Push	Signaller push the receiver away, with hands or feet.	Tactile	29 (27)	10	
		Slap object	Signaller slaps cage element or ground with an open hand.	Audible	52 (37)	14	
		Slap body part	Signaller hits a receiver's body part with an open hand.	Tactile	41 (38)	11	
		Slap self	Signaller hits him/herself with an open hand, in a unique or repeated movement.	Visual	7 (7)	1	
		Touch	Signaller gently puts one or two open hands on receiver's body.	Tactile	19 (14)	6	

Body postures and movements	Throw arm	Signaller throws one or two arms in the receiver's direction.	Visual	232 (190)	22
	Throw leg	Signaller throws one leg in the receiver's direction.	Visual	3 (2)	2
	Bang object	Signaller jumps on cage wall or perches after having taken a run-up, or grabs and shakes cage wall or perches (with hands only or with hands and feet), producing tremors and noise.	Audible	47 (21)	16
	Crouch	Signaller bent his/her four limbs, belly touching the ground.	Visual	11 (8)	6
	Hang	Signaller hangs with arms or legs to the cage or perches, in front of the receiver.	Visual	6 (5)	3
	Hop	Signaller jumps repetitively, in one position or moving around.	Visual	3 (3)	3
	Jump	Signaller jumps and land in front of the receiver or on him/her.	Visual	39 (18)	10
	Prepare to jump	Signaller is oriented toward receiver, limbs bent, in tension, staring at the receiver.	Visual	2 (0)	2
	Lie down	Signaller lays down on his/her back, in front of the receiver.	Visual	2 (2)	1
	Present body part	Signaller exposes one particular body part (head, neck, limb, back, chest, belly, side or crotch) to the receiver, by orienting his/her body appropriately in the direction and/or close to him/her.	Visual	170 (49)	22
	Present rear	Signaller puts his/her rear in the direction and/or close to the receiver.	Visual	376 (227)	24
	Roll on ground	Signaller rolls on ground in front of the receiver.	Visual	2 (1)	1
	Salto	Signaller jumps and turns in the air in front of the receiver.	Visual	4 (3)	2
Shove away	Signaller produces a brief movement with a body part that the receiver is touching, to push him away.	Tactile	3 (0)	3	

		Sit on receiver	Signaller sits on a receiver's body part.	Tactile	1 (1)	1
		Speed up toward	Signaller runs toward the receiver, in a fast movement, and stops close to him/her.	Visual	5 (4)	2
		Stretch torso	Signaller raises his/her chest, torso stretched.	Visual	1 (1)	1
		Throw body	Signaller produces a brief movement toward the receiver with his/her upper body.	Visual	15 (7)	12
		Up-down movement	Signallers produces unique or repeated up-and-down movements with his/her body, in bipedal or quadrupedal posture.	Visual	10 (7)	6
Facial signals	Facial displays ²	Ears back	Signaller puts his/her ears backwards, stretching the upper part of his/her face.	Visual	9 (7)	5
		Lipsmack	Signaller sticks out his/her tongue and moves it between the lips with rapid repeated movements.	Visual	163 (63)	23
		Open mouth	Signaller opens his/her mouth completely (uncovering upper and lower teeth), half or slightly (forming an oval shape with the lips, teeth covered or slightly visible).	Visual	252 (237)	15
		Raise eyebrows	Signaller raises his/her eyebrows, enlarging the white part of eyelids.	Visual	28 (26)	16
		Stick tongue out	Signaller sticks his/her tongue out and retracts it briefly (not repeated).	Visual	8 (5)	5
	Facial actions	Yawn	Signaller yawns, opening the mouth to inspire deeply.	Visual	27 (17)	10
		Bite self	Signaller bites herself/himself or an object, staring at the receiver.	Visual	38 (36)	3
		Bite	Signaller closes his/her mouth on a body part of the receiver.	Tactile	114 (114)	9

Vocal signals ³	A+ / Ti+	Signaller produces series of "A" or "Ti" vocal units (“food call”, “contact call”).	Audible	18 (8)	5
	Oe+	Signaller produces series of "Oe" vocal units (“sexual call”).	Audible	13 (5)	4
	Ro+	Signaller grunts, producing series of "Ro" vocal units (“contact call”, “grunt”).	Audible	126 (92)	19
	Un+	Signaller produces series of "Un" vocal units (“threat call”).	Audible	87 (64)	20
	Alarm	Signaller produces WaHoo calls (“alarm calls”) or Whoop-Gobble (“loud call”).	Audible	1 (1)	1
	Scream	Signaller screams, producing "Wi" vocal unit (“distress call”).	Audible	2 (2)	1
	ND	Signaller produces unidentified vocalisations.	Audible	12 (12)	5

¹Schel et al., under review; ²Aychet et al., in press; ³Bouchet et al., 2010

Contexts of signal production

We categorized the social contexts in which signals were produced according to the signaller and recipient’s behaviours observed within the 5 seconds before and the 5 seconds after the signal production (Aychet et al., in press). Six social context categories were distinguished: affiliative, grooming, sexual, playful, aggressive, and submissive (**Table 3**). Moreover, for the purpose of weighting contextual data in our analysis according to the overall importance of each of these categories, we also established a population-level time budget. Thus, we also coded every 10 sec (scan sampling method, (Altmann, 1974) the social and non-social contexts in which the focal individual was involved, for one session per individual (totalizing 2250 scans for the population).

Table 3. Social contexts of signal production

Social context	Associated behaviours in signaller and receiver
Affiliative	Physical proximity between subjects (at less than one arm length), calm approach of recipient or gentle physical contact
Grooming	Grooming, tactile examination
Sexual	Touching, smelling, licking genital parts or mounting
Playful	Play-fight, rough or gentle (involving manual fighting, biting, gentle or rough touching and grabbing), or locomotor-rotational play (play with few physical contacts, but involving pursuits, jumps, somersaults)
Aggressive	Physical aggression of recipient by signaller (biting, beating, rough manipulation), flight or avoidance of signaller by recipient, or intergroup conflict in which signaller and recipient were in different social groups
Submissive	Flight or avoidance of recipient by signaller
Unclear	Behaviours accompanying the signal were not sufficient to classify the context, or the interaction could be classified in several categories.

Relationship between signaller and receiver

In order to evaluate their potential effect on the production of signal sequences, we determined the relationship between signaller and receiver in terms of dominance relationship, kinship, age difference and sex difference. The dominance relationship was based on avoidance behaviours (Easley & Coelho, 1991). All avoidance behaviours involving focal subjects were analysed, considering turning away from another individual, avoiding an individual by changing direction, avoiding contact with an individual by moving a body part away from the proximity of another individual, fleeing an individual by walking or running in the opposite direction (see “contact rupture behaviours”, Baraud, 2007). When at least 3 occurrences were observed for a dyad, we computed the percentage of avoidance of subject A from subject B over the total number of avoidance behaviours between A and B (Zumpe & Michael, 1986);

and subject A was considered subordinate to subject B if this percentage was above 50%. Kinship was known for all individuals in the colony, and signaller and receiver were considered as “kin” if they were first-degree relatives (parents or siblings). Finally, age difference was not assessed based on the absolute number of years old but on the age category (juveniles, middle-aged and old adults).

Sequence analysis

Sequence definition and characteristics

We defined as “sequence of signals” a series of signals that were directed by a same signaller towards a same receiver, and whose initiations were separated by latencies from 0 to 8 seconds. We determined this time window graphically (Lemasson et al., 2010, 2018; Levréro et al., 2019), based on the observed frequency distribution of latencies between two consecutive signal initiations by a same signaller toward a same receiver in our red-capped mangabeys (**Figure 1**).

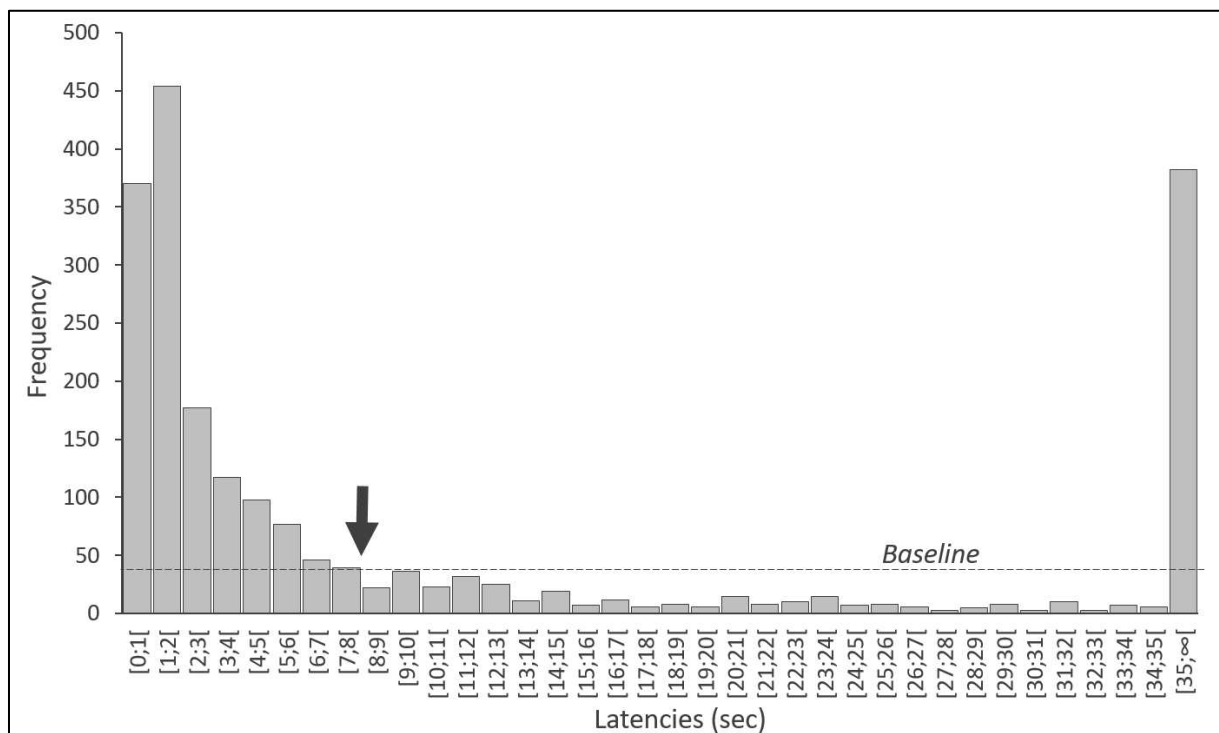


Figure 1. Distribution of the latencies between two consecutive signal productions from a same signaller toward a same receiver (n = 2081 latencies). Black arrow: threshold indicating the maximum latency between two signals from the same communicative sequence.

We extracted all the so-defined communicative sequences from our data set, and used the package {TraMineR} (Gabadinho et al., 2011) from the software R v.3.6.2 (R Core Team, 2018) to visualize and analyse them. Communicative sequences were characterized based on their length (number of signals within the sequence), diversity (number of different signals within the sequence), and complexity. The

complexity index, ranging from 0 to 1, is based on longitudinal entropy and number of transitions within the sequence (Gabadinho et al., 2010, 2011). Thus, sequences composed of few different signals, consecutively repeated, will have low complexity indices; in contrast, the index will raise if signals are less repeated among the sequence and more diverse. Moreover, we defined as “multicomponent”, as opposed to “unicomponent”, the sequences that were composed of more than one type of signal (for instance those that were composed of both body and facial signals). We also defined as “multimodal”, as opposed to “unimodal”, the sequences that were composed of more than one modality of signal (i.e. “free” multimodality, Fröhlich & van Schaik, 2018; Higham & Hebets, 2013; Partan & Marler, 2005: for instance visual and tactile signals, or visual and audible signals).

Sequence clustering and representative sequences

In order to describe the typical communicative sequences produced by red-capped mangabeys, we grouped them based on their composition similarities and extracted “representative sequences” for each group. To do so, we used the package {TraMineR} (Gabadinho et al., 2011) and first computed dissimilarities between observed sequences, based on “optimal matching” method (Abbott & Forrest, 1986; Levenshtein, 1966; Needleman & Wunsch, 1970; Studer & Ritschard, 2016). A distance was measured for each sequence dyad of our dataset, corresponding to the minimum cost needed to transform one sequence into another, considering that each insertion, deletion or substitution of signal has a particular cost. The insertion / deletion cost was set at a constant value (indel = 1). The substitution costs were derived from the observed transition rates between signals, so that the cost of substituting between signals that were frequently produced consecutively was lower than substituting between signals that were rarely produced one after the other. Moreover, as we analysed sequences of different lengths, we applied Abbott’s normalization (Gabadinho et al., 2011) to the “optimal matching” distances, by dividing each distance by the length of the longest of the two corresponding sequences. Based on these normalized distances, we made a hierarchical clustering of the sequences using Ward method (Ward, 1963), and the number of sequence groups was determined graphically based on the generated dendrogram plot.

For each sequence group, we extracted a set of representative sequences based on the “neighbourhood density” criterion (Gabadinho et al., 2011; Gabadinho & Ritschard, 2013). This method permits to define an as small as possible set of non-redundant representatives which cover a minimum percentage of the sample sequences in their “neighbourhood”. Here, we chose to set this minimum coverage at 50%, but we dropped this threshold to 25% for the most heterogeneous groups, i.e. when the needed number of representatives to cover 50% of the group was about half of the group size. Were considered as “neighbours” the sequences for which the distance was under 10% of the maximum theoretical distance (radius = 0.10).

Sequence context

The contexts of production of the communicative sequences were determined based on the context category already assigned to the signal occurrences they were composed of (see above, **Table 3**). When more than one context were identified, we categorized the overall sequence context following the one that was the most represented among the given sequence, and in case of equal representation the one that was attributed to the first signal of the sequence.

Signal combinations

In order to represent and quantify the combinations of different signals, signal types and signal modalities among the communicative sequences of red-capped mangabeys, we applied graphical and statistical methods of network analysis. We discarded here the communicative sequences composed of a unique repeated signal, given that they did not imply different signal combinations. We used SOCPROG 2.9 software (Whitehead, 2009) to compute association indices (simple ratio, Ginsberg & Young, 1992) for each signal dyad, based on the idea that signals produced within a same communicative sequence were combined and thus associated. We then computed four different network statistics for each of the studied signal, in order to test for possible differences of combination potential between signal types and modalities. For each signal we computed: (i) the degree, which corresponds to the number of associates, so the number of different combinations including the corresponding signal; (ii) the strength, which is the sum of all signal's association index (high values thus indicating frequent and/or numerous associations with other signals); (iii) the affinity, which corresponds to the average strength of the signal's associates, weighted by their association indices with the signal (Whitehead, 2008, 2009); and (iv) the clustering coefficient, which represents the extent to which a signal's associates were themselves associated within the signal combination network (Holme et al., 2007; Sosa, Sueur, et al., 2020; Whitehead, 2008, 2009). Finally, we used GEPHI 0.9.2 (Bastian et al., 2009) to represent graphically the network of the most common signal combinations we observed. We represented signal combinations observed in at least two signallers (discarding idiosyncratic associations), and for which association indices were greater or equal to the third quartile value.

Statistical analyses

Besides the descriptive approach explained above, statistical tests were run to complete the description of communicative sequence groups, to test for factors affecting communicative sequence production, multimodality and multicomponentiality, and to compare signal types and modalities' integration in the "combination network". We used R v.3.6.2 (R Core Team, 2018), all tests were two-tailed and alpha-level was set at 0.05. For all multiple comparisons, p-values were adjusted using "False Discovery Rate" (FDR) method (Noble, 2009).

Firstly, after having grouped the sequences depending on their composition similarities, we completed the description by comparing the main sequence characteristics depending on groups: sequence length, diversity and complexity were compared using Kruskal-Wallis rank sum tests and post-hoc Mann-Whitney tests.

Secondly, we analysed the effect of social context on sequence production. The frequency of communicative sequence of each group was weighted for each focal signaller based on the general time budget (affiliative context typically representing 2.40% of total time; grooming: 5.82%; sexual: 0.09%; play: 0.62%; aggressive: 0.53%; submissive: 2.13%; unclear: 4.89%; other –nonsocial- contexts: 83.51%). These weighted frequencies were then compared between social contexts using Friedman rank sum tests and post-hoc Wilcoxon signed rank tests. Moreover, we tested the effect of social contexts on sequence characteristics. We used Generalised Linear Mixed Model (GLMM) of the Gamma family, Poisson family and a Linear Mixed Model (LMM) to analyse this effect on sequence length, diversity and complexity respectively. In each model, the context was included as a fixed effect and identities of signaller and receiver were taken into account as random effects. Model quality was assessed by verifying the normality of the residuals, using normal probability plots. The proportions of multicomponent and multimodal sequences were compared to a theoretical proportion of 0.5 in each context, using exact binomial tests. Then, the proportions of sequences involving different combinations of signal types and signal modalities were compared to theoretical distributions in each context using Fisher exact tests (except for the submissive context, for which the number of sequences observed was not sufficient, i.e. < 35).

Thirdly, we evaluated the effect of socio-demographic factors on sequence production. The effects of focal signallers' age and sex on the number of sequence of each group produced were tested using Mann-Whitney tests. Then, the proportion of communicative sequences produced toward dominant (as opposed to subordinate) receivers, toward kin (as opposed to non-kin) and to receivers of same age or same sex, were compared to a theoretical proportion of 0.5 using exact binomial tests. The proportion of different signaller-receiver sex differences (male-to-male, male-to-female, female-to-male, female-to-female) were also compared to a theoretical distribution for each sequence group using Fisher exact tests.

Finally, after having described the main signal combinations occurring among communicative sequences, we tested whether different types and modalities of signal had different potentialities of being combined with other signals. To do so, we compared signal network statistics (degree, strength, affinity and clustering coefficient) between types and modalities using Mann-Whitney tests.

Results

We recorded 2651 signals produced by or in the direction of focal red-capped mangabeys, of which 1919 were produced as part of communicative sequences (70.17% of the body signals, 79.03% of the facial signals and 71.04% of the vocalisations). We identified a total of 479 communicative sequences, produced by 24 different signallers and involving 47 of the 49 different signals of the repertoire (**Table 2**). Sequences were composed of up to 27 signals (mean length $\pm S.E.$ = 4.00 ± 0.15), and up to 12 different signals (mean diversity $\pm S.E.$ = 2.75 ± 0.09 ; mean complexity index $\pm S.E.$ = 0.34 ± 0.01). 112 of the 479 sequences were repetitions of one unique signal, 260 were multicomponent (i.e. composed of more than one signal type), and 261 were multimodal (i.e. involved more than one sensory modality).

Sequence groups and representative sequences of each group

We grouped the communicative sequences according to their composition, in order to describe the typical communicative sequences of red-capped mangabeys. Based on the dendrogram of the hierarchical clustering of the sequence dissimilarities (**Figure 2**, agglomerative coefficient = 0.97), we found that the best solution was to classify the 479 sequences in 10 groups. Thus, sequence groups differed in their general composition (**Figure 3**), length (Kruskal-Wallis rank sum test: $X^2_9 = 75.25$, $P < 0.001$), diversity ($X^2_9 = 141.85$, $P < 0.001$) and complexity indices ($X^2_9 = 110.26$, $P < 0.001$). Representative sequences of each group, selected using “neighbourhood density” criterion, are presented in **Table 4**. For most sequence groups we could extract a set of representatives covering at least 50% of their sequences, however groups 7, 9 and 10 were too heterogeneous and we had to choose representatives covering 25, 25.2 and 26% of these groups respectively.

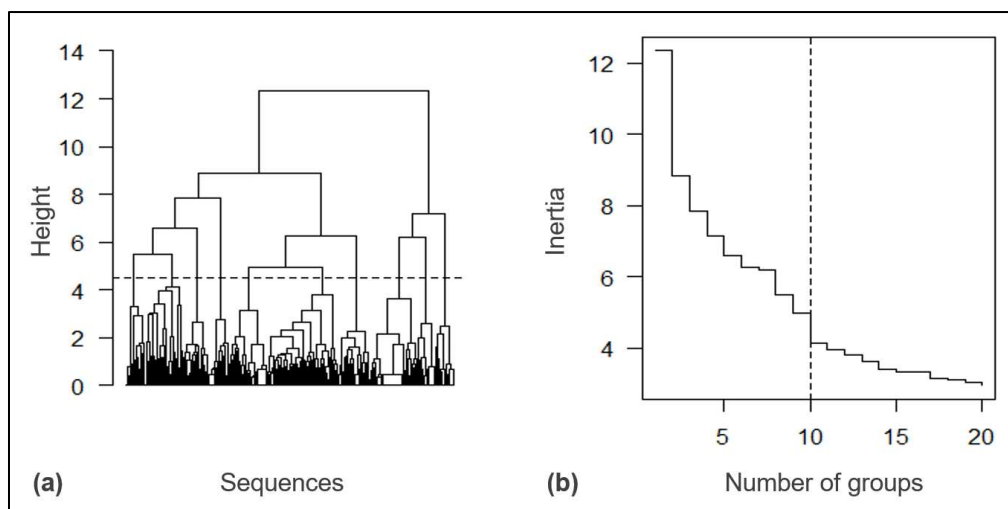


Figure 2. (a) Dendrogram of the hierarchical clustering (Ward method) made on sequence dissimilarities ($N = 479$). (b) Representation of the dendrogram inertia. The 10-group solution (indicated by a dotted line in both graphs) presented the best between-cluster distance.

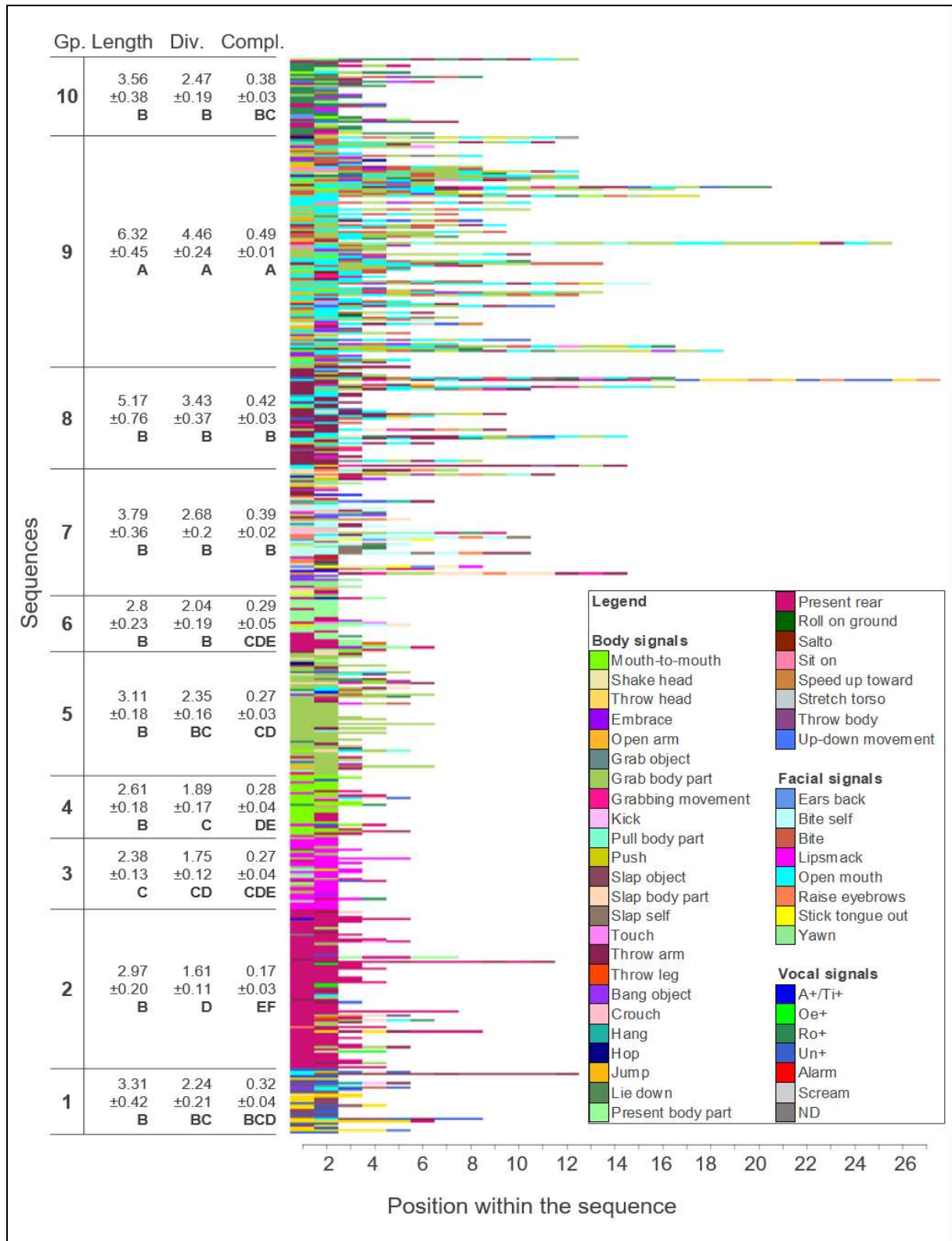


Figure 3. Sequence index plot and sequence group characteristics. Each sequence is represented by a line and each signal by a colour. Sequences are sorted by groups, and characteristics are given on the left as mean values \pm S.E. Gp.: group number; Length: number of signals within the sequence; Div.: diversity (number of different signals within the sequence); Compl.: complexity index (from 0 to 1, based on longitudinal entropy and number of transitions within the sequence. Gabadinho et al., 2010, 2011). Different capital letters indicate significant differences between groups (Mann-Whitney tests with FDR correction: $P < 0.05$).

Table 4. Sequence group description and summary of production context. *Gp.*: group number; *Nb (%)*: number of sequences within the group, and corresponding percentage of the total sample; *N*: number of different signallers; *Nb.sq*: number of representative sequences. Representative sequences are ordered by respective coverage importance. Each representative sequence is described by separating consecutive signals by a semicolon, and if signals are consecutively repeated, “x k” indicates the number k of consecutive instances.

Gp.	<i>Nb (%)</i>	<i>N</i>	Representative sequences			Sequence production		
			<i>Nb.sq</i>	Coverage	Description	Main social context	Age and sex of signallers	Signaller and receiver relationship
1	29 (6.1%)	15	6	51.7%	- Un+ x2 - Slap object; Un+ - Throw head; Slap object - Un+; Slap object - Throw head x4 - Throw head; Un+	Aggressive	Males	Dominant-to-subordinate Non kin Male-to-male
2	71 (14.8%)	18	2	52.1%	- Present rear x2 - Present rear x3	-	Females	Subordinate-to-dominant Non kin
3	32 (6.7%)	15	3	53.1%	- Lipsmack x2 - Grab body part; Lipsmack - Present body part; Lipsmack	Affiliative and grooming	Old adults	Different age category Same sex
4	28 (5.8%)	12	3	57.1%	- Mouth-to-mouth x2 - Mouth-to-mouth; Present rear - Lipsmack; Mouth-to-mouth	Affiliative	Juveniles	-
5	55 (11.5%)	16	8	50.9%	- Grab body part x2 - Grab body part x3 - Grab body part; Throw arm - Grab body part x2; Throw arm - Grab body part x4	Aggressive and play	No specific age and sex category	Dominant-to-subordinate Non kin

					<ul style="list-style-type: none"> - Grabbing movement; Grab body part - Present body part; Grab body part - Jump; Grab body part; Bite; Grab body part 			
6	25 (5.2%)	11	3	56%	<ul style="list-style-type: none"> - Present body part x2 - Present rear; Present body part - Present body part; Present rear 	-	No specific age and sex category	Same sex
7	56 (11.7%)	19	13	25%	<ul style="list-style-type: none"> - Yawn x2 - Stick tongue out; Lipsmack - Shake head; Throw arm - Crouch; Raise eyebrows - Slap object; Yawn x2 - Bang object x2; Yawn - Bang object; Yawn - Un+; Bang object - Raise eyebrows; Slap body part; Throw arm; Grabbing movement; Grab body part x2; Slap body part x2; Raise eyebrows; Slap body part x2; Throw arm; Grabbing movement; Throw arm - A+/Ti+ x2 - Slap body part; Throw arm; Bite; Grab body part; Present rear x2 - Ears back; Stick tongue out; Shake head x2; Stick tongue out; Ears back; Shake head; Lipsmack - Slap body part; Ro+ 	Aggressive	No specific age and sex category	Same sex

8	46 (9.6%)	12	11	50%	<ul style="list-style-type: none"> - Throw arm x2 - ND; Throw arm - Throw arm; ND - Throw arm; ND; Throw arm - ND; Throw head; Grabbing movement; Throw arm x7; Throw body; Throw arm; Grab body part; Throw arm - Throw arm x2; ND x2; Grab body part; Throw arm; ND; Grab body part - Throw arm; Slap object - Throw arm; Lipsmack; Throw arm - Throw arm; Grab body part - Throw body; Throw arm; Grabbing movement - Throw arm; Bite x2 	Play and aggressive	Juveniles	Same age category Male-to-male
9	103 (21.5%)	12	15	25.2%	<ul style="list-style-type: none"> - Open mouth; Grab body part - Grab body part; Open mouth - Open mouth x2 - Grab body part; Bite; Open mouth - Embrace; Bite; Embrace - Jump; Throw arm - Grab body part x2; Open mouth - Jump; Open mouth - Grab body part; Bite - Open mouth; Grab body part; Open mouth; Throw arm - Mouth-to-mouth; Embrace; Bite; Grab body part; Open mouth - Embrace; Open mouth 	Play and aggressive	Juveniles	Kin Same age category Male-to-male

					<ul style="list-style-type: none"> - Mouth-to-mouth; Open mouth x2; Grab body part; Bite; Ro+; Push; Ro+; Throw arm; Open mouth; Ro+; Grab body part x3; Push; Embrace; Grab body part; Open mouth - Ro+; Throw arm; Push x3; Grab body part; Open mouth; Ro+ - Open mouth; Grab body part x3; Open mouth x2; Bite; Grab body part x2; Bite; Open mouth; Touch; Grab body part; Push; Open mouth; Ro+ 			
10	34 (7.1%)	15	4	26%	<ul style="list-style-type: none"> - Ro+ x2 - Present rear; Ro+; Present rear - Ro+; Present body part - Ro+; Lipsmack; Throw head; Ro+ x3 	-	Females	-

Social contexts of sequence production

Communicative sequences of most different groups were produced by red-capped mangabeys in specific social contexts (**Figure 4**, Friedman rank sum tests: group 1: $X^2_{11} = 32.81$, $P < 0.001$; group 3: $X^2_{12} = 22.75$, $P < 0.001$; group 4: $X^2_7 = 42.00$, $P < 0.001$; group 5: $X^2_{12} = 12.68$, $P = 0.048$; group 7: $X^2_{14} = 32.92$, $P < 0.001$; group 8: $X^2_7 = 12.95$, $P = 0.044$; group 9: $X^2_9 = 24.90$, $P < 0.001$), except for groups 2, 6 and 10 for which contexts of production were unclear (group 2: $X^2_{14} = 11.45$, $P = 0.075$; group 6: $X^2_8 = 8.52$, $P = 0.202$; group 10: $X^2_{10} = 6.99$, $P = 0.322$). Main social contexts of the different sequence groups are summarized in **Table 4**.

Moreover, communicative sequence characteristics were dependent on the production context. Sequences produced in playful context were longer than in other contexts (Figure 5.a) and involved more different signals (Figure 5.b), followed by sequences produced in contexts of aggression. Communicative sequences were more complex in playful context (Figure 5.c), followed by aggression and submission contexts, and the less complex sequences were produced in sexual context. Communicative sequences were mostly multimodal in playful context (Exact binomial test: $P < 0.001$), and tended to be multimodal in aggression context ($P = 0.072$), but not in affiliative ($P = 0.896$), grooming ($P = 0.274$) and submission contexts ($P = 0.151$). On the contrary, communicative sequences produced in sexual contexts tended to be mainly unimodal ($P = 0.055$) (**Figure 5.d**). The proportions of signal types and modalities' combinations among communicative sequences were also dependant on the social context (**Figure 5.d** and **e**, Fisher exact test: $P < 0.001$ for multicomponentality and multimodality). Grooming and sexual contexts elicited mainly unicomponent sequences (Exact binomial test: $P < 0.001$ for grooming and $P = 0.002$ for sexual context), specifically sequences of body signals. Affiliative and submissive contexts elicited mainly sequences of body signals or body signals combined with facial and vocal signals. Finally, communicative sequences produced in play context were mainly multicomponent (Exact binomial test: $P < 0.001$), i.e. combinations of body and facial signals, and sequences produced in aggressive contexts were mainly combinations of body signals with facial and/or vocal signals (**Figure 5.d**).

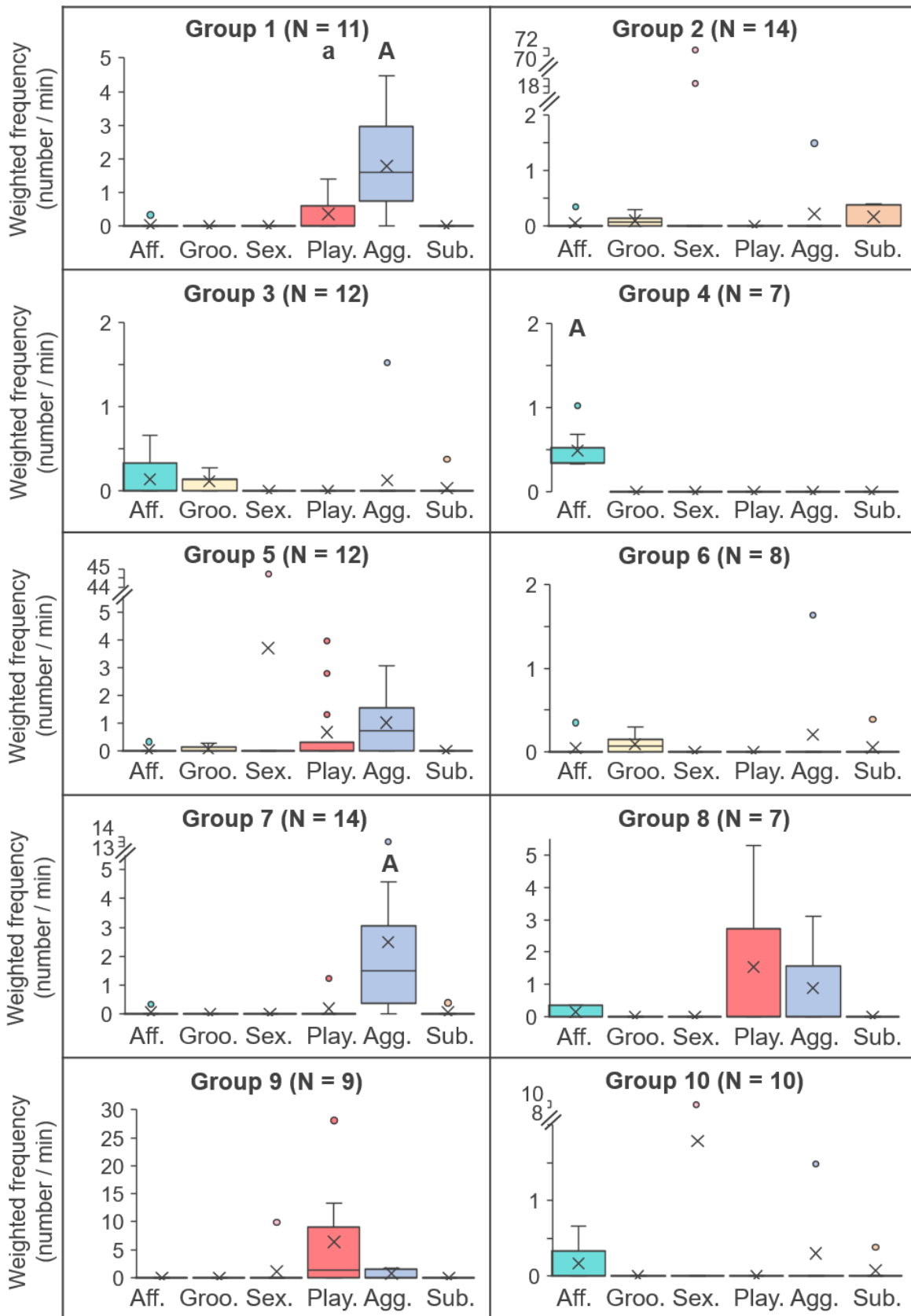


Figure 4. Social contexts of sequence production of different groups. N: number of signallers. Different capital letters indicate significant differences between groups (Wilcoxon signed rank test with FDR correction: $P < 0.05$), and minor letters are used when these are tendencies: $P < 0.01$. **Aff.:** affiliation; **Groo.:** grooming; **Sex.:** sexual context; **Agg.:** aggression; **Sub.:** submission.

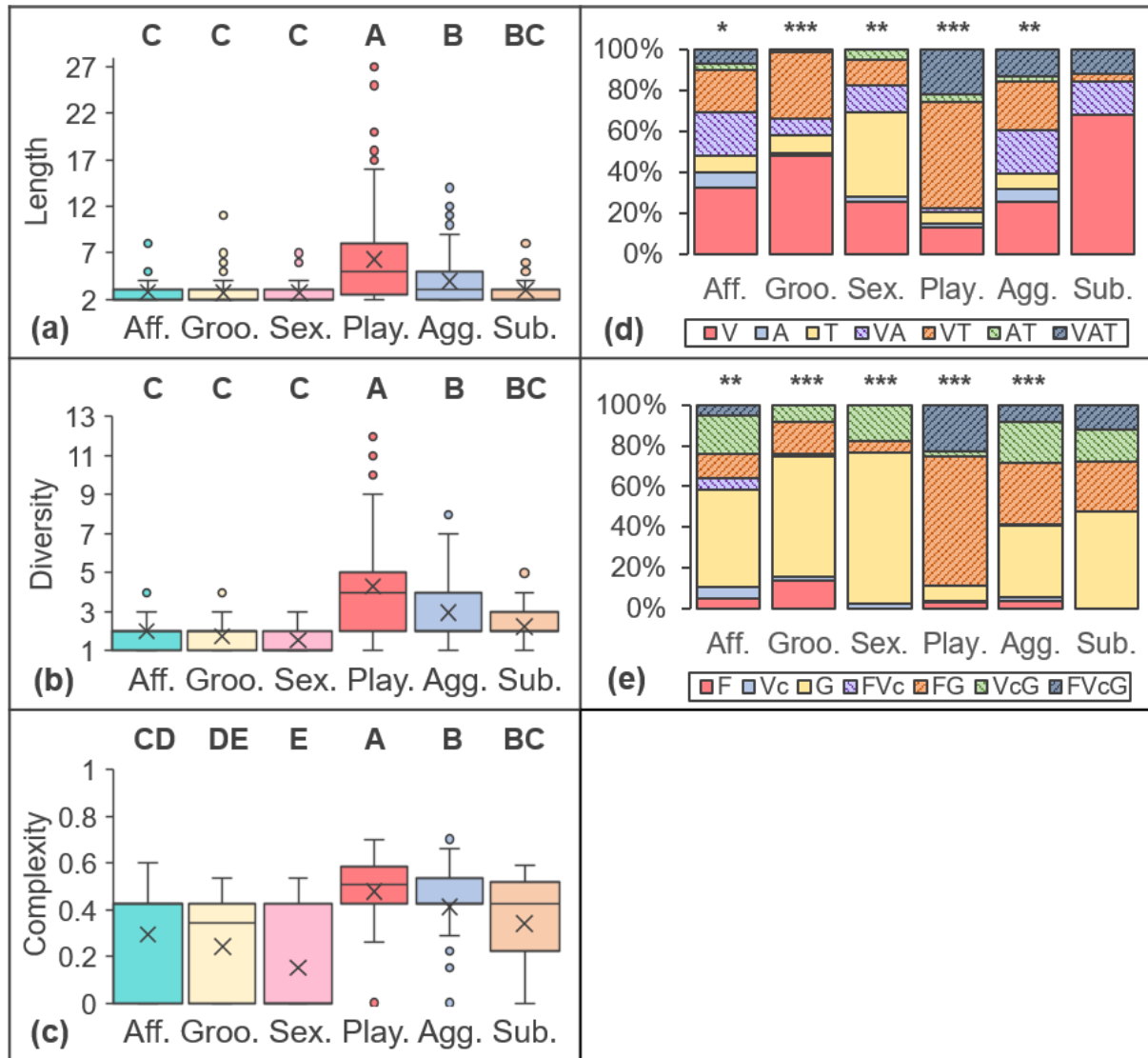


Figure 5. Sequence characteristics depending on social contexts. (a) **Sequence length** (number of signals within the sequence), (b) **diversity** (number of different signals within the sequence) and (c) **complexity** (indices from 0 to 1, based on longitudinal entropy and number of transitions within the sequence. Gabadinho et al., 2010, 2011) were compared between contexts using a GLMM of Gamma family, of Poisson family and a LMM respectively. Different capital letters indicate significant differences between contexts. (d) **Multimodality** and (e) **multicomponentiality** of communicative sequences. Proportion of sequences combining different signal types and modalities were compared to theoretical distributions using Fisher exact tests with FDR correction: *: $P < 0.05$; **: $P < 0.01$; ***: $P < 0.001$. **V**: “visual only” signals; **A**: audible signals; **T**: tactile signals; **F**: facial signals; **Vc**: vocal signals; **G**: gestural and body signals. Plain filling indicates unimodal or unicomponent sequences, hatching indicates multimodal or multicomponent sequences.

Socio-demographic factors’ effect on sequence production for each sequence group

Age and sex of subjects did not have any effect on the overall frequency of communicative sequences produced (Mann-Whitney tests: $N_{males} = 14$, $N_{females} = 10$, $N_{juveniles} = 3$, $N_{middle-aged} = 14$, $N_{old} = 7$; $20 < W < 94$, $P > 0.05$ for all sex and age category comparisons), however these characteristics

affected the group of sequences produced. Particularly, males produced more sequences of group 1 than females ($W = 37, P = 0.038$), and females produced more sequences of group 2 ($W = 117, P = 0.005$), and sequences of group 10 ($W = 107.5, P = 0.016$), than males. Old adults produced more sequences of group 3 than middle-aged ($W = 15.5, P = 0.027$), juveniles produced more sequences of group 4 than middle-aged adults ($W = 42, P = 0.004$), and more sequences of group 8 (juveniles vs middle-aged: $W = 41, P = 0.015$; juveniles vs old adults: $W = 21, P = 0.015$) and 9 (juveniles vs middle-aged: $W = 41, P = 0.017$; juveniles vs old adults: $W = 21, P = 0.030$) than other individuals.

Moreover, the relationship between the signaller and the receiver (dominance relationship, kinship, difference of age and sex) had some significant effects on the production of communicative sequences (all summarised in **Table 4**). Notably, sequences of group 1 were more produced toward subordinate (Exact binomial tests: $P = 0.002$), non-kin ($P = 0.008$) receivers, and mainly produced by males toward other males (Fisher exact tests: male-to-male vs male-to-female: $P = 0.006$). Sequences of group 2 were more produced by subordinates (Exact binomial test: $P = 0.002$), toward non-kin ($P = 0.002$), and sequence of group 3 toward receivers of different age categories ($P < 0.001$). Sequences of group 5 were more produced by dominant signaller toward non-kin ($P = 0.014$) subordinate receivers ($P = 0.001$), and more produced from males to females than females to males (Fisher exact tests: $P = 0.034$). Sequences of group 6 and 7 were more produced toward receivers of the same sex (Exact binomial tests: $P < 0.001$ and $P = 0.002$ respectively). Sequences of group 8 were mainly produced by males toward other males (Fisher exact tests: male-to-male vs female-to-female: $P = 0.006$; vs female-to-male: $P = 0.004$; vs male-to-female: $P = 0.050$), and mainly of the same age (Exact binomial test: $P < 0.001$). Finally, sequences of group 9 were more produced toward kin receiver ($P < 0.001$) of same age ($P < 0.001$).

Signal combinations

We found that 367 of the 479 sequences were composed of at least two different signals. They involved 37 different signals of the repertoire, and on the 1081 theoretically possible combinations associations, we observed 166 different combinations that were produced by at least two signallers (combination network density = 15%). The main combinations of signals that were observed, i.e. for which association indices were above the third quartile value (median association index $\pm IQR = 0.04 \pm 0.05$; third quartile = 0.07), involved 28 different signals of the repertoire and are represented in **Figure 6**. On the whole, the signals that were combined with the most others were the body signals “grab body part” (degree (D) = 34, strength $\pm S.E$ (S) = 2.29 ± 0.12), “throw arm” (D = 32, S = 1.94 ± 0.14), and “present rear” (D = 27, S = 1.07 ± 0.08), as well as the facial signal “open mouth” (D = 32, S = 2.29 ± 0.13) and the vocal signals “Ro+” (D = 27, S = 1.42 ± 0.13) and “Un+” (D = 27, S = 1.43 ± 0.18).

We then tested whether the potentiality of signals of being combined with others was dependent on their types or modalities, by comparing their network measures. We found no significant differences between signal types and modalities regarding these network statistics (degree strength, affinity and clustering coefficient, **Table 5**), except that the clustering coefficient was higher for tactile signals than for audible ones (Mann-Whitney test: $N_{tactile} = N_{audible} = 10$, $W = 11$, $P = 0.031$).

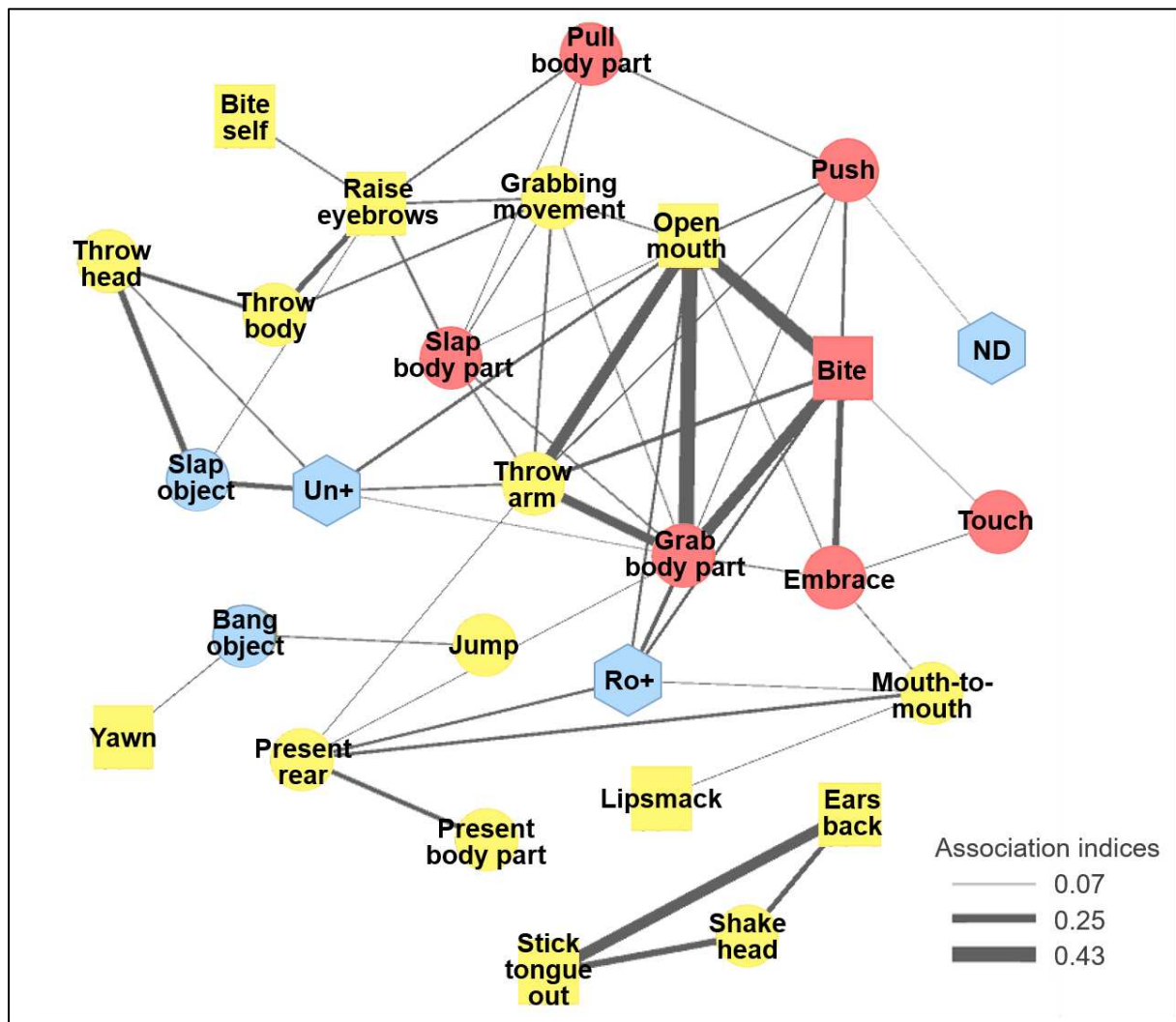


Figure 6. Network of signal combinations among communicative sequences. Are represented only combinations produced by at least 2 signallers, and for which association indices are above or equal to the third quartile value (0.07). Signal types are indicated by node forms (**circles**: body signals; **squares**: facial signals; **hexagons**: vocal signals), and signal modalities are indicated by node colours (**yellow**: “visual only”; **red**: tactile; **blue**: audible).

Table 5. Signal network statistics. Values are given as median $\pm IQR$ for each category. Different letters in superscript indicate significant differences (Mann-Whitney tests with FDR correction: $P < 0.05$)

Signal categories		Degree	Strength	Affinity	Clustering coefficient
Type	Body signals	11.50 \pm 9.75	0.61 \pm 0.55	1.11 \pm 0.44	0.14 \pm 0.10
	Facial signals	18.00 \pm 16.50	0.92 \pm 1.14	0.96 \pm 0.64	0.16 \pm 0.20
	Vocal signals	7.00 \pm 25.00	0.57 \pm 1.28	1.02 \pm 0.52	0.11 \pm 0.09
Modality	Visual only	10.00 \pm 11.00	0.61 \pm 0.47	1.04 \pm 0.48	0.13 \pm 0.12 ^{ab}
	Audible	10.00 \pm 14.50	0.62 \pm 0.90	1.02 \pm 0.30	0.11 \pm 0.08 ^b
	Tactile	15.50 \pm 16.50	0.87 \pm 1.02	1.30 \pm 0.62	0.18 \pm 0.11 ^a

Discussion

We applied sequential and network analyses to describe systematically the use of multiple signals in the spontaneous communication of captive red-capped mangabeys. Sequential analysis, based on dissimilarity measures, permitted to identify rigorously the typical sequences of communicative signals produced by red-capped mangabeys, completing previous descriptions of gestural, facial and vocal communication in this species (Schel et al., under review; Aychet et al. in press; Bouchet et al. 2010). We found that captive mangabeys frequently produce communication signals in sequences, particularly combining different signal types and modalities in a flexible way. Our results brought to light contextual and socio-demographic effects on such complex communication, which gives perspectives to test for current hypotheses on multimodal communication functions. Network analysis permitted to visualize the signal combinations among communicative sequences, and network measures showed equal relative importance of signal types and modalities in those combinations. We believe that applying the present analysis methods to the communication of other species and in different environments should permit reliable comparisons to investigate the causes leading to multimodal and multicomponent communication.

One first aspect that could permit to enhance the reliability of these future comparisons of multimodal and multicomponent communication is the temporal definition used to identify signal combinations. Instead of using different arbitrary criterion to identify signal combinations, basing the temporal definition on observed between-signal latencies would allow to both use a relevant analysis time-window in regard of the species biology, while using the same method from one study to another. Applying here the same graphical method as in studies on vocal exchanges (Lemasson et al., 2010, 2018; Levréro et al., 2019), we identified 479 communicative sequences in total in our sample, which could then be grouped in 10 categories based on their composition. This clustering of communicative sequences was performed using the toolbox {TraMineR} on R (Gabadinho et al., 2011), initially developed for social science but which could be applied to any sequence analysis. The clustering of communicative sequences based on their similarities allows identifying the typical signal sequences

produced in a population, while conserving the observed variability in the analysis. Moreover, sequence index plots and network diagrams permit rapid visualisation of communicative sequence variability and of common signal combinations. To analyse the signal combination network in a population, numerous network analyses softwares exist, such as SOCPROG 2.9 software (Whitehead, 2009) that we used, and a new package was recently developed in R, permitting both statistical measures and network visualisation (Sosa, Puga-Gonzalez, et al., 2020), which could even facilitate such approach. Overall, the method we used permitted systematic description of multimodal and multicomponent communication in an integrated way, taking into account body, facial and vocal signals of their repertoire (completed from Schel et al., under review, Aychet et al., in press and Bouchet et al. 2010), that were delivered on the visual, audible and/or tactile modality. We focused here on these three sensory modalities, which are the most investigated in primate communication (Liebal et al., 2014b), but we note that red-capped mangabey communication may even encompass other sensory channels, which would need specific methods to be measured. For instance, although this has rarely been investigated in catarrhine species, “presenting rear” in sexual context may be a way for females to deliver olfactory signals (Dixon, 2015; Liebal et al., 2014b; Reichert et al., 2002), and some other mangabey body signals are likely to be perceived on the seismic modality, such as “bang object”, which typically provoke tremors of substrates, in addition of noise.

We found that the major part of mangabey signal instances were produced in sequences, i.e. 70% of their body signals, 79% of facial ones and 71% of vocalisations, and most sequences were multicomponent and/or multimodal. Captive mangabeys of all sex and age categories produced communication signals in sequences. Nevertheless, the typical communicative sequences produced by captive red-capped mangabeys (grouped in 10 categories) were generally produced under specific social contexts, and we found significant effects of signaller’s age, sex and relationship with the receiver on the production of communicative sequence types. This permits to refine the previous descriptions of mangabeys’ communication from “unimodal” studies. For instance, even though we did not found any effect of dominance relationship and kinship between the signaller and the receiver regarding the production of facial displays when studied alone (Aychet et al. in press), we report here significant effects of these social factors on the production of communicative sequences involving facial signals. The context-specificity of sequence production may be in favour of the “refinement hypothesis”, which suggest that combining one signal with another permits the first one to be accurately understood by the receiver (Fröhlich & van Schaik, 2018). As a matter of fact, when looking at the contexts of signal production, facial expressions and vocalizations were identified as context-specific (Aychet et al., in press; Bouchet et al., 2010), but red-capped mangabeys have been suggested to produce gestures in a flexible way across different contexts (Schel et al. under review). This “means-ends dissociation” (Bruner, 1981) may imply that some gestures have different possible meanings and need to be combined with facial expressions or vocalizations to encode the specific signaller’s intention (Moore, 2014).

Investigation at the signal-level, using the same approach as proposed by Genty (2019), should permit to test for this hypothesis, comparing receiver response to one specific signal when produced alone, or in combination with whether one or another signal. The present description permits to identify, in the repertoire of red-capped mangabeys, the signals that are the most frequent, and the most frequently produced alone and in combinations with others. We thus believe that the “refinement hypothesis” could be tested in future studies by investing specifically the meanings of these signals under different uses.

Aside from the context-specificity of each sequence type, we found that different social contexts affected the production and characteristics of communicative sequences. Playful contexts, and aggression context in a slightly lower extent, elicit longer, more diverse and complex communicative sequences, and favour both multimodal and multicomponent communication. Particularly, play elicited a wide use of body and facial signal combinations, produced on the visual and tactile modalities. Playful interactions are known to elicit a wider and more flexible use of communication signals in primates than other contexts, with more diverse signals (e.g. gesture use in apes: Call & Tomasello, 2007; Liebal et al., 2006; Pika et al., 2003), production of idiosyncratic gestures (e.g. in gorillas: Pika et al., 2003) and frequent use of signal combinations (e.g. in orangutans Liebal et al., 2006). Thus, more complex signalling in red-capped mangabeys during play compared to other contexts, particularly for juveniles, corroborates theories proposing social play as a way to develop behavioural flexibility, notably by exploring and exercising communicative actions (e.g. Fagen, 1982, 2002; Tomasello et al., 1989). The length of communicative sequences in play and aggression events may also result from the high level of arousal in those contexts, compared to affiliation or grooming, as hypothesized for orangutans gestural sequences (Tempelmann & Liebal, 2012). Another explanation for the observed communication complexity and multimodal/multicomponent use of signals is the higher need for context disambiguation in play and aggression, which both imply close contact between interactants (“refinement hypothesis”). The high proportion of body and facial signal combinations during play might reflect the use of “open mouth” having the role of metacommunicative signals (Altmann, 1967; Bateson, 1955; Bekoff, 1975) to elucidate the meaning of agonistic-like gestures (Demuru et al., 2015; Palagi, 2008; Waller & Cherry, 2012; Waller & Dunbar, 2005). Other contexts, such as grooming or sexual interactions, elicited less complex communication and mainly unimodal (visual or tactile) and unicomponent (mainly gestures) sequences of signals. Studies in apes previously report significantly less signal sequences (e.g. Tempelmann & Liebal, 2012) and less or no multimodal combinations (e.g. Liebal et al., 2006) in such situations, maybe because of more context-specific signals. Despite being rare, signal type combinations (particularly body and vocal signals) in sexual context may support the “complementarity hypothesis”. Indeed, vocalizations in grooming and socio-sexual contexts have been hypothesized to add informative values to other sensory signals, increasing the efficiency of interactions and decision making process (Baraud et al., 2016).

On the whole, all signal types and modalities seem to have important role in red-capped mangabey communication and are equally integrated in complex signalling events: most sequences were multimodal and/or multicomponent; the most frequent signals that were combined with others were of all types and modalities; the proportion of body, facial and vocal signals produced in sequences were almost equal. Additionally, we found no difference in combination network measures between signal types and modalities, except that the clustering coefficient of tactile signals was higher than for audible ones (possibly because of their wide use in playful interactions). These results show that the communication of captive mangabeys relies on all these channels with equal importance, suggesting their complementary roles in communication. This complementarity between signal types, sometimes distinguished as different “communication systems”, is one key argument for the “multimodal theory” of language origins, which advocates that human language emerged from the co-evolution of gestural, vocal and oro-facial communication in the primate lineage, under different ecological and social constraints (e.g. Arbib et al., 2008; Fröhlich et al., 2019; Ghazanfar et al., 2012; Lemasson & Barbu, 2011; Levinson & Holler, 2014; Liebal et al., 2014; Masataka, 2008; Prieur et al., 2019; Vauclair, 2013). Therefore, our results confirm that red-capped mangabey communication has to be studied in an integrated way to take into account its whole complexity, and this might be true for all species particularly when addressing the origin of complex communication and human language.

In that respect, we believe that the descriptive and quantitative method we used to study multimodal and multicomponent communication should permit to make reliable comparisons between species and environments, by enhancing the objectivity of signal sequence description. This should permit to understand the evolutionary determinants leading to more or less frequent use of multiple signalling, such as species sociality or arborealism. Indeed, according to the “social complexity hypothesis” (Dunbar, 2009; Freeberg et al., 2012), species organized in larger groups, with more complex social interactions, might be more likely to use multimodal or multicomponent signalling than others. Additionally, arboreal species may rely less on multicomponent communication than others, because of constraints on the use of gestures, but the modality of signals might be adapted to the distance of communication (Call & Tomasello, 2007; Lemasson, 2011; Liebal, Pika, et al., 2004). Environmental factors might also influence the use of multimodal signalling, which is particularly appropriate for short-distance communication and when animals live in dense habitats (see “efficacy-backup hypothesis”, Fröhlich & van Schaik, 2018; Hebets & Papaj, 2005; Partan & Marler, 2005), as it is the case for red-capped mangabeys which naturally live in high and swamp forest (Gautier-Hion et al., 1999; Jones & Sabater-Pi, 1968; Orimaye, 2017). Comparisons of primate populations living in different environments could also permit to assess the effect of captivity on the frequency of multimodal and multicomponent signalling, giving important insights into the function of multimodal communication. Specifically, the “multiple message hypothesis”, which suggest that multiple signals convey different information that complete each-others (Fröhlich & van Schaik, 2018; Johnstone, 1996; Moller & Pomiankowski, 1993;

Partan & Marler, 1999), predicts that multimodal and multicomponent communication would be more frequent in captivity, due to more socially complex environments and short-distance interactions (Fröhlich & van Schaik, 2018). On the contrary, the “efficacy-backup hypothesis”, which states that multimodality serves to overcome environmental constraints and increase the perceptibility of signals (Fröhlich & van Schaik, 2018; Hebets & Papaj, 2005), predicts that less-dense captive environments would elicit more frequent visual and unimodal signals than in the wild (Fröhlich & van Schaik, 2018).

Conclusion

Captive red-capped mangabeys frequently combined their communicative signals in multimodal and/or multicomponent sequences, under specific contextual and socio-demographic conditions. Completing previous findings from “unimodal” studies, our results highlight the need for a multimodal and multicomponent approach to understand the complexity of mangabey communication. The study of primate multimodal communication is at its beginning, and we believe that the present methodology would enhance future comparisons between species, regarding their use of multimodal and/or multicomponent signalling in different contexts, particularly with the perspective of investigating the evolutionary roots of complex communication and human language.

Conflict of interests: The authors declare that they have no conflict of interest.

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Analyses complémentaires

Suite à la description des séquences de signaux produits par les mangabeys, des analyses complémentaires de nos données d'observation ont été réalisées afin d'explorer la fonction des combinaisons de signaux chez les mangabeys à collier, en termes d'efficacité de la communication.

Certaines hypothèses ont été formulées quant à la fonction de la communication multimodale, en particulier au regard d'une potentielle « interaction » fonctionnelle entre différents signaux combinés (Hebets et Papaj 2005). L'une de ces hypothèses, qui peut être testée en s'intéressant au comportement du receveur suite à la réception de signaux communicatifs, suggère que la communication multimodale permet d'améliorer la détection et la discrimination des signaux (« increased detection and discrimination hypothesis », Fröhlich et van Schaik 2018; Hebets et Papaj 2005). Ainsi, la production de signaux en combinaisons spécifiques, plutôt que seuls, altérerait la réponse du receveur. La probabilité d'obtenir une réponse, la latence nécessaire pour obtenir une réponse, ou bien l'intensité de la réponse reçue pourraient être augmentées (Hebets et Papaj 2005). Une autre possibilité est que la nature même de la réponse du receveur soit modifiée, la combinaison de plusieurs signaux pouvant permettre d'en affiner le sens (Fröhlich et van Schaik 2018), voire de faire émerger une nouvelle signification (Partan et Marler 1999, 2005).

Elargissant cette hypothèse à la combinaison de signaux en général (uni/multimodale ou uni/multicomposante), nous avons supposé que produire des signaux en séquence soit un moyen pour les mangabeys de rendre leur communication plus efficace. En particulier, les mangabeys pourraient utiliser cette stratégie de communication pour augmenter la probabilité d'obtenir une réponse du receveur, notamment après l'échec d'un premier signal. En l'absence d'une réponse satisfaisante de la part du receveur, les mangabeys pourraient en effet répéter leur premier signal (persistance) ou bien produire de nouveaux signaux (élaboration), comme cela a été montré dans la communication gestuelle des grands singes (e.g. Leavens *et al.* 2005; Cartmill et Byrne 2007. **Hypothèse 1 : persistance/élaboration de la communication**). La combinaison de signaux pourrait également être spécifique à un contexte, et être un moyen de préciser le sens des signaux utilisés, lorsque ceux-ci peuvent avoir plusieurs significations (**Hypothèse 2 : combinaison de signaux pour affiner le message**, Fröhlich et van Schaik 2018). Cela a par exemple été mis en évidence chez les bonobos, qui produisent des vocalisations « contest hoot » aussi bien en contextes de jeu ou d'agression. Genty *et al.* (2014) ont cependant montré que la combinaison de ces vocalisations avec des gestes est spécifique au contexte, ce qui suggère que les gestes permettent d'affiner le message convié par les « contest hoots », le receveur pouvant ainsi répondre de manière adéquate.

Hypothèse 1 : Les combinaisons de signaux sont le reflet d'une persistance ou d'une élaboration de la communication en cas d'échec d'un premier signal.

Selon cette hypothèse, un signal qui ne recevrait pas de réponse de la part du receveur devrait plus probablement être suivi de nouveaux signaux communicatifs de la part de l'initiateur, en comparaison à un signal ayant reçu une réponse. Ces nouveaux signaux seraient soit des répétitions du signal initial (persistance), soit des signaux différents (élaboration). Pour chaque mangabey ayant produit des séquences de signaux ($N = 24$), nous avons extrait les occurrences de signaux dits « indépendants », c'est-à-dire produits seuls ou initiant une séquence communicative. Nous avons ensuite comparé la probabilité qu'un signal initie une séquence communicative, selon qu'une réponse du receveur soit observée ou non, une réponse étant définie comme un changement de comportement de la part du receveur entre les 5 secondes précédant et suivant le signal. Pour cela, un modèle linéaire généralisé mixte (GLMM) de type binomial a été utilisé, avec pour effets aléatoires le signal utilisé, le contexte de production, et les identités du signaleur et du receveur. Nous n'avons alors pas trouvé d'effet significatif de la réponse du receveur sur la probabilité que le signal initie une séquence communicative (**Figure 1**, $\chi^2_1 = 2.554$, $P = 0.110$).

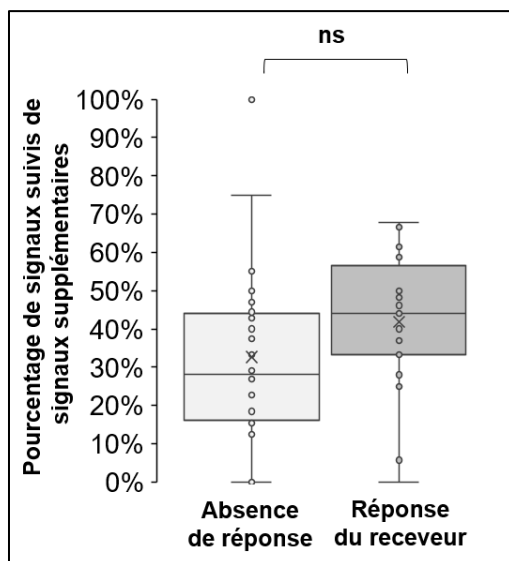


Figure 1. Production de signaux supplémentaires selon que le receveur ait répondu ou non au signal initial ($N = 24$ signaleurs). *ns* : différence non significative (GLMM binomial).

L'hypothèse 1 ne semble donc pas vérifiée. Néanmoins, une analyse plus détaillée de la réponse du receveur serait nécessaire pour l'écarter complètement. En effet, les mangabeys pourraient chercher à améliorer l'efficacité de leur communication non seulement en l'absence de réponse du receveur, mais également lorsque celui-ci donne une réponse qui est insatisfaisante. Nos précédentes observations ont mis en évidence la capacité des mangabeys à persister dans leur communication gestuelle lorsqu'ils n'atteignaient pas leur but (voir **Article 1**). Si cette capacité à produire davantage de signaux de manière tactique existe chez les mangabeys à collier, elle ne semble en tout cas pas être la seule fonction des combinaisons de signaux.

Hypothèse 2 : Les combinaisons de signaux permettent d'affiner le message.

Selon cette hypothèse, un même signal ne devrait pas être observé dans le même contexte selon qu'il soit produit seul ou combiné à d'autres, et ne devrait pas éliciter les mêmes réponses chez le receveur. Afin d'étudier cette hypothèse, nous nous sommes intéressés aux signaux les plus communément combinés à d'autres et produits dans une variété de contextes sociaux chez les mangabeys à collier : les gestes « grab body part » et « throw arm ».

Nous avons tout d'abord comparé la distribution des différents contextes de production de ces signaux, selon qu'ils soient produits seuls ou au sein de séquences communicatives, grâce à des tests exacts de Fisher dont les p-values ont été corrigées avec la méthode FDR. Dans les deux cas, la distribution des contextes de production des gestes « grab body part » et « throw arm » différaient d'une distribution théorique basée sur le budget temps des mangabeys (tests exacts de Fisher : $P < 0.001$ pour chacune de ces comparaisons). De plus, les contextes n'étaient pas les mêmes selon que ces gestes soient produits seuls ou combinés à d'autres signaux (**Figure 2**). En particulier, les ratios de « grab body part » produits en contexte socio-sexuel et en contexte de jeu différaient ($P < 0.001$), ce geste étant davantage produit seul en contexte sexuel et combiné à d'autres signaux en contexte de jeu. Le même effet a été trouvé pour les ratios de « throw arm » produits en contextes de jeu et d'agression ($P = 0.048$), ce geste étant davantage retrouvé en contexte d'agression lorsque produit seul, et en contexte de jeu lorsque combiné à d'autres signaux.

Ces résultats supportent l'hypothèse que certains signaux permettent de clarifier le sens de ceux auxquels ils sont combinés. Ils sont appuyés par les observations préliminaires que nous avons faites des comportements des receveurs suite à la production de « grab body part » et « throw arm » seuls ou au sein de séquences communicatives. La **Figure 3** représente les proportions de comportements du receveur relevés dans les 5 secondes suivant la production du signal, lorsqu'une réponse était observée. Le nombre d'occurrences des gestes seuls étant trop faible pour permettre une analyse statistique, ces résultats sont uniquement descriptifs. Alors que les gestes « grab body part » et « throw arm » seuls semblent principalement provoquer la fuite du receveur, ainsi que l'acceptation d'un contact sexuel dans le cas de « grab body part », leur utilisation en combinaison à d'autres signaux paraît éliciter plus fréquemment des comportements de jeu.

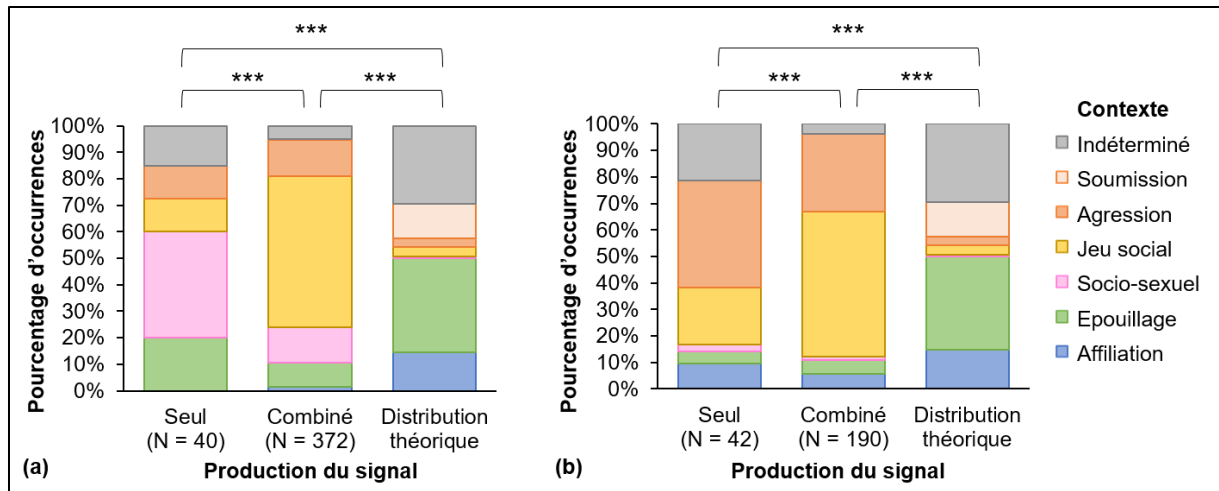


Figure 2. Distribution des contextes de production des gestes « grab body part » (a) et « throw arm » (b) seuls ou combinés à d’autres signaux communicatifs. Les proportions des différents contextes de production des signaux seuls ou en combinaison ont été comparés entre eux et à une distribution théorique grâce à des tests exacts de Fisher. *** : $P < 0.001$; N : nombre d’occurrences du geste.

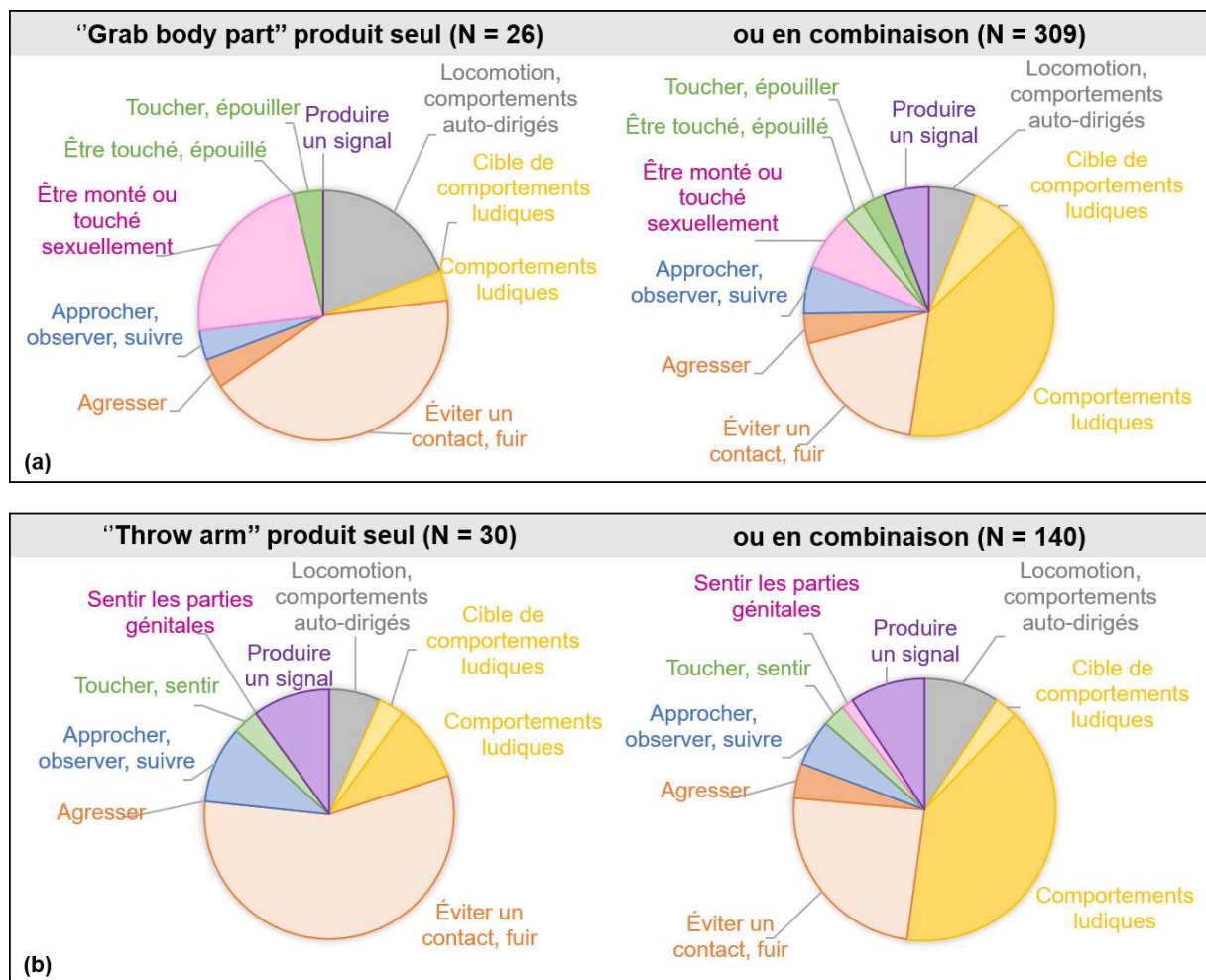


Figure 3. Comportements du receveur observés dans les 5 secondes suivant la production des gestes « grab body part » (a) et « throw arm » (b) seuls ou en combinaisons, lorsqu’une réponse a été observée. N : nombre d’occurrences du geste.

Ces premiers résultats exploratoires sont en faveur de l'hypothèse d'une fonction d'« affinement » du message convié par des combinaisons de signaux (Fröhlich et van Schaik 2018). De futures recherches pourraient permettre d'aborder plus finement cette question, notamment en détaillant les réponses du receveur suite aux différents types de séquences impliquant les gestes « grab body part » et « throw arm », et en prenant en compte une probable variabilité interindividuelle. Il est à noter que les deux hypothèses testées ici ne sont pas mutuellement exclusives, et pourraient expliquer la fonction de la communication multimodale/multicomposante conjointement aux autres hypothèses formulées au regard de la signification ou de l'efficacité de la communication (« content-based and efficacy-based hypotheses », Fröhlich et van Schaik 2018; Hebets et Papaj 2005).

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Chapitre VI

Intentionnalité et multimodalité des gestes : Approche expérimentale





Article 5

Red-capped mangabeys (*Cercocebus torquatus*) adapt their interspecific gestural communication to the recipient's behaviour

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SYNTHESE DE L'ARTICLE 5

Contexte

La sensibilité à l'état attentionnel du receveur et l'adaptation de la communication au comportement de celui-ci sont des marqueurs clés de communication flexible et intentionnelle. De précédentes observations ont montré que la communication gestuelle intraspécifique des mangabeys à collier présentait des marques d'intentionnalité. De plus, une première expérience a été mise en place, impliquant une communication avec un humain, et a montré que la fréquence des gestes des mangabeys dépendait de l'état attentionnel de leur receveur (perçu via l'orientation de sa tête et de son corps).

Méthode

Cherchant à caractériser plus finement l'effet du comportement du receveur sur la communication gestuelle et multimodale des mangabeys, nous avons réalisé une expérience impliquant une quémade alimentaire envers un humain. Un nouveau dispositif a été mis au point, permettant aux mangabeys de se déplacer autour de l'expérimentateur et d'utiliser différentes modalités (visuelle ou acoustique) pour communiquer. Quinze mangabeys à collier ont été testés, selon plusieurs conditions expérimentales en faisant varier l'état attentionnel de l'expérimentateur (i.e. posture de la tête et du corps) ou sa réponse aux gestes des mangabeys, satisfaisante ou non (i.e. récompense alimentaire donnée ou non).

Résultats

Les mangabeys ont produit des gestes de quémade en face de l'expérimentateur uniquement, et en alternant le regard entre leur receveur et la récompense alimentaire. Quand l'expérimentateur leur tournait le dos, les mangabeys se déplaçaient de manière à se repositionner dans le champ visuel de celui-ci, mais n'ont pas utilisé de signaux acoustiques pour attirer son attention. A la différence des grands singes dans des conditions similaires, les mangabeys n'ont pas élaboré leur communication en cas d'absence de réponse satisfaisante de leur receveur. En revanche, ils ont répété leurs gestes lorsque leur but n'était pas atteint (persistance), et n'ont pas produit de gestes lorsque les positions du receveur et de la récompense étaient dissociées.

Conclusion

Ces résultats permettent de confirmer la capacité des mangabeys à adapter leur communication visuelle au comportement de leur receveur : leurs gestes sont dirigés, dépendant de l'attention visuelle du receveur, et répétés en cas d'échec d'un premier signal. Cependant, les mangabeys semblent ne pas utiliser la modalité acoustique de manière flexible pour attirer l'attention ou élaborer leur communication.





OPEN

Red-capped mangabeys (*Cercocebus torquatus*) adapt their interspecific gestural communication to the recipient's behaviour

Juliette Aychet[✉], Pablo Pezzino, Arnaud Rossard, Philippe Bec, Catherine Blois-Heulin & Alban Lemasson

Sensitivity to recipient's attention and responsiveness are critical markers of intentional communication. Although previous research showed that ape gestures can be intentional, few studies have yet addressed this question concerning monkeys. Here, we characterise the effect of a recipient's presence, attentional state and responsiveness on the interspecific gestural communication of captive red-capped mangabeys (*Cercocebus torquatus*). Previous reports showed that they produced learnt begging gestures towards a human recipient preferentially when the latter was facing them. We used here a novel setup that allows subjects to move around an experimenter and to use different modalities (visual and acoustic) to communicate. We found that when the recipient was not facing them, mangabeys moved to a position in the visual field of their recipient rather than using attention-getters. Interestingly, unlike apes, they did not elaborate their communication visually or acoustically when the experimenter did not respond favourably to their begging. However, our results may suggest that begging gestures were goal-directed, since mangabeys inhibited them when the experimenter was not available to answer immediately (i.e. give a reward). Overall, red-capped mangabeys' interspecific visual communication presented intentionality features, but their use of begging gestures was less flexible than that of great apes in similar situations.

Intentionality of non-human primate communication is a key feature for the study of language origins^{1,2}. The first degree of intentionality, first formulated by Dennett³ and studied in animal communication, corresponds to a signal voluntarily transmitted by a signaller toward a recipient in order to change the latter's behaviour^{4,5}, the signaller choosing between different strategies to achieve its social goal⁶. Behavioural indicators, mainly adapted from human developmental studies (e.g.⁷), enable the assessment of the intentionality of a communication signal, notably by evaluating whether the signaller acts as if the signal is social- and goal-directed or not⁸⁻¹⁰. Among these indicators, the social use of the signal, the sensitivity to and manipulation of recipient's attentional state, as well as the goal-dependent persistence and elaboration in signalling, are critical markers of intentional communication.

Therefore, intentionality may be reflected by the effect that the presence and characteristics of a recipient may have on the communication, including the adaptation of the signaller to the recipient's attentional state or its understanding of the signal (e.g.⁸⁻¹¹). Studies addressing this topic on primate gestural communication have focussed mainly on apes, showing that their gestures can be intentional (see reviews:^{5,12,13}), while few studies focus on other non-human primate species^{9,14}. Intentionality markers accompanying non-human primates' gestural communication can be studied by observing intraspecific interactions (e.g.¹⁵⁻²⁰), however control of the recipient's behaviour cannot be applied practically in this context to evaluate rigorously the effects of different characteristics. Consequently, intentionality of non-human primate gestures is often investigated at an interspecific level through an experimental approach, using setups in which subjects produce learnt begging or pointing gestures directed towards a human, in order to obtain a food reward (e.g.²¹⁻³³).

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The social use of begging gestures, that is, the effect of the mere presence of a recipient on the production of the gestures, is a requirement to qualify them as communicative, and thus to study their intentionality^{9,10,12,34,35}. It has been evidenced in great apes (chimpanzees, *Pan troglodytes*, bonobos, *Pan paniscus*, orangutans, *Pongo pygmaeus*, gorillas, *Gorilla gorilla*: e.g.^{21,24,34,36}), but also in several monkey species (Tonkean, rhesus and bonnet macaques, *Macaca tonkeana*, *M. mulatta* and *M. radiata*^{31,33,37,38}; olive baboons, *Papio anubis*^{28,29}; capuchins, *Cebus apella*^{39,40}; and squirrel monkeys, *Saimiri sciureus*²⁶). Moreover, pointing and begging gestures in great apes are accompanied by gaze alternations between the recipient and the food^{21,35,36,41,42}, considered an indicator of intentional communication acquisition during human development^{43,44}. This has been evidenced also in some monkey species' interspecific gestures (i.e. squirrel monkeys⁴⁵; olive baboons^{46,47}; Tonkean and rhesus macaques^{31,38}).

While the effect of recipient's presence reveals the social-dependency of a signal, sensitivity to recipient's attentional state also reflects the fact that signaller intends to direct its signal in order to reach its goal^{9,10}. In that regard, Roberts et al.^{48–50} suggested that intentional gestures themselves evolved from the need to direct effectively the recipient's attention to the goal. To adapt its gestural communication to its recipient's attentional state, a signaller can use different modalities (visual, acoustic, tactile) or display attention-getters before producing a visual gesture⁵¹. The first demonstration was made by Tomasello and colleagues⁵², based on observations of chimpanzees displaying different gestural modalities depending on the recipient's visual attentional state. Then this trait was reported for all great ape genera based on both observational and experimental data (e.g. chimpanzees^{19,22,34,53,54}; bonobos^{15,55}; orangutans^{16,20,56}; and gorillas^{18,56}). Another strategy to deal with recipient's attentional state is to move to a position in the recipient's visual field before gesturing. Reports showed that chimpanzees moved so that they could stay in front of their human recipient before gesturing²³, and a recent study demonstrated this ability in wild bonnet macaques³³. To our knowledge, this has not yet been investigated in other catarrhine or platyrrhine monkeys, although several species are known to be sensitive to a recipient's attentional state for displaying begging gestures, based on the human's head or body posture (olive baboons²⁸; red-capped mangabeys²⁷; Tonkean and rhesus macaques^{31,38}; capuchin monkeys^{39,40}).

Moreover, the flexibility of monkeys' gestural communication regarding their strategy to deal with their recipient's response has been poorly studied (but see recent reports on olive baboons⁵⁷ and bonnet macaques⁵⁸). Indeed, after a signal has been emitted the recipient can either respond favourably regarding the signaller's goal, not respond at all, or respond in an incongruent way. In an intentional communication event, a signaller can be expected to act strategically in order to reach its goal, and so to persist (by repeating the signal) or to elaborate its communication (by modulating the signal or using new ones) when the recipient does not give a satisfying answer^{9,10}. Both persistence and elaboration were brought to light in great apes^{12,13,59,60}, notably using experimental paradigms of interspecific communication where a human either does not give a response or gives a partial response to an ape's begging gestures^{8,25}.

In the current study, we addressed all these aspects of intentionality on the gestural communication of a still poorly studied species of catarrhine monkeys, the red-capped mangabey (*Cercocebus torquatus*), via an experimental approach in captivity. An observational study previously showed that red-capped mangabeys' gestures were adapted to their recipient's attentional state and accompanied by other indices of intentionality such as goal persistence [Schel et al., under review]. Moreover, a first study in controlled conditions showed that red-capped mangabeys produced learnt begging gestures towards a human experimenter preferentially when the latter was facing them²⁷. Our aim here is to characterise more precisely the gestural communication strategies that mangabeys adopt to deal with changes of the recipient's attentional state, and complete the previous findings by evaluating other aspects of intentional communication. For this purpose, we used a novel experimental setup that allowed the subjects to move freely around the experimenter and to use different sensory modalities (visual and audible) to communicate. First, we investigated the social-dependency of learnt begging gestures in red-capped mangabeys, in order to confirm that they were communicative. We hypothesised that (i) red-capped mangabeys would produce them only in the presence of a human recipient and (ii) would display gaze alternation while gesturing. Second, we studied the effect of changes in the recipient's attentional state, based on change of head and body postures. We hypothesised that mangabeys (iii) would produce less begging gestures in front of an inattentive than an attentive recipient, (iv) would position themselves in the visual field of their recipient to communicate, or (v) would use audible attention-getters when gesturing in front of the recipient was not possible. Third, we tested the effect of different recipient's response on the gestural communication of mangabeys, hypothesising that (vi) they would persist in gesturing if the recipient did not respond favourably to their begging, or (vii) would elaborate their communication visually (by changing their gesture amplitude, or producing other visual signals) or acoustically (by producing audible gestures or vocalisations).

Methods

Ethical note. The current study and its experimental procedure have been approved by the Rennes Ethical Committee for Animal Experiment (Authorization N°2019012915271260). The living conditions of the captive mangabeys at the Station Biologique de Paimpont (University Rennes 1, France) follow all applicable international, national and institutional guidelines for the care and use of animals, and are regularly monitored by the local responsible authorities [Housing agreement for research D35-211-18, delivered by the "Direction Départementale de la Cohésion Sociale et de la Protection des Populations" (DDCSPP)].

Subjects and housing conditions. We tested the effect of a recipient's presence and characteristics on the gestural communication of fifteen red-capped mangabeys (*C. torquatus*). Our subjects were ten females and five males between 4 and 31 years old (Table 1), living in social groups of two to thirteen individuals, whose compositions had been stable for at least 20 months. These mangabeys were housed in outdoor-indoor enclosures of

Social group	Subject	Sex	Date of birth	Test location	Previous training experience:	
					Pointing gestures ^{72,80}	Begging gestures ²⁷
I	Bell	Female	31/03/2002	A	Trained	Naive
	Chipie	Female	28/06/1992	A	Trained	Trained
	Chipse	Female	03/01/2006	A	Trained	Trained
	Gofrette	Female	08/11/1996	A	Trained	Trained
	Joly	Female	22/10/2000	A	Trained	Naive
	Julie	Female	08/05/2004	A	Trained	Trained
	Kargi	Male	19/05/2005	A	Naive	Naive
	Litchi	Male	20/04/2015	A	Naive	Naive
	Maillette	Female	29/12/2009	A	Trained	Naive
	Many	Female	14/08/2008	A	Trained	Naive
	Triskelle	Female	21/04/2015	A	Naive	Naive
	Zunie	Female	03/07/1987	A	Trained	Trained
II	Roby	Male	18/11/2010	B	Naive	Naive
III	Coët	Male	31/08/2011	B	Naive	Naive
	Tips	Male	10/07/2011	B	Naive	Naive

Table 1. Characteristics of our red-capped mangabey subjects.

different sizes (from 8 to 26.4 m² for indoor enclosures, 14.7–37.2 m² for outdoor enclosures, and height from 2.5 to 4.4 m). Indoor temperature was maintained at 22 °C, and enclosures were enriched with wood and metal perches, chains and hessian ribbons. The floor of the indoor enclosures was covered with straw and sawdust, while the floor of the outdoor enclosures was covered with cement or bark. Mangabeys were fed twice a day with fresh fruits, vegetables and monkey chow, and water was available ad libitum.

These experiments were conducted between January and April 2019, in the morning or in the afternoon, always before feeding. The tests took place in two outdoor enclosures (A and B, Table 1), depending on the focal social group, each time in the subjects' home cage or an adjacent one. Subjects were trained and tested alone, in physical isolation from their social group but this setup allowed visual and auditory contact with their conspecifics.

Experimental setup. The experimenter was placed in a cubic cage (1.70 × 1.70 × 1.70 m), built for the occasion, in the centre of the test area, thus allowing the subjects to move freely around the experimental setup (Fig. 1a). The experimenter was seated on a 20 cm-high platform, and was able to turn his body towards one side of the cage or another. The metallic grid composing the cage was tight enough to prevent the mangabeys from sticking an arm directly through it (dimensions 2 × 2 cm). Plates of Plexiglas (20 × 40 cm) were hooked on two opposite sides of the cage, with two apertures (diameter 6 cm, 7 cm apart horizontally) through which mangabeys could produce begging gestures (Fig. 1b). The height of the begging-plates was adjustable in relation to the size of the subject (i.e. positioned at the level of the subject's shoulders: 35 cm for juveniles and adult females, and 50 cm for adult males). Velcro strips were placed above 'begging apertures', allowing the experimenter to fix a row of four hanging metallic bells, thus begging through the corresponding aperture was audible. During the tests, the bells were hung only above one aperture of each begging plate, so that the mangabeys could chose to beg through an aperture with or without bells. Moreover, an opaque PVC plate could be fixed on the apertures, to prevent begging gestures on one side of the cage.

Training and habituation. *Begging gesture training.* Begging gestures studied here correspond to an extension of the arm with hand open in the direction of a recipient in order to obtain a reward. Given that red-capped mangabeys do not naturally produce this type of gesture, all our subjects were trained to produce them before conducting the tests. Some subjects had already been trained to produce pointing and/or begging gestures for previous experiments and others were naive (Table 1), yet we used the same methodology for all individuals, ritualizing reaching actions into gestures. Applying the same procedure as in previous studies^{28,29,31}, each training session was composed of three steps during which the experimenter presented a peanut in front of the mangabey, increasing progressively the distance between the reward and the subject. First, the mangabey was able to grasp the reward directly on the hand of the experimenter; second, the reward was held at the limit of the subject's reach, and given as soon as the extension of the arm was produced; finally, the peanut was out of subject's reach and was given only when the arm was extended towards it with hand open, without any grasping movement. Daily training sessions of 5–20 min were performed until the criterion of two consecutive sessions with only valid begging gestures was reached (between 2 and 5 sessions were needed, depending on the subject), and were then regularly performed until the experiments took place. Begging gestures were considered valid if they did not imply any rotation of the subject's body to reach the reward and any grasping actions at the end of arm extension. Training sessions were performed in the indoor enclosure of the subjects' home cage, using the same begging-plates as the ones used subsequently during the experiments, but without the bells (Fig. 1b).

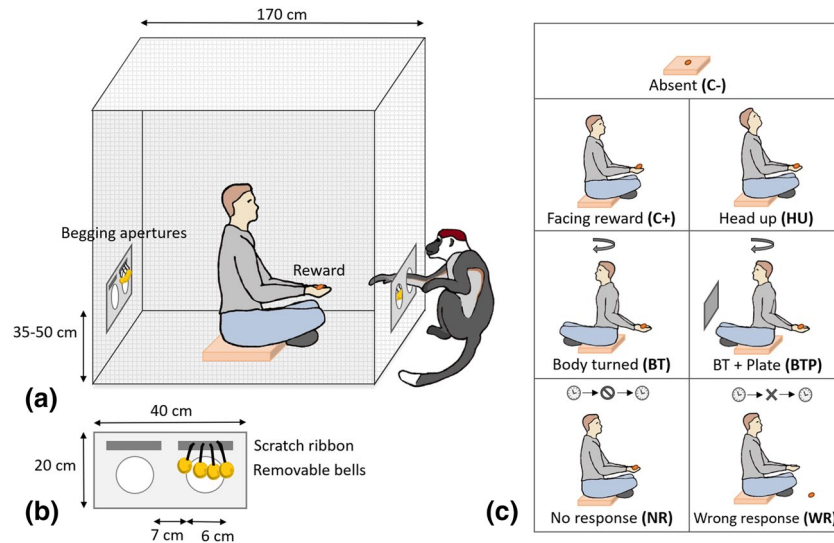


Figure 1. Experimental setup and procedure. (a) The experimenter was placed in a cubic cage in the centre of the test area and presented a peanut in his hands. The mangabey could thus beg for the reward and move freely around the experimenter. (b) Begging-plates were fixed on two opposite sides of the cage, with two apertures above which it was possible to fix a row of bells so that begging gestures would be audible. (c) The presence and attentional state of the experimenter, as well as his responsiveness (i.e. rewarding behaviour) varied with the experimental condition.

Habituation to the bells. Once the mangabeys had acquired the begging gesture, we habituated them to beg with bells hanging in front of the begging apertures, for them to experiment the sound production resulting from the manipulation of the bells, and to reduce neophobia of these objects. Thus, rows of bells were hung above both apertures of the begging-plates (Fig. 1b). We followed the same training procedure as before, alternating training sessions with and without bells, and the same criterion of two consecutive valid sessions was required (between 2 and 7 sessions were needed depending on the subject). These training sessions were then repeated regularly until the experiments took place.

Habituation to the test area and to the cage setup. Two sessions of 10 min—habituation to the test area and to the cage setup were carried out for each individual. Subjects were introduced individually into the test area where the experimenter was sitting inside the cage, presenting a peanut in his hand in front of one of the begging-plates. Subjects could explore the area freely and were encouraged to produce begging gestures, as during the trainings, alternatively through the two accessible sides of the cage.

Experimental procedure. The experimenter sat in the centre of the cage and presented a peanut in his hands at an unreachable distance from the ‘begging apertures’ (50 cm), hands always joint and approached at the same time to the subject when rewarding him, to avoid any laterality bias. The experimenter’s head and body positions and his rewarding behaviour varied with the experimental condition (Fig. 1c). Each subject was exposed to seven different experimental conditions. At the end of each trial, the subject was rewarded regardless of its response. All test trials started when the mangabey positioned itself in front of one begging plate, where it had been rewarded during the preceding trial to standardize the beginning of the trials.

During the positive control condition (C+), the experimenter held a reward in front of him in a standardized position (as during training), with his head and eyes directed towards the subject. The reward was given to the mangabey after 10 s, regardless of its gestural communication²⁷. The ‘head up’ condition (HU) was the same as the positive control condition and lasted 10 s, but the experimenter had modified his attentional state by changing the direction of his head and eyes, to look upwards. In the ‘body turned’ (BT) condition, the experimenter also modified his attentional state by turning his body and head in the opposite direction, but maintained the reward on the same side, i.e. holding the peanut behind his back. After 10 s, the experimenter moved back to his initial position and rewarded the subject. To evaluate mangabeys’ use of attention-getters when they were not able to communicate facing their recipient, we presented a condition where the experimenter’s body and head were turned away from the subject and the ‘begging apertures’ in front of the experimenter were blocked with an opaque plate (BTP condition). The ‘no response’ condition (NR) was similar to the positive control, except that the experimenter did not respond (i.e. give the reward) after the first 10 s (NR.a), and waited instead for 10 supplementary seconds (NR.b) before rewarding the subject. During the ‘wrong response’ condition (WR), the experimenter mimicked giving a reward after 10 s (WR.a) and then took up again the same position as in the positive control condition for 10 more seconds (WR.b) to evaluate whether the subjects would persist or elaborate their begging gestures after not receiving the expected response. In this condition, in order to carry the exact same action of rewarding but without making the peanut reachable to the monkey, the reward was put

Behaviour category	Variable	Variants	Description
Begging gestures	Number of begging gestures	–	Extension of arm through one begging aperture, with hand open and without grasping movement
	Latency for first begging gesture (s)	–	Duration between the start of the experimental trial and the initiation of the first begging gesture
	Begging gesture amplitude	Amplified (Beg+)	Begging gesture amplified so that the entire arm passed through the begging aperture and the arm moved up in front of the experimenter, still without grasping movement of the hand
		Normal	Begging gesture mangabeys had been trained to produce, with forearm extended through the begging aperture, without grasping movement of the hand
		Lessened (Beg–)	Begging gesture with arm not very extended, so that only the hand passed through the begging aperture
Begging aperture chosen	With/without bells	Begging aperture through which the arm is extended when producing the begging gesture	
Other signals	Number of other communication signals	–	Vocalisations ⁸¹ , gestures (Schel et al. <i>under review</i>) or facial expressions (Aychet et al. <i>under review</i>) directed towards the experimenter
Gazes	Number of gaze alternations	–	Three consecutive gazes in a row (i.e. two eye movements) directed alternatively towards the experimenter's face and the reward
	Number of gazes upwards	–	Head and eyes directed upwards
Displacements	Time spent in different locations (s)	Front	Time the subject spent in front of the experimenter
		Back	Time the subject spent behind the experimenter
		Away	Time spent away from the begging sides of the cage, i.e. $> \pm 45^\circ$ from the front of the begging sides
	Change of begging side	Yes/no	Movement around the cage to switch begging side during a trial
	Side chosen to circumvent the cage	Same/different	Side chosen to circumvent the cage being the same or not as the side the experimenter chose to turn his body in BT and BTP conditions

Table 2. Behavioural variables studied.

on the ground in front of the experimenter instead of in the experimenter's hands (see Supplementary Video S1 for examples of each experimental condition).

Each mangabey was subjected to two experimental sessions (2×9 trials in a row), each one included the six abovementioned conditions plus three “motivational trials” (as in Maille et al.'s study²⁷) presented in a random order. Motivational trials were similar to the positive control trials but, contrarily to the experimental trials, the subjects were rewarded as soon as they produced a begging gesture. Moreover, before or after each session, we carried out a negative control trial (C–) for which the experimenter was absent but a reward was visible in the centre of the cage, to evaluate whether begging gestures would be performed in the absence of a human recipient. The two experimental sessions were separated by 1–12 days according to the subject.

We randomized the order of the conditions within a session, and semi-randomized the order in which the individuals were tested (taking into account subjects' social groups and dominance rank within groups). Moreover, we balanced, between sessions of each subject, the position of the bells (above the left or right begging aperture), the direction of rotation of the experimenter when he turned his body (towards the left or towards the right), and the order of the negative control trial (before or after presentation of the other conditions).

Data collection. *Video recording and coding.* The experimental sessions were recorded from inside the test cage by two GoPro White Hero 7 cameras attached to the experimenter's chest and back, so that monkeys were visible on videos of both ‘begging sides’ of the cage. Moreover, a JVC Full HD GZ-RX615 camcorder was positioned outside the test area. Videos were then extracted and coded by a first observer using the software BORIS v.5.1.0⁶¹. Videos taken from inside the cage were used to code the gestures and gazes of the mangabeys during the experiment, and the videos taken from outside were used to code the movements of the subjects around the cage. The detailed variables collected are presented in Table 2. In order to characterize mangabeys' begging gestures depending on experimental conditions, as well as the potential communication elaboration or use of attention-getters, we recorded: the number of begging gestures produced, the latency for first gesture, the gesture amplitude, the aperture chosen to beg and the number of any other communicative signals. We quantified gaze alternations, which are indicator of intentional communication^{43,44}, and upward gazes, which were considered as indices of monkeys' perception of the experimenter's attentional state in HU condition. Finally, in order to assess whether mangabeys preferred to position themselves in the visual field of their recipient, we quantified the time spent in different locations, and recorded whether they circumvented the cage and on which side.

Inter-observer reliability. In order to assess the reliability of the video coding, a second observer coded the behavioural variables for eight random experimental sessions, corresponding to 27% of the total amount of data. We computed Kendall's coefficients of concordance for the quantitative variables (gazes, begging gestures, latency for first gesture, time spent in different locations) and Cohen's kappa coefficients for the qualitative one (gesture amplitude)⁶². A strong agreement^{63,64} was found between the two observers (Gaze alternations: $W = 0.833$, $P < 0.001$; Upward gazes: $W = 0.886$, $P < 0.001$; Begging gestures: $W = 0.958$, $P < 0.001$; Latency for first gesture: $W = 0.882$, $P < 0.001$; Time spent in front, in the back of the experimenter and away from begging sides:

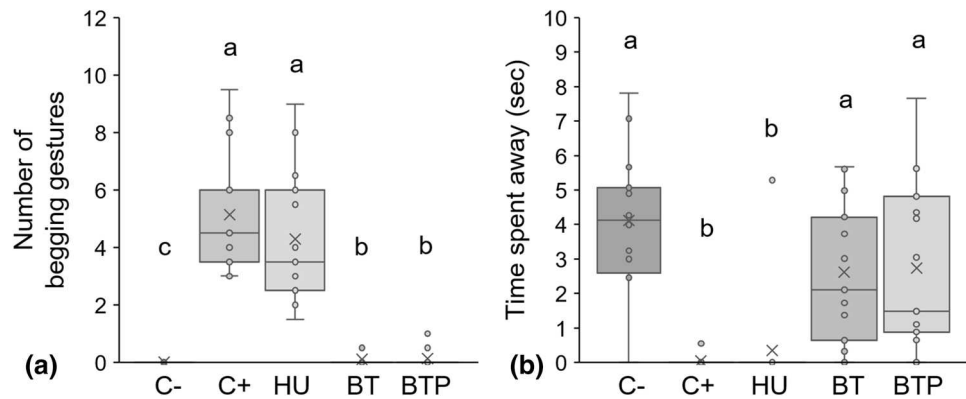


Figure 2. (a) Number of begging gestures produced and (b) time spent away from the ‘begging side’ of the cage (in seconds) in relation to the experimenter’s presence and attentional state. Individual data are plotted as means of sessions A and B. C- experimenter absent, C+ experimenter facing reward and subject, HU head up, BT body turned, BTP body turned and opaque plate blocking begging apertures in front of the experimenter. GLMM negative binomial was used to analyse the number of begging gestures (a) and LMM to analyse the time spent away from the ‘begging side’ of the cage (b). Different lower-case letters indicate significant differences between conditions ($P < 0.05$).

$W = 0.944$, $P < 0.001$, $W = 0.964$, $P < 0.001$ and $W = 0.919$, $P < 0.001$ respectively; Gesture amplitude: $\kappa = 0.841$, $P < 0.001$).

Data analysis. We used R 3.5.0 software⁶⁵ to run all statistical tests and models. All tests were two-tailed and alpha-level was always set at 0.05. First, to assess the effect of the recipient’s presence and attentional state, we compared the mangabeys’ behaviour between C- (absence), C+ (presence), HU (head up), BT and BTP (body turned without and with opaque plate) conditions. Then, we analysed the effect of the recipient’s responsiveness. Within the NR condition, we compared the first 10 s (NR.a) and the last 10 s (NR.b) to assess the effect of receiving no response from the recipient on the mangabeys’ communication gestures. Similarly, C+, WR.a and WR.b conditions were compared to assess the effect of a wrong response from the recipient.

Therefore, generalized linear mixed models (GLMM) and linear mixed models (LMM) were used to analyse the following behavioural variables depending on the relevant experimental conditions (see Supplementary Table S1 for detailed list of models used): number of begging gestures, latencies for first begging gestures, proportions of inhibited and amplified begging gestures, proportions of audible begging gestures, change of begging apertures when gesturing, number of gaze alternations, number of upward gazes, as well as the time that mangabeys spent in front or behind the experimenter, or away from the begging sides of the cage. In each statistical model, the individual, the experimental session and the order of the different conditions within the session were taken into account as random effects. Model quality was assessed by verifying the normality of the residuals, using normal probability plots. When comparing more than two conditions, p-values were adjusted for multiple comparisons using the ‘False Discovery Rate’ (FDR) method, controlling the proportion of false significant p-values⁶⁶.

We tested the correlation between the number of begging gestures and the number of gaze alternations using a Spearman correlation test. Finally, the proportions of individuals who circumvented the cage when the experimenter turned his body, and the proportions of individuals who followed the same side as the experimenter when circumventing the cage, were all tested to differ from a random distribution using exact binomial tests, and were compared between conditions using Fisher’s exact tests for count data.

Results

Effect of presence and attentional state of the recipient. *Presence of a recipient.* Red-capped mangabeys produced approximately 4.5 begging gestures (Median \pm IQR = 4.5 ± 2.5) per trial when the experimenter was present and facing them (C+), while no begging gestures were produced when the experimenter was absent (Fig. 2a, GLMM negative binomial C- vs C+: $Z = -3.915$, $P < 0.001$. See Supplementary Table S2 for detailed results of all models). Moreover, when the experimenter was absent, the subjects spent more time away from the ‘begging side’ of the cage than during the C+ condition (Fig. 2b, LMM C- vs C+: $t = 7.095$, $P < 0.001$). Furthermore, the number of begging gestures produced during the C+ condition was significantly positively correlated with the number of gaze alternations between the reward and the experimenter (Fig. 3, Spearman correlation: $S = 179.65$, $r_s = 0.679$, $P = 0.005$).

Attentional state of the recipient: change of head position. Neither numbers of begging gestures (GLMM negative binomial C+ vs HU: $Z = 1.487$, $P = 0.196$) nor latencies before first begging gesture differed significantly between C+ and HU (Fig. 2a, GLMM Gamma C+ vs HU: $t = -0.247$, $P = 0.960$). However, mangabeys exhibited significantly less gaze alternations when the experimenter held his head up than in the control condition

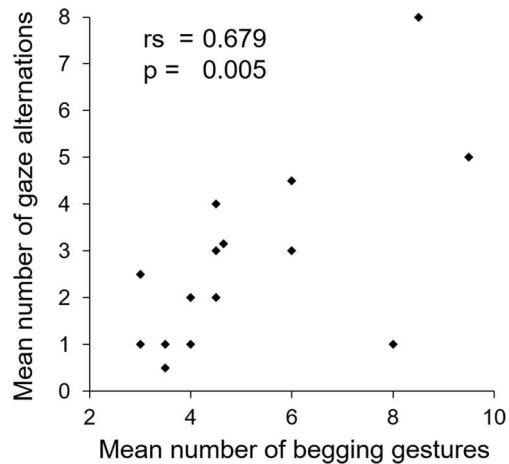


Figure 3. Begging gestures produced by mangabeys in relation to number of gaze alternations between the experimenter and the reward in the positive control condition.

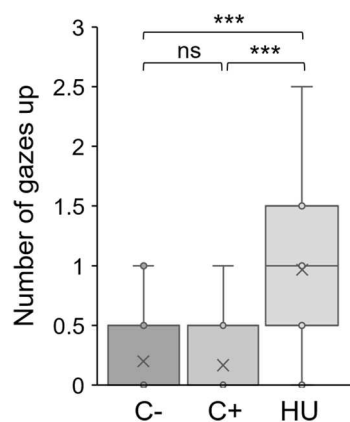


Figure 4. Upward gazes in relation to the experimenter's presence and head position. Individual data are plotted as means of sessions A and B. C- experimenter absent, C+ experimenter facing reward and subject; HU: Head up. GLMM Poisson: *** $P < 0.001$; ns non-significant difference.

(GLMM Poisson C+ vs HU: $Z = -2.679$, $P = 0.007$), and they exhibited more upward gazes (Fig. 4, GLMM Poisson C+ vs HU: $Z = 3.630$, $P < 0.001$).

Attentional state of the recipient: change of body position. Red-capped mangabeys produced few or no begging gestures when the experimenter turned his body away (Fig. 2a, GLMM negative binomial BT vs C+: $Z = -6.954$, $P < 0.001$, BT vs C-: $Z = -2.865$, $P = 0.006$), and there were no significant differences between BT and BTP conditions (GLMM negative binomial BT vs BTP: $Z = 0.417$, $P = 0.846$). Almost all individuals circumvented the cage when the experimenter turned his body, despite the position of the reward (Exact binomial tests: $P < 0.001$ for BT and BTP), while none of them changed side during C+ trials (Fisher exact tests BT vs C+: $P < 0.001$, BT vs BTP: $P = 1.000$). Thus, red-capped mangabeys spent more time away from the 'begging sides' of the cage during BT and BTP than during C+ trials (Fig. 2b, LMM BT and BTP vs C+: $t = 5.231$ and $t = 5.434$, $P < 0.001$), but it tended to be less than during C- trials (LMM BT and BTP vs C-: $t = 2.554$, $P = 0.062$, and $t = 2.409$, $P = 0.066$). Moreover, when circumventing the cage, individuals preferred to use the same side as the experimenter (Exact binomial tests: $P = 0.035$ for BT and $P = 0.007$ for BTP). Taking into account all conditions, subjects spent more time in front of the experimenter than behind him (LMM 'Front' vs 'Back': $t = 13.607$, $P < 0.001$).

Effect of recipient's responsiveness. *No response.* After 10 s without a response from the experimenter, subjects produced less begging gestures (Fig. 5a, GLMM Poisson NR.a vs NR.b: $Z = -4.624$, $P < 0.001$), and the number of gaze alternations decreased (GLMM negative binomial NR.a vs NR.b: $Z = -2.502$, $P = 0.012$). The amplitude of the gestures did not vary when the experimenter did not answer (Fig. 5b, LMM NR.a vs NR.b: $Z = 1.082$, $P = 0.285$ for Beg-, $Z = 1.619$, $P = 0.114$ for Beg+). Moreover, when comparing NR.a and NR.b, subjects

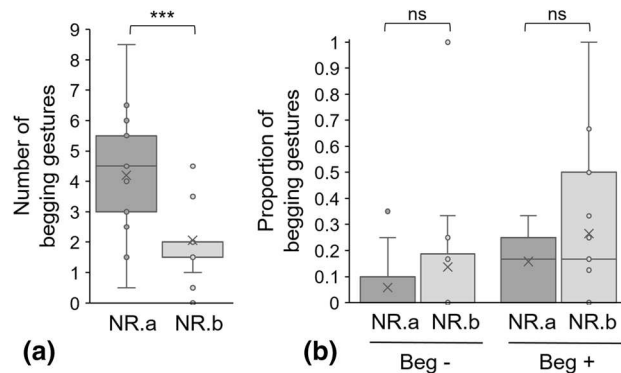


Figure 5. (a) Begging gestures and (b) proportions of lesser (Beg⁻) and amplified (Beg⁺) begging gestures when the experimenter did not answer. Individual data are plotted as means of sessions A and B. NR.a: first 10 s; NR.b: last 10 s. GLMM Poisson was used to analyse the numbers of begging gestures and LMM to analyse the proportions of lesser and amplified begging gestures. *** $P < 0.001$; ns non-significant difference.

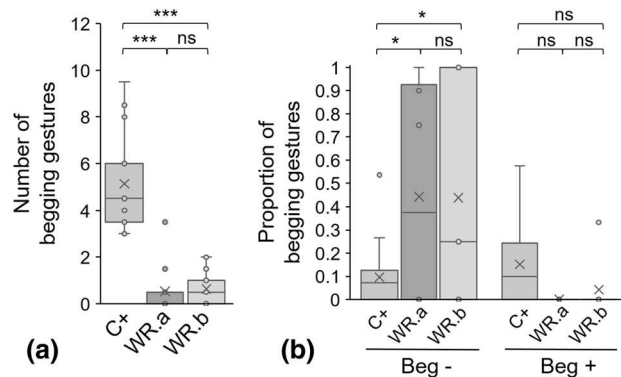


Figure 6. (a) Number of begging gestures and (b) proportion of lesser (Beg⁻) and amplified (Beg⁺) begging gestures when the experimenter gave a wrong response. Individual data are plotted as means of sessions A and B. WR.a: first 10 s; WR.b: last 10 s, after a false response. GLMM Poisson was used to analyse the number of begging gestures (a), and LMM to analyse the proportion of lesser and amplified begging gestures (b). *** $P < 0.001$; * $P < 0.050$; ns non-significant difference.

did not use more the ‘begging apertures’ with bells (LMM NR.a vs NR.b: $t = 0.153$, $P = 0.879$) and did not produce other communication signals in the direction of the experimenter (visual or vocal).

Wrong response. Numbers of begging gestures produced by the subjects when the experimenter gave a wrong response, i.e. mimicked rewarding them (Fig. 6a, GLMM Poisson WR.a vs WR.b: $Z = 0.511$, $P = 0.610$), and latencies before first begging gesture (GLMM Gamma WR.a vs WR.b: $t = -0.016$, $P = 0.988$) did not differ significantly between WR.a and WR.b. In addition, amplitude of gestures did not vary significantly between WR.a and WR.b (LMM WR.a vs WR.b: $t = -0.595$, $P = 0.556$ for Beg⁻, $t = 0.616$, $P = 0.543$ for Beg⁺) and none of the subjects used the begging aperture with bells or produced other communication signals directed towards the experimenter.

In fact, very few begging gestures were produced in these situations, i.e. when the reward was on the ground in front of the experimenter instead of in his hands (Fig. 6a, GLMM Poisson WR.a vs C+: $Z = -8.577$, $P < 0.001$), and latencies before first beg thus increased (GLMM Gamma WR.a vs C+: $t = 5.357$, $P < 0.001$). Moreover, the gestures produced then were of lesser amplitude than during positive control trials (Fig. 6b, LMM WR.a vs C+: $t = 2.978$, $P = 0.014$), and we observed less gaze alternations (GLMM Poisson WR.a vs C+: $Z = -5.220$, $P < 0.001$).

Discussion

The present study aimed to characterise the effect of recipient’s presence, attentional state and responsiveness on red-capped mangabeys’ interspecific gestural communication. We showed that the production of learnt begging gestures depended on the presence and attentional state of the recipient, and our results helped refine our knowledge on the visual cues used by mangabeys to perceive their recipient’s attentional state. We found that when the recipient was not facing them, mangabeys moved to a position in their recipient’s visual field. Interestingly, unlike great apes, our mangabeys did not elaborate their communication visually nor acoustically when the experimenter did not respond or responded incongruently to their begging gestures. Finally, our results suggest

that, when the recipient was not immediately available to answer (i.e. to give a reward), red-capped mangabeys inhibited their begging gestures, which may indicate the goal-directedness of these displays.

The fact that begging gestures were produced only in the presence of the experimenter demonstrates that they are for communication^{34,35}. Moreover, the fact that they were accompanied by gaze alternations between the recipient and the referent (i.e. reward) may reflect red-capped mangabeys' ability to master joint attention, which is notably associated with intentional communication in human infants^{43,67}. In this way, mangabeys may indeed direct the attention of the experimenter toward the food reward⁵⁰. This corroborates previous results showing that gaze alternations accompany learnt begging or pointing gestures in other non-human primate species (e.g., orangutans²¹; chimpanzees^{35,36}; olive baboons^{28,29,47}; rhesus and Tonkean macaques^{31,36}; squirrel monkeys⁴⁵). In olive baboons, the frequency of gaze alternations during requesting-gesture events was not associated with an individual's communication experience with humans⁴⁶. Thus, we assume that present results on gaze alternation in red-capped mangabeys were not conditioned by training but reflect features of spontaneous visual communication.

Red-capped mangabeys produced begging gestures regardless of the upward direction of the recipient's head and eyes. This was surprising regarding previous results showing that they produced less gestures towards an experimenter when she turned her head laterally²⁷. In our experiment, this change of head posture was however discriminated since they produced more upward gazes when experimenter's eyes and head were directed upwards. Thus, in addition to their ability to follow conspecifics' gazes⁶⁸, red-capped mangabeys exhibit abilities to follow a gaze in interspecific interactions, as do rhesus macaques⁶⁹. Moreover, we assume that even when subjects perceive the upward head direction of the experimenter, it does not necessarily mean to them that the recipient is unable to see their gestures. In a terrestrial species of monkeys such as red-capped mangabeys, which may keep monitoring their upward environment even during a social interaction, we hypothesise that head posture is not the most significant cue to predict recipient's incapacity to perceive their visual gesture. Instead, we hypothesise that similarly to gorillas or orangutans, this assessment is mainly based on recipient's body orientation^{56,70}.

Indeed, as Maille and colleagues²⁷ showed previously, red-capped mangabeys perceived body posture as a cue of a recipient's attentional state, as they did not produce any begging gestures when the experimenter turned his back to them. Moreover, this study sheds a new insight into the strategy that mangabeys adopt to deal with this change of recipient's attentional state. Similarly to great apes²³ and wild bonnet macaques³³, red-capped mangabeys moved to position themselves in front of the experimenter, regardless of the position of the reward. They even chose preferentially the same side as the experimenter to turn around the setup, thus avoiding breaking visual contact with him just to be able to attempt to grasp the food. Nevertheless, mangabeys did not produce begging gestures once they had moved in front of the human experimenter in BT condition, and two explanations could account for this. We believe that when the experimenter was facing the subjects but holding the reward in his hands behind his back, the mangabeys did not perceive him as 'available' to give the food reward directly, so therefore they did not beg for it. Additionally, together with the fact that mangabeys produced gaze alternations when gesturing, this suggests that begging gestures could be functionally referential to the food reward^{35,47,71}, especially considering that previous research highlighted red-capped mangabeys' ability for referential gestures⁷². One could also say that the production of the learnt begging gesture is just not very flexible and that during BT condition, the experimenter's posture was too different from the human's posture during training. Reports on olive baboons suggest that associative learning plays an important role in their ability to discriminate human attention cues, yet all communication features of learnt begging gestures do not rely exclusively on training⁷³. Here, mangabeys did gesture in HU condition, in which the experimenter's posture was also different from the one of training phase, which calls into questions the assumption that associative learning would be the only explanation of our subjects' behaviour in BT and BTP conditions.

Interestingly, we did not observe any use of vocalisations or auditory gestures as manipulators of the recipient's attentional state when the latter turned away, even when an opaque plate prevented begging gestures in front of the experimenter. This agrees with observations in macaques (rhesus, Tonkean and bonnet macaques^{31,33,38}), gorillas and orangutans⁵⁶, who did not produce vocalisations or auditory gestures as getters of attention in similar interspecific communication contexts. Chimpanzees produce vocalisations preferentially to gestures in front of a visually-inattentive human^{22,34}, however in a setup when they had the choice to move into their recipient's visual field, they did not use any attention-getters²³. We thus hypothesise that mangabeys did not use visual or auditory attention-getters because they preferred to move directly in front of the human they were interacting with. A supplementary hypothesis is that they do not resort to attention-getters to deal with a recipient's inattentive state in such contexts, or prefer to use tactile signals instead of auditory signals, as do olive baboons in intraspecific communication⁵⁷, but had no possibility to express them in the present situation.

Mangabeys repeated their gestures in the positive control condition, i.e. when, contrarily to training and motivational trials, they were not immediately rewarded. However, considering the decrease of begging occurrences in NR.b condition, this persistence in gesturing seem to not extend after more than 10 s without receiving a response from the recipient. Moreover, when the experimenter gave an incongruent response, we expected that the subjects would persist in the production of begging gestures, as apes can do^{8,25,36,59,74,75}. We noted that red-capped mangabeys produced the same number of gestures before getting any reward (WR.a) and after obtaining a wrong response (WR.b), although few gestures were performed in this specific experimental condition. Since mangabeys did repeat their gestures in the absence of their goal being reached, our hypothesis on communication persistence as a function of recipient's responsiveness seems partially verified, and two explanations could account to explain that the number of begging gestures decreased with time. This could be due to a decrease in their motivation to communicate with a non-responsive recipient, or be related to the steep hierarchical social system of red-capped mangabeys⁷⁶, in which requesting something for too long from a higher-ranking individual (as could be the experimenter) would be avoided.

Cartmill and Byrne²⁵ showed that orangutans do not repeat a gesture that is not efficient, but instead elaborate their communication when they are totally misunderstood by their recipient. Yet, contrary to what we expected based on results for baboons²⁸ and apes (chimpanzees^{8,23,36,64,74}; bonobos¹⁵; gorillas⁷⁷ and orangutans²⁴), we did not observe any elaboration in the visual or auditory modality when the recipient did not answer. Even if we assume that due to the training and habituation to the bells, red-capped mangabeys were able to understand that bells make a noise and can attract attention, as can do Japanese macaques (*Macaca fuscata*⁷⁸), they did not use them as a way to elaborate their begging gesture through the auditory channel. Overall, one hypothesis could be that red-capped mangabeys' interspecific communication possesses only a weak flexibility, due to training or to real interspecific differences with great apes. Other explanations of the absence of elaboration could be related to a lack of possibility to elaborate in the tactile modality, or a lack of motivation from mangabeys to elaborate their signalling, since the begging gesture they learnt is already efficient in most cases.

Finally, considering the few begging gestures recorded when the experimenter had his hands behind him (BT and BTP) or when the reward was on the ground instead of held in his hands (WR), we believe that red-capped mangabeys inhibited their begging when the recipient was not directly available to give the reward. Indeed, Kaminski et al.⁷⁹ suggested that the experimenter's body posture is not only perceived as a cue of attentional state but also encodes disposition to answer. Previous results suggested that great apes^{23,56}, bonnet macaques³³ and capuchin monkeys³⁹ produced less begging gestures when the experimenter and the food location were dissociated. Therefore, this inhibition of gesturing might reflect the fact that red-capped mangabeys are less motivated to beg when communication is less likely to be efficient and may suggest the 'aboutness' of their begging gestures, in other words their intentionality^{3,10}.

Conclusion

To sum up, this study brings to light the adaptation of red-capped mangabeys' interspecific visual communication to their recipient's behaviour. We observed key features of social-directedness in their begging gestures (i.e. gestures depend on the presence and visual attentiveness of a recipient and are accompanied by gaze alternations) and of potential goal-directedness (i.e. gestures depend on the likelihood of recipient to give a satisfying response), which are indices of intentional communication. Furthermore, we refined our knowledge on the visual cues mangabeys perceive as indicators of their recipient's attentional state, and showed that they prefer moving to maintain visual contact with the recipient instead of using acoustic attention-getters. However, mangabeys did not exhibit any audible or visual elaboration of their interspecific communication when recipient did not respond favourably to their gestures. Future research on this species should investigate to what extent the experimental conditions may affect gesture flexibility, to elucidate the significance of the present results regarding red-capped mangabeys' ability to gesture intentionally.

Data availability

All data analysed during this study are available as a supplementary table (Supplementary Table S3).

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Author contributions

J.A., P.P., C.B.H. and A.L. conceived, designed and coordinated the study. P.B. conceived the set-up, P.P. and A.R. carried out the experiment. P.P. and J.A. performed the statistical analyses and J.A. drafted the manuscript with C.B.H. and A.L. All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Competing interests

The authors declare no competing interests.

Additional information

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Supplementary files

Supplementary Table S1. Mixed models used to analyse mangabeys' behaviour depending on experimental conditions.

https://static-content.springer.com/esm/art%3A10.1038%2Fs41598-020-69847-6/MediaObjects/41598_2020_69847_MOESM1_ESM.pdf

Supplementary Table S2. Results of mixed models.

https://static-content.springer.com/esm/art%3A10.1038%2Fs41598-020-69847-6/MediaObjects/41598_2020_69847_MOESM2_ESM.pdf

Supplementary Table S3. Data on red-capped mangabeys' behaviours during the experiment.

https://static-content.springer.com/esm/art%3A10.1038%2Fs41598-020-69847-6/MediaObjects/41598_2020_69847_MOESM3_ESM.xlsx

Supplementary Video V1. Experimental sessions of the female mangabey Bell.

https://static-content.springer.com/esm/art%3A10.1038%2Fs41598-020-69847-6/MediaObjects/41598_2020_69847_MOESM4_ESM.mp4



Chapitre VII

Discussion générale





1. Principaux résultats

L'objectif de ce travail de thèse était de caractériser la communication gestuelle et multimodale de mangabeys à collier, dans le but d'en comprendre les causes et mécanismes cognitifs sous-jacents, et de questionner l'existence de précurseurs du langage dans la communication de singes cercopithécidés (i.e. non-hominoïdes). Nos observations ont permis de compléter la description du répertoire communicatif des mangabeys à collier en captivité (**Articles 1, 2 et 4**), ouvrant la voie à une analyse de leur communication en termes de production intentionnelle, latéralisée et flexible de signaux.

Par une approche observationnelle et expérimentale (**Articles 1 et 5**), nous avons montré que les gestes communicatifs des mangabeys sont accompagnés de tous les marqueurs comportementaux définis pour identifier un signal intentionnel (Townsend *et al.* 2017). De plus, certains gestes sont utilisés de manière flexible dans différents contextes (**Article 1 et 4S** : analyses supplémentaires de l'article 4), et ce phénomène de « means-ends dissociation » peut être un indicateur d'utilisation stratégique de signaux pour atteindre un but social précis (Bruner 1981). Conjointement aux résultats récents concernant les gestes intraspécifiques des babouins olives et des macaques à bonnet (Molesti *et al.* 2019; Gupta et Sinha 2019), cela suggère une capacité des cercopithécidés à communiquer intentionnellement grâce à leurs gestes, y compris des gestes manuels « libres », une capacité jusqu'alors considérée comme unique aux primates hominoïdes. Nos observations offrent également de premiers éléments en faveur d'une production intentionnelle d'expressions faciales par les mangabeys à collier (**Article 2**), et soulignent la valeur communicative de ces signaux, au-delà de simples indices de l'état émotionnel du signaleur.

Nous n'avons pas décelé de latéralisation significative à échelle individuelle ou populationnelle pour la production de gestes brachio-manuels intraspécifiques. En revanche, l'analyse multifactorielle que nous avons utilisée a permis de mettre en lumière un effet important du contexte social sur la main utilisée par les mangabeys pour communiquer (**Article 3**). Ces résultats corroborent des observations de gorilles et de chimpanzés dans leur communication gestuelle spontanée (Prieur *et al.* 2016a, 2017a), et nous suggérons qu'une même méthode soit adoptée pour analyser la communication d'autres primates, en particulier des cercopithécidés, dans la perspective d'une large approche comparative. Les substrats cérébraux de la communication gestuelle intentionnelle des catarrhiniens sont supposément homologues aux aires impliquées dans le langage chez l'humain, ainsi l'analyse des facteurs impactant leur latéralité gestuelle nous renseigne sur les causes ultimes et proximales de la latéralisation du langage (e.g. Meguerditchian *et al.* 2013a; Prieur *et al.* 2019a).

Enfin, nous avons montré que les mangabeys à collier combinent fréquemment différents types et modalités de signaux dans leur communication intraspécifique, et ce de manière flexible, en fonction du contexte et des caractéristiques sociodémographiques du signaleur et du receveur (**Article 4**). La fonction d'une telle complexité de la communication chez les primates est encore indéterminée (e.g. Fröhlich et van Schaik 2018). Nos résultats suggèrent une utilisation flexible de différents types et

modalités de signaux par les mangabeys non pas pour élaborer la communication en cas d'échec d'un premier signal (**Article 4S et 5**), mais possiblement comme un moyen d'affiner le message convié par un signal (notamment gestuel) lorsque celui-ci est associé à différents contextes (**Articles 1, 4 et 4S**). Nos résultats soulignent l'importance d'étudier la communication des primates via une approche multimodale pour en comprendre toute la complexité, en particulier dans le cadre de l'étude des origines évolutives du langage. Nous avons décrit ici la communication multimodale et multicomposante des mangabeys en utilisant une méthode d'analyse de séquences et d'analyse de réseaux. Pour favoriser de futures comparaisons entre espèces, nous proposons cette méthode comme un moyen d'améliorer l'objectivité de telles descriptions, en particulier dans la perspective d'élucider les causes et fonctions de la communication multimodale.

Nous présenterons ici les implications qu'ont nos résultats pour la compréhension des capacités sociocognitives sous-tendant la communication gestuelle et multimodale des cercopithécidés, dans le cadre de l'étude des origines évolutives du langage. Nous discuterons également des limites et perspectives méthodologiques, suggérées par le présent travail, concernant l'étude de l'intentionnalité, de la latéralité et de la multimodalité de la communication des primates non-humains.

2. Intentionnalité de la communication visuelle chez les cercopithécidés

2.1. Communication gestuelle intentionnelle chez des non-hominoïdes

La communication gestuelle des grands singes est reconnue comme étant intentionnelle et flexible (Liebal *et al.* 2014; Byrne *et al.* 2017; Tomasello et Call 2018). Une hypothèse a ainsi été formulée, selon laquelle l'intentionnalité du langage humain a émergé de cette propriété de la communication gestuelle chez l'ancêtre commun des hominoïdes actuels, il y a environ 20 millions d'années (e.g. Pollick et De Waal 2007). Les résultats récents dont ceux présentés ici, émanant d'espèces de cercopithécidés donc plus éloignés de l'humain phylogénétiquement (e.g. Perelman *et al.* 2011; Springer *et al.* 2012), suggèrent cependant une origine encore plus ancienne de la communication intentionnelle, il y a au moins 29 millions d'années, dont aurait émergé le langage.

2.1.1. Mise en évidence de marqueurs d'intentionnalité

La communication gestuelle chez les singes non-hominoïdes a historiquement attiré moins d'attention que celle des grands singes (Slocombe *et al.* 2011) et l'intentionnalité de leurs gestes est débattue. Plusieurs études expérimentales ont mis en évidence certains marqueurs d'intentionnalité dans les gestes interspécifiques (appris) de singes catarrhiniens et platyrrhiniens (e.g. Hattori *et al.* 2007; Anderson *et al.* 2010; Maille *et al.* 2012; Bourjade *et al.* 2013a; Meunier *et al.* 2013c; Canteloup *et al.* 2015a; Defolie *et al.* 2015; Deshpande *et al.* 2018), comme la sensibilité à l'état attentionnel d'un receveur humain ou l'alternance de regards, mais ces approches ne permettaient de valider qu'un seul

des critères d'intentionnalité (« social-directedness », Liebal *et al.* 2014; Townsend *et al.* 2017; Graham *et al.* 2019). Récemment, deux études ont mis en évidence d'autres marqueurs d'intentionnalité dans la production de gestes intraspécifiques des babouins olives (*Papio anubis*, i.e. directionnalité, attente d'une réponse du receveur : Molesti *et al.* 2019) et des macaques à bonnet (*Macaca radiata*, i.e. directionnalité, signal stoppé quand le but supposé est atteint, persistance ou élaboration dans le cas contraire, changement de comportement chez le receveur : Gupta et Sinha 2019). Dans la présente thèse, nous avons complété ces résultats en démontrant que les gestes communicatifs des mangabeys à collier sont accompagnés de *tous* les marqueurs comportementaux définis pour identifier un signal intentionnel.

Les mangabeys produisent leurs gestes communicatifs de manière dirigée vers un receveur et regardent en sa direction avant de produire le signal (« audience checking »). Les gestes visuels sont préférentiellement produits en direction de receveurs attentifs (**Articles 1 et 5**), et les mangabeys adaptent la modalité de leurs gestes dans le cas contraire (**Article 1**). Quand cela est possible cependant, ils se déplacent dans le champ visuel de leur receveur plutôt que d'utiliser des signaux audibles (**Article 5**), comme observé chez les macaques à bonnet et les chimpanzés (*M. radiata* et *Pan troglodytes* : Liebal *et al.* 2004b; Deshpande *et al.* 2018). En contexte expérimental, contrairement au contexte de communication intraspécifique, nous n'avons pas observé d'utilisation de signaux non-visuels par les mangabeys pour attirer l'attention du receveur. Ces résultats sont possiblement dûs à l'impossibilité pour les mangabeys durant l'expérience d'utiliser des signaux tactiles, qu'ils semblent préférer aux signaux acoustiques en contexte intraspécifique (**Article 1** et observations personnelles), similairement aux babouins olives (Molesti *et al.* 2019). En situation expérimentale, les mangabeys ont alterné leur regard entre le receveur et la récompense alimentaire, comme observé chez plusieurs espèces de grands et petits singes (e.g. chez les chimpanzés : Leavens *et al.* 1996, 2004a ; les orang-outans, *Pongo pygmaeus* : Call et Tomasello 1994 ; les babouins olives : Bourjade *et al.* 2013a; Meunier *et al.* 2013c; Lamaury *et al.* 2017 ; les macaques Rhésus et de Tonkéoan, *M. mulatta* et *tonkeana* : Canteloup *et al.* 2015a, b ; les singes écureuils, *Saimiri sciureus* : Anderson *et al.* 2007). Bourjade *et al.* (2015) ont montré que des babouins olives, non entraînés à produire des gestes de quémande, pouvaient produire ces gestes face à un humain et alterner leurs regards entre ce dernier et une récompense alimentaire, à la même fréquence que des singes entraînés. La combinaison de ces alternances de regard avec les gestes dépendaient toutefois de l'entraînement que les babouins avaient reçus, suggérant que les expériences individuelles façonnent le développement de ces marqueurs d'intentionnalité (Bourjade *et al.* 2015). Ce comportement d'alternance de regard, qui suggère une capacité des individus à communiquer de manière référentielle (Franco et Butterworth 1996; Desrochers *et al.* 2014), n'a cependant pas été observé lors d'interactions intraspécifiques, ni chez les mangabeys ni, à notre connaissance, chez d'autres cercopithécidés, probablement en raison de l'extrême rareté des situations élicitant une communication gestuelle triadique chez les primates (Liebal *et al.* 2014). Nous notons qu'une telle alternance de regard peut cependant être observée conjointement à la production de vocalisations chez les mangabeys à

collier, bien que la présence d'aucun autre marqueur d'intentionnalité n'ait jusqu'alors été testée dans leur communication vocale. Les vocalisations « Un+ », produites par les mangabeys lors de conflits, peuvent être accompagnées de regards alternés entre leur opposant et d'autres membres du groupe, de manière à demander une alliance (« recruiting for help », Bouchet *et al.* 2010).

En plus des marqueurs précédemment cités, montrant la directionnalité sociale des gestes des mangabeys, nous avons mis en évidence plusieurs indices suggérant qu'ils sont produits dans un but précis (« goal-directed », Townsend *et al.* 2017). Similairement aux babouins olives (Molesti *et al.* 2019), les mangabeys à collier maintiennent leur regard en direction de leur receveur après avoir produit leur geste, comme une attente de réponse (**Article 1**, « response waiting » : Liebal *et al.* 2014; Townsend *et al.* 2017). Ce marqueur seul ne peut néanmoins pas permettre de démontrer avec certitude que le signal est produit dans un but précis (Liebal *et al.* 2014; Graham *et al.* 2019), et doit être corroboré par une utilisation stratégique d'autres signaux communicatifs pour atteindre ce but (« goal-persistence » : Townsend *et al.* 2017). Il a récemment été montré, pour la première fois dans la communication intraspécifique d'un non-hominoïde, que les macaques à bonnet persistaient ou élaboraient leur communication gestuelle lorsque leur but n'était pas immédiatement atteint (Gupta et Sinha 2019). Nous avons montré qu'il en était de même pour les mangabeys à collier, qui répètent leurs gestes communicatifs lorsque leur premier geste ne reçoit pas de réponse satisfaisante (persistance) (**Article 1 et 5**). En contexte intraspécifique, nous avons montré que les mangabeys pouvaient également élaborer leur communication, en produisant d'autres signaux communicatifs, bien que la persistance soit la stratégie privilégiée (**Article 1**). En contexte expérimental, nous n'avons cependant observé aucune élaboration de la communication, ni visuelle ni acoustique (**Article 5**). Une première explication est que la communication des mangabeys puisse être moins flexible, en termes de capacités d'élaboration, que celle des grands singes dans des conditions expérimentales similaires (e.g. *Pan troglodytes*, *Gorilla gorilla* et *Pongo pygmaeus* : Liebal *et al.* 2004b; Leavens *et al.* 2005; Poss *et al.* 2006; Cartmill et Byrne 2007). Une autre possibilité est l'effet du contexte expérimental, empêchant les mangabeys de communiquer sur la modalité tactile, ou ayant potentiellement un impact sur leur motivation. Enfin, les résultats de notre expérience suggèrent que les mangabeys ne produisent des gestes que lorsque leur receveur est perçu comme susceptible de leur répondre. En effet, nous avons noté qu'ils produisaient moins de gestes lorsque la position de la récompense alimentaire et de l'expérimentateur humain étaient dissociées, comme observé chez les grands singes (Povinelli *et al.* 2003; Botting et Bastian 2019), les macaques à bonnet (Deshpande *et al.* 2018) ou les singes capucins (*Sapajus paella*, Hattori *et al.* 2010). Ces résultats constituent un indice supplémentaire de la capacité des mangabeys à produire des gestes intentionnellement.

Les gestes des mangabeys à collier remplissent donc les trois grands critères d'intentionnalité de premier ordre (i.e. « social-directedness », « goal-directedness » et changement de comportement chez le receveur : Townsend *et al.* 2017)(**Articles 1 et 5**). De plus, certains de ces gestes peuvent être utilisés

de manière flexible dans différents contextes (**Article 1 et 4S**), comme observé chez les macaques de Barbarie (*Macaca sylvanus*, Hesler et Fischer 2007), les macaques à bonnet (Gupta et Sinha 2019) et les babouins olives (Molesti *et al.* 2019).

2.1.2. Implications pour les origines évolutives du langage

Les présents résultats obtenus chez les mangabeys à collier, et ceux obtenus récemment par l'étude d'autres *Papionini* (Molesti *et al.* 2019; Gupta et Sinha 2019), sont des indices convergents en faveur d'une **intentionnalité des gestes des cercopithécidés**. Il est à noter que ces études ne sont pas les premières à mettre en évidence des marqueurs d'intentionnalité dans la communication spontanée d'animaux non-hominoïdes, puisque de tels comportements accompagnent les signaux visuels d'oiseaux (*Corvus corax* : Pika et Bugnyar 2011) et de poissons (*Plectropomus pessuliferus* et *leopardus* : Vail *et al.* 2013) en contexte de coopération. En revanche, en raison de l'éloignement phylogénétique de ces espèces avec les grands singes, cette similarité est sans doute le résultat d'une *convergence évolutive* (Chen *et al.* 2012). Pour retracer l'histoire évolutive de l'intentionnalité de la communication telle qu'elle existe dans le langage humain, nous recherchons ici des traits *homologues* au langage, ce qui pourrait être le cas pour l'intentionnalité des gestes des cercopithécidés. Cette capacité sociocognitive pourrait ainsi être plus ancienne que ce que nous pensions dans l'histoire évolutive des primates, et avoir déjà existé dans la communication gestuelle des ancêtres des catarrhiniens, il y a environ 29 millions d'années. Cette hypothèse pourrait être renforcée ou contredite par la description de la communication gestuelle d'autres cercopithécidés, en dehors des *Papionini*, comme les colobinés dont la communication visuelle n'est que très peu décrite (mais voir par exemple chez les langurs du Nilgiri, *Trachypithecus johnii* : Poirier 1970).

Outre l'intentionnalité des gestes des cercopithécidés, l'une des implications importantes des présents résultats pour les origines du langage concerne la description de **gestes brachio-manuels dits « libres »**, c'est-à-dire n'impliquant pas de contact avec un receveur ou un substrat. Les gestes brachio-manuels intentionnels des grands singes ont attiré jusqu'alors une attention toute particulière pour l'étude des origines du langage, en raison de leur latéralisation, ayant possiblement une origine commune avec la spécialisation hémisphérique des humains pour les fonctions langagières (e.g. Call et Tomasello 2007; Pollick et Dec Waal 2007; Hopkins *et al.* 2012; Roberts *et al.* 2012a; Meguerditchian *et al.* 2013a; Prieur *et al.* 2019a). Bien que ces gestes brachio-manuels « libres » aient longtemps été supposés absents du répertoire communicatif des singes non-hominoïdes (e.g. Call et Tomasello 2007; Pollick et De Waal 2007; Roberts *et al.* 2012a, 2014a), nos observations chez les mangabeys (**Articles 1, 3 et 4**), et celles qui ont été faites chez des babouins olives (Molesti *et al.* 2019) montrent que de tels gestes existent bel et bien dans leur communication intraspécifique. Nous pouvons faire l'hypothèse que la production de ces gestes soit favorisée par les caractéristiques écologiques d'espèces telles que les babouins olives ou les mangabeys à collier, à locomotion semi-terrestre ou terrestre (Jones et Sabater-

Pi 1968; Patel et Wunderlich 2010; Cooke 2012; Mitani *et al.* 2012). En effet, les gestes visuels semblent être davantage présents chez les espèces non-arboricoles, évoluant dans des environnements moins denses qui facilitent la perception de cette modalité de signaux (Marler 1965; Gautier 2001; Lemasson et Barbu 2011; Parr *et al.* 2015). Certains auteurs font l'hypothèse que cet effet de la densité de l'environnement physique des primates ait constitué une contrainte évolutive déterminante pour l'émergence du langage. Selon cette hypothèse, des changements d'habitats arboricoles à terrestres chez les ancêtres communs aux humains et aux autres primates actuels, avec des changements de milieux forestiers à des milieux ouverts, auraient fait partie des contraintes ayant favorisé une communication gestuelle, intentionnelle et latéralisée, dont auraient émergé certaines propriétés langagières (e.g. Gentilucci et Corballis 2006; McNeill 2012; Prieur *et al.* 2019a).

2.2. Intentionnalité des expressions faciales des cercopithécidés : des gestes pas comme les autres ?

Certains auteurs incluent les expressions faciales des primates dans la description de leur communication gestuelle (e.g. Altmann 1962; Maestripieri 1997, 2005; Call et Tomasello 2007; Hesler et Fischer 2007; Molesti *et al.* 2019), tandis que d'autres considèrent les expressions faciales et les gestes comme des signaux différents, considérant qu'ils ne sont peut-être pas sous-tendus par les mêmes mécanismes cognitifs, en particulier en termes d'intentionnalité (e.g. Pollick et De Waal 2007; Genty *et al.* 2009; Hobaiter et Byrne 2011b; Roberts *et al.* 2014a; Byrne *et al.* 2017). En effet, l'intentionnalité de premier ordre des expressions faciales des primates non-humains est encore en question, et peu explorée (e.g. Arbib *et al.* 2008; Hopkins *et al.* 2011b; Slocombe *et al.* 2011; Graham *et al.* 2019. Voir introduction partie 3.1.3.). Nos observations ont permis de montrer que les expressions faciales des mangabeys à collier pouvaient être dirigées vers un receveur, précédées de regards en direction du receveur (« audience checking »), être produites préférentiellement face à un receveur attentif, être suivies d'une attente de réponse (« response waiting »), et induire un changement de comportement chez le receveur (**Article 2**). Ces mêmes marqueurs accompagnent la production de certaines expressions faciales chez les babouins olives (Molesti *et al.* 2019). Cependant, bien que tous les marqueurs comportementaux de directionnalité sociale soient présents (« socially-directed signal », Townsend *et al.* 2017), ces résultats ne permettent pas encore d'affirmer que les expressions faciales des mangabeys et des babouins remplissent les trois critères d'intentionnalité. En effet, le marqueur « response waiting », qui correspond à un maintien du regard du signaleur en direction du receveur après avoir produit le signal, ne peut être à lui seul une preuve que le signal est produit dans un but précis (« goal-directed signal », Townsend *et al.* 2017). En effet, ce maintien de regard peut avoir d'autres explications que l'attente d'une réponse, en particulier dans des contextes élicitant une grande attention sociale, et doit être complété par d'autres marqueurs comme la persistance ou l'élaboration de la communication en cas d'absence de réponse (Liebal *et al.* 2014; Graham *et al.* 2019). Les présents résultats, qui

constituent un premier pas dans l'exploration de l'intentionnalité des expressions faciales des cercopithécidés, devront donc être complétés par d'autres analyses testant la présence de ces marqueurs. Nous pensons que cette perspective pourrait être facilitée par une approche multimodale / multicomposante, pour permettre une analyse plus complète des événements communicatifs impliquant des expressions faciales.

Nos résultats ne permettent pas actuellement de considérer les expressions faciales comme faisant partie de la communication gestuelle intentionnelle des cercopithécidés, mais fournissent de premiers éléments en faveur d'une intentionnalité de premier ordre. De plus, nous avons montré que la plupart des expressions faciales des mangabeys étaient socialement dirigées et induisaient un changement de comportement chez le receveur (**Article 2**), soulignant leur *valeur communicative*, au-delà de simples *indices* d'état interne du signaleur (e.g. Ruxton et Schaefer 2011).

2.3. Perspectives méthodologiques pour l'étude de l'intentionnalité des signaux visuels

Plusieurs perspectives sont envisageables pour améliorer notre approche concernant l'étude de la communication visuelle intentionnelle des cercopithécidés. L'un des principaux axes d'amélioration envisageables réside dans la méthode de description-même des expressions faciales. Nous avons décrit ici le répertoire d'expressions faciales des mangabeys à collier en décrivant les mouvements directement visibles de la bouche, des yeux, des oreilles (**Article 2**). Nous avons identifié, dans ce premier répertoire, différentes variantes pour les expressions faciales impliquant des mouvements de la bouche (« open mouth » et bâillements). Il est cependant très probable que cette première description soit une simplification de la réelle diversité de mouvements faciaux produits par les mangabeys, et nécessiterait d'être complétée par une mesure plus fine des variations d'amplitude de ces mouvements. Le codage des expressions faciales par le système FACS (« Facial Action Coding System », Ekman 1997; Prince *et al.* 2017), développé pour plusieurs espèces de primates non-humains (chimpanzés, gibbons, orang-outans, macaques : Parr *et al.* 2007; Waller *et al.* 2012; Caeiro *et al.* 2013; Julle-Danière *et al.* 2015), permet de coder les expressions faciales selon les mouvements de chaque faisceau de muscles faciaux (identifiés comme des « Action Units »). Son utilisation chez les mangabeys pourrait permettre de différencier ces variantes et d'analyser ainsi plus précisément l'effet du comportement du receveur sur leur production. Chez les orang-outans, cette méthode a notamment permis de mettre en évidence un effet de l'état attentionnel du receveur sur l'amplitude des expressions faciales de jeu (Waller *et al.* 2015). Cela pourrait également permettre de tester une possible élaboration de la communication faciale par les primates non-humains en fonction de la réponse du receveur, car cette élaboration pourrait résider dans une modulation fine des mouvements faciaux. Chez les macaques à crête (*Macaca nigra*), de subtiles variations dans la morphologie de l'expression faciale « silent bared-teeth » induisent des réponses différentes chez le receveur, correspondant à différents contextes (affiliation, socio-sexuel, jeu social, soumission. Clark *et al.* 2020). Ainsi, différentes variantes d'une même expression faciale

pourraient être associées à des intentions différentes de la part du signaleur, qui devraient être distinguées les unes des autres pour pouvoir tester la présence de persistance ou d'élaboration pour satisfaire cette intention.

L'analyse des marqueurs d'intentionnalité accompagnant les signaux des primates non-humains est parfois faite à échelle des différents types de signaux, comptabilisant le pourcentage d'occurrences en présence / absence des différents marqueurs (e.g. Call et Tomasello 2007; Cartmill et Byrne 2010; Gupta et Sinha 2019), comme nous l'avons fait ici pour les expressions faciales et les gestes spontanés des mangabeys (**Articles 1 et 2**). La prise en compte de la variabilité interindividuelle entre les différents signaleurs, pas toujours accessible car nécessitant un échantillonnage important, serait cependant pertinente. Des différences interindividuelles avaient par exemple été mises en lumière dans la capacité des mangabeys à communiquer de manière référentielle (Maille *et al.* 2013), et nous pouvons faire l'hypothèse que ce type de différences existe pour l'intentionnalité de leur communication. En particulier, des caractéristiques comme l'âge du signaleur pourraient impacter sa capacité à produire des signaux intentionnels. Molesti *et al.* (2019) ont par exemple mis en évidence des différences entre les babouins olives nouveau-nés (moins d'un an) et les autres individus juvéniles et adultes, leurs gestes étant moins fréquemment suivis d'une attente de réponse. Ces observations suggèreraient qu'il existe chez les babouins olives, comme chez les humains, un développement des capacités de communication gestuelle intentionnelle dans les premières années de vie des individus (e.g. Bretherton et Bates 1979). Des études longitudinales, sur un plus grand nombre d'individus et sur différentes espèces, permettraient d'éclaircir cet effet de l'âge sur l'intentionnalité de la communication gestuelle des primates non-humains (Liebal *et al.* 2014, 2019). L'intentionnalité de la communication pourrait être acquise par un apprentissage social, par exemple à travers le jeu (e.g. Fagen 1982; Demuru *et al.* 2015), les interactions des jeunes individus avec leurs congénères renforçant peu à peu la directionnalité de leurs signaux et leur capacité à s'adapter au comportement de leurs receveurs (Liebal *et al.* 2019). L'acquisition de cette capacité pourrait aussi être le résultat d'une maturation des régions cérébrales contrôlant la communication intentionnelle, comme suggéré par l'effet de l'âge des individus sur la latéralité gestuelle chez les primates non-humains (e.g. Hopkins et Leavens 1998; Meguerditchian et Vauclair 2006; Prieur *et al.* 2016a).

Outre ces perspectives pour compléter les présentes analyses, la méthodologie d'évaluation de l'intentionnalité de la communication des primates non-humains, basée sur la présence de marqueurs comportementaux, est elle-même actuellement discutée. Les marqueurs comportementaux utilisés pour analyser l'intentionnalité de premier ordre dans la communication des animaux présentent certaines limites de validité lorsqu'ils sont considérés individuellement (e.g. voir Introduction partie 3.1.2. Liebal *et al.* 2014; Graham *et al.* 2019). En effet, chaque marqueur peut avoir une explication autre que l'intentionnalité, et c'est la raison pour laquelle un maximum d'indices différents doivent être pris en compte, plusieurs éléments convergents étant probablement le résultat d'un même mécanisme cognitif

(e.g. Byrne et Bates 2006; Schel *et al.* 2013; Liebal *et al.* 2014; Townsend *et al.* 2017). Malgré tout, l'intentionnalité de premier ordre ne peut jamais être prouvée de manière irréfutable, et certains auteurs ont récemment suggéré des pistes de réflexion méthodologique pour améliorer la distinction entre l'intentionnalité de premier ordre et d'ordre zéro (mécanismes non intentionnels) (Graham *et al.* 2019). Bien que les émotions sous-tendant potentiellement les signaux communicatifs n'excluent pas une production intentionnelle de ces derniers, les marqueurs comportementaux d'intentionnalité doivent théoriquement être produits indépendamment de l'état émotionnel du signaleur pour être valides. Ainsi, afin d'évaluer la part d'émotion et en particulier de niveau d'excitation du signaleur dans l'expression de ces comportements, il est suggéré de compléter l'évaluation comportementale par des mesures physiologiques. Le développement d'outils de mesures compatibles avec l'observation des primates est encore nécessaire (i.e. permettant des mesures en temps réel, sur des individus en mouvement, sans perturber leurs interactions sociales), mais pourrait représenter une nouvelle avancée dans l'évaluation de l'intentionnalité de la communication (Graham *et al.* 2019). Enfin, il est proposé que des expériences soient développées pour évaluer l'intentionnalité de second ordre plutôt que de premier ordre dans la communication des primates, en testant l'effet du niveau de connaissance du receveur sur la communication (Graham *et al.* 2019). L'évaluation de l'intentionnalité de second ordre semble moins largement applicable à différentes espèces et à différents types de signaux communicatifs, car elle implique une capacité des animaux à attribuer un état mental à leurs receveurs, et une fonction *informative* plutôt qu'*impérative* des signaux (voir Introduction, partie 3.1.1., Liebal *et al.* 2014; Townsend *et al.* 2017). Cependant, sa démonstration impliquerait une preuve d'une intentionnalité de premier ordre, tout en contournant la nécessité de s'appuyer sur des critères comportementaux dont la validité est limitée (Graham *et al.* 2019).

3. Facteurs déterminant la latéralité gestuelle

D'après des données comportementales, neuro-anatomiques et fonctionnelles, les gestes intentionnels des primates catarrhiniens, en particulier leurs gestes brachio-manuels, seraient contrôlés par des structures cérébrales homologues aux substrats neuronaux de la production langagière chez l'humain, dans l'hémisphère gauche (Rizzolatti *et al.* 1996; Meunier *et al.* 2013a; Meguerditchian et Vauclair 2014; Prieur *et al.* 2018, 2019a, b). Ainsi, l'étude des facteurs ultimes et proximaux affectant la latéralité gestuelle des primates est un moyen d'élucider les contraintes évolutives ayant contribué à une spécialisation hémisphérique pour le contrôle du langage.

3.1. La communication gestuelle des mangabeys à collier est-elle latéralisée ?

Après avoir identifié des gestes brachio-manuels remplissant les trois critères comportementaux d'intentionnalité dans la communication intraspécifique des mangabeys à collier, nous avons cherché à caractériser la potentielle latéralité de ces gestes. En nous intéressant aux gestes brachio-manuels

intentionnels dans leur ensemble, nous n'avons pas mis en évidence de latéralisation significative, à échelle individuelle ou populationnelle (**Article 3**). Etant donné la latéralité gestuelle à droite observée chez plusieurs singes catarrhiniens (e.g. des babouins olives et des macaques de Tonkéoan : Meguerditchian et Vaclair 2006; Meguerditchian *et al.* 2011b; Meunier *et al.* 2012, 2013a, b), nous faisons l'hypothèse que l'absence de latéralité significative à échelle individuelle ou populationnelle dans la présente étude est due à la taille de notre échantillon, probablement trop faible pour permettre de déceler un biais significatif s'il existe. Le faible nombre d'occurrences de gestes relevés par individu dans cette étude exploratoire pourrait nous empêcher de déceler des latéralisations à échelle individuelle (Hopkins *et al.* 2012). De plus, le nombre d'individus étudiés est souvent limitant pour pouvoir détecter un biais à échelle populationnelle, en particulier lorsqu'il existe une forte variabilité interindividuelle (Hopkins et Cantalupo 2005; Hopkins 2006; Chapelain 2010). Une précédente étude expérimentale avait mis en évidence des préférences manuelles à échelle individuelle pour la production de gestes communicatifs interspécifiques chez les mangabeys à collier (Maille *et al.* 2013). Cette expérience avait montré que les mangabeys ayant les meilleures capacités à produire des gestes référentiels face à un humain (i.e. pointage) étaient latéralisés à droite, mais une grande variabilité interindividuelle avait été observée. Ainsi, cette variabilité pourrait exister également dans la communication gestuelle intraspécifique des mangabeys. Nous suggérons qu'augmenter la taille d'échantillon permettrait également de tester une potentielle latéralité gestuelle des individus pour chaque type de gestes indépendamment les uns des autres. En effet, la direction et la force de la latéralité peuvent dépendre du geste étudié (Hopkins et Leavens 1998; Hopkins et Wesley 2002; Hobaiter et Byrne 2013a; Prieur *et al.* 2016a, 2017a, b). Tester l'hypothèse d'une latéralité gestuelle à échelle populationnelle chez les mangabeys, avec un échantillon plus important, pourra permettre des comparaisons avec d'autres espèces. Cette approche comparative est un moyen de déterminer les facteurs écologiques et sociaux impactant la latéralité gestuelle, comme le degré d'arboricolisme ou la complexité sociale (MacNeilage 2007; MacNeilage *et al.* 2009; Schaafsma *et al.* 2009; Hopkins *et al.* 2011b; Meguerditchian 2014).

Bien que nous n'ayons pas décelé de latéralisation significative à échelle individuelle ou populationnelle pour la production des gestes des mangabeys, une analyse multifactorielle nous a permis de mettre en évidence l'effet de certains facteurs contextuels sur la main utilisée pour communiquer.

3.2. Des facteurs contextuels influencent la latéralité gestuelle

Grâce à un modèle linéaire mixte généralisé, nous avons analysé l'effet de différents facteurs sur la main utilisée par les mangabeys pour communiquer (**Article 3**). Les facteurs liés à la production du geste (posture du signaleur, modalité sensorielle) ainsi que les caractéristiques sociodémographiques des sujets (âge, sexe, relations de dominance et parenté entre le signaleur et le receveur) ne semblent pas avoir d'influence sur la latéralité gestuelle des mangabeys. En revanche, la main utilisée par les mangabeys pour produire leurs gestes dépend de facteurs liés au contexte social, en particulier de la

valence émotionnelle associée à ce contexte et des positions relatives du signaleur et du receveur durant leur interaction.

Les mangabeys à collier utilisent préférentiellement leur main droite pour produire des gestes en contextes négatifs, c'est-à-dire d'agression ou de soumission. Ce même effet du contexte a été observé chez les chimpanzés et les gorilles dans leur communication intraspécifique (Prieur *et al.* 2016a, 2017a). Ces résultats sont étonnants au regard des théories formulées quant aux asymétries cérébrales pour le traitement des émotions (Demaree *et al.* 2005). En effet, une première théorie propose que l'hémisphère droit contrôle la perception et l'expression des émotions (« Right hemisphere theory » : Borod *et al.* 1983; Lindell 2013). La théorie de la valence ou d'approche / recul (« Valence theory » ou « Approach/withdrawal theory » : Silberman et Weingartner 1986; Ehrlichman 1987; Davidson 1992) quant à elle, propose que l'hémisphère droit contrôle les émotions négatives, associées à des comportements de recul, et l'hémisphère gauche les émotions positives, associées à des comportements d'approches. Selon l'une ou l'autre de ces théories, nous pourrions ainsi nous attendre à ce que le côté gauche soit davantage utilisé en contexte social négatif. Rohlfs et Ramirez (2006) notent cependant que les régions préfrontales de l'hémisphère gauche sont activées chez l'humain en contexte d'agression, et que la théorie de la valence est pertinente pour expliquer ces observations. En effet, les contextes sociaux d'agression ne sont pas seulement susceptibles d'induire des émotions négatives, mais impliquent également de fortes motivations d'approches, associées à l'hémisphère gauche selon cette théorie (Silberman et Weingartner 1986; Ehrlichman 1987). Chez d'autres espèces de vertébrés, des comportements d'agression sont également latéralisés à droite et associés à un contrôle de l'hémisphère gauche (e.g. chez des poissons, *Gambusia holbrooki*, *Xenotoca eiseni*, *Betta splendens* : Bisazza et de Santi 2003 ; chez des reptiles comme les anoles verts, *Anolis carolinensis*, et anoles bruns, *Anoles sagnei* : Deckel 1995 ; chez des mammifères non-primates comme le daim européen, *Dama dama* : Jennings 2012 ; mais voir à l'inverse chez les chevaux domestiques et les chevaux de Przewalski, *Equus caballus* et *E. przewalskii* : Austin et Rogers 2012, 2014). Ainsi, la théorie de la valence ou « d'approche / recul » pourrait ainsi expliquer les résultats obtenus sur la latéralité gestuelle intraspécifique des chimpanzés, gorilles et mangabeys à collier (Prieur *et al.* 2016a, 2017a ; **Article 3**). Cette hypothèse est renforcée par la corrélation entre la latéralité manuelle à droite chez les chimpanzés et des comportements d'approche en contexte expérimental (Hopkins et Bennett 1994).

Nous pouvons également faire l'hypothèse que la latéralité gestuelle à droite des catarrhiniens est plus marquée en contextes négatifs en raison d'une flexibilité moins importante induite par ces contextes. Les vocalisations d'alarmes sont plus conservées et moins flexibles au sein d'une espèce que des vocalisations associées à des contextes moins urgents (Bouchet *et al.* 2016). De même, les gestes produits dans des situations d'agressions pourraient être plus latéralisés car moins soumis à l'influence d'autres facteurs proximaux, et plus déterminés par des influences sociales au moment de leur acquisition (théorie de l'origine sociale de la latéralité : Ghirlanda et Vallortigara 2004; Vallortigara et

Rogers 2005; MacNeilage *et al.* 2009). Inclure l'effet du type de geste dans l'analyse chez les mangabeys permettrait de tester cette hypothèse, en s'intéressant en particulier à la latéralité de mêmes gestes produits en contextes négatifs ou positifs. En renouvelant les présentes analyses sur un échantillon plus important, il serait également intéressant de tester l'interaction de plusieurs effets sur la latéralité gestuelle, et notamment le possible effet conjoint du contexte et de la relation de dominance entre signaleur et receveur, pouvant induire des niveaux plus ou moins importants de stress social (Prieur *et al.* 2016a). Le même type d'analyse sur d'autres espèces de cercopithécidés permettrait également de savoir si cet effet de la valence du contexte est généralisable ou non aux catarrhiniens, et ainsi évaluer l'effet de ce facteur dans l'émergence de la latéralité gestuelle. Nous pouvons par exemple tester l'existence de cet effet chez les babouins olives, une latéralité gestuelle à droite étant observée à échelle populationnelle pour un geste produit en contexte agressif, le « hand-slapping » (Meguerditchian et Vauclair 2006; Meguerditchian *et al.* 2011b).

En plus de l'effet de la valence du contexte, nous avons mis en évidence un effet significatif des positions relatives du signaleur et du receveur sur la latéralité gestuelle (**Article 3**). Comme les chimpanzés et les gorilles (Prieur *et al.* 2016a, 2017a, b), les mangabeys à collier communiquent préférentiellement avec la main ipsilatérale à la position de leur receveur, probablement pour diriger plus efficacement leur geste. En effet, chez les chimpanzés et les gorilles, la position du signaleur impacte la main utilisée pour communiquer spécifiquement lorsque le geste utilisé est tactile ou visuel, et donc supposément plus dirigé vers le receveur. De précédentes analyses de la latéralité sociale chez les mangabeys captifs ont montré que les mangabeys approchent préférentiellement leurs congénères dans leur champ visuel droit (Baraud *et al.* 2009). Nous pouvons ainsi faire l'hypothèse que les signaleurs initiant une interaction soient plus susceptibles d'approcher le receveur en se positionnant à sa droite, justement pour mieux diriger leurs gestes si ces derniers sont préférentiellement produits avec le bras droit. Ce lien entre latéralité sociale et latéralité gestuelle pourrait être plus amplement exploré, car potentiellement influencé par le contexte comme l'est la latéralité sociale et visuelle chez de nombreux mammifères (e.g. chez les chevaux domestiques : De Boyer Des Roches *et al.* 2008; Farmer *et al.* 2018 ; les daims européens : Jennings 2012 ; les chimpanzés et gorilles : Quaresmini *et al.* 2014 ; les humains : Lemasson *et al.* 2018b, 2020). En outre, nos résultats soulignent l'importance de prendre en compte la position du receveur lorsque nous étudions la latéralité gestuelle intraspécifique des primates non-humains, ou de contrôler ce paramètre en conditions expérimentales.

Cette analyse exploratoire a mis en lumière l'importance du contexte interactionnel sur la latéralité des gestes des mangabeys (**Article 3**), de la même façon que chez les chimpanzés et les gorilles (Prieur *et al.* 2016a, 2017a, b), suggérant une importance particulière de facteurs sociaux dans l'émergence de la latéralité gestuelle des catarrhiniens. De plus, l'influence de la valence du contexte sur la production de gestes intentionnels souligne le lien étroit entre les mécanismes émotionnels et intentionnels pouvant sous-tendre la communication (e.g. Liebal *et al.* 2014). Cette étude devra être complétée par l'analyse

d'un échantillon plus important de mangabeys à collier, et par une analyse multifactorielle de la latéralité gestuelle d'autres espèces. Ainsi, une large approche comparative permettra de déterminer si les effets observés sont généralisables ou non aux catarrhiniens (voire à d'autres primates), et d'identifier les facteurs ayant pu représenter des contraintes évolutives pour l'émergence de la latéralité des gestes intentionnels, possiblement à l'origine de la spécialisation de l'hémisphère gauche chez l'humain pour les fonctions langagières.

4. Combinaison flexible de différents types et modalités de signaux communicatifs

Nous avons montré que les mangabeys à collier utilisaient leurs gestes de manière intentionnelle et flexible vis-à-vis du contexte (**Articles 1, 2 et 5**), et que la latéralité de ces gestes dépendait de facteurs contextuels (**Article 3**). Nous nous sommes alors intéressés à la flexibilité d'utilisation de leurs signaux en termes de communication multimodale et multicomposante (**Article 4, 4S et 5**). Elucider la fonction d'une telle complexité de la communication chez les primates, et les mécanismes cognitifs qui la sous-tendent, pourrait permettre une meilleure compréhension des origines du langage, dans une perspective multimodale et multicausale.

4.1. Quelles causes et fonctions de la multimodalité de la communication ?

Nos observations ont montré que les mangabeys à collier captifs combinent fréquemment leurs signaux communicatifs, en particulier différentes modalités (visuelle, acoustique, tactile) et types de signaux (gestes, expressions faciales, vocalisations), et ce de manière flexible, en fonction du contexte social et de facteurs sociodémographiques (**Article 4**). De plus, tous les types et modalités de signaux utilisés par les mangabeys sont combinés à la même fréquence, et la plupart des séquences communicatives que nous avons identifiées étaient multimodales et/ou multicomposantes. Nos résultats montrent ainsi que la communication des mangabeys à collier captifs repose sur tous ces modes de communication de manière égale, suggérant leur complémentarité, un argument clé en faveur de l'hypothèse d'une origine multimodale du langage (e.g. Arbib *et al.* 2008; Masataka 2008a; Lemasson et Barbu 2011; Ghazanfar *et al.* 2012; Vauclair 2013; Liebal *et al.* 2014; Levinson et Holler 2014; Fröhlich *et al.* 2019; Prieur *et al.* 2019a). De plus, ces observations soulignent l'importance d'étudier la communication de manière multimodale pour en comprendre la complexité et l'histoire évolutive (e.g. Slocombe *et al.* 2011; Waller *et al.* 2013; Partan 2013; Liebal *et al.* 2014; Fröhlich et van Schaik 2018).

La comparaison de nos résultats avec des observations de mangabeys à l'état sauvage pourrait permettre d'évaluer l'effet de l'environnement captif des mangabeys sur la multimodalité de leur communication, pour en comprendre la fonction. L'hypothèse selon laquelle la communication multimodale ou multicomposante permet de convier différents messages à la fois (« multiple message

hypothesis » : Moller et Pomiankowski 1993; Johnstone 1996; Partan et Marler 1999, 2005; Fröhlich et van Schaik 2018) prédit que ce type de communication soit favorisé en captivité. En effet, certains auteurs suggèrent cet effet de la captivité en raison des courtes distances entre les individus, permettant la perception de signaux sur plusieurs modalités sensorielles (Partan et Marler 2005; Wilke *et al.* 2017; Fröhlich et van Schaik 2018). De plus, la proximité entre individus d'un même groupe en captivité pourrait nécessiter l'utilisation d'une communication plus complexe pour limiter les tensions sociales (Wilke *et al.* 2017). Au contraire, selon l'hypothèse d'une fonction de « backup » des signaux combinés, la communication multimodale et/ou multicomposante serait plus fréquente dans des environnements naturels, qui impliquent davantage de perturbations visuelles et acoustiques contraignant la perceptibilité des signaux (Hebets et Papaj 2005; Fröhlich et van Schaik 2018). Cette fonction de « backup » des signaux multimodaux, lorsque la communication est contrainte par des bruits environnementaux, a été mise en évidence chez d'autres espèces animales. Par exemple, chez les araignées-loups (*Scizocosa retrorsa*), la production de signaux multimodaux visuels et sismiques permet une perceptibilité aussi bien dans des environnements sombres que lumineux, ou aussi bien sur des substrats transmettant les vibrations que ne les transmettant pas (Hebets *et al.* 1996; Hebets et Uetz 1999).

Nos résultats suggèrent que la multimodalité de la communication des mangabeys n'est pas (ou pas seulement) le reflet d'une élaboration de la communication en cas d'absence de réponse satisfaisante de la part du receveur. En effet, les mangabeys ne produisent pas moins de signaux en séquence lorsque le receveur répond à leur premier signal (**Article 4S**), et ne semblent pas privilégier l'élaboration de leurs signaux sur d'autres modalités en cas d'échec de la communication (**Article 1 et 5**). Une autre hypothèse pour expliquer la production fréquente de combinaisons de signaux, y compris de manière multimodale et multicomposante, pourrait être liée à la nature exploratoire des contextes de jeu. En effet, les contextes de jeu font partie des contextes dans lesquels les mangabeys produisent le plus de combinaisons de signaux, produisant les plus longues et diverses séquences communicatives de leur répertoire (**Article 4**). Le jeu social chez les primates élicite une utilisation plus riche et plus flexible de signaux communicatifs que les autres contextes (e.g. chez les grands singes : Pika *et al.* 2003; Liebal *et al.* 2006; Call et Tomasello 2007), avec davantage de gestes idiosyncratiques (e.g. chez les gorilles : Pika *et al.* 2003) et de combinaisons de signaux (e.g. chez les orang-outans : Liebal *et al.* 2006). Ainsi, une communication plus complexe des mangabeys à collier durant le jeu, en particulier pour les juvéniles, corrobore les théories suggérant que le jeu social est un moyen d'explorer et d'expérimenter l'utilisation de signaux communicatifs (e.g. Fagen 1982, 2002; Tomasello *et al.* 1989). La longueur des séquences communicatives en contexte de jeu et d'agression chez les mangabeys pourrait également être le résultat d'une plus forte excitation sociale, en comparaison aux interactions affiliatives et aux épouillages mutuels, comme suggéré chez les orang-outans produisant des séquences de gestes (Tempelmann et Liebal 2012).

Enfin, d'après nos analyses, nous faisons l'hypothèse que les mangabeys à collier combinent leurs signaux communicatifs dans le but d'affiner le message convié, comme chez les grands singes (« refinement hypothesis » : e.g. Genty *et al.* 2014, 2015; Moore 2014; Wilke *et al.* 2017; Fröhlich et van Schaik 2018). En effet, les gestes des mangabeys peuvent être associés à différents contextes (**Article 1** et **4S**) (« means-ends dissociation », Bruner 1981), et leur combinaison à d'autres signaux comme des expressions faciales ou des vocalisations, plus spécifiques à des contextes particuliers (**Article 2**, Bouchet *et al.* 2010), pourrait être nécessaire pour élucider leur signification (Moore 2014). Cette hypothèse est renforcée par le fait que la production de combinaisons de signaux par les mangabeys ait été principalement observée en contextes de jeu et d'agression (**Article 4**), dans lesquels le besoin de lever l'ambiguïté des signaux est plus important que dans d'autres situations. En particulier, en contexte de jeu social, les mangabeys produisent fréquemment des gestes en combinaison à des expressions faciales (**Article 4**), ce qui pourrait refléter une fonction des « open mouth » de préciser la signification ludique de gestes pouvant sembler agressifs (Bateson 1955; Altmann 1967; Bekoff 1975; Waller et Dunbar 2005; Palagi 2008; Waller et Cherry 2012; Demuru *et al.* 2015; Špinka *et al.* 2016). Des contextes tels que l'épouillage mutuel ou les interactions socio-sexuelles élicitent quant à eux moins de combinaisons de signaux, et ces combinaisons sont principalement unimodales (visuelles ou tactiles) et unicomposantes (combinaison de gestes). Chez les grands singes, ces contextes élicitent également moins de combinaisons de signaux et moins de multimodalité (e.g. chez les orang-outans, *P. pygmaeus* : Liebal *et al.* 2006; Tempelmann et Liebal 2012), les signaux utilisés étant supposément plus spécifiques au contexte. Les résultats des premières analyses que nous avons réalisées concernant l'utilisation des gestes « throw arm » et « grab body part » sont elles aussi en faveur de cette hypothèse de « refinement » (**Article 4S**). En effet, les contextes d'utilisation de ces gestes seuls diffèrent de ceux dans lesquels ils sont produits en combinaison à d'autres signaux, et les réponses des receveurs ne sont pas les mêmes. Alors que les gestes « grab body part » et « throw arm » seuls semblent principalement provoquer la fuite du receveur, ainsi que l'acceptation d'un contact sexuel dans le cas de « grab body part », leur utilisation en combinaison à d'autres signaux paraît éliciter plus fréquemment des comportements ludiques. Ces premières analyses pourront être complétées par davantage d'observations des mangabeys dans leur communication spontanée, afin d'augmenter l'échantillon de ce type de combinaisons et tester statistiquement les éventuelles différences de réponses des receveurs. Une approche expérimentale pourrait également être développée pour tester cette hypothèse de « refinement », pour vérifier que ces gestes seuls ou en combinaison à d'autres signaux sont perçus différemment. Quelques expériences ont été menées pour étudier la perception qu'ont les primates des signaux visuels ou multimodaux de leurs congénères. Ces expériences sont basées sur des paradigmes « match-to-sample », dans lesquels les sujets sont incités à sélectionner des images sur un écran tactile et à associer des stimuli congruents (e.g. Parr 2004; Parr et Heintz 2009; Micheletta *et al.* 2015; Waller *et al.* 2016b). Ce type de paradigme pourrait être utilisé pour tester si les mangabeys associent la production de signaux seuls ou en

combinaison à des interactions sociales différentes entre un receveur et un signaleur (voir la perception des expressions faciales chez les macaques à crête : Waller *et al.* 2016b).

Ainsi, nos résultats soulignent l'importance d'une approche « multimodale » pour comprendre la complexité de la communication des primates. Nos résultats apportent de premiers éléments de compréhension quant à la fonction des combinaisons de signaux. De futures comparaisons à d'autres espèces et dans différents environnements permettront d'affiner nos connaissances quant aux possibles contraintes évolutives ayant favorisé une telle complexité de la communication des primates humains et non-humains. Dans cette perspective, la méthodologie que nous avons utilisée pourrait permettre d'améliorer l'objectivité de la description des combinaisons de signaux, et favoriser les approches comparatives.

4.2. Développement d'une méthodologie descriptive pour l'étude de la multimodalité

Un premier aspect de notre méthodologie que nous proposons comme un moyen d'améliorer l'objectivité de futures comparaisons entre espèces est la définition temporelle des combinaisons de signaux. Nous proposons de définir les combinaisons de signaux comme faisant partie d'une même séquence communicative, cette séquence correspondant à des signaux produits par un même signaleur, vers un même receveur, et dont l'initiation est séparée par une latence déterminée sur une base d'observation des primates étudiés. Pour déterminer cette latence « seuil », nous nous sommes basés sur la fréquence des latences entre signaux observés dans notre population de mangabeys, et avons utilisé une méthode graphique utilisée dans les études sur les échanges vocaux (Lemasson *et al.* 2010, 2018a; Levréro *et al.* 2019). Nous pensons que cette méthode est un moyen d'utiliser la même définition pour toutes les espèces et populations de primates étudiés, tout en utilisant une fenêtre temporelle cohérente avec la biologie de l'espèce. Pour décrire de manière systématique les combinaisons de signaux produites par les mangabeys à collier dans leur communication intraspécifique, et en particulier les combinaisons multimodales et multicomposantes, nous avons utilisé une méthodologie basée sur de l'analyse séquentielle et de l'analyse de réseau. L'analyse de séquence avec l'outil {TraMineR} (Gabadinho *et al.* 2011), initialement développé pour les études de sciences sociales, nous a permis de regrouper les séquences communicatives des mangabeys sur la base de leurs similarités. L'analyse de séquence permet ainsi d'identifier les séquences de signaux typiquement produites au sein d'une population, tout en prenant en compte et en représentant la diversité des événements communicatifs observés (Baraud *et al.* 2016). De plus, l'analyse des combinaisons de signaux par une analyse de réseau est un moyen de représenter graphiquement et de quantifier objectivement les combinaisons les plus fréquentes au sein d'une population. L'utilisation de ce type de méthode chez d'autres espèces et dans d'autres environnements permettrait des comparaisons objectives de la fréquence de combinaisons multimodales ou multicomposantes dans différents contextes. Une plus large approche comparative permettrait de comprendre l'effet de caractéristiques de l'espèce sur la multimodalité, comme le degré

de socialité et l'arboricolisme, ou comme expliqué précédemment, l'effet de l'environnement des primates étudiés. De plus, la description systématique de la communication multimodale et multicomposante des primates ouvre la voie à une étude plus approfondie et plus intégrative de la communication, telle qu'elle est produite par le signaleur et perçue par le receveur.

5. Principales perspectives

En résumé, ce travail de thèse pourra être complété par des observations et expérimentations supplémentaires pour investiguer plus en détail la communication des mangabeys à collier, mais également la communication d'autres primates dans une perspective comparative.

D'une part, nous notons que la taille de notre échantillon a parfois été limitante dans nos analyses sur les propriétés de la communication gestuelle et multimodale des mangabeys. Répliquer les présentes études sur un nombre d'individus et de signaux plus important pourrait permettre de compléter l'étude de l'intentionnalité des gestes et expressions faciales avec une plus grande prise en compte de la variabilité interindividuelle (voir partie 2.3.). Comme évoqué précédemment, l'étude de cette variabilité pourrait, par exemple, nous renseigner sur l'ontogénie de l'intentionnalité de la communication. La flexibilité d'utilisation des gestes devra également être examinée à échelle individuelle, pour examiner dans quelles mesures de *mêmes* individus utilisent un geste dans différents contextes. La latéralité des gestes intentionnels devra elle-même être caractérisée sur un échantillon plus conséquent, afin de prendre en compte les potentiels effets d'autres facteurs que ceux étudiés ici, comme le type de gestes produits ou l'interaction entre plusieurs facteurs contextuels et sociodémographiques (voir partie 3.2.). De même, la fonction des combinaisons de signaux chez les mangabeys pourra être testée avec plus de certitude par la collecte de données d'observations supplémentaires et/ou par la mise en place d'expériences sur la perception de ces signaux.

D'autre part, nous soulignons que la méthodologie utilisée dans cette thèse pour évaluer l'intentionnalité de la communication présente certaines limites (voir partie 2.3.). Nous avons évoqué la perspective d'utiliser d'autres outils de description des signaux (e.g. la description des expressions faciales par le système FACS) pour en étudier l'intentionnalité de premier ordre. Il est à noter toutefois que la pertinence de l'analyse de l'intentionnalité de premier ordre par des marqueurs comportementaux peut elle-même être discutée (voir partie 2.3., Liebal *et al.* 2014; Graham *et al.* 2019). A ce jour, les perspectives d'amélioration de la fiabilité de l'étude de l'intentionnalité consistent au développement de méthodes d'analyses physiologiques, afin de mesurer l'excitation des individus lors de la communication, voire des expériences pour évaluer l'intentionnalité de second ordre (Graham *et al.* 2019).

Enfin, les présents résultats devront être complétés par des analyses semblables chez d'autres populations de mangabeys à collier, notamment à l'état sauvage, pour estimer l'effet de l'environnement

captif sur les présents résultats (voir partie 4.1.). Une approche comparative entre différentes espèces de cercopithécidés, et de primates non-humains en général, pourrait permettre d'évaluer les causes proximales et ultimes de la communication gestuelle et multimodale, et tenter de reconstituer l'histoire évolutive des différents traits sociocognitifs impliqués.

6. Conclusion

Pour conclure, les présentes études observationnelles et expérimentales chez des mangabeys à collier captifs mettent en évidence la présence de potentiels précurseurs du langage dans la communication gestuelle et multimodale de singes cercopithécidés.

Nous avons montré que les gestes des mangabeys à collier remplissent les trois critères d'intentionnalité de premier ordre, puisqu'ils semblent produits dans un but social précis, sont dirigés vers un receveur pour atteindre ce but, et induisent un changement de comportement chez celui-ci. De plus, certains de ces gestes peuvent être utilisés de manière flexible dans différents contextes. Ces résultats et les récentes observations faites sur des babouins olives et des macaques à bonnet constituent des indices convergents en faveur d'une **intentionnalité des gestes des cercopithécidés**. Cette propriété sociocognitive langagière pourrait ainsi être plus ancienne que ce que nous pensions dans l'histoire évolutive des primates, et être héritée de la communication gestuelle des ancêtres des catarrhiniens, il y a environ 29 millions d'années. Nos résultats fournissent également de premiers éléments en faveur d'une intentionnalité de premier ordre des expressions faciales des cercopithécidés.

Parmi les gestes intentionnels décrits dans la communication intraspécifique des mangabeys, nous avons identifié des **gestes brachio-manuels dits « libres »**, longtemps supposés absents du répertoire communicatif des singes non-hominoïdes. La caractérisation de la production de gestes brachio-manuels chez les mangabeys a mis en lumière l'**effet significatif du contexte interactionnel sur leur latéralité**. De même que les chimpanzés et les gorilles, les mangabeys utilisent préférentiellement le côté droit pour communiquer en contextes négatifs, et préférentiellement la main ipsilatérale à la position du receveur, de manière à diriger leurs gestes. Nos résultats suggèrent ainsi une importance particulière de facteurs sociaux dans l'émergence de la latéralité gestuelle des catarrhiniens. Ils devront être complétés par l'analyse d'un échantillon plus important de mangabeys à collier, et par une analyse multifactorielle de la latéralité gestuelle d'autres espèces, pour comprendre les origines évolutives de la spécialisation de l'hémisphère gauche chez l'humain pour les fonctions langagières.

Enfin, nous avons décrit la **communication multimodale et multicomposante** des mangabeys à collier, et montré qu'ils combinent de manière **flexible** des signaux de différentes modalités (visuelle, tactile, audible) et différents types (gestes, expressions faciales, vocalisation), en fonction du contexte et de facteurs sociodémographiques. Nos résultats soulignent l'importance d'une approche « multimodale » pour comprendre la complexité de la communication des primates, et suggèrent une

complémentarité des différents systèmes de communication, un argument clé en faveur de l'hypothèse d'une origine multimodale du langage. De plus, nos analyses apportent de premiers éléments de compréhension quant à la fonction des combinaisons de signaux chez les cercopithécidés, qui pourraient être un moyen d'affiner le message convié, comme chez les grands singes et les humains.

Les présents résultats pourront être complétés par une caractérisation de la communication gestuelle et multimodale, en termes d'intentionnalité, de latéralité et de flexibilité, chez d'autres espèces de singes catarrhiniens, avec divers systèmes sociaux et caractéristiques écologiques. La méthode que nous avons utilisée pour décrire la communication multimodale et multicomposante des mangabeys pourrait être appliquée à d'autres espèces et d'autres environnements, à la fois dans la perspective d'étudier les causes ultimes et proximales de la communication multimodale des primates, dont le langage, mais également pour évaluer l'intentionnalité et la flexibilité de la communication de manière plus intégrative.



Chapitre VIII

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Chapitre IX

Annexes





Annexe 1 - Liste des publications

Publications dans des revues internationales avec comité de lecture

- **Aychet, J.**, Pezzino, P., Rossard, A., Bec, P., Blois-Heulin, C., Lemasson, A. (2020). Red-capped mangabeys (*Cercocebus torquatus*) adapt their interspecific gestural communication to the recipient's behaviour. *Scientific Reports* 10, 12843. <https://doi.org/10.1038/s41598-020-69847-6>
- **Aychet, J.**, Blois-Heulin, C., Palagi, E., Lemasson, A. (2020). Facial displays in red-capped mangabeys (*Cercocebus torquatus*): repertoire, social context, and potential intentionality. *Journal of Comparative Psychology*. <https://doi.org/10.1037/com0000252>

Articles en préparation ou en révision pour publication

- Schel, A. M., Bono, A., **Aychet, J.**, Pika, S., Lemasson, A. (under review). Intentional gesturing in red-capped mangabeys (*Cercocebus torquatus*).
- **Aychet, J.**, Blois-Heulin, C., Lemasson, A. (in prep.). Using sequential and network analyses to describe multimodal and multicomponent communication in captive red-capped mangabeys.
- **Aychet, J.**, Blois-Heulin, C., Lemasson, A. (in prep.). Multifactorial analysis of gestural laterality in captive red-capped mangabeys (*Cercocebus torquatus*).



Annexe 2 - Communications dans des colloques nationaux et internationaux

Communication orale (*voir résumé page suivante*)

- **Aychet, J.**, Pezzino, P., Rossard, A., Bec, P., Blois-Heulin, C., Lemasson, A. (2019). Effet d'audience sur la communication gestuelle des mangabeys à collier (*Cercocebus torquatus*). 32ème colloque de la Société Francophone de Primatologie (SFDP), 2-5 Octobre 2019, Parc de Branféré, France.

Communications affichées (*voir poster page suivante*)

- **Aychet, J.**, Palagi, E., Blois-Heulin, C., Lemasson, A. (2019). Social and intentional use of facial expressions in red-capped mangabeys (*Cercocebus torquatus*). Summer Conference of the Association for the Study of Animal Behaviour (ASAB), 26-28 Août 2019, Université de Konstanz, Allemagne.
- **Aychet, J.**, Palagi, E., Blois-Heulin, C., Lemasson, A. (2019). Social and intentional use of facial expressions in red-capped mangabeys (*Cercocebus torquatus*). 32ème colloque de la Société Francophone de Primatologie (SFDP), 2-5 Octobre 2019, Parc de Branféré, France.
- **Aychet, J.**, Palagi, E., Blois-Heulin, C., Lemasson, A. (2019). Social and intentional use of facial expressions in red-capped mangabeys (*Cercocebus torquatus*). Journées scientifiques de l'école doctorale Biologie Santé (BS), 10-11 Décembre 2019, Angers, France.

32ème colloque de la Société Francophone de Primatologie (SFDP)

Effet d'audience sur la communication gestuelle des mangabeys à collier (*C. torquatus*)

Aychet Juliette, Pezzino Pablo, Rossard Arnaud, Bec Philippe, Blois-Heulin Catherine, Lemasson Alban
Univ Rennes, Normandie Univ, CNRS, EthoS (Éthologie animale et humaine) - UMR 6552

L'intentionnalité de la communication chez les primates non-humains est une problématique clé dans l'étude des origines du langage. Des critères comportementaux permettent d'évaluer l'intentionnalité des signaux communicatifs, comme la directionnalité des signaux envers une audience, la persistance ou l'élaboration de la communication lorsque le receveur ne répond pas favorablement... Parmi ces critères, l'effet d'audience est un marqueur central de communication intentionnelle. Il se définit comme l'effet de la présence d'une audience sur la communication, mais également comme l'adaptation de l'émetteur à l'état attentionnel de son audience, et à sa compréhension des signaux communicatifs. L'effet d'audience sur la communication gestuelle des primates peut être étudié expérimentalement, via des paradigmes impliquant la production de gestes de quémade d'une récompense en direction d'un expérimentateur humain. Bien que l'effet d'audience sur les gestes communicatifs ait été principalement étudié chez les grands singes, de précédentes études ont mis en évidence une sensibilité à l'état attentionnel du receveur chez des singes de l'Ancien Monde. En particulier, de précédents travaux sur les mangabeys à collier (*Cercocebus torquatus*) ont montré que ces derniers produisaient davantage de gestes de quémade face à un expérimentateur visuellement attentif, leur perception de l'état attentionnel du receveur reposant sur la position de la tête et du corps de celui-ci.

Grâce à un dispositif expérimental original, nous avons cherché ici à mieux caractériser les stratégies de communication gestuelle des mangabeys face à ces modifications de l'état attentionnel de l'audience ; notamment en permettant aux sujets de se déplacer autour de l'expérimentateur ou d'utiliser différentes modalités pour communiquer. De plus, nous nous sommes intéressés à la flexibilité de la communication des mangabeys face à différents degrés de réponse du receveur, en terme de persistance (répétition des signaux communicatifs), d'élaboration (modification des signaux communicatifs) ou d'inhibition de la communication. Quinze individus captifs ont ainsi été entraînés à produire des gestes de quémade envers un expérimentateur, et ont été testés à la Station Biologique de Paimpont (France), à raison de deux sessions expérimentales chacun. Chaque session comprenait sept conditions expérimentales, dans lesquelles l'état attentionnel de l'expérimentateur et le degré de réponse face aux quémades étaient variables.

Nous avons pu noter que la production des gestes de quémade par les mangabeys était dépendante de la présence d'une audience, et s'accompagnait d'alternances de regards entre la récompense et le receveur humain, attestant de la valeur communicative de ces gestes. Nos résultats ont également permis de préciser les indices visuels utilisés par les mangabeys pour évaluer l'état attentionnel de leur audience. De plus, nous avons montré que les mangabés cherchaient à être placés dans le champ visuel du receveur, en dépit de la position de la récompense. Lorsque l'audience n'était pas attentive ou pas disposée à répondre, nous avons observé une inhibition de la production des gestes de quémade, ces gestes étant bien produits volontairement et dans un but précis.

Par ailleurs, nous avons observé une modulation de l'amplitude des gestes de quémade en comparaison aux gestes auxquels les sujets avaient été entraînés, mais ces différentes amplitudes de gestes n'étaient pas modulées en fonction de l'audience. De plus, nous n'avons pas noté d'élaboration de la communication via la modalité acoustique lorsque le receveur ne répondait pas ou en partie aux gestes de quémade. Ces résultats sont particulièrement intéressants au regard de ceux obtenus chez les grands singes dans des conditions expérimentales similaires, suggérant différents niveaux de flexibilité de la communication gestuelle.

Singes de l'Ancien Monde, geste, intentionnalité, état attentionnel, flexibilité



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Social and intentional use of facial expressions in red-capped mangabeys

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INTRODUCTION

Primates produce a wide range of expressive facial movements, thanks to their complex facial musculature¹. The dual intentional and emotional use of facial expressions has been recently suggested for apes^{2,3,4}. However, the question **whether monkeys produce facial expressions intentionally to communicate** remains open. We tested here whether red-capped mangabeys (*Cercocebus torquatus*) use facial displays socially and concomitantly to behavioural markers of intentional communication⁵.

METHODS

Focal animal sampling (15.67 ± 0.10 min per individual)

25 captive mangabeys living in five social groups -10 ♀ and 15 ♂ (from 3 to 31 yo)

Facial expressions = all facial movements (i.e. mouth and lips, eyebrows, ears) that could be produced either alone or combined with others, during social interactions or not^{6,7,8}.



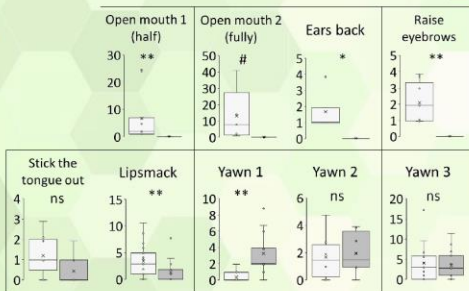
Station Biologique de Paimpont

SOCIAL CONTEXTS OF FACIAL DISPLAYS

Context determination was based on signaller's behaviours 5 sec before and 5 sec after facial display.

Mean numbers of occurrences in social / non social contexts: (Wilcoxon tests)

□ SOCIAL
■ NONSOCIAL



Total numbers of occurrences depending on contexts: (Fisher's exact tests)

	Open mouth 1 (half)	Open mouth 2 (fully)	Ears back	Raise eyebrows	Stick the tongue out	Lipsmack	Yawn 1 (teeth covered)	Yawn 2 (canines visible)	Yawn 3 (all teeth visible)	
***	***	***	***	NS	***	***	***	**	***	
> 90%	0	0	8	0	4	24	0	0	0	Affiliative
75-90%	0	0	0	0	1	47	0	0	0	Grooming
50-75%	0	0	0	0	0	1	0	0	0	Sexual
25-50%	62	63	0	0	0	0	0	0	0	Playful
10-25%	9	1	0	22	1	1	4	7	32	Agonistic
< 10%	1	0	0	1	0	1	0	0	0	Submissive
	0	0	0	0	0	0	0	1	21	Alarm
	2	0	4	5	5	7	1	6	10	Other
	0	0	0	0	4	31	50	16	53	Nonsocial

- All used in **social contexts** + context specificity
- "Stick the tongue out", lipsmacks and yawns also displayed in non-social contexts (Yawn 1 mostly)
- Different variants of intensity = different functions?

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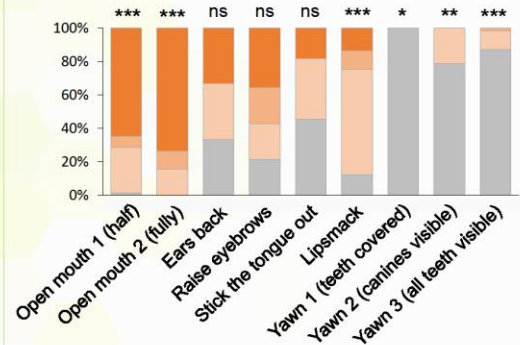
Repertoire of 6 facial expressions (+ variants of intensity)

531 occurrences

INTENTIONALITY

Distributions of the cumulative behavioural markers of intentionality (grouped in 3 criteria)⁵: (Fisher's exact tests)

Recipient-directed (Social directionality, Audience checking)	Goal-directed (Response waiting)	Response of receiver
X	X	
X	X	X
X		



- Open mouth fulfilled the 3 criteria of intentionality
- Other facial expressions = recipient-directed
- Except for yawns = dissociated from intentional dyadic communication

CONCLUSION: Most of the facial expressions were produced in **specific social contexts** and **directed to a recipient**. Playful "open mouth" displays were associated with all markers of **intentionality**, and the distributions of the markers were substantially variable depending on the facial expressions.



We are thankful to the French Society for the Study of Animal Behaviour for the grant which supported the participation to this conference.



Annexe 3 - Activités de vulgarisation scientifique

- Octobre 2018 | **Fête des Sciences – Portes ouvertes de la Station Biologique de Paimpont** | Accueil du public et visite de l’animalerie de primates, présentation des thématiques de recherche de l’UMR EthoS.
- Mai 2019 | **Festival Pint of Science - Rennes** | Présentation « Le langage est-il le propre de l’Homme ? – Sur les traces de l’origine gestuelle du langage »
- Mai 2019 | **Entretien pour la radio C-lab** | Discussion en amont du festival Pint of Science : « La communication chez les primates non-humains »
- Mai 2019 | **Intervention en classe de collège** | Présentation de l’éthologie et des possibles cursus en biologie animale au collège St Yves, Mordelles (35)
- Octobre 2019 | **Communication web sur le 32^{ème} colloque de la Société Francophone de Primatologie (SFDP)** | <https://paimpont.univ-rennes1.fr/actualites/retour-sur-le-32eme-colloque-de-la-societe-francophone-de-primatologie>
- Octobre 2020 | **Festival Imaginascience 8 : Science et bande-dessinée** | Podcast « Planches sonores » sur la zoologie | <https://soundcloud.com/user-793450297/202009-mcst-imaginasciences-zoologiste>

Responsabilités collectives

- Janvier 2019 – Septembre 2020 | Co-crédation et animation du **Journal Club** du laboratoire





Annexe 4 - Activités d'enseignement et d'encadrement de projets scientifiques

- 2017 - 2020 | **Monitorat d'enseignement** | Travaux pratiques de Licence | Université de Rennes 1, UFR Sciences de la Vie et de l'Environnement
 - U.E. Ethologie et Physiologie Animale (L1 Sciences de la vie) – 70 heures
 - U.E. L'animal et son milieu (L2 Sciences de la vie) – 12 heures
 - U.E. Chronobiologie (L3 Biologie des organismes) – 64 heures
 - U.E. Mineur de complément de Biologie (L3 Psychologie) – 4 heures

- Octobre 2018 – Juin 2019 | **Co-encadrement d'un étudiant de Master 2** | Pablo Pezzino | Master Comportement animal et humain, Université de Rennes 1 | Effet d'audience sur la communication gestuelle des mangabeys à collier (*Cercocebus torquatus*).

- Janvier 2020 | **Encadrement d'une étudiante de Master 1** | Lise Le Vern | Université de Brest | Contagion des bâillements chez les mangabeys à collier (*Cercocebus torquatus*)

- Avril – Juin 2020 | **Co-encadrement d'une étudiante de Master 1** | Noémie Monchy | Master Comportement animal et humain, Université de Rennes 1 | Latéralité gestuelle chez les mangabeys à collier (*Cercocebus torquatus*)



Annexe 5 - Formations suivies et bourses

Formation continue

- Novembre - Décembre 2017 | **Se former pour enseigner dans le supérieur** | MOOC avec certification | Ministère de l'Enseignement Supérieur, de la Recherche et de l'Innovation
- Janvier 2018 | **Expérimentation animale**, N.1 : Concepteur de procédures expérimentales | Oniris
- Juillet 2018 | **Formation aux modèles mixtes linéaires et non linéaires** | Anastats
- Octobre – Décembre 2018 | **Bien-être des animaux en élevage** | MOOC avec certification | VetAgroSup, Oniris, AgroParisTech, INRA, Agreenium
- Novembre 2018 et Mai 2019 | **Ethique de la recherche scientifique, Ethique en expérimentation animale et humaine** | Ecole doctorale Biologie Santé
- Mars – Juin 2020 | **Vivre avec les autres animaux** | MOOC avec certification | Université Virtuelle Environnement et Développement durable (UVED)

Bourses

- 2017 - 2020 | **Bourse de thèse : Contrat doctoral d'établissement (CDE)**
- 2019 | **Bourse internationale de la Société Française pour l'Etude du Comportement Animal (SFECA)**, pour participation au colloque de l'ASAB, 26-28 Août 2019, Konstanz, Allemagne



Titre : Communication gestuelle et multimodale chez les mangabeys à collier (*Cercocebus torquatus*)

Mots clés : Primates, Communication intentionnelle, Expressions faciales, Latéralité gestuelle, Flexibilité

Résumé : Ce travail s'inscrit dans l'étude des origines évolutives du langage, par la recherche de propriétés langagières dans la communication gestuelle et multimodale de primates cercopithécidés en captivité, les mangabeys à collier. Par une double approche observationnelle et expérimentale, nous avons montré que les gestes des mangabeys remplissent les critères de définition d'une communication intentionnelle, et peuvent être produits de manière flexible dans différents contextes. Nos observations fournissent également de premiers éléments en faveur d'une intentionnalité des expressions faciales des cercopithécidés, souvent considérées comme de simples indices d'état émotionnel. Cette propriété sociocognitive langagière pourrait ainsi être plus ancienne que ce que nous pensions dans l'histoire évolutive des primates, et être héritée de la communication gestuelle des ancêtres des catarrhiniens, il y a environ 29 millions d'années. De plus, nous avons mis en évidence un effet significatif du contexte interactionnel sur la latéralité

gestuelle des mangabeys, suggérant une importance particulière de facteurs sociaux dans l'émergence d'une spécialisation hémisphérique pour la communication intentionnelle, dont le langage humain. Enfin, par une méthode originale, reposant sur des analyses de séquences et de réseau, nous avons décrit la communication multimodale et multicomposante des mangabeys à collier, et montré qu'ils combinent de manière flexible différents types et modalités de signaux en fonction du contexte et de facteurs sociodémographiques. Nos résultats soulignent l'importance d'une approche multimodale pour comprendre la complexité de la communication des primates, et apportent de premiers éléments de compréhension sur la fonction des combinaisons de signaux. De futures comparaisons à d'autres espèces et dans différents environnements pourraient permettre d'affiner nos connaissances quant aux possibles contraintes évolutives ayant favorisé une telle complexité de la communication des primates humains et non-humains.

Title : Gestural and multimodal communication in red-capped mangabeys (*Cercocebus torquatus*)

Keywords : Primates, Intentional communication, Facial expressions, Gestural laterality, Flexibility

Abstract : In order to address the evolutionary origins of human language, we searched for key language characteristics in the gestural and multimodal communication of captive cercopithecids, red-capped mangabeys. Through both an observational and experimental approach, we demonstrated that red-capped mangabey gestures meet all criteria of intentional communication, and are flexibly used in different social contexts. Our observations also provide first elements in favour of an intentional use of facial expressions by non-hominoid primates, beyond a mere function of emotional state indices. Our results suggest that intentionality, a key socio-cognitive language characteristic, could be older than we thought in the evolutionary history of primates, and be inherited from the gestural communication of Catarrhines' ancestors, about 29 million years ago. Moreover, highlighting the significant effect of interactional context on mangabey gestural laterality,

our results suggest a particular importance of social factors in the emergence of a hemispheric specialization for intentional communication, including human language. Finally, using an original method of sequence and network analyses, we described the multimodal and multicomponent communication of red-capped mangabeys, and showed that they flexibly combine different types and modalities of signals depending on contextual and socio-demographic factors. Our results underline the importance of a multimodal approach to study and understand the complexity of primate communication, and provide first insights into the function of signal combinations. Future comparisons with other species living in different environments may allow us to refine our knowledge about the possible evolutionary constraints that shaped such a complex communication in human and non-human primates.