



HAL
open science

Sur les traces de la théorie de l'Esprit chez les singes : compréhension de l'attention, des perceptions et des intentions d'autrui

Charlotte Canteloup

► To cite this version:

Charlotte Canteloup. Sur les traces de la théorie de l'Esprit chez les singes : compréhension de l'attention, des perceptions et des intentions d'autrui. Biologie animale. Université de Strasbourg, 2016. Français. NNT : 2016STRAJ087 . tel-01675044v1

HAL Id: tel-01675044

<https://theses.hal.science/tel-01675044v1>

Submitted on 4 Jan 2018 (v1), last revised 9 Jan 2018 (v2)

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

ÉCOLE DOCTORALE des Sciences de la Vie et de la Santé

Centre de Primatologie de l'UDS / LNCA UMR 7364

THÈSE présentée par :

Charlotte CANTELOUP

soutenue le: **28 Novembre 2016**

pour obtenir le grade de : **Docteur de l'université de Strasbourg**

Discipline/ Spécialité : Sciences du Vivant / Ecologie - Ethologie

**Sur les traces de la Théorie de l'Esprit chez les
singes : compréhension de l'attention, des
perceptions et des intentions d'autrui**

THÈSE dirigée par :

Dr. MEUNIER Hélène

Ingénieur de recherche, Université de Strasbourg

RAPPORTEURS :

Pr. BLOIS-HEULIN Catherine

Professeur, Université de Rennes 1

Pr. VERCAUTEREN Martine

Professeur, Université Libre de Bruxelles

AUTRES MEMBRES DU JURY :

Dr. MASI Shelly

Maître de Conférence, MNHN de Paris

Pr. ROHMER Odile

Professeur, Université de Strasbourg

Dr. VAN DE WAAL Erica

Docteur, Université de Zürich

A Zébulon et Prunelle,

Mes compagnons de vie à longues oreilles, partis pendant ma thèse

« Some philosophers think that animals are not conscious because they do not have language. I am autistic and I think in pictures. If the philosophers are correct, I would have to conclude that I am not conscious. »

Temple Grandin

Evolution and Cognition, 2002

SOMMAIRE

REMERCIEMENTS	5
PUBLICATIONS	9
COMMUNICATIONS	10
INTRODUCTION GENERALE	13
1. Quelques notions historiques	13
2. Les théories de l'évolution de la cognition	15
3. La Théorie de l'Esprit	16
3.1. Des premières études...	16
3.2. ...A un changement de paradigme	18
3.3. Etat de l'art	19
3.3.1. <i>Discrimination de l'attention</i>	20
3.3.2. <i>Prise de perspective</i>	21
3.3.3. <i>Manipulation sociale</i>	23
3.3.4. <i>Compréhension des intentions</i>	24
4. Objectifs de la thèse	27
ARTICLE 1	31
Do Tonkean macaques (<i>Macaca tonkeana</i>) tailor their gestural and visual signals to fit the attentional states of a human partner?	
ARTICLE 2	47
Intentional gestural communication and discrimination of human attentional states in rhesus macaques (<i>Macaca mulatta</i>)	
ARTICLE 3	61
Do Tonkean macaques (<i>Macaca tonkeana</i>) perceive what conspecifics do and do not see?	

ARTICLE 4	87
Functionally deceptive behaviours in Tonkean macaques (<i>Macaca tonkeana</i>)	
ARTICLE 5	115
‘Unwilling’ versus ‘unable’: Tonkean macaques understanding of human goal-directed actions	
DISCUSSION GENERALE	143
1. Discrimination de l’attention	143
2. Prise de perspective	146
3. Manipulation sociale	148
4. Compréhension des intentions	150
5. Lecture de comportement ou lecture d’esprit ?	152
5.1. Casse-tête méthodologique	152
5.2. Casse-tête théorique	153
6. Quelles solutions à ce puzzle ?	155
7. Conclusion générale	157
REFERENCES BIBLIOGRAPHIQUES	161

REMERCIEMENTS

Mes sincères et profonds remerciements sont adressés à :

Hélène Meunier pour m'avoir permis de rédiger et de construire mon propre projet de thèse sur le sujet de mon choix, ce qui m'a permis d'acquérir une grande liberté et autonomie dans ma recherche. Un grand merci pour ta confiance, ton soutien depuis maintenant de nombreuses années, tes relectures et pour m'avoir guidée au long de ce travail. Je te suis aussi infiniment reconnaissante de m'avoir fait bénéficier d'un financement de deux ans.

Catherine Blois-Heulin, Martine Vercauteren, Odile Rohmer, Shelly Masi et Erica van de Waal pour avoir accepté de faire partie de mon jury de thèse et d'évaluer ce travail.

L'école Doctorale 414 des Sciences de la Vie et de la Santé de l'Université de Strasbourg et plus particulièrement son directeur **Serge Potier** pour m'y avoir acceptée malgré mon parcours semé d'embûches. Merci aussi à **Mélanie Muser** et **Géraldine Schverer** pour leur disponibilité.

Jean-Christophe Cassel du Laboratoire de Neurosciences Cognitives et Adaptatives (LNCA UMR 7364) pour ses conseils avisés et pour m'avoir soutenue depuis le début.

Christian Kelche du LNCA pour m'avoir fait l'honneur de faire partie de mon comité de mi-thèse ainsi que pour ses conseils et questionnements scientifiques enrichissants.

Mes soutiens financiers : l'Institut d'Etudes Avancées de l'Université de Strasbourg (USIAS), le Centre de Primatologie de l'Université de Strasbourg, La Société Francophone de Primatologie pour m'avoir remis la bourse Tremplin ainsi que la **Région Alsace** pour m'avoir accordé une bourse « Expériences de jeunes » pour un projet innovant.

Les équipes du Centre de Primatologie de l'Université de Strasbourg et de SILABE ADUEIS : leurs directeurs respectifs **Yves Larmet** et **Fanélie Wanert**, ainsi que **Pascal Ancé, Antoine Beauvy, Helen Beyer, Xavier Brochet, Marc Charlier, Cédric Cizek,**

Manon Dirheimer, Nicolas Herrenschmidt, Lyne Fellmann, Cédric Gaertner, Christelle Gandon, Lucien Huot, Jennifer Jund Riegert, Laurent Laeuffer, Martine Ohl, Frédéric Quiriet, Pierrick Regnard, Adam Rimele et Laetitia pour leur accueil chaleureux et leurs bons soins prodigués aux animaux. Je tiens à remercier vivement et tout particulièrement **Steve Lapp, Adrien Panter et Jean-Marc Woock** pour leur aide logistique précieuse dans la construction et la réparation des dispositifs expérimentaux dans la bonne humeur et avec l'accent alsacien ! Je souhaite aussi remercier fortement mon collègue **Jonas Fizet** avec qui j'ai pu partager, de la meilleure des façons, les joies et les peines de la vie d'un doctorant. Enfin, je voudrais remercier **Jean-Jacques Roeder** pour m'avoir ouvert les portes de la primatologie lors de mon premier stage au CdP il y a maintenant six ans.

Mes stagiaires : Myriam Gerardin, Justine Guillaumont, Lucie Hoornaert, Sophie Le Ray, Lucie Ligault, Emilie Piraux, Clémence Simart et Ondine Walter sans qui je n'aurais pu mener les expériences. Spéciale dédicace à **Isis Poitrasson** qui a passé des mois à analyser minutieusement des vidéos image par image, qui a construit des dizaines de tableaux Excel et qui m'a fait gagner un temps précieux à la fin de ma thèse !

Nicolas Poulin pour son aide considérable en statistiques, pour m'avoir formée aux modèles et pour avoir toujours répondu présent lors de mes innombrables mails, rendez-vous et questions sur les maths.

James R. Anderson pour sa bienveillance, ses corrections en anglais ultra rapides et pour le partage de ses connaissances passionnantes.

Nadège Krebs de Noldus, pour sa gentillesse, sa disponibilité et son aide à de maintes reprises pour percer les mystères du logiciel *The Observer*.

Dalila Bovet pour avoir accepté de collaborer et de m'accorder un peu de son temps lors de la première partie de ma thèse et pour avoir fait partie de mon comité de mi-thèse.

Marie Bourjade pour ses conseils statistiques bienvenus et pour m'avoir initiée à la recherche fascinante sur la communication gestuelle des primates.

Mes amis de Paris, de Strasbourg et d'ailleurs : **Aude** et **François**, **Amélie**, **Benjamin**, **Cécile**, **Charlotte**, **Cinzia**, **Coralie**, **Fabien**, **Floriane** et **Julien**, **Laura**, **Paula**, **Pierre**, **Raphaëlle**, **Ruth**, **Sabrina**, **Sarah** ainsi que **Taoufik**, pour avoir été présents pour moi, pour m'avoir soutenue dans les moments de doutes et pour tous les bons moments passés ensemble. Enfin, je me dois de remercier comme il se doit **Ameline Bardo**, mon « dindon », ma « scientific sister », mon alter-ego, pour son amitié forte et irremplaçable !

Gaël, pour m'avoir supportée dans tous les sens du terme pendant ma thèse, pour avoir servi de second observateur à la dernière minute, pour ta patience, ta présence, tes gentilles attentions, ta compréhension, tes encouragements...

Ma famille, tout d'abord **mes parents** qui m'ont toujours soutenue sans inquiétude, ont cru en moi et m'ont encouragée à me battre pour accomplir mes rêves. Je vous suis très reconnaissante de m'avoir laissé autant de liberté dans mes choix d'orientation qui pouvaient paraître pourtant bien fermés et de m'avoir transmis votre force d'acharnement et votre ténacité. Merci à vous, à **ma sœur Camille** ainsi qu'à **Alain** pour avoir relu mon manuscrit avec attention et intérêt.

Les macaques de Tonkean, tout d'abord **Yannick**, mon meilleur sujet pour lequel j'ai une affection particulière, mais aussi **Gaëtan**, **Lady**, **Nema**, **Nenno**, **Néréis**, **Shan**, **Olli**, **Ulrich**, **Ulysse**, **Uruk**, **Vishnu**, **Wallace**, **Walt**, **Wotan**, **Yang**, et **Yin** ainsi que **les macaques rhésus** : **Chourros**, **Grenadine**, **Grimm**, **Kasparov** et **Printemps** qui ont volontairement participé à mes expériences et qui m'ont fait découvrir avec drôlerie, émotion et étonnement les méandres de la cognition simiesque.

PUBLICATIONS

Canteloup C., Poitrasson I., Anderson J.R., Poulin N. & Meunier H. *Submitted*. Functionally deceptive behaviours in Tonkean macaques (*Macaca tonkeana*)

Canteloup C., & Meunier H. *Submitted*. ‘Unwilling’ versus ‘unable’: Tonkean macaques’ understanding of human goal-directed actions.

Canteloup C., Piraux E., Poulin N., & Meunier H. 2016. Do Tonkean macaques (*Macaca tonkeana*) perceive what conspecifics do and do not see? *PeerJ*, e1693, 4: DOI 10.7717/peerj.1693

Canteloup C., Bovet D., & Meunier H. 2015. Intentional gestural communication and discrimination of human attentional states in rhesus macaques (*Macaca mulatta*). *Animal Cognition*, 18(4): 875-883.

Canteloup, C., Bovet D., & Meunier H. 2015. Do Tonkean macaques (*Macaca tonkeana*) tailor their gestural and visual signals to fit the attentional states of a human partner? *Animal Cognition*, 18(2): 451-461.

Bourjade M., **Canteloup C.**, Meguerditchian A., Vauclair J. & Gaunet F. 2015. Training experience in gestures affects the display of social gaze in baboons’ communication with a human. *Animal Cognition*, 18(1): 239-250.

Canteloup C., Vauclair J., & Meunier H. 2013. Hand preferences on unimanual and bimanual tasks in tonkean macaques (*Macaca tonkeana*). *American Journal of Physical Anthropology*, 152(3), 315-321.

Meunier H., Fagard J., Maugard A., Briseno M., Fizet J., **Canteloup C.**, Defolie C. & Vauclair J. 2013. Patterns of hemispheric specialization for a communicative gesture in different primate species. *Developmental Psychobiology*, 55(6), 662-671.

COMMUNICATIONS

COMMUNICATIONS ORALES

Canteloup C., & Meunier H. Les macaques de Tonkean discriminent-ils les actions intentionnelles d'un humain? *29ème colloque de la Société Francophone de Primatologie (SFDP)*, Rennes, France. 18/10/16 – 20/10/16.

Canteloup C., Piraux E., Poulin N., & Meunier, H. Are Tonkean macaques able to take the visual perspective of their conspecifics ? *6ème colloque de la Fédération Européenne de Primatologie (EFP)*, Rome, Italie 25/08/15 – 28/08/15.

Canteloup C., Piraux E., & Meunier H. Les macaques de Tonkéan sont-ils capables de perspective-taking visuel? *Colloque de la Société Française pour le Comportement Animal (SFECA)*, Strasbourg, France, 21/04/15 – 23/04/15.

Canteloup C. On the tracks of Theory of Mind in monkeys: attention, perception and intention reading abilities. *Journées de l'Ecole Doctorale des Sciences de la Vie et de la Santé de l'Université de Strasbourg (ED 414)*. 26/02/15 – 27/02/15.

Canteloup C., Piraux E., & Meunier H. Les macaques de Tonkean perçoivent-ils ce que peuvent et ne peuvent pas voir leurs congénères? *27ème colloque de la SFDP*, Poitiers, France, 04/11/14 – 07/11/14.

Canteloup C., Bovet D., & Meunier H. Les macaques de Tonkean (*Macaca tonkeana*) ajustent-ils leur geste de pointage en fonction de l'état attentionnel d'un partenaire humain ? *26ème colloque de la SFDP*, Kinshasa, République démocratique du Congo. 29/10/13 – 10/11/13.

Canteloup C., Bovet D., & Meunier H. Which social cues are taken into account by Tonkean macaques to communicate with a human partner? *Colloque de l'EFP "Primates in our hands"*, Anvers, Belgique. 11/09/13 – 13/09/13.

Canteloup C., Vauclair J., & Bourjade, M. Les babouins olive ajustent leur comportement de quémande en fonction de l'état d'attention d'un partenaire humain. *25ème colloque de la SFDP*, Lyon, France. 17/10/12 – 19/10/12.

COMMUNICATIONS AFFICHÉES

Pouydebat E., Bardo A., **Canteloup C.**, & Borel A. Preliminary observation of coconut cracking open among capuchins monkeys and humans: proto-tool use costs and benefits. *25ème congrès de la Société Internationale de Primatologie (IPS)*, Hanoï, Vietnam, 11/08/2014 – 16/08/2014.

Canteloup C., Bovet D. & Meunier H. Rhesus macaques (*Macaca mulatta*) discriminate more finely human attentional cues than Tonkean macaques (*Macaca tonkeana*). *Colloque de la SFECA*, Nanterre, France, 08/07/14 – 11/07/14.

Canteloup C., & Meunier H. Manual laterality in rhesus macaque (*Macaca mulatta*) and Tonkean macaque (*M. tonkeana*). *Colloque de la SFECA "l'animal dans tous ses sens"*, Tours, France, 17/05/11 – 19/05/11.

VULGARISATION SCIENTIFIQUE

2013 : Participation à un documentaire TV CanalSat « l'Homme et son évolution »

2014 : Rédaction d'un article pour le bulletin de la SFDP : *Les macaques intolérants discriminerait-ils des indices attentionnels plus subtils que les macaques tolérants ?*

2016 : Participation à un reportage AFP sur la Théorie de l'Esprit chez les primates

DISTINCTIONS

Novembre 2013 : Bourse Tremplin de la SFDP (1500€)

Novembre 2013 : Bourse « Expériences de jeunes » (1500€) de la Région Alsace

Février 2015 : Premier prix du meilleur blitz de l'Ecole Doctorale Vie et Santé de l'Université de Strasbourg – présentation de thèse en trois minutes

INTRODUCTION GENERALE

L'espèce humaine a historiquement été considérée comme la seule ayant développé des capacités cognitives extrêmement complexes allant du langage articulé aux mathématiques, en passant par le raisonnement scientifique, la création de machines et celle d'institutions sociales ingénieuses (Tomasello & Rakoczy 2003 ; MacLean 2016). Bien que certains critères définissant l'unicité de l'Homme à savoir l'utilisation d'outils (*e.g.* chimpanzés : Goodall 1986), la culture (Fragaszy & Perry 2003) ou encore le rire (*e.g.* rats : Panksepp 2007) aient été remis en question, d'autres comme la conscience, le langage et la capacité de se représenter les états mentaux d'autrui (Théorie de l'Esprit) semblent plus résistants à la controverse (Penn et al. 2008 ; Bolhuis & Wynne 2009). Ce que signifie « être humain » continue ainsi de nourrir les passions tant parmi les philosophes que les biologistes (Corballis & Lea 2000 ; Michaud 2000 ; Picq et al. 2003 ; Lestel 2007 ; Tomasello 2014) et l'une des plus grandes questions animant aujourd'hui le monde scientifique concerne l'origine de la cognition humaine, son évolution et la nature des forces qui lui ont permis d'émerger.

Dans ce chapitre, après une brève introduction concernant le contexte historique du développement des sciences cognitives, j'exposerai les différentes théories concernant l'évolution de la cognition. Dans un second temps, j'établirai un état de la recherche portant sur l'un des critères considéré comme une spécificité de l'Homme, la Théorie de l'Esprit, en faisant notamment un état de l'art de nos connaissances chez les primates non-humains (ci-après « primates »). Enfin, je terminerai cette introduction en présentant les objectifs de ma thèse.

1. Quelques notions historiques

La cognition a été définie comme l'ensemble des processus mentaux par lesquels les êtres vivants acquièrent, traitent et enregistrent les informations de l'environnement tels que l'apprentissage, la mémoire et la prise de décisions (Shettleworth 2010). L'intelligence, quant à elle, se réfère à l'évaluation d'une performance sur la base d'un critère fonctionnel donné (McFarland 1989). Au cours de l'histoire des sciences cognitives, deux approches différentes se sont imposées. La première doit son héritage à Descartes (1637) et à sa notion d'animal-machine. L'objectif du projet cartésien d'isoler le corps de l'esprit afin de pouvoir les étudier

séparément a conduit à discerner l'homme, doté d'une pensée, de l'animal dénué d'esprit. Ce dualisme entre le physique et le psychique a fait le lit du courant behavioriste qui s'est ensuite développé dans la première moitié du XX^{ème} siècle (Gillot 2007). Behaviorisme qui, en se focalisant exclusivement sur les relations stimulus-réponse des animaux (humains et non-humains), s'est interdit toute investigation de la « boîte noire » contenant les mécanismes mentaux impliqués dans les comportements (*e.g.* Watson 1913). La deuxième approche a été insufflée par Darwin (1871) qui proposa que notre intelligence diffère en degré et non en nature de celle des animaux supérieurs. La continuité mentale suggérée par Darwin suppose donc que la cognition d'*Homo sapiens* partage certains attributs avec celles d'espèces lui étant phylogénétiquement proches. De telles similarités sont appelées homologues. Toutefois, des capacités cognitives semblables peuvent aussi être observées chez des espèces bien plus éloignées au sein de l'arbre phylogénétique mais subissant des contraintes écologiques et/ou sociales similaires: on parle alors d'analogies par convergence évolutive (Butler 2009).

Le raisonnement darwinien est à la base de la psychologie comparée et de l'éthologie cognitive contemporaines (Vauclair 2016). Ainsi, la recherche de similarités et de différences entre des espèces évolutivement proches contribue à l'identification des dynamiques de l'évolution de la cognition (Byrne 2000 ; Shettleworth 2010 ; Boesch 2012 ; MacLean et al. 2012 ; MacLean 2016). Les primates, nos plus proches cousins, se révèlent de ce fait être de bons candidats afin de tenter d'élucider certains processus évolutifs et notamment l'histoire évolutive de la cognition. Parmi les hominidés, le dernier ancêtre commun entre chimpanzés, bonobos et humains vivait il y a environ 6,6 millions d'années. Les gorilles et les orangs-outans se seraient séparés de la lignée humaine il y a respectivement 8,9 et 15,8 millions d'années. La séparation entre *Homo sapiens* et les singes de l'Ancien Monde (*e.g.* macaques et babouins) daterait d'environ 29,1 millions d'années et celle d'avec les singes du Nouveau Monde (*e.g.* tamarins et capucins) remonterait à 43,1 millions d'années (www.timetree.org; Herlyn 2016). D'autre part, les primates ont un cerveau approximativement deux fois plus gros que ceux de mammifères de taille équivalente (Passingham 1981 ; Barton 2006) et, parmi les primates, la taille du cerveau est positivement corrélée à leur proximité phylogénétique avec l'humain ; les grands singes ayant de plus gros cerveaux que les petits singes, eux-mêmes ayant de plus gros cerveaux que les prosimiens (Montgomery et al. 2010). Il apparaît alors légitime de s'interroger sur les causes de ce développement cérébral chez les primates au cours de l'évolution.

2. Les théories de l'évolution de la cognition

L'évolution ne pouvant aboutir à un net handicap pour les espèces, chaque désavantage apparaissant en son cours se doit d'être surpassé par d'importants bénéfices (Byrne 2000). Les nombreux coûts associés à l'accroissement du volume cérébral (*e.g.* augmentation de la dépense énergétique ; complication de l'enfantement) doivent ainsi être contrebalancés par des avantages considérables au cours de l'évolution des espèces. L'intelligence semble en être l'atout essentiel (Byrne 2013). Deux théories principales ont été proposées pour tenter d'expliquer l'émergence de l'intelligence : l'une prône une origine écologique tandis que l'autre soutient une origine sociale (van Schaik & Deaner 2003 ; Byrmit 2006). Selon les hypothèses écologiques, la taille du cerveau des primates aurait augmenté en réponse à des contraintes environnementales complexes. Ainsi, la saisonnalité de ressources alimentaires inégalement distribuées comme par exemple celle des fruits aurait nécessité le développement d'une mémoire spatiale pour localiser de tels aliments parvenus à maturité et disséminés dans l'environnement (Milton 1988). D'autre part, certains aliments riches comme des noix, racines, tubercules ou encore larves d'insectes logées dans des troncs nécessitent une habileté considérable pour être consommés. Le traitement de nourriture encastrée ou d'aliments extraits aurait aussi requis l'acquisition d'une intelligence technique *via* l'utilisation d'outils par exemple (Parker & Gibson 1977 ; Gibson 1986).

Les hypothèses en faveur d'une origine sociale suggèrent que c'est la vie en société complexe qui aurait exercé de fortes pressions de sélection sur la cognition des primates (Jolly 1966 ; Humphrey 1976). En effet, les primates, incluant notre espèce, considérée comme « ultra sociale » (Herrmann et al. 2007), sont amenés dans leur vie quotidienne à former des associations sociales complexes, à raisonner par analogie et à procéder à des inférences afin d'anticiper les réactions de leurs congénères (Vauclair 1992 ; 1996). Cette Hypothèse de l'Intelligence Sociale selon laquelle les individus faisant face à des relations sociales multiples et complexes auraient des capacités cognitives supérieures aux autres animaux a eu un écho particulier chez les primatologues s'intéressant aux comportements de manipulation sociale et de tromperie (Hypothèse de l'Intelligence Machiavélienne : Byrne & Whiten 1988 ; Whiten & Byrne 1997). Cette hypothèse sociale a par ailleurs été renforcée par la mise en lumière d'une relation entre la taille relative du cerveau (et plus précisément du néocortex) et certaines variables sociales dont l'organisation sociale (*e.g.* monogamie, système familial, groupe multi-mâles-multi-femelles et système de fission-fusion chez les primates), la taille de

la colonie et du groupe de toilettage (Hypothèse du Cerveau Social : Dunbar 1998 ; 2003 ; Dunbar & Schultz 2007 ; Dunbar 2009) et par l'absence de relation avec des variables écologiques (*e.g.* taille du domaine vital ; style de fourragement) chez les primates mais également chez d'autres mammifères et oiseaux.

Une autre théorie ayant une composante sociale, l'Hypothèse de l'Intelligence Culturelle, a été proposée pour expliquer l'émergence de la cognition humaine. Van Schaik et Burkart (2011) ont proposé que les espèces ayant de grandes opportunités d'apprentissage social devraient être les plus culturelles et ainsi les plus intelligentes. A la différence de nos cousins primates, nous, humains, développerions tôt au cours de notre ontogenèse, les facultés extraordinaires que sont la communication déclarative, la coopération et l'attribution d'états mentaux en raison de notre extrême socialité et de notre motivation unique à participer à des activités sociales et à partager des connaissances au sein de groupes culturels (Tomasello 1999 ; Tomasello et al. 2005 ; Herrmann et al. 2007).

Toutefois, d'autres chercheurs accordent davantage de crédit à une théorie socio-écologique de l'évolution de l'intelligence simiesque qui mixerait pressions écologiques et sociales (Reader & Laland 2002 ; Deaner et al. 2006 ; Reader et al. 2011). Selon ces auteurs, l'innovation, l'utilisation d'outils et l'apprentissage social seraient des caractéristiques clés du développement de fonctions cognitives supérieures, physiques et sociales confondues. Cette hypothèse suggère l'existence d'une « intelligence générale » au sein des primates, et plus largement des mammifères, pour laquelle les performances dans des tâches relevant de différents domaines cognitifs sont positivement corrélées (Burkart et al. 2016), plutôt que plusieurs intelligences spécialisées issues de domaines plus spécifiques.

L'ensemble de ces hypothèses sur les origines de notre gros cerveau convergent sur le fait que cette caractéristique est d'un intérêt particulier pour la compréhension de l'émergence de nos capacités mentales complexes et contribue à considérer les primates comme un modèle de choix pour l'étude de l'évolution de la cognition.

3. La Théorie de l'Esprit

3.1. Des premières études...

« Le chimpanzé a-t-il une théorie de l'esprit ? » Telle est la question pionnière posée par Premack et Woodruff (1978) qui sera à l'origine d'un débat scientifique considérable. Ces

auteurs ont défini la Théorie de l'Esprit comme la capacité à imputer des états mentaux à soi-même et à autrui, tels que des intentions, des croyances, des savoirs et des désirs. Ce système d'inférences tient son appellation de « théorie » du fait que ces états mentaux sont inobservables et qu'un tel système permet de prédire le comportement d'autres organismes (Premack & Woodruff 1978). Dans leur étude fondatrice, Premack et Woodruff (1978) ont montré à un chimpanzé, Sarah, des films illustrant un humain confronté à un problème physique (*e.g.* l'acteur tentait d'attraper une banane hors de sa portée). Sarah devait ensuite sélectionner la photographie correspondant à la solution du problème. Par exemple, lorsqu'on lui montrait la vidéo d'un expérimentateur cherchant à obtenir une banane attachée au plafond, Sarah devait cliquer sur l'image dans laquelle l'humain était monté sur une boîte. Ce qu'elle fit. Elle fit aussi de même dans d'autres situations expérimentales, ce qui amena les primatologues à conclure que Sarah reconnaissait le problème, comprenait le but de l'acteur et choisissait des solutions compatibles avec les situations expérimentales. Cette conclusion a toutefois été remise en question par d'autres chercheurs pour lesquels Sarah ne se représentait pas les buts de l'humain mais était simplement capable de prédire des séquences comportementales sur la base de similarités perceptuelles entre les films et les alternatives proposées ou encore par apprentissage associatif (*e.g.* Savage-Rumbaugh & Rumbaugh 1979).

La controverse autour de cette étude a été le point de départ dans les années 1980 d'une recherche florissante sur la Théorie de l'Esprit, notamment en psychologie du développement à travers des expériences testant la compréhension des fausses croyances chez les enfants (Wimmer & Perner 1983 ; Baron-Cohen et al. 1985 ; Perner et al. 1987). Dans ces études, les enfants, témoins d'une scénette dans laquelle un premier personnage cache un jouet à un endroit précis avant de quitter la scène puis d'y revenir après qu'un second personnage ait changé le jouet de cachette hors de sa vue, devaient répondre verbalement à la question : où le premier personnage va-t-il chercher le jouet en revenant ? Seuls les enfants âgés d'au moins quatre ans réussissaient ce test en reconnaissant que le premier personnage avait une fausse croyance concernant la localisation du jouet (Wimmer & Perner 1983). La recherche en cognition chez les enfants s'est ensuite focalisée sur la compréhension des buts, intentions et perspectives d'autrui en utilisant des paradigmes expérimentaux non-verbaux dont par exemple l'analyse du temps de regard. Ainsi, les enfants de six mois comprennent qu'une action est dirigée vers un but et vers l'âge de deux ans ils attribuent des intentions et perceptions à autrui (Woodward 1998 ; Gergely et al. 2002 ; Behne et al. 2005 ; Onishi & Baillargeon 2005 ; Southgate et al. 2007). Ces études ont montré que les enfants ne naissent

pas avec une Théorie de l'Esprit complète mais développent ces capacités mentales au cours de leur ontogenèse jusqu'à atteindre leur plein développement vers l'âge de quatre à cinq ans.

A la suite de l'étude emblématique de Premack et Woodruff (1978), la recherche sur la Théorie de l'Esprit chez les primates s'est considérablement développée dans les années 1990. Les premières données proviennent d'observations spontanées suggérant de la tromperie et de la manipulation chez de nombreuses espèces de primates (Byrne & Whiten 1988 ; 1990 ; 1992), mais celles-ci ne permettant pas d'investiguer spécifiquement les mécanismes sous-jacents aux comportements observés, les expériences en laboratoire se sont imposées comme plus adéquates (Povinelli et al. 1990 ; Call & Tomasello 1994 ; Povinelli & Eddy 1996). Dans leur expérience, Povinelli, Nelson et Boysen (1990) apprirent à des chimpanzés à sélectionner parmi plusieurs gobelets, celui pointé par un expérimentateur qui savait qu'il contenait une récompense alimentaire plutôt que celui montré par un expérimentateur qui ne connaissait pas la localisation de la nourriture. Les chimpanzés furent ensuite testés dans un test de transfert dans lequel l'expérimentateur « ignorant » portait un sac sur la tête l'empêchant de voir une tierce personne cacher la nourriture alors que l'expérimentateur « savant », lui, était autorisé à voir la scène. Les chimpanzés choisirent le gobelet pointé par l'expérimentateur « savant » de préférence à celui pointé par l'« ignorant », ce qui amena les chercheurs à conclure que les chimpanzés étaient capables de comprendre ce que les humains pouvaient et ne pouvaient pas voir (Povinelli et al. 1990). Ces résultats ont toutefois par la suite été critiqués: les chimpanzés auraient simplement pu apprendre à discriminer et à préférer un expérimentateur n'ayant pas de sac sur la tête à un autre en étant pourvu (Povinelli 1994 ; Heyes 1998). A la fin des années 1990, l'opinion majoritaire est alors que les grands singes n'ont pas de Théorie de l'Esprit (Tomasello & Call 1997).

3.2. ...A un changement de paradigme

La méthodologie utilisée dans les années 1990 – ou la tâche de choix d'objet - a été remise en question dans les années 2000 : elle ne permettrait pas de révéler les capacités cognitives réelles des primates (Hare 2001 ; Hare & Tomasello 2004 ; Johnson & Karim-D'Arcy 2006). En effet, selon certains auteurs, cette tâche place les sujets dans une situation où ils doivent coopérer avec un humain pour obtenir de la nourriture, contexte considéré comme trop artificiel pour des primates dont la vie sociale est majoritairement régulée par des règles de compétition entre congénères (Byrne & Whiten 1988). Les années 2000 furent ainsi le témoin d'un changement fondamental de paradigme expérimental : Hare et ses collègues

(2000 ; 2001) proposèrent de tester désormais les primates dans un contexte écologiquement plus valide pour eux, à savoir en compétition avec leurs congénères plutôt qu'en coopération avec des humains. Ces chercheurs tâchèrent de savoir si un chimpanzé subordonné préférerait récupérer un morceau de nourriture visible par un congénère dominant ou bien un morceau hors de la vue de ce dominant. Ils choisirent préférentiellement le morceau caché à la vue du dominant, ce qui amena les auteurs à conclure que les chimpanzés faisaient preuve du premier niveau de prise de perspective visuelle c'est-à-dire la compréhension de ce que les autres peuvent et ne peuvent pas voir, tant au présent (Hare et al. 2000) que dans un passé proche (Hare et al. 2001). Bien que ces résultats aient aussi suscité la critique (*e.g.* Povinelli & Vonk 2004 ; Lurz & Krachun 2011), l'adoption de cette nouvelle méthodologie a permis de mettre au jour des capacités cognitives jusqu'alors insoupçonnées chez les primates.

3.3. Etat de l'art

La recherche sur la Théorie de l'Esprit s'est d'abord principalement focalisée sur l'étude des grands singes et notamment du chimpanzé, négligeant les autres espèces de primates dont les « petits » singes (ci-après « singes »). Ce « chimpocentrisme », critiqué par certains auteurs (Beck 1982 ; Miklósi 2002), entrave notre compréhension de l'évolution de la cognition. En effet, des études comparatives entre grands singes, singes et autres espèces sont nécessaires afin de retracer l'histoire évolutive de la cognition. Une des raisons pour laquelle les singes ont été délaissés est probablement due au fait que les études portant sur les capacités mentales des primates ont souvent rapporté que les grands singes surpassaient les singes dans de telles tâches (Byrne 1995). Toutefois, les différences de résultats obtenus entre grands singes et singes pourraient s'expliquer ici aussi par des disparités de méthodologie ; les grands singes ayant été principalement étudiés dans des conditions expérimentales en laboratoire contrairement aux singes qui furent davantage observés dans leur milieu naturel. De plus, même dans les études utilisant des protocoles semblables, les performances des grands singes testés, fortement acculturés, étaient comparées à celles de singes naïfs, surestimant ainsi les différences observées (Tomasello & Call 1997).

Il apparaît désormais nécessaire d'étudier un plus large panel d'espèces, au sein et au-delà des primates, à travers des paradigmes similaires standardisés afin de mieux comprendre les processus cognitifs sous-tendant la cognition. Cet effort en est à ses balbutiements mais de plus en plus d'études adoptent une approche comparative et certaines ont même révélé des

performances comparables chez les singes de l’Ancien Monde et les grands singes (Amici et al. 2010 ; MacLean et al. 2012 ; Schmitt et al. 2012 ; 2013).

Pour en revenir à la Théorie de l’Esprit, cette capacité cognitive a été définie comme constituée de différents composants de complexité variable se développant graduellement au cours de l’ontogénie (Premack 1990 ; Leslie 1994 ; Baron-Cohen 1995). Dans la recherche sur la Théorie de l’Esprit chez les animaux non-humains (animaux ci-après), les composants généralement étudiés sont les suivants : suivi du regard, discrimination de l’attention, prise de perspective, duperie, compréhension des intentions et des fausses-croyances ainsi que la conscience de soi. Je présenterai dans les pages suivantes un état de l’art focalisé sur la discrimination de l’attention, la prise de perspective, la tromperie et la compréhension des intentions chez les primates, sujets de ma thèse.

3.3.1. *Discrimination de l’attention*

Etre capable d’estimer l’état attentionnel d’autrui est une faculté essentielle notamment lors d’interactions sociales impliquant des signaux visuels (Chance 1967). Dans ce sens, la communication sera plus efficace si l’émetteur d’un signal visuel choisit de communiquer avec le récepteur lorsqu’il est particulièrement attentif (Liebal et al. 2013). La discrimination des états attentionnels d’autrui est considérée par ailleurs comme un des critères de la communication intentionnelle (Leavens et al. 2005). La discrimination de l’attention a été majoritairement étudiée *via* un paradigme coopératif de quémade, par exemple la tâche de choix d’objet. Comme il a été vu précédemment, dans ce test, le sujet doit, afin d’obtenir une récompense alimentaire hors de sa portée, communiquer sa localisation grâce à un geste de pointage ou de quémade à un expérimentateur humain dont l’état d’attention varie. De nombreuses expériences de la sorte ont été menées chez les grands singes (*e.g.* chimpanzés : Hostetter et al. 2001 ; orangs-outans et bonobos : Zimmermann et al. 2009) et plus récemment chez les singes (*e.g.* saïmiris : Anderson et al. 2010 ; babouins : Bourjade et al. 2013 ; capucins : Hattori et al. 2010 ; mangabeys : Maille et al. 2012) mais les résultats concernant les indices attentionnels pris en compte par ces espèces ne font pas l’unanimité.

La grande majorité des études a montré que les grands singes sont sensibles à l’orientation du corps (Povinelli & Eddy 1996 ; Krause & Fouts 1997 ; Hostetter et al. 2001 ; Kaminski et al. 2004 ; Liebal et al. 2004 ; Poss et al. 2006 ; Bania & Stromberg 2013 ; Genty et al. 2015), du visage (Kaminski et al. 2004 ; Tempelmann et al. 2011) ainsi qu’à des indices

plus subtils comme l'état des yeux de l'expérimentateur (Barth et al. 2005 ; Hostetter et al. 2007 ; Bulloch et al. 2008). Peu d'espèces de singes ont quant à elles été testées mais la plupart de ces études ont montré que les singes ne prennent en compte que des indices grossiers comme l'orientation du corps et du visage du partenaire humain dans l'appréciation de son état attentionnel (capucins : Defolie et al. 2015 ; mangabeys : Maille et al. 2012 ; babouins : Meunier et al. 2013 ; Vick & Anderson 2003). Il se pourrait toutefois que cette prétendue absence de sensibilité aux yeux soit due à des caractéristiques méthodologiques des expériences car certaines études ont rapporté que des singes y sont sensibles. Certains singes discriminent en effet l'état des yeux (ouverts *versus* fermés) de l'expérimentateur humain et cela a été mesuré à travers leur comportement visuel et non gestuel (capucins : Hattori et al. 2007) et lorsque la nourriture convoitée était posée dans la main du partenaire humain et non sur une entité externe comme une table (babouins : Bourjade et al. 2013 ; capucins : Hattori et al. 2010).

Il semblerait donc que les singes, comme les grands singes, soient capables d'adapter leur comportement selon l'état d'attention d'un humain, en se basant au moins sur l'orientation de son corps et de son visage si ce n'est l'état de ses yeux. Cette faculté dont ils font preuve amène la question suivante : sont-ils pour autant capables de comprendre ce que les autres voient et ne voient pas ?

3.3.2. *Prise de perspective*

La capacité à comprendre ce que les autres voient et ne voient pas, appelée aussi prise de perspective visuelle, est considérée comme un composant phare de la Théorie de l'Esprit (Emery 2000). Chez les enfants, cette capacité se développe en deux étapes (Flavell 1992). Vers l'âge de deux ans, les enfants comprennent que quelqu'un peut voir quelque chose qu'ils ne voient pas (niveau 1) et ce n'est qu'autour de leur troisième année qu'ils sont ensuite capables de se représenter mentalement les différentes perceptions visuelles d'une scène observée par des personnes ayant différents points de vue (niveau 2 ; *e.g.* Moll & Meltzoff 2011).

La tâche de choix d'objet fut également pendant longtemps considérée comme le paradigme de référence pour tester le niveau 1 de la prise de perspective chez les primates mais les résultats furent peu probants chez les grands singes (Povinelli & Eddy 1996 ; Peignot & Anderson 1999 ; Call et al. 2000) comme chez les singes (Anderson et al. 1995 ; 1996 ; Burkart & Heschl 2007). Les premiers résultats positifs de prise de perspective visuelle chez

les chimpanzés ont émergé de l'utilisation de tâches compétitives (Hare et al. 2000 ; 2001 : voir p. 20-21 ; Bräuer et al. 2007 ; voir aussi Melis et al. 2006 pour prise de perspective auditive). Ce type de paradigme expérimental a été utilisé chez peu d'espèces de singes et les résultats obtenus sont mitigés. Les capucins et les marmousets se comportaient comme s'ils comprenaient ce que pouvait et ne pouvait pas voir un dominant mais leur choix pouvait s'expliquer par un mécanisme cognitif plus simple de lecture de comportement (Hare et al. 2003 ; Burkart & Heschl 2007). Ainsi, les singes auraient simplement évité de s'approcher d'un morceau de nourriture « contaminé » par le regard pesant d'un dominant (Kaminski et al. 2008). Toutefois, Overduin-de Vries, Spruit et Sterck (2014) ont récemment mis au point un protocole plus contrôlé : le subordonné pouvait voir le dominant à travers un miroir sans tain empêchant ce dernier d'avoir un accès visuel à son congénère et à la nourriture avant et pendant le test. Les auteurs conclurent ainsi que les macaques à longue queue étaient capables de prise de perspective visuelle (Overduin-de Vries et al. 2014). D'autres expériences en situation de compétition ont rapporté que lémuriens (Sandel et al. 2011 ; MacLean et al. 2013 ; Bray et al. 2014) et macaques rhésus (Flombaum & Santos 2005 ; Bray et al. 2014 ; voir Santos et al. 2006 pour domaine auditif) préféraient voler de la nourriture à un humain compétiteur qui ne pouvait pas les voir, suggérant ainsi qu'ils soient dotés du niveau 1 de prise de perspective visuelle.

Très récemment, des chercheurs ont voulu déterminer si les chimpanzés comprenaient comment les autres voyaient les choses (niveau 2 de prise de perspective visuelle : Karg et al. 2016). Ils ont cherché à savoir si les chimpanzés étaient capables d'attribuer une fausse perception visuelle, différente de la leur et de la réalité, à leurs congénères. Un subordonné était testé face à un dominant, un panneau vertical opaque les séparant jusqu'à mi-hauteur, leur permettant ainsi de se voir. Deux bâtons de Bretzel de taille identique étaient accrochés sur le panneau du côté du subordonné, l'un des deux dépassant plus que l'autre du bord supérieur, apparaissant ainsi illusoirement plus grand à la vue du dominant. Le subordonné, quant à lui, voyait de son côté que les deux bâtonnets étaient de la même taille. Le choix entre les deux items était ensuite proposé au dominant hors de portée de vue du subordonné, puis au subordonné qui ignorait donc lequel venait d'être choisi par son compétiteur. Le subordonné ne pouvait obtenir une récompense que s'il choisissait le morceau non choisi par le dominant. L'hypothèse des auteurs était la suivante : si le subordonné est capable de se représenter mentalement la perception visuelle du dominant, alors il devrait préférentiellement choisir le bâton de Bretzel apparaissant plus petit au dominant, supposant que celui-ci a préalablement manifesté une préférence pour le morceau apparemment plus grand. Les chercheurs ont

rapporté que, face au dominant, les subordonnés choisissaient un bâtonnet au hasard et montraient curieusement une préférence pour le « grand » bâton dans un test contrôle c'est-à-dire testés seuls. Il semblerait donc que les chimpanzés projettent leur propre préférence à leur congénère sans comprendre que la motivation du dominant est basée sur une fausse perception (Karg et al. 2016). Aucune étude de ce genre n'a encore été menée chez des singes. Bien qu'il soit désormais de plus en plus admis qu'au moins les grands singes, si ce n'est certaines espèces de singes, semblent être capables d'inférer ce que les autres peuvent et ne peuvent pas voir (Call & Tomasello 2008 ; Whiten 2013), le mystère reste entier quant à leur capacité à utiliser ces informations à des fins de manipulation intentionnelle.

3.3.3. *Manipulation sociale*

Les premiers indices de tromperie tactique chez les primates proviennent d'un catalogue d'anecdotes, émanant d'un grand nombre de chercheurs, récoltées pour la plupart en milieu naturel (Byrne & Whiten 1990). Bien que plusieurs termes et définitions aient été proposées pour la tromperie tactique (de Waal 1992 ; Mitchell 1993 ; Semple & McComb 1996 ; Hauser 1997), la définition la plus communément acceptée est celle de Byrne et Whiten (1985) selon laquelle il s'agit d'un acte appartenant au répertoire comportemental normal d'un individu, utilisé à faible fréquence dans un contexte différent de l'utilisation « honnête » du signal, de sorte qu'un autre individu interprète mal la signification du dit comportement, et ce, à l'avantage de l'émetteur. Cette définition est toutefois purement fonctionnelle et ne contient pas de postulat quant aux mécanismes cognitifs sous-jacents impliqués (Byrne 2003).

Une première approche expérimentale fut de tester si un sujet pouvait tromper un expérimentateur humain compétiteur à propos de la localisation d'une récompense alimentaire cachée. Dans l'étude originale de Woodruff et Premack (1979), quatre chimpanzés, préalablement entraînés à pointer en direction d'un conteneur rempli de nourriture, furent ensuite testés avec un partenaire humain soit coopératif, soit compétitif. S'ils pointaient correctement face à l'humain coopératif, ils étaient récompensés ; en revanche ils devaient signaler le récipient vide à l'expérimentateur compétitif pour obtenir la nourriture. Les chimpanzés ne firent pas de différence entre les deux personnes au cours des soixante premiers essais et il leur aura fallu plus d'une centaine d'essais pour apprendre à garder pour eux l'information ou encore pour indiquer le récipient vide au compétiteur. Des résultats similaires ont été rapportés chez des saïmiris (Anderson et al. 2001), des capucins bruns

(Mitchell & Anderson 1997) ainsi que des lémurs noirs et bruns (Genty & Roeder 2006 ; Genty et al. 2008). Deux critiques peuvent être énoncées concernant ce protocole. D'une part, les singes ayant, lors d'un pré-test, fait l'expérience d'un expérimentateur conciliant et coopératif pendant de très nombreux essais, il se pourrait qu'il ait été ensuite difficile pour eux de passer à un mode compétitif. D'autre part, les sujets auraient pu apprendre au fil des essais constituant l'expérience, des règles comportementales simples par apprentissage associatif comme par exemple « si le coopérateur approche, montrer le récipient contenant la nourriture » ou « si le compétiteur approche, montrer le récipient vide » (Heyes 1993 ; 1998).

Une deuxième approche expérimentale, écologiquement plus valide pour des primates, permet de tester des individus dans un contexte social compétitif avec leurs congénères. Dans ce paradigme, un subordonné, précédemment informé de la cachette d'une source de nourriture, était autorisé à chercher cette nourriture en présence d'un congénère dominant. Dans l'étude pionnière de Menzel (1971 ; 1974), les chimpanzés subordonnés ayant assisté à la cache de la nourriture étaient capables de garder cette information pour eux et essayaient même d'attirer le dominant loin de la nourriture convoitée (voir aussi Hirata & Matsuzawa 2001). Des stratégies similaires ont été observées chez des espèces de singes comme les mangabeys couronnés (Coussi-Korbel 1994) et les macaques de Tonkean (Ducoing & Thierry 2003). Bien que ce type de protocole semble plus pertinent et ait révélé des comportements de duperie chez les singes et les grands singes, ces résultats peuvent aussi être expliqués par un apprentissage au fil du temps, basé sur des mécanismes simples d'association. Ainsi, les subordonnés pourraient avoir appris à ajuster leur comportement en fonction de celui du dominant en utilisant une règle simple telle que « si présence du dominant, pas d'accès à la nourriture ». La question de l'intentionnalité de ces comportements de duperie reste de ce fait entière et en nourrit une seconde : les primates sont-ils capables de reconnaître les intentions d'autrui ?

3.3.4. Compréhension des intentions

Etre capable de comprendre les intentions des autres a de nombreux avantages dans la vie sociale. Déceler les buts d'autrui permet aux individus d'extraire des informations de l'environnement et d'anticiper le comportement futur d'autres individus, par exemple lors d'un face à face avec un compétiteur dans une situation inédite (Call & Tomasello 2008 ; Call 2009). Cela permet aussi de discerner un bon partenaire social de celui qui ne l'est pas (Woodward 2009). Dans la littérature sur le sujet, plusieurs termes tels que « action dirigée

vers un but », « intention » et « intentionnalité » sont utilisés de manière interchangeable, se référant parfois à la même chose, parfois pas. Il est donc avant tout nécessaire de poser quelques définitions.

Selon certains auteurs, une action dirigée vers un but est un acte moteur dont le but est intérieurement représenté, ce qui implique une connaissance des relations de causalité entre les actions et leurs conséquences (de Wit & Dickinson 2009 ; Pezzulo & Castelfranchi 2009). Pour d'autres, il s'agit simplement d'une relation entre un agent et un objet sans avoir recours à une représentation interne du but ni de l'intention (Penn & Povinelli 2009). Une distinction peut être faite entre intention et intentionnalité : la première se réfère à ce qui est communiqué tandis que la seconde renvoie à la façon dont le contenu est communiqué (Scott-Phillips 2015). L'intentionnalité a ainsi été définie par les philosophes de l'esprit comme la propriété qui rend les états mentaux et actions dirigés vers, ou relatifs à des objets et situations du monde (Dennett 1971 ; Searle 1983 ; Brentano 1995). L'intention est considérée quant à elle comme le plan d'action émis pour que le but soit atteint (Tomasello et al. 2005). L'intention est ainsi incrustée dans l'action. Comprendre qu'une action est dirigée vers un but reviendrait à percevoir un premier niveau d'intention : l'intention dans l'action (Searle 1983). Dans ce sens, il est admis que les animaux peuvent avoir des intentions mais la question qui se pose est de savoir s'ils peuvent comprendre que les autres en ont aussi.

Différentes méthodes expérimentales ont été utilisées pour tester la compréhension des intentions chez les enfants et les primates. La mesure la plus fréquemment utilisée en psychologie développementale est la « violation de l'expectative par le temps de regard ». Pendant une phase d'habituation, les enfants visionnent sur un écran plusieurs essais dans lesquels un agent attrape un objet situé derrière une barrière. La barrière est ensuite retirée et les enfants se voient proposer deux types d'essais : un essai dans lequel l'agent attrape directement l'objet et un essai dans lequel il saisit l'objet après avoir contourné une barrière imaginaire qui n'est plus présente. Les enfants âgés de neuf mois regardent plus longtemps les images de saisies indirectes, signe qu'ils sont surpris par ce mouvement incohérent (Woodward 1998 ; Phillips & Wellman 2005 ; Brandone & Wellman 2009). Il semblerait donc qu'ils comprennent que le but de l'agent est d'obtenir l'objet. Un résultat similaire a été rapporté chez des macaques (Rochat et al. 2008), suggérant ainsi que primates humains et non-humains partagent au moins certains précurseurs de la compréhension des intentions.

Une autre méthode souvent utilisée chez les enfants est basée sur l'imitation. Le protocole « accidentel *versus* intentionnel » consiste à montrer aux enfants un acteur réalisant une action de manière accidentelle ou intentionnelle. Après ces démonstrations, l'opportunité

de produire l'action par eux-mêmes est donnée aux sujets. Carpenter, Akhtar et Tomasello (1998) ont montré que les enfants de 14 à 18 mois imitaient significativement plus les actions intentionnelles qu'accidentelles ce qui les amena à conclure que les jeunes enfants comprenaient quelque chose des intentions d'autrui. Call et Tomasello (1998) ont utilisé le même protocole chez des enfants de deux et trois ans ainsi que chez des chimpanzés et orangs-outans adultes. Les sujets avaient appris à utiliser un indice visuel utilisé par un expérimentateur comme signal fiable pour localiser une récompense alimentaire se trouvant dans une boîte parmi trois. Lors du test, l'expérimentateur marquait une boîte intentionnellement en plaçant délibérément la cible dessus, et une autre accidentellement en la laissant tomber dessus. Les auteurs rapportèrent que les enfants et les grands singes testés choisissaient préférentiellement la boîte marquée intentionnellement que celle marquée accidentellement, suggérant ainsi une sensibilité particulière à la nature intentionnelle des actions chez ces espèces (mais voir Povinelli et al. 1998 pour des résultats discordants). D'autres auteurs, utilisant un protocole quelque peu différent, ont rapporté que les chimpanzés, tamarins et macaques rhésus sélectionnaient plus fréquemment le récipient intentionnellement ciblé qu'accidentellement, les amenant à conclure que ces espèces étaient capables d'inférer des actions rationnelles et dirigées vers un but par un humain (Wood et al. 2007 mais voir Costes-Thiré et al. 2015 pour des résultats négatifs chez les capucins bruns et les macaques de Tonkéoan; voir aussi Gergely et al. 2002 et Buttelmann et al. 2007 pour des résultats positifs quant à la compréhension de la rationalité des actions chez les enfants et les chimpanzés).

Une dernière méthode utilisée pour tester l'attribution d'intention est le paradigme « réticent *versus* incapable ». Dans l'étude originale utilisant ce paradigme (Call et al. 2004), un expérimentateur avait préalablement habitué les chimpanzés à recevoir une récompense alimentaire à travers un petit trou percé dans un mur de plexiglas. Lors du test, il s'arrêtait subitement de nourrir le sujet soit parce qu'il ne le voulait plus alors qu'il le pouvait (réticent) soit parce qu'il ne le pouvait plus à cause d'une barrière physique (incapable). Les auteurs rapportèrent que les chimpanzés qu'évitaient plus la nourriture et quittaient la zone de test plus rapidement, car frustrés, face à un expérimentateur mal intentionné que bien intentionné, ce qui amena les chercheurs à conclure que les chimpanzés interprétaient les actions de l'humain comme dirigées vers un but (Call et al. 2004). Des résultats similaires ont été observés chez des enfants de neuf mois (Behne et al. 2005) et chez des capucins pour des actions accomplies par un humain mais pas par un robot (Phillips et al. 2009).

Malgré des points de vue divergents (Povinelli & Vonk 2003 ; Lurz & Krachun 2011), de plus en plus d'études rapportent des résultats posant question chez les grands singes et les singes suggérant qu'ils comprennent quelque chose des intentions d'autrui bien que ce « quelque chose » demeure à l'heure actuelle obscur.

4. Objectifs de la thèse

Pour résumer, le consensus prédominant de la fin des années 1990 imposa que la Théorie de l'Esprit était une capacité spécifiquement humaine et que les animaux, petits et grands singes compris, n'avaient nullement accès aux états mentaux des autres (*e.g.* Heyes 1993 ; Tomasello & Call 1997 ; Heyes 1998). Les années 2000 marquèrent un virage méthodologique qui proposa de tester les primates dans un contexte écologiquement plus valide pour eux c'est-à-dire en compétition avec leurs congénères (Hare et al. 2000 ; 2001). Ce nouveau souffle a permis à la recherche sur la Théorie de l'Esprit chez les primates de faire peau neuve et de révéler des capacités cognitives inédites chez ces espèces. Les grands singes, et notamment les chimpanzés, seraient capables de discriminer différents états attentionnels (*e.g.* Barth et al. 2005), d'adopter la perspective visuelle d'autrui (*e.g.* Hare et al. 2001), de se servir de ce savoir pour manipuler activement leurs congénères (*e.g.* Hare et al. 2006) et de comprendre que les autres peuvent avoir des intentions (*e.g.* Call et al. 2004).

Les singes, quant à eux, ont souffert d'un « chimpocentrisme » leur accordant peu de place et peu d'intérêt dans cette recherche, mais depuis une dizaine d'années, les études portant sur les composants et prérequis à la Théorie de l'Esprit chez les singes font florès. Ainsi, certaines espèces de petits singes dont notamment les capucins, les babouins et les macaques, révèlent des comportements d'intérêt dans le domaine de la communication intentionnelle (*e.g.* Bourjade et al. 2013), de la discrimination de l'attention (*e.g.* Defolie et al. 2015), des perceptions (*e.g.* Flombaum & Santos 2005) et intentions d'autrui (*e.g.* Wood et al. 2007). Ces données sont encore rares et il est aujourd'hui plus que souhaitable que davantage d'études portent sur de plus nombreuses espèces de singes, en particulier sur des espèces encore peu étudiées, afin de tenter de retracer l'histoire évolutive de la cognition des primates.

C'est pourquoi je me suis intéressée au cours de ma thèse aux capacités socio-cognitives des macaques. Les macaques sont des primates semi-terrestres, essentiellement frugivores qui vivent en groupes sociaux multimâles-multifemelles de plusieurs dizaines d'individus (Thierry et al. 2004). Parmi les macaques, le macaque rhésus (*Macaca mulatta*)

est l'espèce la plus étudiée en cognition. Les macaques rhésus ont une vie sociale gouvernée par une hiérarchie stricte et leurs interactions, à l'instar des sociétés despotiques, sont très dépendantes de leurs relations hiérarchiques. Ainsi, chez les macaques rhésus, les membres du groupe surveillent sans cesse leurs congénères, sont à l'affut et réagissent au moindre changement de leur comportement. Les conflits sont unidirectionnels, les subordonnés se soumettant la plupart du temps au dominant. Les macaques de Tonkean (*Macaca tonkeana*) entretiennent quant à eux des relations plus orientées par leurs affinités, ils font preuve d'une grande tolérance sociale, ponctuant leurs conflits par de nombreuses protestations et des réconciliations diverses et variées (Thierry et al. 2004). Cette espèce a été beaucoup moins étudiée et les connaissances en cognition la concernant sont peu abondantes, c'est la raison pour laquelle je me suis principalement intéressée à cette espèce.

L'objectif de ma thèse était ainsi de répondre aux questions suivantes :

1. Les macaques rhésus et les macaques de Tonkean sont-ils capables d'utiliser intentionnellement un geste de pointage et de discriminer différents états attentionnels d'un expérimentateur humain ? (**Article 1 & 2**)
2. Les macaques de Tonkean sont-ils capables de percevoir ce que peuvent et ne peuvent pas voir leurs congénères ? (**Article 3**) Sont-ils capables de tromperie ? (**Article 4**)
3. Les macaques de Tonkean sont-ils capables de discriminer les intentions d'autrui ? (**Article 5**)

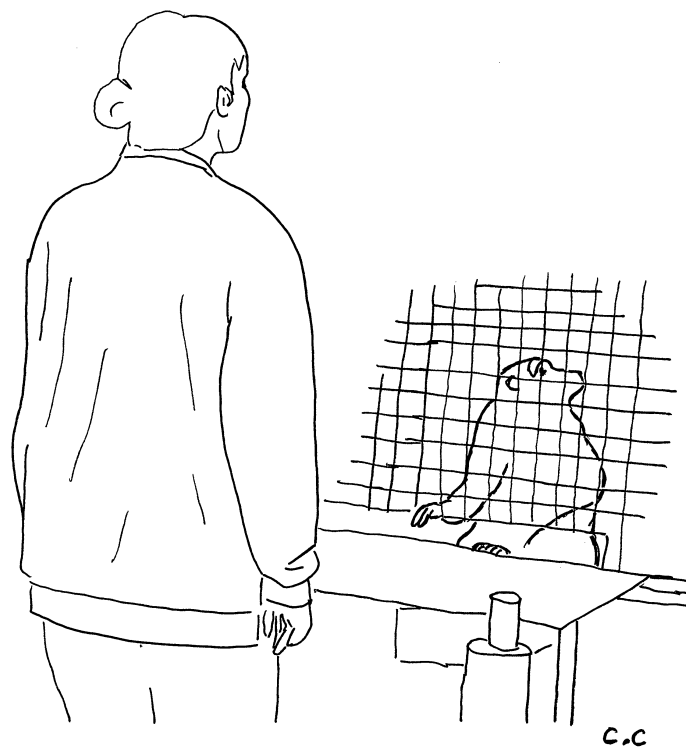
ARTICLE 1

Do Tonkean macaques (*Macaca tonkeana*) tailor their gestural and visual signals to fit the attentional states of a human partner?

Canteloup C., Bovet D. & Meunier H.

Animal Cognition 2015, 18(2) : 451-461

Avec la permission de Springer



Synthèse de l'article 1:

Do Tonkean macaques (*Macaca tonkeana*) tailor their gestural and visual signals to fit the attentional states of a human partner?

Canteloup C., Bovet D. & Meunier H.

Animal Cognition 2015, 18(2) : 451-461

Questions

Etre capable de discriminer l'état d'attention d'autrui rend la communication plus efficace et est considéré comme un critère d'une communication intentionnelle. Les macaques de Tonkean sont-ils capables d'utiliser intentionnellement un geste de pointage et de discriminer différents états attentionnels d'un expérimentateur humain ? Si oui, sur quels indices attentionnels se basent-ils ?

Méthode

Six macaques de Tonkean, préalablement entraînés à produire un geste de pointage en direction d'une récompense alimentaire pouvant leur être délivrée par une expérimentatrice, ont été testés dans sept conditions expérimentales variant selon l'état d'attention de cette dernière (*e.g.* différant selon l'orientation de ses yeux, de son visage ou de son corps).

Résultats

Les macaques de Tonkean ajustent leurs signaux de communication à l'état d'attention de l'expérimentatrice en prenant en compte des indices attentionnels « grossiers » comme la présence, l'orientation du corps et du visage de l'expérimentatrice mais pas d'indices plus subtils comme l'état des yeux.

Conclusion

Les macaques de Tonkean sont capables de communication gestuelle intentionnelle et de discriminer l'état d'attention d'un humain sur la base de l'orientation de son visage et de son corps. Cette faculté est un prérequis à la Théorie de l'Esprit mais n'implique par forcément une capacité de prise de perspective visuelle.

Do Tonkean macaques (*Macaca tonkeana*) tailor their gestural and visual signals to fit the attentional states of a human partner?

Charlotte Canteloup · Dalila Bovet ·
Hélène Meunier

Received: 31 January 2014/Revised: 26 September 2014/Accepted: 7 October 2014/Published online: 14 October 2014
© Springer-Verlag Berlin Heidelberg 2014

Abstract We tested here whether Tonkean macaques (*Macaca tonkeana*), trained to produce a pointing gesture, modify their behaviour in response to different human's attentional states. More specifically, we investigated the macaque's ability to communicate intentionally about the location of an unreachable hidden food reward in several contexts which differ by the human partner's attentional state. The experimenter displayed seven attentional states differing on the basis of body, head and gaze orientation. Our study validates several criteria of an intentional communication. We showed that macaques produce more pointing gestures when an audience, i.e. the human partner, is present than absent. We also revealed an adjustment of gaze alternation between the face of the experimenter and the hidden food reward according to several experimental conditions. However, in our study, macaques did not produce auditory attention-getting behaviours when the human partner was inattentive. Finally, only rough cues, i.e. presence, body and face orientation of the observer, seem to be taken into account by macaques. However, our results also supposed the importance of joint attention for macaques since they display more gaze alternation when the head and/or eyes of the human partner are mobile.

Keywords Intentional communication · Social cognition · Attention · Cues · Monkeys

Introduction

Effective communication is a prerequisite for social animals that routinely share information about their social and physical environment, and in this aim, it is especially important for animals to be sensitive to what others are paying attention to (Chance 1967; Maynard Smith and Harper 2003; Partan and Marler 1999). Identifying the attentional states of others can thus make the communication more efficient and optimize the cost of the communicative act by choosing the right time to start communicating (Tomasello et al. 1998, 2001). For example, when you want to attract the attention of someone who is away from you and do not look at you, it is cheaper for you—in terms of expended energy—to wait until his gaze turns towards you in which case you could make him a sign. This will save you gesticulate or shout to get his attention! Comprehension of attentional states of others has been reported as a criterion of intentional communication (Leavens et al. 2005b) and has aroused great interest among researchers in the framework of gestural communication.

Numerous researchers seeking to understand when and how human language evolved are interested in gestural communication in primates. The theory of the gestural origin of language proposes that language evolved from gestures (Corballis 2002; Vauclair 2004) and emphasizes similarities between non-human primates' gestural communication and human language (Hewes 1973). First studies on gestural communication in primates date back to the 1960s (Goodall 1968; van Lawick-Goodall 1967), and

C. Canteloup (✉) · H. Meunier
Primate Centre of Strasbourg University, Fort Foch,
67207 Niederhausbergen, France
e-mail: charlotte.canteloup@gmail.com

C. Canteloup · H. Meunier
Laboratoire de Neurosciences Cognitives et Adaptatives,
UMR 7364, Strasbourg University, Strasbourg, France

D. Bovet
Laboratory of Ethology, Cognition, Development, University
Paris Ouest Nanterre La Défense, BSL Building, 200 Avenue de
la République, 92001 Nanterre Cedex, France

more recently, researchers have established gestural repertoires in monkeys (e.g. *Macaca nemestrina*: Maestripiéri 1996a; *M. arctoides*: Maestripiéri 1996b) and described intentional gestures such as “grooming hand-slap” (McGrew et al. 2001), “leaf-clipping” (Nishida 1980; Matsumoto-Oda and Tomonaga 2005) and “directed scratching” (Pika and Mitani 2006) predominantly in great apes as wild chimpanzees (*Pan troglodytes*). Some authors (Hobaiter and Byrne 2011a; Liebal et al. 2004a) adopted a wide definition of gestural communication including movements of the whole body, limbs and head, whereas others (Roberts et al. 2012a, b) focused their definition on movements of the hands without the use of objects or a substrate.

A gesture has been especially examined in primates’ gestural communication: pointing, defined as extended fingers point to distal objects with the putative goal of directing the attention of an observer to those distal objects (Leavens et al. 1996). Spontaneous pointing gestures have been recorded in a wild bonobo (*Pan paniscus*) (e.g. Veà and Sabater-Pi 1998), in wild chimpanzees (Hobaiter et al. 2014; Roberts et al. 2012b), in captive orangutans (*Pongo pygmaeus*) (e.g. Call and Tomasello 1994), captive bonobos (e.g. Zimmerman et al. 2009) and captive chimpanzees (e.g. Krause and Fouts 1997; Leavens et al. 1996, 2004a, 2005a, b; Leavens and Hopkins 1998, 1999). Although almost no spontaneous pointing gestures have been reported in monkeys (e.g. olive baboons (*Papio anubis*): Bourjade et al. 2014), they can be trained to exhibit pointing gestures to communicate the location of a food reward to a human experimenter (squirrel monkeys (*Saimiri sciureus*): Anderson et al. 2007, 2010; olive baboons: Bourjade et al. 2013; Meunier et al. 2013; capuchins (*Sapajus apella*): Hattori et al. 2007, 2010; mangabeys (*Cercocebus torquatus*): Maille et al. 2012). Studying learned pointing gestures in monkeys allow researchers to investigate three main questions: (1) the referential property of such gestures, (2) the intentionality of such gestural communication and (3) monkeys’ attention reading abilities. Moreover, we know that primates (1) have sophisticated social systems relying on visual behaviour and visual signals (Tomasello et al. 1998), (2) have brains containing neurons responding to eye gaze and head orientation (Perrett et al. 1985) and (3) are closely related to humans, which make them good candidates to evaluate the contribution of eye gaze perception to attributing attention and mental states.

Several studies have focused on the referential property of pointing gestures, which convey information about objects or environmental events (e.g. Call and Tomasello 1994; Cartmill and Byrne 2007; Pika and Mitani 2006; Roberts et al. 2012a, 2013, 2014a, b). The study of pointing gestures regarding intentional communication and attention

reading abilities was mostly studied in humans and great apes, neglecting monkeys, perhaps mainly because they have been thought to have poor cognitive abilities in comparison with great apes (Byrne 2000; Tomasello et al. 2003).

In humans, pointing becomes an act of intentional communication at about 12 months of age, and infants aged from 16 months precede significantly more their pointing behaviour by a visual monitoring of the social partner (Franco and Butterworth 1996). This verification is done in three steps: (1) the child checks the attentional state of the partner before pointing, (2) he directs the attention of the partner to the event of interest by pointing and (3) he shares an internal state (Franco and Butterworth 1996). Such pointing gesture was believed to be a uniquely human ability until some reports of spontaneous pointing in our nearest living relatives, the great apes that set up a new deal (Leavens et al. 2005b). In this context, pointing gesture has been defined as intentional communication when the emitter has a goal and modifies its gestural communicative act according to the attention and comprehension state of the recipient (Tomasello and Call 2007). Leavens et al. (2005b) have proposed a definition of intentional communication in non-human primates based on several criteria initially established for humans (e.g. Bates et al. 1979). According to this definition, an act of communication is intentional when: (a) the display of the communicative signal is dependent upon the presence of an audience: the gesture is produced and directed towards a recipient; (b) the attentional state of the observer has an influence on the propensity to emit gestures; (c) the subject do some gaze alternation between the social partner and the object or event of interest; (d) the subject deploys apparent attention-getting behaviours such as vocalizations; and (e) persists; and (f) elaborates new types of communicative behaviours when attempts to get the attention of the observer fail (the signaller flexibly repeated and substituted the original gesture by alternative gesture type).

The criterion of an audience (criterion a) was validated in a lot of studies in great apes (e.g. Hostetter et al. 2001; Kaminski et al. 2004; Leavens et al. 2004a; Roberts et al. 2012b; Schel et al. 2013a, b) and in monkeys (saimiris: Anderson et al. 2010; olive baboons: Bourjade et al. 2013; Meunier et al. 2013).

The criterion (b) regarding the influence of the attentional state of the recipient on the basis of different cues (body, head, eyes) on the gestural communication of the emitter was approved in several studies mentioned in the previous paragraph. When requesting food, all great apes species and numerous monkeys’ species are sensitive to a human’s attention. However, studies investigating which cues are relevant for these different species to assess the attentional state of others have produced inconsistent

results. Thus, chimpanzees have been reported to exhibit more gestures and faster when the experimenter was oriented towards them (Krause and Fouts 1997; Liebal et al. 2004b; Povinelli and Eddy 1996) and to emit more vocalizations when the human partner was oriented away from them (Hostetter et al. 2001). Kaminski et al. (2004) concluded that chimpanzees, bonobos and orangutans are able to discriminate the front-back body orientation and face orientation when begging for food from a human, but have little sensitivity for the state of the eyes, whereas Tempelmann et al. (2011) found that all great apes species were sensitive only to face orientation. Few studies reported sensitivity to subtle cues such as eyes state in great apes (Barth et al. 2005; Hostetter et al. 2007). In monkeys, mangabeys have been shown to gesture more and faster when both the body and the head of the experimenter were oriented towards them than when they were oriented away (Maille et al. 2012). Meunier et al. (2013) have reported that olive baboons adjusted their requesting gestures to the body orientation of the experimenter. Capuchins have been reported to be sensitive to eyes state. This was recorded when considering their visual orienting behaviour, but not when considering their gestural behaviour (Hattori et al. 2007) and when the food was held in the human's hand, but not when the food was on a table (Hattori et al. 2010). More recently, Bourjade et al. (2013) have shown that olive baboons paid attention to the visual attention, i.e. direction and focus of attention of the experimenter with special emphasis on the state of her eyes (open vs. closed). In this study, the food was held in the experimenter's hand and baboons gestured more and looked more at the experimenter when she was with her eyes open compared with a situation with her eyes closed. Considering macaques, Blaschke and Ettliger (1987) have successfully trained four rhesus monkeys (*Macaca mulatta*) to point towards a box containing food in an object-choice task and Flombaum and Santos (2005) have shown that rhesus macaques are able to deduce what a human competitor perceive on the basis of where he is looking. However, no information is available on the cues taken into account by macaques to discriminate attentional states.

It has been reported that gaze alternation between the human partner and the desired food (criterion c) add to vocal communication in wild chimpanzees (Schel et al. 2013b), and to gestural communication in great apes (Leavens and Hopkins 1998, 1999; Leavens et al. 2004a; Tomasello et al. 1994) and in monkeys (saïmiris: Anderson et al. 2007, 2010; olive baboons: Bourjade et al. 2013; Meunier et al. 2013).

Deployment of attention-getting behaviours (criterion d) when the communicative intent was not satisfied has been demonstrated in human infants (e.g. Liszkowski et al. 2008), great apes (Hopkins et al. 2007; Hostetter et al.

2001; Krause and Fouts 1997; Leavens et al. 2004b; Tomasello et al. 1994) and recently for the first time in a monkey species (olive baboons: Bourjade et al. 2013). However, few studies have reported evidences of persistence and elaboration (criteria e and f) of communication when communicative bids failed (orangutans: Cartmill and Byrne 2007; chimpanzees: Leavens et al. 2005b; Roberts et al. 2013, 2014b; olive baboons: Bourjade et al. 2013).

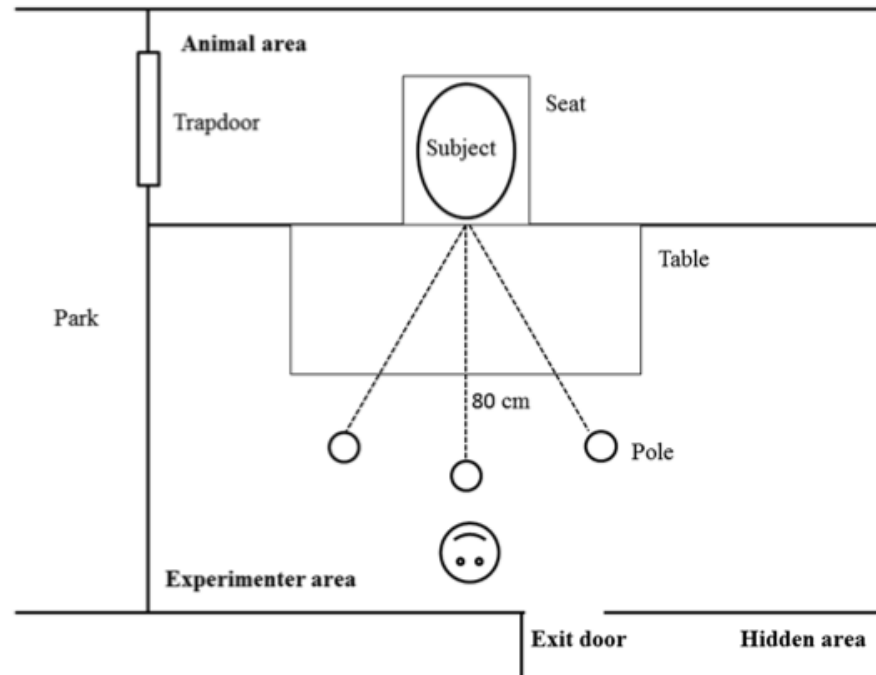
In this context, our study has two main goals, the first being to test the intentional property of a learned pointing gesture in a not-yet-studied Old World Monkey species, the Tonkean macaque (*Macaca tonkeana*). The second is to determine which rough and/or subtle cues are discriminated by macaques in order to assess the attentional state of the human partner. For this, we set up an experimental procedure in which macaques should communicate the location of a hidden raisin by pointing to an experimenter whom attentional state varied and who was ignorant of its location. The attentional state of the human partner differed according to her body, face and eyes orientation. We expected that, as great apes and other monkeys' species, macaques would not point when the human was inattentive and rather use other means to try to get her attention. However, facing an attentive human, we expected that macaques would point more and realize more gaze alternation between experimenter face and the hidden food reward. We also hypothesized that, as demonstrated in other studies (e.g. Ferrari et al. 2000), Tonkean macaques can follow the gaze of the experimenter, so are capable of visually co-orientation with others (Rosati and Hare 2009). If macaques are able to use subtle cues as eyes, they should produce more pointing gestures and gaze alternation when the experimenter's eyes are open than when they are closed. However, if macaques rely on more global cues such as body orientation, they should emit more pointing gestures when the experimenter is facing them than when she is oriented away, but should not be influenced by the other experimental conditions.

Methods

Subjects

The subjects were six Tonkean macaques (*Macaca tonkeana*), all housed and raised at the Primatology Centre of Strasbourg University, France (Number of agreement for conducting experiments on primates: AL/46/53/02/13). Six individuals (five males and one female aged 5–13 years), trained to produce a pointing gesture towards a hidden food reward, were tested between October 2012 and March 2013. The macaques lived in a one-acre wooded enclosure. Animals were fed with commercial pellets and water

Fig. 1 Schema of the experimental apparatus. Opaque cylinders allowing hiding raisin were put on the three poles



ad libitum. Fruits and vegetables were distributed twice a week, outside the experimental sessions.

Apparatus

Subjects were tested in an outdoor area opened and placed along their outdoor enclosure. The apparatus consisted in an adaptation of Bishop's QHP task (Bishop et al. 1996), initially designed to quantify manual preferences in human infants, and adapted to non-human primates by Meunier et al. (2011). The apparatus (Fig. 1) was composed of a concrete block placed inside the primates' outside area perpendicularly to the mesh, at about 1 m from the ground, used as a seat by the individual tested. A table in front of the subject and three unreachable wooden poles, each topped with containers and separated by 30° from the seated subject's perspective, were placed in the experimenter's area. A 10 × 60-cm hole in the mesh allowed subjects to point towards the baited container. A video camera was placed about 2 m in front of the wire mesh on the left side of the experimenter.

Testing procedure

All subjects were trained to produce a pointing gesture towards a food reward (a raisin) hidden under one of the three containers in a previous study (see Meunier et al. 2013 for details). One assistant and one experimenter

conducted the test. In the experimental trials, the assistant came to the subject and hid a raisin under one of the three containers in view of the subject according to a randomized order, including position of the raisin and hand used by both the assistant and experimenter to handle the raisin. Then, the experimenter, unaware of the location of the raisin, came to the subject; adopted one of the seven attentional states described below during 10 s and rewarded it after it pointed towards the container hiding the raisin. If no food was present under the pointed container, the experimenter showed the subject that there was nothing and the assistant came and removed the raisin in order to start a new trial. The seven different conditions varying according the attentional state are the following: in the "eyes open" condition, the experimenter was facing and looking at the subject with her eyes open. In the "alternation" condition, she followed the subject's gaze, copying its gaze alternation. In the "eyes closed", "eyes up" and "head aside" conditions, the experimenter was facing the subject with her eyes closed, or she looked up or she turned her head aside towards the park. In the "back turned" condition, the experimenter placed herself back turned to the subject. In the "absent" condition, the experimenter did not come to the subject after the assistant hide the raisin. Each testing session comprised, in a randomized order, the seven 10-s experimental trials, alternated with 16 motivational trials in which the experimenter gave the subject the reward, without any delay, just waiting for the subject

pointing towards one of the container. Each macaque received a total of 10 testing sessions (one session of test maximum per day) consisting of a total of 70 experimental trials and 160 motivational trials per individual. Due to a loss of four videos, we analysed only nine sessions for four subjects (the lacking sessions are session 1 of Wallace, session 2 of Ulrich, session 2 of Uruk and session 3 of Shan).

Data analysis

Experiments were recorded by a video camera HD (Canon, Legria HF S20). Videos were blindly analysed (without any cue about the experimental condition) frame by frame (one frame = 0.04 s) by CC using the software The Observer XT 10.1.548. During the analysis, we focused on gaze direction (to the experimenter, to the hidden food reward, to the park, up and to the exit door, see Fig. 1), on gaze duration, on frequency of gaze alternation between the experimenter and the hidden food reward and on frequency of pointing. Pointing was defined as an extension of the subject's arm through the hole of the wire mesh towards one of the three positions. We recorded one pointing when the extension of the gesture was at its peak just before the subject begins to retract or lower his arm. We also recorded several behaviours: noisy behaviours (vocalizations, strikes against the wire mesh) and other behaviours (yawn, scratch itself and lick the wire mesh).

Statistical analysis

We used two types of mathematical models in order to determine which attentional cues influenced different behavioural variables. Generalized linear mixed models (GLMM) for data following a Poisson law were used to test which attentional cues influenced two discontinuous variables: numbers of begging gestures and number of gaze alternations. Linear mixed-effects models (LME) for data following a normal law were used to test the effect of experimental conditions on four different continuous variables: durations of (1) gaze to the experimenter; (2) gaze to the hidden food reward; (3) gaze up and (4) gaze to the exit door. Graphic verifications (QQ plot of continuous variables) were in accordance with the normal law and allowed us to establish LME. Experimental condition ("alternation"; "eyes open"; "eyes closed"; "eyes up"; "head aside"; "back turned"; and "absent") was considered as fixed effect and individual factor was considered as a random effect. Each condition was compared with the reference condition: the "eyes open" condition. All tests were performed with R 3.1.0 software with level of significance set at 0.050.

Results

Gestural communication

The mean success rate of pointing in the right direction was of 92.78 % [standard error of the mean (SEM) = 2.09]. The frequency of pointing (Fig. 2) was significantly influenced by the experimenter's attentional state (AIC = 1,749.1; LRT = 77.1; $df = 6$; $P < 0.0001$). GLMM reveals that Tonkean macaques pointed significantly more in the "eyes open" condition (mean = 4.98 pointing gestures per trial ± 0.39) than in the "eyes up" (4.14 ± 0.44 ; $P = 0.038$), "head aside" (4.02 ± 0.34 ; $P = 0.016$), "back turned" (3.70 ± 0.44 ; $P = 0.001$) and "absent" conditions (2.59 ± 0.34) ($P < 0.0001$). However, there were no significant differences of frequencies of pointing gestures between the condition "eyes open" and "alternation" (5.60 ± 0.36) and "eyes closed" (4.48 ± 0.38) conditions ($P > 0.05$).

Visual orienting behaviour

The duration of gaze to the experimenter was significantly influenced by the experimenter's attentional state (numDF = 6; denDF = 380; F value = 31.18; and P value < 0.0001). LME reveals that Tonkean macaques looked significantly longer at the experimenter in the "eyes open" condition (mean = 2.02 s/trial ± 0.25) than in the "eyes up" (1.41 ± 0.14), "head aside" (1.28 ± 0.15) and "back turned" (1.28 ± 0.16) ($P < 0.001$) conditions. However, there were no significant differences of duration of gaze to the experimenter between the "eyes open" condition and "alternation" (2.40 ± 0.25) and "eyes closed" (2.17 ± 0.22) conditions ($P > 0.05$).

The duration of gaze to the hidden food reward was significantly influenced by the experimenter's attentional state (numDF = 6; denDF = 380; F value = 7.36; and $P < 0.0001$). LME reveals that rhesus macaques looked significantly longer at the hidden food reward in the "eyes open" condition (2.21 ± 0.18) than in the "back turned" (1.74 ± 0.19 ; $P = 0.024$) and "absent" (1.31 ± 0.15 ; $P < 0.0001$) conditions. However, there were no significant differences of duration of gaze to the hidden food reward between the "eyes open" condition and "alternation" (2.30 ± 0.18), "eyes closed" (2.59 ± 0.19), "eyes up" (1.97 ± 0.17) and "head aside" (2.02 ± 0.15) conditions ($P > 0.05$).

The frequency of gaze alternation (Fig. 3) was significantly influenced by the experimenter's attentional state (AIC = 1,571.7; LRT = 81.0; $df = 5$; and $P < 0.0001$). GLMM reveals that Tonkean macaques displayed significantly more gaze alternation between the face of the

Fig. 2 Mean frequency of pointing per session \pm SEM in function of the seven experimental conditions. $N = 6$. * $P < 0.05$; ** $P < 0.01$; and *** $P < 0.001$

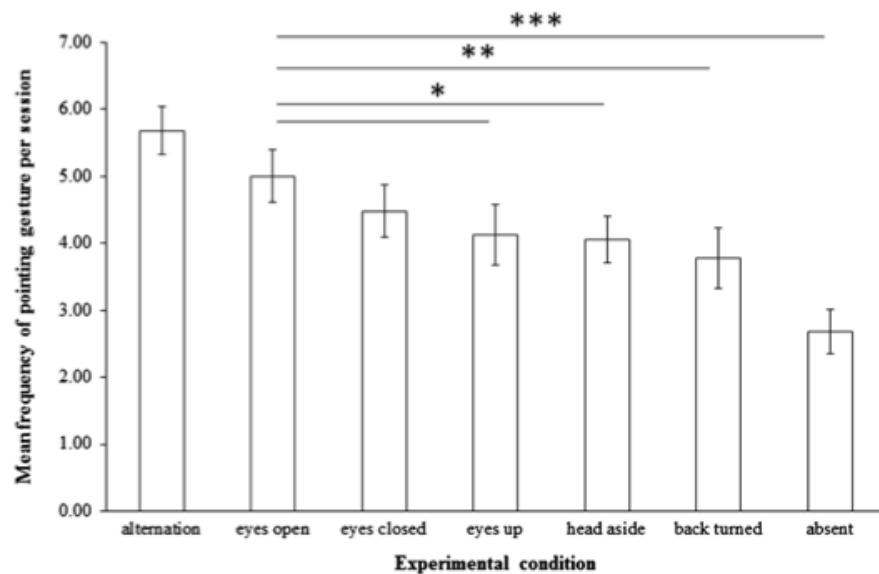
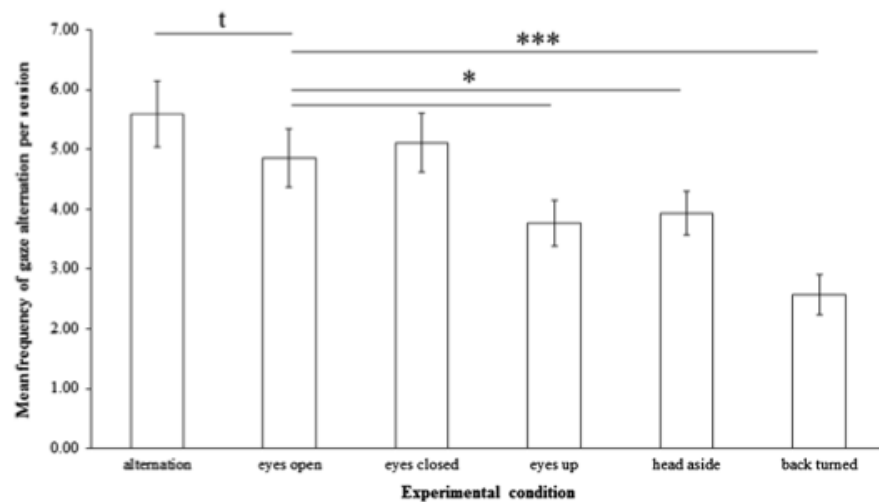


Fig. 3 Mean frequency of gaze alternation between the face of the experimenter and the hidden food reward per session \pm SEM in function of the six experimental conditions in which the experimenter was present. $N = 6$. t tendency; * $P < 0.05$; *** $P < 0.001$



experimenter and the hidden food reward in the “eyes open” condition (mean = 4.77 gaze alternation per trial \pm 0.49) than in the “eyes up” (3.77 ± 0.39 ; $P = 0.010$), “head aside” (3.91 ± 0.37 ; $P = 0.030$) and “back turned” (2.54 ± 0.33 ; $P < 0.0001$) conditions. Furthermore, Tonkean macaques tended to display more gaze alternation in the “alternation” (5.59 ± 0.53) condition than in the “eyes open” condition ($P = 0.07$).

Gaze following

The duration of gaze up (Fig. 4) was significantly influenced by the experimenter’s attentional state (numDF = 6;

denDF = 380; F value = 8.27; and $P < 0.0001$). LME reveals that Tonkean macaques looked up significantly longer in the “eyes up” condition ($0.86 \text{ s/trial} \pm 0.17$) than in the “alternation” (0.08 ± 0.04), “eyes open” (0.19 ± 0.08) “eyes closed” (0.12 ± 0.06), “head aside” (0.28 ± 0.09), “back turned” (0.19 ± 0.11) and “absent” (0.14 ± 0.08) conditions ($P < 0.001$).

Importance of the human partner

The duration of gaze to the exit door (Fig. 5) in the “absent” condition was significantly influenced by the experimenter’s presence (numDF = 6; denDF = 380;

Fig. 4 Mean duration of gaze to the sky per session \pm SEM in function of the seven experimental conditions. $N = 6$. $***P < 0.001$

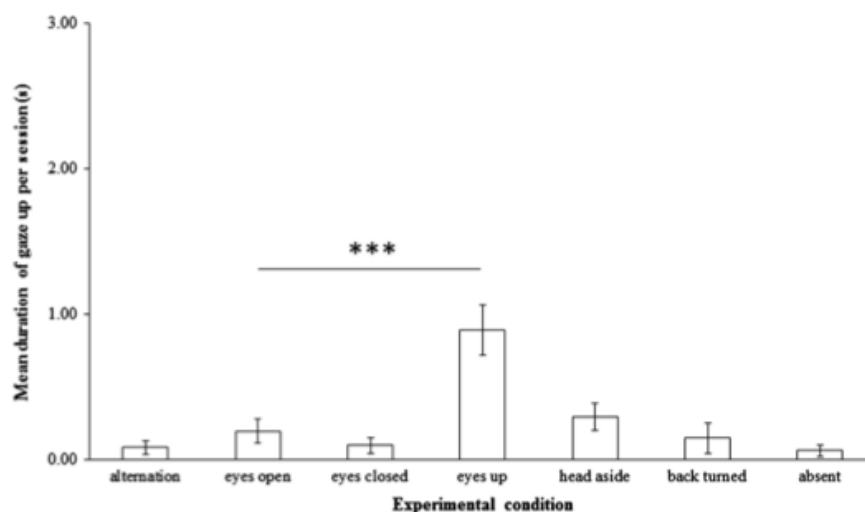
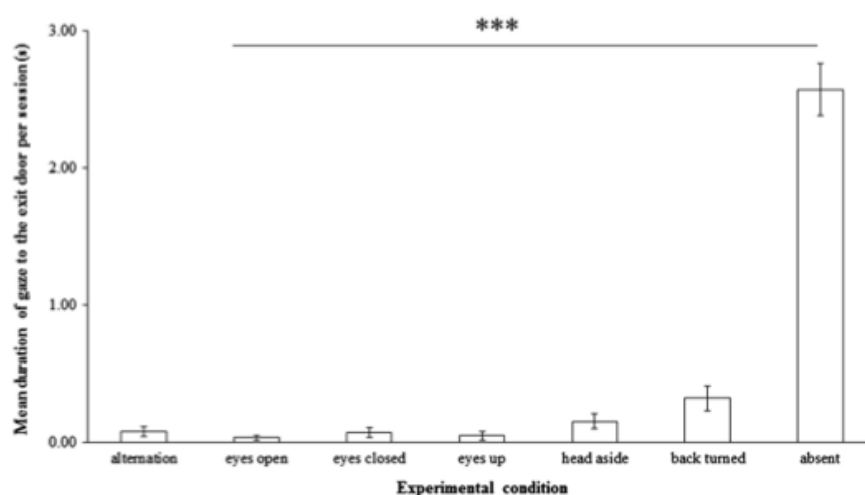


Fig. 5 Mean duration of gaze to the area where the exit door in the “absent” condition per session \pm SEM in function of the seven experimental conditions. $N = 6$. $***P < 0.001$



F value = 119.83; and $P < 0.0001$). LME reveals that Tonkean macaques looked significantly longer at the exit door in the “absent” condition ($2.51 \text{ s/trial} \pm 0.19$) than in the “eyes open” condition (0.03 ± 0.02 ; $P < 0.0001$). Subjects also looked significantly longer at the exit door in the “back turned” condition (0.31 ± 0.09) than in the “eyes open” condition ($P = 0.02$).

Discussion

This study is, to our knowledge, the first to investigate attention understanding and intentional gestural communication in Tonkean macaques. While previous studies have shown that great apes can use gestural communication

intentionally (orangutan: Cartmill and Byrne 2007, 2010; gorilla: Genty et al. 2009; Pika et al. 2003; chimpanzee: Hobaiter and Byrne 2011b; Roberts et al. 2013; bonobo: Pika et al. 2005), we provide here that Tonkean macaques also have similar abilities. Indeed, we reported that Tonkean macaques validate three criteria of intentional communication: they behaved differently when the human partner was present; they adjusted their communicative behaviour according to the attentional state of the human partner by taking into account her body and face orientation; and they displayed some gaze alternation between the human’s face and the hidden food reward. However, Tonkean macaques did not produce attention-getting behaviours and did not elaborate new types of communicative behaviours.

The mean success rate of pointing in the correct direction is very high, more than 90 %, and this is an evidence of referential signalling defined as the capacity to direct the attention of an observer to a distal object or entity (Leavens et al. 2004a). In the studied group, Tonkean macaques pointed significantly more when the human partner was present than when absent. The discrimination of the presence of an audience, which is one of the criteria of intentional communication formulated by Leavens et al. (2005b), is taken into account by macaques. This result is strengthened by the fact that when the experimenter was not visible for the subject—in the “absent” condition—macaques looked more at the exit door than in the others conditions when she was present. Moreover, Tonkean macaques pointed significantly more when the human was facing them with her eyes open rather than when she was looking up with her head oriented up, when her head was turned aside, and when she was back turned showing thus that macaques took into account the body and face orientation of the human partner in order to communicate with her. This result is in agreement with a lot of studies demonstrating a discrimination of both body and face orientation in great apes (Genty et al. 2009; Kaminski et al. 2004; Liebal et al. 2004b; Pika et al. 2005; Roberts et al. 2014a; Tempelmann et al. 2011) and in monkeys (mangabeys: Maille et al. 2012; olive baboons: Bourjade et al. 2013; Meunier et al. 2013). However, it seems that they do not discriminate subtle cues as eyes. Indeed, there were no differences in frequency of pointing between the conditions varying according to the state of the eyes (i.e. the “alternation”, “eyes open” and “eyes closed” conditions). In the literature, very few studies reported a discrimination of the state of the eyes, notably during gestural communication (chimpanzees: Hostetter et al. 2007; olive baboons: Bourjade et al. 2013; capuchins: Hattori et al. 2010). One possible explanation is that macaques are more arboreal than baboons; thus, the low visibility within the trees compared with savannah could explain the lack of distinction of eyes state. Another hypothesis is that the vast majority of studies on this topic having required that primates collaborate with humans in object-choice tasks are not naturalistic enough for primates. Some authors (Hare 2001; Vick and Anderson 2003) have proposed that competitive paradigms would be more suited to reveal attention reading abilities than the more frequently used object-choice paradigm.

On the whole, Tonkean macaques looked more at the experimenter when she was attentive rather inattentive. This shows that macaques behaved differently according to the attentional state of the human. These results are confirmed by those concerning gaze alternation. Our study reported that Tonkean macaques produced some gaze alternation between the face of the human partner and the

hidden food reward, maybe as an attempt to get the attention of the experimenter, which validates at least one criterion of intentional communication. We put in evidence that macaques displayed more gaze alternation when the experimenter had her eyes open in comparison when she looked up, turned her head aside and was back turned. These results confirm those obtained by analysing their gestural communication: Tonkean macaques discriminate both body and face orientation of the human partner. On the other hand, Tonkean macaques tended to display more gaze alternation when the experimenter displayed alternation too in the “alternation” condition than when her eyes were fixed open in the “eyes open” condition. We can thus suppose that, maybe, macaques take into account a supplementary cue as a combination of head and eyes mobility, and this ability would be highlighted only in their visual orienting behaviour and not in their pointing. To clarify what is the most important cue, it should be interesting to test individuals in a condition in which only the eyes and not the head would be mobile. Moreover, this “alternation” condition corresponds to a joint attention situation in which the subject and the human bring their attention on the same thing and, maybe, this is this situation which is meaningful for macaques. This “alternation” condition is particularly interesting because it had been tested in only one study on squirrel monkeys but researchers focused on pointing gestures and gaze to the experimenter’s face, but not on gaze alternation of subjects (Anderson et al. 2010). These authors concluded that joint attention did not influence the frequency of pointing, and they also hypothesized that their assistant failed to establish true joint attention with the subjects, whereas in our study, it is this condition in which the individuals responded more. We can thus hypothesize that gaze alternation, which was not trained and can thus be considered as a spontaneous behaviour, would be more informative, in terms of indication of their sensitivity to attentional states, than pointing, which was learned by conditioning. Hattori et al. (2007) showed in a similar paradigm that capuchins had sensitivity to eyes state and that this sensitivity was revealed through the measure of their looking behaviour and not of their gestural behaviour. The same authors (Hattori et al. 2010) reported later that capuchins took into account subtle cue of eye gaze only when they requested food held by the human partner, whereas they did not pay attention when they requested food that was on a table. Other evidences of discrimination of eyes state have been reported in chimpanzees (Hostetter et al. 2007) and baboons (Bourjade et al. 2013) in comparable contexts. In these studies, the situation was dyadic: the food was handled in the experimenter’s hand, and the primates were required only to attract the human’s attention. The task was thus less cognitively difficult than our task corresponding

to a triadic situation. Indeed, in our study, macaques were required to both attract the experimenter's attention and direct it towards the hidden food reward, which was more cognitively demanding.

In this study, we also investigated gaze following and we reported that macaques followed the human gaze in the "eyes up" condition. This is in agreement with some studies having reported that crested macaques (*Macaca nigra*: Micheletta and Waller 2012) followed the gaze of conspecifics and rhesus macaques followed the gaze of conspecifics (Tomasello et al. 1998) and of a human only on the basis of their eyes state (Ferrari et al. 2000; Tomasello et al. 2001). Nevertheless, in our "eyes up" condition, the eyes but also the head of the human were directed up and we can hypothesize that maybe macaques reacted to the head rather than to the eyes' orientation. It would have been interesting to design an experimental condition in which only the eyes were directed up and not the head.

Contrary to one of our assumptions, but in accordance with others studies (Roberts et al. 2014a; Tempelmann et al. 2011; Theall and Povinelli 1999), Tonkean macaques did not produce and elaborate some attention-getting behaviours such as vocalizations or strikes against the wire mesh when the human partner was inattentive. Several studies reported the use of audition-based behaviours as a means of gaining an inattentive audience's attention in several primates' species (gorillas: Pika et al. 2003; chimpanzees: Hopkins et al. 2007; Hostetter et al. 2001; Leavens et al. 2004b; Tomasello et al. 1994, 1997; olive baboons: Bourjade et al. 2013). In the Bourjade et al.'s study (2013), experimental trials lasted 30 s, whereas our trials lasted 10 s. We can think that subjects would be able to emit more attention-getting behaviours in longer trials, and maybe if our trials lasted longer, there would have been more noisy behaviours. However, in literature, there are no studies on the intentionality of vocal communication in Tonkean macaques, so it is difficult to know if this species uses intentionally audition-based behaviours towards particular conspecifics in their natural behaviour. Even if Tonkean macaques used such communication with their conspecifics, would they use it with a human partner? Another explanation would be that in our study, the food reward was hidden, contrary to the Bourjade and collaborators' study. Seeing the food reward could enhance subjects' motivation and/or frustration and thus increase their propensity to produce attention-getting behaviours. It would thus be interesting to compare these two conditions in macaques, as Hattori et al. (2010) did with capuchins.

To summarize, our study reported the first evidence of intentional gestural communication in Tonkean macaques. Tonkean macaques adapt their visual orienting behaviour according to the attentional state of the human partner more flexibly than their gestural behaviour. Indeed, a

sensitivity to body and face orientations was highlighted with the measure of pointing gestures and gaze alternation. Furthermore, our study indicates that Tonkean macaques were more sensitive to the "alternation" condition in their visual orienting behaviour, consisting of a joint attention situation in which both the human head and eyes were mobile. This result highlights the importance of considering more deeply joint attention impact and to investigate what are the cues considered by macaques, and more generally by non-human primates, that reflect a joint attention. Is the face mobility and/or the eyes mobility and/or a combination of cues that indicates to the subject a particular attentional state? These investigations, crucially lacking in monkeys studies, are strongly hoped.

Acknowledgments This study was funded by the Primatology Centre of Strasbourg University. The authors are sincerely grateful to Nicolas Herrens Schmidt and his whole team for allowing them to conduct this study at the Primatology Centre of Strasbourg University in France. The authors are particularly thankful to the assistant Myriam Gerardin for helping in data collection during the experiments and to Nicolas Poulin from CeStatS of Strasbourg University, Marie Bourjade from the Aix-Marseille University and Jonas Fizet from the Primatology Centre of Strasbourg University for statistical assistance. Sarah Lux is greatly thanked for her valuable proofreading and correction of the manuscript in English. Authors also thank, on one hand, Nadège Krebs from Noldus for her advices concerning the use of the software *The Observer* and, on the other hand, the "Conservation Sauvage Internationale" association for providing internship agreement to CC. Finally, the two anonymous reviewers are thanked for their valuable and helpful corrections and commentaries. All the experiments adhered to the current French laws concerning laboratory animal care and were approved by the French ethical committee CREMEAS (Number of agreement for conducting experiments on primates: AL/46/53/02/13).

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

References

- Anderson JR, Kuwahata H, Fujita K (2007) Gaze alternation during "pointing" by squirrel monkeys (*Saimiri sciureus*)? *Anim Cognit* 10:267–271
- Anderson JR, Kuroshima H, Hattori Y, Fujita K (2010) Flexibility in the use of requesting gestures in squirrel monkeys (*Saimiri sciureus*). *Am J Primatol* 72:707–714
- Barth J, Reaux JE, Povinelli DJ (2005) Chimpanzees' (*Pan troglodytes*) use of gaze cues in object-choice tasks: different methods yield different results. *Anim Cognit* 8:84–92
- Bates E, Benigni L, Bretherton I, Camaioni L, Volterra V (1979) The emergence of symbols: cognition and communication in infancy. Academic Press, New York
- Bishop D, Ross V, Daniels M, Bright P (1996) The measurement of hand preference: a validation study comparing three groups of right handers. *Br J Psychol* 87:269–285
- Blaschke M, Ettliger G (1987) Pointing as an act of social communication by monkeys. *Anim Behav* 35(5):1520–1523
- Bourjade M, Meguerditchian A, Maille A, Vauclair J (2013) Olive baboons, *Papio anubis*, adjust their visual and auditory

- intentional gestures to the visual attention of others. *Anim Behav* 87:121–128
- Bourjade M, Canteloup C, Meguerditchian A, Vauclair J, Gaunet F (2014) Training experience in gestures affects the display of social gaze in baboons' communication with a human. *Anim Cognit*. doi:10.1007/s10071-014-0793-5
- Byrne RW (2000) Evolution of primate cognition. *Cognit Sci* 24:543–570
- Call J, Tomasello M (1994) Production and comprehension of referential pointing by orangutans (*Pongo pygmaeus*). *J Comp Psychol* 108:307–317
- Cartmill EA, Byrne RW (2007) Orangutans modify their gestural signaling according to their audience's comprehension. *Curr Biol* 17:1345–1348
- Cartmill EA, Byrne RW (2010) Semantics of primate gestures: intentional meaning of orangutan gestures. *Anim Cognit* 13:193–804
- Chance MRA (1967) Attention structure as the basis of primate rank orders. *Man* 2(4):503–518
- Corballis MC (2002) From hand to mouth. The origins of language. Princeton University Press, Princeton
- Ferrari PF, Kohler E, Fogassi L, Gallese V (2000) The ability to follow eye gaze and its emergence during development in macaque monkeys. *PNAS* 97(25):13997–14002
- Flombaum JI, Santos LR (2005) Rhesus monkeys attribute perceptions to others. *Curr Biol* 15:447–452
- Franco F, Butterworth G (1996) Pointing and social awareness: declaring and requesting in the second year. *J Child Lang* 23(2):307–336
- Genty E, Breuer T, Hobaiter C, Byrne RW (2009) Gestural communication of the gorilla (*Gorilla gorilla*): repertoire, intentionality and possible origins. *Anim Cognit* 12:527–546
- Goodall J (1968) The behaviour of free-living chimpanzees in the Gombe stream reserve. *Anim Behav Monogr* 1:163–311
- Hare B (2001) Can competitive paradigms increase the validity of experiments on primate social cognition? *Anim Cognit* 4:269–280
- Hattori Y, Kuroshima H, Fujita K (2007) I know you are not looking at me: capuchin monkeys' (*Cebus apella*) sensitivity to human attentional states. *Anim Cognit* 10:141–148
- Hattori Y, Kuroshima H, Fujita K (2010) Tufted capuchin monkeys (*Cebus apella*) show understanding of human attentional states when requesting food held by a human. *Anim Cognit* 13:87–92
- Hewes GW (1973) Primate communication and gestural origin of language. *Curr Anthropol* 14:5–24
- Hobaiter C, Byrne RW (2011a) The gestural repertoire of the wild chimpanzee. *Anim Cognit* 14:745–767
- Hobaiter C, Byrne RW (2011b) Serial gesturing by wild chimpanzees: its nature and function for communication. *Anim Cognit* 14:827–838
- Hobaiter C, Leavens DA, Byrne RW (2014) Deictic gesturing in wild chimpanzees (*Pan troglodytes*)? Some possible cases. *J Comp Psychol* 128(1):82–87
- Hopkins WD, Tagliatalata JP, Leavens DA (2007) Chimpanzees differentially produce novel vocalizations to capture the attention of a human. *Anim Behav* 73:281–286
- Hostetter AB, Cantero M, Hopkins WD (2001) Differential use of vocal and gestural communication by chimpanzees (*Pan troglodytes*) in response to the attentional status of a human (*Homo sapiens*). *J Comp Psychol* 115(4):337–343
- Hostetter AB, Russell JL, Freeman H, Hopkins WD (2007) Now you see me, now you don't: evidence that chimpanzees understand the role of the eyes in attention. *Anim Cognit* 10:55–62
- Kaminski J, Call J, Tomasello M (2004) Body orientation and face orientation: two factors controlling apes' begging behaviour from humans. *Anim Cognit* 7:216–223
- Krause MA, Fouts RS (1997) Chimpanzee (*Pan troglodytes*) pointing: hand shapes, accuracy, and the role of eye gaze. *J Comp Psychol* 111:330–336
- Leavens DA, Hopkins WD (1998) Intentional communication by chimpanzees: a cross-sectional study of the use of referential gestures. *Dev Psychol* 34:813–822
- Leavens DA, Hopkins WD (1999) The whole-hand point: the structure and function of pointing from a comparative perspective. *J Comp Psychol* 113(4):417–425
- Leavens DA, Hopkins WD, Bard KA (1996) Indexical and referential pointing in chimpanzees (*Pan troglodytes*). *J Comp Psychol* 110:346–353
- Leavens DA, Hopkins WD, Thomas RK (2004a) Referential communication by chimpanzees (*Pan troglodytes*). *J Comp Psychol* 118(1):48–57
- Leavens DA, Hostetter AB, Wisley MJ, Hopkins WD (2004b) Tactical use of unimodal and bimodal communication by chimpanzees, *Pan troglodytes*. *Anim Behav* 67:467–476
- Leavens DA, Hopkins WD, Bard KA (2005a) Understanding the point of Chimpanzee pointing. *Curr Dir Psychol Sci* 14:185–189
- Leavens DA, Russell JA, Hopkins WD (2005b) Intentionality as measured in the persistence and elaboration of communication by chimpanzees (*Pan troglodytes*). *Child Dev* 76(1):296–306
- Liebal K, Call J, Tomasello M (2004a) Use of gesture sequences in chimpanzees. *Am J Primatol* 64:377–396
- Liebal K, Pika S, Call J, Tomasello M (2004b) To move or not to move: how apes alter the attentional state of humans when begging for food. *Interact Stud* 5:199–219
- Liszkowski U, Albrecht K, Carpenter M, Tomasello M (2008) Infants' visual and auditory communication when a partner is or not visually attending. *Infant Behav Dev* 31:157–167
- Maestriperi D (1996a) Gestural communication and its cognitive implications in pigtail macaques (*Macaca nemestrina*). *Behaviour* 133:997–1022
- Maestriperi D (1996b) Social communication among captive stump-tailed macaques (*Macaca arctoides*). *Int J Primatol* 17(5):785–802
- Maille A, Engelhart L, Bourjade M, Blois-Heulin C (2012) To beg, or not to beg? That is the question: mangabey modify their production of requesting gestures in response to human's attentional states. *PLoS ONE* 7(7):e41197. doi:10.1371/journal.pone.0041197
- Matsumoto-Oda A, Tomonaga M (2005) 'Intentional' control of sounds production found in the leaf-clipping display of Mahale chimpanzees. *Jpn Ethol Soc* 23:109–112
- Maynard Smith J, Harper D (2003) Animal signals. Oxford University Press, Oxford
- McGrew WC, Marchant LF, Scott S, Tutin CEG (2001) Intergroup differences in a social custom of wild chimpanzees: the grooming hand-clasp of the Mahale Mountains, Tanzanian. *Curr Anthropol* 42:148–153
- Meunier H, Blois-Heulin C, Vauclair J (2011) A new tool for measuring hand preference in non-human primates: adaptation of Bishop's quantifying hand preference task for Olive baboons. *Behav Brain Res* 218:1–7
- Meunier H, Fizez J, Vauclair J (2013) Tonkean macaques communicate with their right hand. *Brain Lang* 126:181–187
- Micheletta J, Waller BM (2012) Friendship affects gaze following in a tolerant species of macaque, *Macaca nigra*. *Anim Behav* 83:459–467
- Nishida T (1980) The leaf-clipping display: a newly-discovered expressive gesture in wild chimpanzees. *J Hum Evol* 9:117–128
- Partan S, Marler P (1999) Communication goes multimodal. *Science* 26(283):1272–1273
- Perrett DI, Smith PAJ, Potter DD, Mistlin AJ, Head AS, Milner AD, Jeeves MA (1985) Visual cells in the temporal cortex sensitive to

- face view and gaze direction. *Proc R Soc Lond Biol Sci* 223:293–317
- Pika S, Mitani JC (2006) Referential gestural communication in wild chimpanzees (*Pan troglodytes*). *Curr Biol* 16:R191–R192
- Pika S, Liebal K, Tomasello M (2003) Gestural communication in young gorillas (*Gorilla gorilla*): gestural repertoire, learning and use. *Am J Primatol* 60:95–111
- Pika S, Liebal K, Tomasello M (2005) Gestural communication in subadults bonobos (*Pan paniscus*): repertoire and use. *Am J Primatol* 65:39–61
- Povinelli DJ, Eddy TJ (1996) What young chimpanzees know about seeing. *Monogr Soc Res Child Dev* 61(3):1–152
- Roberts AI, Vick SJ, Buchanan-Smith HM (2012a) Usage and comprehension of manual gestures in wild chimpanzees. *Anim Behav* 84:459–470
- Roberts AI, Vick SJ, Roberts SGB, Buchanan-Smith HM, Zuberbühler K (2012b) A structure-based repertoire of manual gestures in wild chimpanzees: statistical analyses of a graded communication system. *Evol Hum Behav* 33:578–589
- Roberts AI, Vick SJ, Buchanan-Smith HM (2013) Communicative intentions in wild chimpanzees: persistence and elaboration in gestural signaling. *Anim Cognit* 16:187–196
- Roberts AI, Roberts SGB, Vick SJ (2014a) The repertoire and intentionality of gestural communication in wild chimpanzees. *Anim Cognit* 17:317–336
- Roberts AI, Vick SJ, Roberts SGB, Menzel CR (2014b) Chimpanzees modify intentional gestures to coordinate a search for hidden food. *Nat Commun* 5:1–8
- Rosati AG, Hare B (2009) Looking past the model species: diversity in gaze-following skills across primates. *Curr Opin Neurobiol* 19:45–51
- Schel AM, Machanda Z, Townsend SW, Zuberbühler K, Slocombe KE (2013a) Chimpanzee food calls are directed at specific individuals. *Anim Behav* 86:955–965
- Schel AM, Townsend SW, Machanda Z, Zuberbühler K, Slocombe KE (2013b) Chimpanzee alarm call production meets key criteria for intentionality. *PLoS ONE* 8(10):e76674. doi:10.1371/journal.pone.0076674
- Tempelmann S, Kaminski J, Liebal K (2011) Focus on the essential: all great apes know when others are being attentive. *Anim Cognit* 14:433–439
- Theall LA, Povinelli DJ (1999) Do chimpanzees tailor their gestural signals to fit the attentional states of others? *Anim Cognit* 2:207–214
- Tomasello M, Call J (2007) *The gestural communication of Apes and monkeys*. Lawrence Erlbaum Associates, London
- Tomasello M, Call J, Nagell K, Olguin R, Carpenter M (1994) The learning and the use of gestural signals by young chimpanzees: a trans-generational study. *Primates* 35(2):137–154
- Tomasello M, Call J, Warren J, Frost GT, Carpenter M, Nagell K (1997) The ontogeny of chimpanzee gestural signals: a comparison across groups and generations. *Evol Commun* 1:223–259
- Tomasello M, Call J, Hare B (1998) Five primate species follow the visual gaze of conspecifics. *Anim Behav* 55:1063–1069
- Tomasello M, Hare B, Fogleman T (2001) The ontogeny of gaze following in chimpanzees, *Pan troglodytes*, and rhesus macaques, *Macaca mulatta*. *Anim Behav* 61:335–343
- Tomasello M, Call J, Hare B (2003) Chimpanzees versus humans: it's not that simple. *Trends Cognit Sci* 7:239–240
- van Lawick-Goodall J (1967) Mother-offspring relationships in free-ranging chimpanzees. In: Morris D (ed) *Primate ethology*. Weidenfeld and Nicolson, London
- Vauclair J (2004) Lateralization of communicative signals in nonhuman primates and the hypothesis of the gestural origin of language. *Int Stud* 5:363–384
- Veà JJ, Sabater-Pi J (1998) Spontaneous pointing behaviour in the wild pygmy chimpanzee (*Pan paniscus*). *Folia Primatol* 69:289–290
- Vick SJ, Anderson JR (2003) Use of human visual attention cues by olive baboons (*Papio anubis*) in a competitive task. *J Comp Psychol* 117(2):209–216
- Zimmerman F, Zemke F, Call J, Gómez JC (2009) Orangutans (*Pongo pygmaeus*) and bonobos (*Pan paniscus*) point to inform a human about the location of a tool. *Anim Cognit* 12:347–358

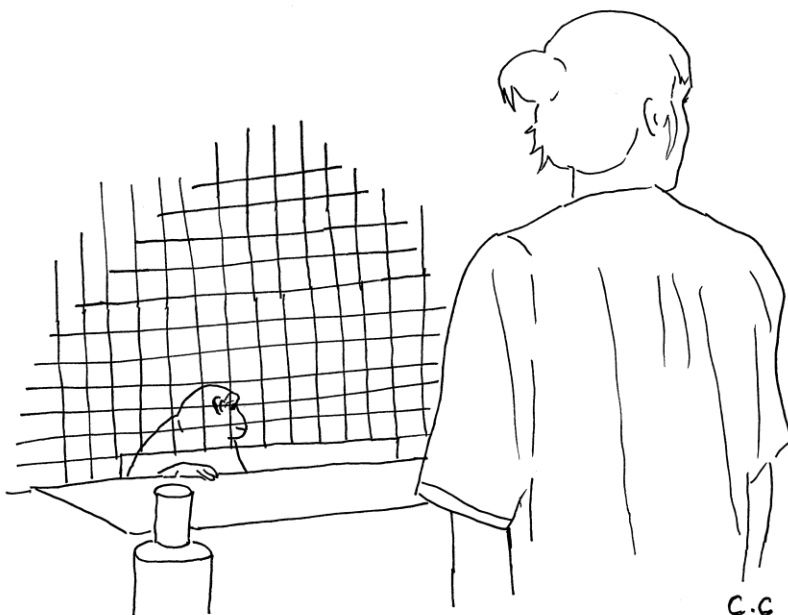
ARTICLE 2

Intentional gestural communication and discrimination of human attentional states in rhesus macaques (*Macaca mulatta*)

Canteloup C., Bovet D. & Meunier H.

Animal Cognition 2015, 18(4) : 875-883

Avec la permission de Springer



Synthèse de l'article 2 :

Intentional gestural communication and discrimination of human attentional states in rhesus macaques (*Macaca mulatta*)

Canteloup C., Bovet D. & Meunier H.

Animal Cognition 2015, 18(4) : 875-883

Questions

Etre capable de discriminer l'état d'attention d'autrui est considéré comme un prérequis de la Théorie de l'Esprit et un critère d'une communication intentionnelle. Les macaques rhésus sont-ils capables d'utiliser intentionnellement un geste de pointage et de discriminer différents états d'attention d'un expérimentateur humain ? Si oui, sur quels indices attentionnels se basent-ils ?

Méthode

Six macaques rhésus, préalablement entraînés à produire un geste de pointage en direction d'une récompense alimentaire pouvant leur être délivrée par une expérimentatrice, ont été testés dans sept conditions expérimentales variant selon l'état d'attention de cette dernière (*e.g.* différant selon l'orientation de ses yeux, de son visage ou de son corps).

Résultats

Les macaques rhésus ajustent leurs signaux de communication à l'état d'attention de l'expérimentatrice en prenant en compte des indices attentionnels « grossiers » comme la présence, l'orientation du corps et du visage de l'expérimentatrice mais pas d'indices plus subtils comme l'état des yeux. Ils font également plus d'alternances de regard quand l'expérimentatrice suit leur regard que quand elle les regarde fixement avec les yeux ouverts.

Conclusion

Les macaques rhésus sont capables de communication gestuelle intentionnelle et de discriminer l'état d'attention d'un humain sur la base de l'orientation de son visage et de son corps. Les macaques rhésus sont toutefois particulièrement sensibles à une situation d'attention conjointe. Cette faculté est un prérequis à la Théorie de l'Esprit mais n'implique par forcément une capacité de prise de perspective visuelle.

Intentional gestural communication and discrimination of human attentional states in rhesus macaques (*Macaca mulatta*)

Charlotte Canteloup^{1,2} · Dalila Bove³ · H el ene Meunier^{1,2}

Received: 12 November 2014 / Revised: 10 February 2015 / Accepted: 2 March 2015 / Published online: 7 March 2015
© Springer-Verlag Berlin Heidelberg 2015

Abstract The present study tested intentionality of a learned begging gesture and attention-reading abilities in rhesus macaques (*Macaca mulatta*). Subjects were trained to produce a begging gesture towards a hidden food reward that could be delivered by a human experimenter. More specifically, we investigated which attentional cues—body, face and/or eyes orientation of a human partner—were taken into account by the macaques in order to communicate with her. Our results provide strong evidence of intentional communication: the monkeys adjusted their behaviour to that of the partner. The latter’s attentional state influenced the monkeys’ likelihood of performing begging gestures and showing gaze alternation between the partner and the hidden food. By contrast, we found no evidence of attention-getting behaviours, persistence or elaboration of new communicative behaviours. Our results also showed that rhesus macaques discriminated gross cues including the presence, body and face orientation of the human experimenter but not her eyes. However, the monkeys emitted more gaze alternation and monitored the human’s attentional state more closely when she also displayed gaze alternation, suggesting an important role of joint attention in gestural communication.

Keywords Social cognition · Attention-reading abilities · Non-human primates · Intentionality · *Macaca mulatta*

Introduction

Being able to assess others’ attentional states during social interactions is an essential skill, particularly in communicative interactions involving visual signals (Chance 1967; Fehr and Exline 1987). Indeed, a visual signal will only be successful if the recipient of the signal is attending to it (Call and Tomasello 2007; Liebal et al. 2013). Discriminating the attentional states of others is considered to be one of the precursors of understanding others’ mental states and one criterion of intentional communication (Leavens et al. 2004a, 2005).

Intentional behaviour, communicative behaviour and intentional communication are often distinguished in the literature and require definition. First, intentionality, a key feature of human language, refers to an individual’s own goal-directed behaviours, without consideration of others’ mental states (Liebal et al. 2013). Second, Bates et al. (1975) distinguished between intentional communication and communicative behaviour. They studied the development of communication in human infants and reported that children initially communicate with adults non-intentionally. For example, a 2-month-old baby reacts innately to the physiological state of hunger by crying, which predictably results in him getting fed by his caregiver. However, the infant is probably unaware of the signal value of his cries. It is only after 10 months of age and before being able to express himself verbally that the child understands the role of adults as agents by intentionally using non-verbal signals such as pointing to direct adults’ attention to objects. Third, Bard (1992) distinguished intentional

✉ Charlotte Canteloup
charlotte.canteloup@gmail.com

¹ Primatology Centre of Strasbourg University, Fort Foch, 67207 Niederhausbergen, France

² Laboratory of Cognitive and Adaptive Neurosciences, Faculty of Psychology, UMR 7364, Strasbourg University, 12 rue Goethe, 67000 Strasbourg, France

³ Laboratory of Ethology, Cognition, Development, University Paris Ouest Nanterre, BSL Building, 200 avenue de la R epublique, 92001 Nanterre Cedex, France

communication from intentional behaviour in a study on food-sharing interactions between orangutan mothers and offspring. She proposed that an intentional behaviour is a goal-directed sequence of behaviours involving either objects or social agents, whereas an intentional communication consists of behavioural sequences requiring coordination between social agents and objects. For example, in their first few months of life, infant orangutans directly and intentionally manipulate food items and also their mother as an intermediate means for obtaining food. From two years of age, orangutans intentionally communicate with their mother by acting with her in coordinated fashion after observing her behaviour (Bard 1992).

Numerous studies have investigated intentionality of gestural communication and attention-reading abilities in non-human primates (e.g. Anderson et al. 2010; Bourjade et al. 2013; Cartmill and Byrne 2010; Genty et al. 2009; Hobaiter and Byrne 2011; Leavens and Hopkins 1998; Liebal et al. 2004). The most often used paradigm in these studies is the cooperative requesting paradigm, in which the subject has to communicate the location of an unreachable food reward to a human partner whose attentional states vary (e.g. Hare and Tomasello 2004; Hattori et al. 2007, 2010; Maille et al. 2012; Zimmermann et al. 2009). Despite the large number of studies, few have tested all the criteria that classify an act as intentional (Leavens et al. 2004a, 2005). Furthermore, the findings are inconsistent in terms of which cues subjects actually attend to. Indeed, while some studies have reported sensitivity to subtle cues such as eye state in great apes (Barth et al. 2005; Hostetter et al. 2007), others have only found discrimination of grosser cues, such as face (Tempelmann et al. 2011) and body orientation of the partner (Bania and Stromberg 2013; Hostetter et al. 2001; Krause and Fouts 1997; Povinelli and Eddy 1996). In contrast, several studies of monkeys have reported discrimination of body and face orientation (Canteloup et al. 2015; Maille et al. 2012; Meunier et al. 2013; Vick and Anderson 2003); a few have also shown sensitivity to eye state (Bourjade et al. 2013; Flombaum and Santos 2005; Hattori et al. 2007, 2010). However, in a recent study on highly socially tolerant Tonkean macaques (*Macaca tonkeana*, see Matsumura 1999; Thierry 2000; Thierry et al. 2004), subjects displayed more gaze alternation between the experimenter's face and the food reward when her head and eyes were mobile and focused on the same object (Canteloup et al. 2015). Thus, in accordance with Anderson et al. (2010), we proposed that a joint attention situation, where individual X follows individual Y's attention onto an object of joint focus Z (cf. Emery 2000; Itakura 2004), is particularly favourable for revealing sensitivity to eyes.

The present study investigated intentionality of gestural communication and attention-reading abilities in rhesus

macaques. Rhesus macaques are of interest in this context for the following reasons. First, to our knowledge, there are no studies on intentional gestural communication in rhesus. Second, of all macaque species, rhesus show the highest degree of nepotism and asymmetry in aggression, in contrast to Tonkean macaques which are the least nepotistic and the most symmetrical in terms of aggressive interactions (Thierry 2000); comparing these two species could provide insights into the effect of sociocultural environment on intention reading and communication. Third, rhesus macaques are phylogenetically more distant from humans than are great apes. We therefore tested rhesus macaques using the same paradigm as in a study of Tonkean macaques (cf. Canteloup et al. 2015): macaques could beg for an unreachable food reward delivered by an experimenter who was unaware of the food's location and whose attentional state varied as a function of body, head and eye orientations. We expected that if rhesus use their trained begging gestures to communicate intentionally, then like other monkeys, they should beg less frequently when facing an inattentive experimenter compared to an attentive experimenter. We also hypothesized that if rhesus discriminate gross attentional cues as body and face orientation, they should look at and beg more towards an experimenter facing them than to an experimenter whose head and/or body is turned away. Finally, based on previous studies, we expected that rhesus would follow the experimenter's gaze and would be sensitive to her eyes. Indeed, due to their strict dominance hierarchies in which the individuals need to be highly attentive to the behaviour of others, we expected that rhesus macaques would pay particular attention to the partner's attentional state and show greater sensitivity to subtle cues as eyes, compared to Tonkean macaques.

Methods

This experiment involved behavioural observations, routine training and non-invasive contact with the monkeys. The procedures were approved by the Animal Experiment Committee of the Primatology Centre of Strasbourg University and by the CREMEAS ethics committee (approval for conducting experiments on primates no. AL/46/53/02/13) and adhered to the French legal requirements.

Subjects

The subjects were five rhesus macaques (*Macaca mulatta*: four females and one male aged 2–18 years), all housed and raised at the Primate Centre of Strasbourg University, France. Testing was conducted between June and August 2013. All subjects lived in a social group in a one-acre

naturally wooded park connected to a 20 m² heated indoor housing unit where feeding with commercial pellets took place and water was available *ad libitum*. Fruit and vegetables were distributed twice a week in the park, outside experimental sessions.

Apparatus

Subjects were tested in an outdoor area adjacent to the outdoor enclosure, connected by a trapdoor. The apparatus consisted of an adaptation of Bishop's Quantifying Hand Preference (QHP) task (Bishop et al. 1996), initially designed to quantify manual preferences in human infants and adapted for use with non-human primates by Meunier et al. (2011). Two compartments were used: the subject area and the experimenter area (Fig. 1), separated by a wire mesh. In the subject area, a wooden platform was placed perpendicular to the separator mesh and served as a seat for the subject. In the experimenter area, a table and three unreachable vertical wooden poles (height: 1 m), each topped with containers and separated by 30° from the seated subject's perspective, were placed in front of the subject (Fig. 1). A horizontal 10 × 60 cm hole, in the mesh separating the subject's area from the experimenter's area, allowed subjects to point towards one of the containers. A hidden area allowed the assistant and the experimenter to move out of view of the subject. A video camera was placed in the experimenters' area, 2 m from the wire mesh, to the left side of the experimenter.

Training procedure

Between December 2012 and May 2013, the monkeys were trained to produce a begging gesture towards an opaque

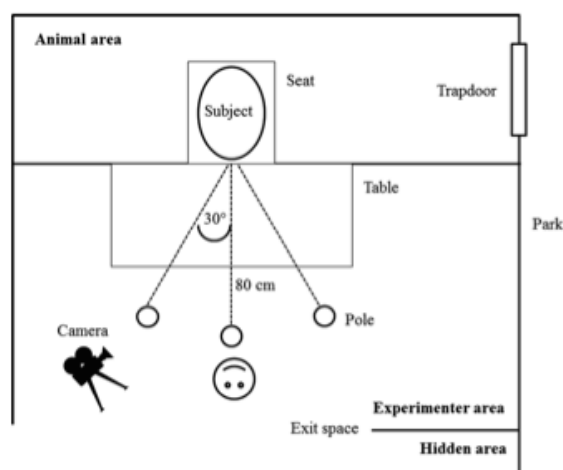


Fig. 1 Schema of the experimental apparatus. Opaque cylinders in which raisins could be hidden were put on the three poles

container baited with a food reward by one assistant. Training consisted of the three following steps: (1) a raisin was put on the table in front of the subject and within its reach, so that the subject could grasp it; (2) the raisin was gradually moved back from the subject who was rewarded with it for initiating the arm extension to grasp it; and (3) the raisin was placed out of reach of the subject and reward withheld until the subject begged for the raisin by extending its arm without attempting to grasp it (see Meunier et al. 2013 for details). Following Meunier et al. (2013), we defined begging as “a manual gesture with arm, hand and/or fingers extended towards one of the three containers with no attempt to grasp it”.

Testing procedure

One assistant and one experimenter took part in the test. Two types of trials were conducted: motivational trials and experimental trials. Each test session comprised seven 10-s experimental trials randomly interspersed among 16 motivational trials. Before starting a trial, the assistant and the experimenter took up position in the hidden area. In a motivational trial, the assistant approached the subject and placed a raisin under one of the three containers in view of the subject according to a randomized list defining position and hand used and then returned to the hidden area. The experimenter, unaware of the location of the raisin, then approached the subject face-on and looking at it, and rewarded the subject as soon as it requested the raisin by begging towards the correct container. An experimental trial consisted of two stages: first, the assistant hid a raisin under one of the three containers as in motivational trials and second, the experimenter, unaware of the raisin's location, approached the subject and then adopted one of seven attentional states described below, for 10 s. At the end of the 10-s trial, the experimenter rewarded the subject only after it begged in the correct direction. If the subject begged towards an unbaited container, the experimenter lifted up that container to show the subject that there was nothing under it, and then, the assistant returned, removed the raisin and started a new trial.

Subjects were tested in seven different experimenter attentional conditions (Fig. 2). In the “alternation” condition, the experimenter faced the subject and mirrored its gaze pattern by moving only her head and eyes. Thus, when the subject displayed gaze alternation between the experimenter's face and a container, she mimicked gaze alternation by displaying alternation between the subject's face and the container. In the “eyes open” condition, the experimenter faced and looked fixedly at the subject with her eyes clearly open. In the “eyes closed”, “head and eyes up” and “head aside” conditions, the experimenter's body was oriented towards the subject but her eyes were closed,



Fig. 2 Pictures of the seven experimental conditions. **a** Alternation; *white arrows* illustrate that experimenter's eyes and head were mobile; **b** eyes open; **c** eyes closed; **d** head and eyes up; **e** head aside; **f** back turned; **g** absent

she looked up with her head oriented upwards, or she turned her head aside to look elsewhere in the park. In the “back turned” condition, the experimenter turned her back towards the monkey. In the “absent” condition, the experimenter did not emerge from hiding after the assistant had baited a container. Each subject participated in 10 test sessions, a total of 70 experimental trials and 160 motivational trials per individual, with no more than one session per day.

Data analysis

Experiments were video recorded using a camcorder HD (Canon, Legria HF S20). CC analysed the videos blindly frame by frame (1 frame = 0.04 s) using the Observer XT 10.1.548 software. For analysis, we focused on gaze direction (to the experimenter, to the baited container, to the park, up, to the exit), gaze duration, number of gaze alternations and number of begging gestures. A begging gesture was defined as extension of the subject's arm through the hole of the wire mesh towards one of the three containers. As in previous studies (Canteloup et al. 2015; Bourjade et al. 2013; Maille et al. 2012), gaze measures were considered as continuous variables defined by a start and an end, whereas gaze alternation and begging were considered as discontinuous variables characterized by occurrences. We considered begging gestures as one-time events, recorded at the moment when the extension of the arm was at its peak just before the subject began to retract

or lower his or her arm. We also recorded auditory attention-getting behaviours as vocalizations and strikes against the wire mesh.

Statistical analysis

Two types of models were used to determine which attentional cues influenced different behavioural variables; both were mixed models in order to deal with pseudo-replication among individuals. Generalized linear mixed models (GLMM) with a Poisson distribution were used for count data to test which attentional cues influenced two discontinuous variables: number of begging gestures and number of gaze alternations. Concerning these measures, each experimental condition was compared with the “eyes open” reference condition. Linear mixed-effects models (LME) were used to test the effect of experimental conditions on four different continuous variables: durations of (1) gaze to the experimenter; (2) gaze to the hidden food reward; (3) gaze up; and (4) gaze to the exit space. Quantile–Quantile plots (QQ plots) were used to assess visual normality of the residuals that is needed for LME. Experimental condition (“alternation”, “eyes open”, “eyes closed”, “head and eyes up”, “head aside”, “back turned” and “absent”) was considered as a fixed effect, and a random intercept was estimated for each individual. Concerning duration of gaze to the park, each experimental condition was compared to the “head aside” condition as a reference. Concerning gaze up duration, each experimental

conditions was compared to the “head and eyes up” condition. Concerning duration of gaze to the exit space, each condition was compared to the “absent” condition. Concerning other gaze durations, each experimental condition was compared with the “eyes open” reference condition. *P* values presented are those of pairwise comparisons with the reference level with Dunnett’s correction. All tests were performed with R 3.1.0 software with significance level set at 0.05.

Results

Gestural communication

Rhesus macaques pointed towards the correct container on average in about 93 % of trials (standard error of the mean (SEM) = 2.89). Regarding begging gestures, experimental condition was a significant factor (likelihood ratio test: LRT = 119.17; *df* = 6; *P* < 0.0001). GLMM revealed that rhesus macaques pointed significantly more in the “eyes open” condition (3.72 ± 0.25) than the “head and eyes up” (2.24 ± 0.20), “head aside” (1.96 ± 0.19), “back turned” (1.58 ± 0.19) and “absent” conditions (1.52 ± 0.20) (*P* < 0.0001). However, there were no significant differences in number of begging gestures between “eyes open” and “alternation” (3.68 ± 0.24) or “eyes closed” (3.60 ± 0.22) conditions (*P* > 0.05) (Fig. 3).

Gaze alternation

Regarding gaze alternation, experimental condition was a significant factor (LRT = 249.84; *df* = 5; *P* < 0.0001). GLMM revealed significantly more gaze alternation between the experimenter’s face and the baited container in

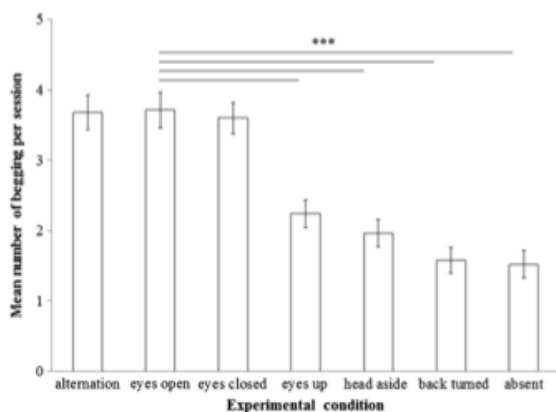


Fig. 3 Mean number of begging gestures per session \pm SEM as a function of the seven experimental conditions. *N* = 5. ****P* < 0.0001

the “alternation” condition (mean = 7.78 gaze alternation per trial \pm 0.61) than the “eyes open” condition (6.48 ± 0.50 ; *P* < 0.0001). The subjects displayed significantly more gaze alternation in the “eyes open” condition than in the “head and eyes up” (3.78 ± 0.33), “head aside” (3.38 ± 0.26) and “back turned” (2.04 ± 0.20) (*P* < 0.0001) conditions. However, there was no significant difference in number of gaze alternations between the “eyes open” and “eyes closed” (5.78 ± 0.50) conditions (*P* > 0.05) (Fig. 4).

Gaze to the experimenter

Regarding gaze to the experimenter, experimental condition was a significant factor (*F* = 26.21; *df* = 6.339; *P* < 0.0001). LME revealed significantly longer looking at the experimenter in the “eyes open” condition (2.27 ± 0.31) than the “head and eyes up” (1.55 ± 0.16), “head aside” (1.14 ± 0.09) and “back turned” (1.35 ± 0.17) (*P* < 0.0001) conditions. However, there were no significant differences in duration of gaze to the experimenter between the “eyes open” condition and “alternation” (2.68 ± 0.24) and “eyes closed” (2.16 ± 0.22) conditions (*P* > 0.05).

Gaze to the baited container

Regarding gaze to the baited container, experimental condition was a significant factor (*F* = 14.04; *df* = 6.339; *P* < 0.0001). LME revealed significantly longer looking at the baited container in the “eyes open” condition (2.70 ± 0.19) than the “head and eyes up” (1.85 ± 0.16), “head aside” (1.74 ± 0.14), “back turned” (1.65 ± 0.14) and “absent” (1.51 ± 0.16) (*P* < 0.0001) conditions.

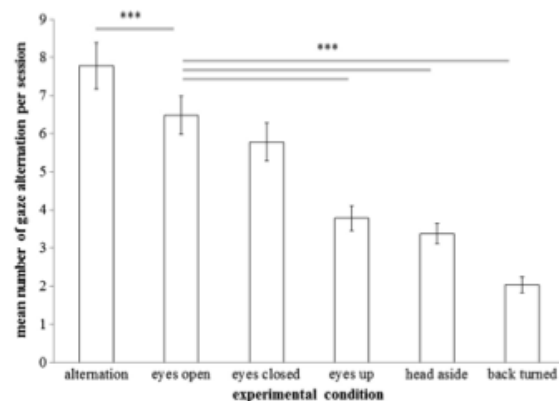


Fig. 4 Mean number of gaze alternations between the face of the experimenter and the hidden food reward per session \pm SEM as a function of the six experimental conditions in which the experimenter was present. *N* = 5. ****P* < 0.0001

However, there were no significant differences in duration of gaze to the baited container between the “eyes open” condition and “alternation” (2.74 ± 0.15) and “eyes closed” (2.72 ± 0.17) conditions ($P > 0.05$).

Gaze up

Regarding gaze up, experimental condition was a significant factor ($F = 52.17$; $df = 6.339$; $P < 0.0001$). LME revealed significantly longer looking in the “head and eyes up” condition (1.51 ± 0.16) than the “alternation” (0.08 ± 0.06), “eyes open” (0.13 ± 0.07), “eyes closed” (0.09 ± 0.04), “head aside” (0.12 ± 0.06), “back turned” (0.05 ± 0.03) and “absent” (0.03 ± 0.02) conditions ($P < 0.0001$) (Fig. 5).

Gaze to the park

Regarding gaze to the park, experimental condition was a significant factor ($F = 8.47$; $df = 6.339$; $P < 0.0001$). LME revealed significantly longer looking in the “head aside” condition, i.e. the experimenter is looking to the park (4.40 ± 0.33), than the “alternation” (1.96 ± 0.25), “eyes open” (2.11 ± 0.28), “eyes closed” (2.56 ± 0.28), “head and eyes up” (2.57 ± 0.34) and “absent” (3.15 ± 0.29) conditions ($P < 0.0001$) (Fig. 6).

Gaze to exit space

Regarding gaze to the exit space, experimental condition was a significant factor ($F = 126.29$; $df = 6.339$; $P < 0.0001$). LME revealed significantly longer looking at the exit space in the “absent” condition (1.69 ± 0.15) than the “alternation” (0.08 ± 0.06), “eyes open” (0.02 ± 0.01), “eyes closed” (0.09 ± 0.04), “head aside” (0.12 ± 0.06), “back turned” (0.05 ± 0.03) and “absent” (0.03 ± 0.02) conditions ($P < 0.0001$).

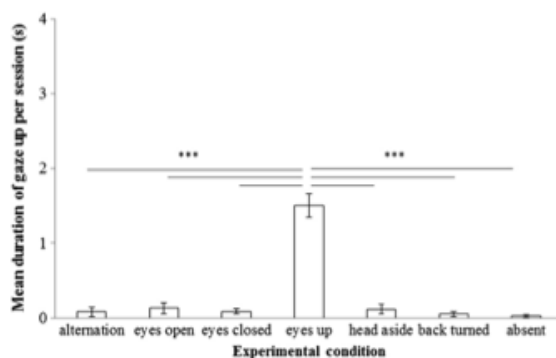


Fig. 5 Mean duration of gaze up per session \pm SEM as a function of the seven experimental conditions. $N = 5$. *** $P < 0.0001$

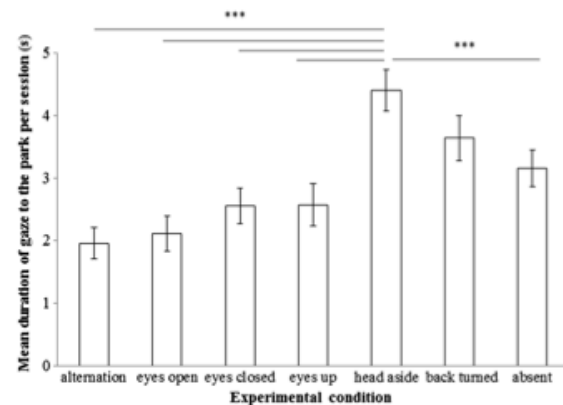


Fig. 6 Mean duration of gaze to the park per session \pm SEM as a function of the seven experimental conditions. $N = 5$. *** $P < 0.0001$

Auditory attention-getting behaviours

Regarding auditory attention-getting behaviours, experimental condition was not a significant factor ($F = 1.27$; $df = 6.339$; $P = 0.27$).

Discussion

The present study follows up a recent study on Tonkean macaques (Canteloup et al. 2015). The goals of this research were to (1) test the intentionality of a learned begging gesture; (2) study which behavioural cues are relevant for rhesus macaques' assessments of attention; and (3) investigate the effect of sociality on attention-reading abilities in macaques.

Our results show that rhesus macaques, like great apes and other monkey species (orangutan: Cartmill and Byrne 2007, 2010; Poss et al. 2006; gorilla: Genty et al. 2009; Pika et al. 2003; Poss et al. 2006; chimpanzee: Hobaiter and Byrne 2011; Roberts et al. 2013; bonobo: Pika et al. 2005; capuchin: Hattori et al. 2007, 2010; mangabey: Maille et al. 2012; olive baboon: Bourjade et al. 2013; Meunier et al. 2013; Tonkean macaque: Canteloup et al. 2015), are able to use a learned gesture intentionally. Indeed, our results confirm that rhesus monkeys meet at least three criteria used to classify an act as intentional (cf. Leavens et al. 2004b, 2005): they begged preferentially when a human was present, they behaved differently towards an inattentive versus an attentive partner, and they showed gaze alternation between the partner and the location of hidden food, notably when the partner was the most attentive. Moreover, the mean success rate of begging in the correct direction was very high, about 93 %, which is evidence that rhesus macaques can direct an observer's

attention to a distal object or entity in accordance with the definition of a referential gesture (Leavens et al. 2004a). However, the rhesus macaques did not produce or elaborate other attention-getting behaviours such as vocalizations or strikes against the wire mesh when the partner was inattentive, whereas several other primate species have used auditory behaviours in similar contexts (gorillas: Pika et al. 2003; chimpanzees: Hopkins et al. 2007; Hostetter et al. 2001; Leavens et al. 2004b; Tomasello et al. 1994, 1997; olive baboons: Bourjade et al. 2013). In Bourjade et al. (2013), experimental trials lasted 30 s, compared to only 10 s in the present study; it is conceivable that the rhesus might have produced more attention-getting behaviours in longer trials. Another procedural difference is that in our study, the food reward was hidden, whereas it was always visible in Bourjade et al. (2013). Seeing the food reward could enhance subjects' motivation and/or frustration and thus increase the likelihood of attention-getting behaviours. It would thus be interesting to compare these two conditions in macaques (see Hattori et al. 2010 for capuchins).

Rhesus macaques begged significantly more towards an experimenter facing them with her eyes open than when she was looking up, when her head was turned aside, when she had her back turned and when she was absent. From these results we conclude, in agreement with studies in great apes (e.g. Kaminski et al. 2004; Liebal et al. 2004; Tempelmann et al. 2011) and monkeys (Tonkean macaques: Canteloup et al. 2015; mangabeys: Maille et al. 2012; olive baboons: Bourjade et al. 2013; Meunier et al. 2013), that rhesus used this begging gesture socially and that they took into account gross attentional cues including the presence and body and face orientation of the human partner to communicate the location of a hidden food reward. However, they did not beg differently as a function of whether the partner's eyes were open or closed, from which we conclude that rhesus monkeys do not discriminate the subtle cue "eye state". Some authors (Kobayashi and Kohshima 2001; Tomasello et al. 2007) proposed that non-human primates are less sensitive to gaze direction than humans because their darker sclera makes the detection of their eyes more difficult than those of humans. However, research has shown that rhesus macaques are able to deduce what others perceive on the basis of where they are looking (Flombaum and Santos 2005). Moreover, several studies on rhesus visual scan patterns demonstrated that they gazed predominantly at human eyes as compared to other facial areas and that they gazed longer at the eyes when the face gazed towards them than when the gaze was averted (Keating and Keating 1982, 1993; Nahm et al. 1997; Sato and Nakamura 2001). Some studies have also reported sensitivity to eye states in chimpanzees during gestural communication (Barth et al. 2005; Bethell et al. 2007; Hostetter et al. 2007), and few

studies have shown it in monkeys (olive baboons: Bourjade et al. 2013; capuchins: Hattori et al. 2010).

It is interesting that the same pattern of results held for the occurrence of gaze alternation. The analysis further showed that the rhesus monkeys displayed more gaze alternation when the experimenter also displayed gaze alternation, in comparison with when she simply looked at the subject. We thus propose that gaze alternation, a spontaneous, untrained behaviour (see also Bourjade et al. 2014), may be a more informative measure of monkeys' sensitivity to attentional states than begging, which was shaped through conditioning. Hattori et al. (2007) also showed that capuchin monkeys were sensitive to humans' eyes, but this sensitivity was revealed only in their visual orienting behaviour, not in their gestural behaviour. This "alternation" condition, corresponding to a joint attention situation (cf. Emery 2000; Itakura 2004) in which the attention of the subject and the human converged on the same thing, seems particularly effective for engaging monkeys' attention. Notably, in this condition, not only did subject and human share the same focus of attention, the human's head and eyes were mobile, which may suggest that a combination of attentional cues is more effective than a single cue for the assessment and processing of attention direction.

Furthermore, rhesus macaques looked up longer in the "gaze up" condition, looked longer to the park in the "head aside" condition and looked longer towards the exit space by which the experimenter left in the "absent" condition compared to all other conditions. These results all accord with previous studies on gaze following in various species of primates (Ferrari et al. 2000; Tomasello et al. 1998, 2001, 2007).

The genus *Macaca* presents a wide variety of social organizations ranging from highly hierarchical and nepotistic (level 1) to highly tolerant and egalitarian (level 4) (Matsumura 1999; Thierry 2000; Thierry et al. 2004). Compared to "despotic" species such as rhesus, "egalitarian" species such as Tonkean macaques exhibit milder and more symmetrical aggression, greater inter-individual proximity during foraging, higher rates of affiliative interactions such as grooming and higher rates of peaceful post-conflict contacts (Thierry 2000). Given their very strict dominance hierarchies and high sensitivity to other's behaviours, we expected rhesus macaques to be more sensitive to attentional states and to more subtle attentional cues than Tonkean macaques. However, our prediction was not confirmed. Why did not we observe discrimination of eye states in our rhesus macaques? We proposed two hypotheses below.

First, an explanation might lie in the procedures we used. Our experiment involved a cooperative task in which the subject had to inform the human partner of the location of the hidden raisin in order to be rewarded. This paradigm

may be too artificial for despotic macaque species such as rhesus. The “social competition hypothesis” (Hare 2001) stipulates that many primates do not engage in cooperative intentional communicative behaviour because they largely compete over food. Another more recent hypothesis, the “abject object-choice hypothesis”, suggests that the sight of spatially close “decoy” containers near to the baited container causes distraction for subjects (Mulcahy and Hedge 2012). Containers directly in front of the subjects draw their attention away from the experimenter’s cue. In line with this hypothesis, dyadic situations in which the food was directly held in the experimenter’s hand have provided strong evidences of discrimination of eye state in great apes (Hostetter et al. 2007) and monkeys (Bourjade et al. 2013; Hattori et al. 2010).

Second, we can hypothesize that macaques process both sources of information—eyes and head orientation—at the same time in order to assess attention. Humans make decisions about the direction of another’s attention based on several different cues. Indeed, observers can assess direction of attention by processing eyes and head cues in parallel (Langton 2000; Langton and Bruce 2000). It would therefore be interesting to test macaques in a condition in which, for example, only the eyes and not the head of the experimenter were mobile.

In conclusion, our results show that rhesus macaques are able to intentionally communicate the location of a hidden food reward to an unaware human. The monkeys used their learned begging gesture socially, adjusted their visual orienting behaviour and their gestural behaviour to the attentional state of the human and engaged in gaze alternations between the human and the location of the desired food. We also showed that, like Tonkean macaques, rhesus take into account gross attentional cues such as body and face orientation in order to assess attention, which suggests that this ability existed in an common ancestor of modern macaques. In addition, we highlighted rhesus macaques’ proclivity to follow a human’s gaze. Finally, our results in the “gaze alternation” condition, consisting of a joint attention situation in which the human’s head and eyes both moved, suggest that a combination of attentional cues has greater salience for macaques than any single cue.

Acknowledgments This study was funded mainly by the Primatology Centre of Strasbourg University. CC also received the “Tremplin” grant of the Francophone Society of Primatology (SFDP) for this work. The authors are sincerely grateful to Nicolas Herrenscheidt and his whole team for allowing them to conduct this study at the Primatology Centre of Strasbourg University in France. The authors are particularly thankful to the assistants Lucie Ligault, Sophie Le Ray, Ondine Walter and Clémence Simart for helping in training the subjects to point and in data collection during the experiments. Nicolas Poulin from CeStatS of Strasbourg University, Marie Bourjade from the Aix-Marseille University and Jonas Fizet from the Primatology Centre of Strasbourg University are greatly thanked for

statistical assistance. Jim Anderson and Sarah Lux are warmly thanked for their proofreading and correction of the English manuscript. Authors also thank Nadège Krebs from Noldus for her valuable advice concerning the use of *The Observer* software and the *Conservation Sauvage Internationale* association for providing internship agreement to CC. The authors declare that they have no conflict of interest. All the experiments adhered to the current French laws concerning laboratory animal care and were approved by the French ethical committee CREMEAS (Number of agreement for conducting experiments on primates: AL/46/53/02/13).

References

- Anderson JR, Kuroshima H, Hattori Y, Fujita K (2010) Flexibility in the use of requesting gestures in squirrel monkeys (*Saimiri sciureus*). *Am J Primatol* 72:707–714
- Bania AE, Stromberg EE (2013) The effect of body orientation on judgments of human visual attention in western lowland gorillas (*Gorilla gorilla gorilla*). *J Comp Psychol* 127(1):82–90
- Bard KA (1992) Intentional behavior and intentional communication in young free-ranging orangutans. *Child Dev* 63(5):1186–1197
- Barth J, Reaux JE, Povinelli DJ (2005) Chimpanzees’ (*Pan troglodytes*) use of gaze cues in object-choice tasks: different methods yield different results. *Anim Cogn* 8:84–92
- Bates E, Camaioni L, Volterra V (1975) The acquisition of performatives prior to speech. *Merr-Palm Q* 21(3):205–226
- Bethell EJ, Vick SJ, Bard KA (2007) Measurement of eye-gaze in chimpanzees (*Pan troglodytes*). *Am J Primatol* 69(5):562–575
- Bishop DVM, Ross VA, Daniels MS, Bright P (1996) The measurement of hand preference: a validation study comparing three groups. *Brit J Psychol* 87:269–285
- Bourjade M, Meguerditchian A, Maille A, Vauclair J (2013) Olive baboons, *Papio anubis*, adjust their visual and auditory intentional gestures to the visual attention of others. *Anim Behav* 87:121–128
- Bourjade M, Canteloup C, Meguerditchian A, Vauclair J, Gaunet F (2014) Training experience in gestures affects the display of social gaze in baboons’ communication with a human. *Anim Cogn*. doi:10.1007/s10071-014-0793-5
- Call J, Tomasello M (2007) The gestural communication of apes and monkeys. Lawrence Erlbaum Associates, Mahwah
- Canteloup C, Bovet D, Meunier H (2015) Do Tonkean macaques (*Macaca tonkeana*) tailor their gestural and visual signals to fit the attentional states of a human partner? *Anim Cogn* 18(2):451–461
- Cartmill EA, Byrne RW (2007) Orangutans modify their gestural signaling according to their audience’s comprehension. *Curr Biol* 17:1345–1348
- Cartmill EA, Byrne RW (2010) Semantics of primate gestures: intentional meaning of orangutan gestures. *Anim Cogn* 13:193–804
- Chance MRA (1967) Attention structure as the basis of primate rank orders. *Man* 2(4):503–518
- Emery NJ (2000) The eyes have it: the neuroethology, function and evolution of social gaze. *Neurosci Biobehav Rev* 24:581–604
- Fehr BJ, Exline RB (1987) Social visual interaction: a conceptual and literature review. In: Siegman AW, Feldstein S (eds) *Nonverbal behavior and communication*, 2nd edn. Erlbaum, Hillsdale
- Ferrari PF, Kohler E, Fogassi L, Gallese V (2000) The ability to follow eye gaze and its emergence during development in macaque monkeys. *Proc Nat Acad Sci USA* 97(25):13997–14002
- Flombaum JI, Santos LR (2005) Rhesus monkeys attribute perceptions to others. *Curr Biol* 15:447–452

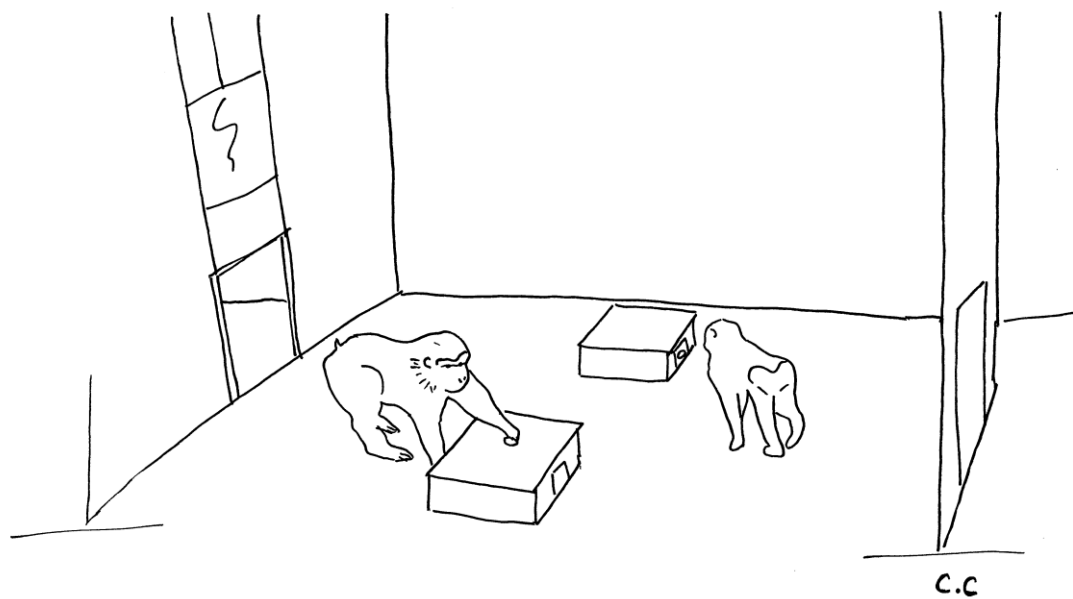
- Genty E, Breuer T, Hobaiter C, Byrne RW (2009) Gestural communication of the gorilla (*Gorilla gorilla*): repertoire, intentionality and possible origins. *Anim Cogn* 12:527–546
- Hare B (2001) Can competitive paradigms increase the validity of experiments on primate social cognition? *Anim Cogn* 4:269–280
- Hare B, Tomasello M (2004) Chimpanzees are more skillful in competitive than in cooperative cognitive tasks. *Anim Behav* 68:571–581
- Hattori Y, Kuroshima H, Fujita K (2007) I know you are not looking at me: capuchin monkeys' (*Cebus apella*) sensitivity to human attentional states. *Anim Cogn* 10:141–148
- Hattori Y, Kuroshima H, Fujita K (2010) Tufted capuchin monkeys (*Cebus apella*) show understanding of human attentional states when requesting food held by a human. *Anim Cogn* 13:87–92
- Hobaiter C, Byrne RW (2011) The gestural repertoire of the wild chimpanzee. *Anim Cogn* 14:745–767
- Hopkins WD, Tagliapietra JP, Leavens DA (2007) Chimpanzees differentially produce novel vocalizations to capture the attention of a human. *Anim Behav* 73:281–286
- Hostetter AB, Cantero M, Hopkins WD (2001) Differential use of vocal and gestural communication by chimpanzees (*Pan troglodytes*) in response to the attentional status of a human (*Homo sapiens*). *J Comp Psychol* 115(4):337–343
- Hostetter AB, Russell JL, Freeman H, Hopkins WD (2007) Now you see me, now you don't: evidence that chimpanzees understand the role of the eyes in attention. *Anim Cogn* 10:55–62
- Itakura S (2004) Gaze-following and joint visual attention in nonhuman animals. *Jap Psychol Res* 46(3):216–226
- Kaminski J, Call J, Tomasello M (2004) Body orientation and face orientation: two factors controlling apes' begging behaviour from humans. *Anim Cogn* 7:216–223
- Keating CF, Keating EG (1982) Visual scan patterns of rhesus monkeys viewing faces. *Perception* 11:211–219
- Keating CF, Keating EG (1993) Monkeys and mug shots: cues used by rhesus monkeys (*Macaca mulatta*) to recognize a human face. *J Comp Psychol* 107:131–139
- Kobayashi H, Kohshima S (2001) Unique morphology of the human eye and its adaptive meaning: comparative studies on external morphology of the primate eye. *J Hum Evol* 40:419–435
- Krause MA, Fouts RS (1997) Chimpanzee (*Pan troglodytes*) begging: hand shapes, accuracy, and the role of eye gaze. *J Comp Psychol* 111:330–336
- Langton SRH (2000) The mutual influence of gaze and head orientation in the analysis of social attention direction. *Q J Exp Psychol* 53(3):825–845
- Langton SRH, Bruce V (2000) You must see the beg: automatic processing of cues to the direction of social attention. *J Exper Psychol: Hum Percept Perform* 26(2):747–757
- Leavens DA, Hopkins WD (1998) Intentional communication by chimpanzees: a cross-sectional study of the use of referential gestures. *Dev Psychol* 34:813–822
- Leavens DA, Hopkins WD, Thomas RK (2004a) Referential communication by chimpanzees (*Pan troglodytes*). *J Comp Psychol* 118(1):48–57
- Leavens DA, Hostetter AB, Wisley MJ, Hopkins WD (2004b) Tactical use of unimodal and bimodal communication by chimpanzees, *Pan troglodytes*. *Anim Behav* 67:467–476
- Leavens DA, Russell JA, Hopkins WD (2005) Intentionality as measured in the persistence and elaboration of communication by chimpanzees (*Pan troglodytes*). *Child Dev* 76(1):296–306
- Liebal K, Pika S, Call J, Tomasello M (2004) To move or not to move: how apes alter the attentional state of humans when begging for food. *Interact Stud* 5:199–219
- Liebal K, Waller BM, Burrows AM, Slocum KE (2013) Primate communication. A multimodal approach. Cambridge University Press, Cambridge
- Maille A, Engelhart L, Bourjade M, Blois-Heulin C (2012) To beg, or not to beg? That is the question: mangabeys modify their production of requesting gestures in response to human's attentional states. *PLoS ONE* 7(7):e41197. doi:10.1371/journal.pone.0041197
- Matsumura S (1999) The evolution of "egalitarian" and "despotic" social systems among macaques. *Primates* 40(1):23–31
- Meunier H, Blois-Heulin C, Vauclair J (2011) A new tool for measuring hand preference in non-human primates: adaptation of Bishop's Quantifying Hand Preference task for Olive baboons. *Behav Brain Res* 218:1–7
- Meunier H, Fizet J, Vauclair J (2013) Tonkean macaques communicate with their right hand. *Brain Lang* 126:181–187
- Mulcahy NJ, Hedge V (2012) Are great apes tested with an object-choice task? *Anim Behav* 83:313–321
- Nahm FKD, Perret A, Amaral DG, Albright TD (1997) How do monkeys look at faces? *J Cogn Neurosci* 9:611–623
- Pika S, Liebal K, Tomasello M (2003) Gestural communication in young gorillas (*Gorilla gorilla*): gestural repertoire, learning and use. *Am J Primatol* 60:95–111
- Pika S, Liebal K, Tomasello M (2005) Gestural communication in subadult bonobos (*Pan paniscus*): repertoire and use. *Am J Primatol* 65:39–61
- Poss S, Kuhar C, Stoinski TS, Hopkins WD (2006) Differential use of attentional and visual communicative signaling by orangutans (*Pongo pygmaeus*) and gorillas (*Gorilla gorilla*) in response to the attentional status of a human. *Am J Primatol* 68(10):978–992
- Povinelli DJ, Eddy TJ (1996) What young chimpanzees know about seeing. *Monogr Soc Res Child Dev* 61(3):1–152
- Roberts AI, Vick SJ, Buchanan-Smith HM (2013) Communicative intentions in wild chimpanzees: persistence and elaboration in gestural signaling. *Anim Cogn* 16:187–196
- Sato N, Nakamura K (2001) Detection of directed gaze in rhesus monkeys (*Macaca mulatta*). *J Comp Psychol* 115(2):115–121
- Tempelmann S, Kaminski J, Liebal K (2011) Focus on the essential: all great apes know when others are being attentive. *Anim Cogn* 14:433–439
- Thierry B (2000) Covariation of conflict management patterns across macaque species. In: Aureli F, de Waal FBM (eds) *Natural Conflict resolution*. University of California Press, Berkeley, pp 106–128
- Thierry B, Singh M, Kaumanns W (2004) *Macaque societies: a model for the study of social organization*. Cambridge University Press, Cambridge
- Tomasello M, Call J, Nagell K, Olguin R, Carpenter M (1994) The learning and the use of gestural signals by young chimpanzees: a trans-generational study. *Primates* 35(2):137–154
- Tomasello M, Call J, Warren J, Frost GT, Carpenter M, Nagell K (1997) The ontogeny of chimpanzee gestural signals: a comparison across groups and generations. *Evol Commun* 1:223–259
- Tomasello M, Call J, Hare B (1998) Five primate species follow the visual gaze of conspecifics. *Anim Behav* 55:1063–1069
- Tomasello M, Hare B, Fogleman T (2001) The ontogeny of gaze following in chimpanzees, *Pan troglodytes*, and rhesus macaques, *Macaca mulatta*. *Anim Behav* 61:335–343
- Tomasello M, Hare B, Lehmann H, Call J (2007) Reliance on head versus eyes in the gaze following of great apes and human infants: the cooperative eye hypothesis. *J Hum Evol* 52:314–320
- Vick S-J, Anderson JR (2003) Use of human visual attention cues by Olive baboons (*Papio anubis*) in a competitive task. *J Comp Psychol* 117(2):209–216
- Zimmermann F, Zemke F, Call J, Gomez JC (2009) Orangutans (*Pongo pygmaeus*) and bonobos (*Pan paniscus*) point to inform a human about the location of a tool. *Anim Cogn* 12:347–358

ARTICLE 3

Do Tonkean macaques (*Macaca tonkeana*) perceive what conspecifics do and do not see?

Canteloup C., Piraux E., Poulin N. & Meunier H.

PeerJ 2016, 4 :e1693 ; DOI 10.7717/peerj.1693



Synthèse de l'article 3:

Do Tonkean macaques (*Macaca tonkeana*) perceive what conspecifics do and do not see?

Canteloup C., Piraux E., Poulin N. & Meunier H.

PeerJ 2016, 4 :e1693 ; DOI 10.7717/peerj.1693

Questions

Etre capable de prendre la perspective visuelle d'autrui est considéré comme un composant de la Théorie de l'Esprit. Les macaques de Tonkean sont-ils capables de comprendre ce que peuvent et ne peuvent pas voir leurs congénères ?

Méthode

Vingt et une paires de dominant-subordonné ont été testées dans un paradigme de compétition alimentaire. Quatre conditions expérimentales ont été proposées: dans les deux premières conditions, le subordonné avait accès visuellement à deux morceaux de nourriture tandis que le dominant n'en voyait qu'un et il était relâché dans la zone de test soit simultanément soit avec un temps d'avance sur le dominant. Dans les deux dernières conditions, le dominant voyait les deux morceaux de nourriture alors que le subordonné n'en voyait qu'un et il était relâché dans la zone de test soit avant soit en même temps que le subordonné.

Résultats

Les subordonnés se dirigent significativement plus vers le morceau de nourriture caché au dominant dans les deux premières conditions expérimentales alors que les dominants ne montrent aucune préférence pour un des deux morceaux de nourriture dans les deux dernières conditions expérimentales.

Conclusion

Les macaques de Tonkean semblent capables de prendre la perspective visuelle de leurs congénères. Toutefois, une explication de plus bas niveau est possible : les subordonnés pourraient simplement lire le comportement du dominant et ainsi éviter de se diriger vers la nourriture visible, convoitée et regardée par celui-ci.



Do Tonkean macaques (*Macaca tonkeana*) perceive what conspecifics do and do not see?

Charlotte Canteloup^{1,2,3}, Emilie Piraux², Nicolas Poulin⁴ and H  l  ne Meunier^{1,2,3}

¹ Laboratoire de Neurosciences Cognitives et Adaptatives, UMR 7364, Strasbourg, France

² Centre de Primatologie de l'Universit   de Strasbourg, Niederhausbergen, France

³ University of Strasbourg Institute for Advanced Study, Strasbourg, France

⁴ Centre Statistique de Strasbourg, IRMA, UMR 7501, Strasbourg, France

ABSTRACT

The understanding of the visual perception of others, also named visual perspective taking, is a component of Theory of Mind. Although strong evidence of visual perspective taking has been reported in great apes, the issue is more open to discussion in monkeys. We investigated whether Tonkean macaques (*Macaca tonkeana*) know what conspecifics do and do not see, using a food competition paradigm originally developed in great apes. We tested individuals in pairs, after establishing the dominance relationship within each pair. Twenty-one pairs were tested in four different conditions. In one condition, the subordinate had the choice between two pieces of food, one that was visible only to it and another that was also visible to the dominant. It was predicted that if the subordinate understands that the dominant cannot see both pieces of food because one is hidden from its view, the subordinate should preferentially go for the food visible only to itself. In the three other conditions, we varied the temporal and visual access to food for both individuals, to control for alternative explanations based on dominance. We recorded the first movement direction chosen by subjects, i.e. towards a) visible food b) hidden food or c) elsewhere; and the outcome of the test, i.e. the quantity of food obtained. Results showed that subordinates moved preferentially for the hidden food when released simultaneously with the dominant and also with a head start on the dominant. By contrast, dominants' choices of the two pieces of food were random. We also describe and discuss some of the strategies used by subordinates in these tests. According to the whole of our results, Tonkean macaques seem capable of visual perspective taking despite the fact that a low-level explanation as behavior reading has not been totally excluded.

Submitted 1 October 2015
Accepted 25 January 2016
Published 22 February 2016

Corresponding author
Charlotte Canteloup,
charlotte.canteloup@gmail.com

Academic editor
Juliane Kaminski

Additional Information and
Declarations can be found on
page 17

DOI 10.7717/peerj.1693

   Copyright
2016 Canteloup et al.

Distributed under
Creative Commons CC-BY 4.0

OPEN ACCESS

Subjects Animal behavior, Neuroscience

Keywords Perspective taking, Theory of mind, Competition, Social cognition, Monkey

INTRODUCTION

Exploiting information from others is an ability that plays a key role in social species' daily interactions. One way of obtaining information is gaze following, defined as "looking where someone else is looking" (Corkum & Moore, 1995), a widespread behavior in nonhuman primates (Emery, 2000; Itakura, 2004). Gaze following may rely

How to cite this article Canteloup et al. (2016), Do Tonkean macaques (*Macaca tonkeana*) perceive what conspecifics do and do not see?. PeerJ 4:e1693; DOI 10.7717/peerj.1693

on simple mechanisms and is adaptive for detecting food during foraging, potential danger from predators, and important social information such as dominance-related interactions (Itakura, 2004). Moreover, it is considered as a prerequisite to complex forms of social cognition such as Theory of Mind (Emery, 2000). The use of another's gaze cues has indeed been implicated in higher order cognitive abilities such as visual perspective taking, deception and empathy (e.g. Anderson, 1998; Tomasello et al., 2005; Byrne & Bates, 2010). In these cases, the observer understands that the observed individual is attending to a particular stimulus because the individual intends to do something with the visual target, or believes something about it. One of the biggest issues faced by comparative cognitive scientists is the extent to which gaze following reflects mental state attribution, especially in our closest relatives, the nonhuman primates (Shepherd, 2010).

Following the gaze of a human experimenter has been reported in many primate species (chimpanzees, *Pan troglodytes*: Povinelli & Eddy, 1996; Call, Hare & Tomasello, 1998; Tomasello, Hare & Fogleman, 2001; gibbons, *Hylobates pileatus*, *H. moloch*, *H. lar*, *Symphalangus syndactylus*: Liebal & Kaminski, 2012; rhesus macaques, *Macaca mulatta*: Tomasello, Hare & Fogleman, 2001; stump-tailed macaques, *Macaca arctoides*: Anderson & Mitchell, 1999; marmosets, *Callithrix jacchus*: Burkart & Heschl, 2006). Conspecific models are also effective (chimpanzees: Tomasello, Call & Hare, 1998; Kano & Call, 2014; bonobos, *Pan paniscus*: Kano & Call, 2014; orangutans, *Pongo abelii*: Kano & Call, 2014; rhesus macaques: Emery et al., 1997; Tomasello, Call & Hare, 1998; stumptailed macaques: Tomasello, Call & Hare, 1998; pigtail macaques, *Macaca nemestrina*: Tomasello, Call & Hare, 1998; sooty mangabeys, *Cercocebus atys torquatus*: Tomasello, Call & Hare, 1998; brown lemurs, *Eulemur fulvus* and black lemurs, *Eulemur macaco*: Ruiz et al., 2009). Furthermore, some scholars have recently reported flexibility in primate gaze following skills. For example, crested macaques (*Macaca nigra*) reacted quicker to a change of gaze direction by a socially close conspecific (Micheletta & Waller, 2012), and long-tailed macaques (*Macaca fascicularis*) showed stronger gaze following responses when a human's gaze shift was accompanied by a social facial expression compared to a neutral expression (Goossens et al., 2008). The latter authors also showed that macaques frequently looked back to the human's face when facing a human who was looking at the ceiling where there was nothing of interest; chimpanzees do likewise (Call, Hare & Tomasello, 1998; Bräuer, Call & Tomasello, 2005). Such results suggest that gaze following is more than a simple reflex, but they provide no evidence that great apes understand that the model is actually seeing something. This ability to understand what another subject can see, also named visual perspective taking, is a component of Theory of Mind (Premack & Woodruff, 1978; Povinelli, Nelson & Boysen, 1990).

The development of visual perspective taking in human infants is a two-step process, according to Flavell (1992). For this author, infants near the age of two years can infer that someone may see something that they do not, and *vice versa* (called Level 1 knowledge of visual perception). Later, around three years of age (e.g. Moll & Meltzoff, 2011), infants are able to recreate the different visual appearances of something viewed by two persons from different locations (called Level 2 knowledge of visual perception). Some researchers have

sought to determine whether nonhuman primates are capable of Level 1 perspective taking by testing great apes and monkeys in various experimental paradigms.

One of the most commonly used paradigms to study visual perspective taking in nonhuman primates is the object-choice task. Typically in this task, a human experimenter hides a piece of food under one of two containers and then attempts to notify the subject about the location of the food by staring or pointing at the baited container. Great apes (chimpanzees: *Call, Agnetta & Tomasello, 2000*; orangutans: *Call & Tomasello, 1998*; gorillas: *Peignot & Anderson, 1999*) and monkeys (brown capuchins: *Anderson, Sallaberry & Barbier, 1995*; rhesus macaques: *Anderson, Montant & Schmitt, 1996*; marmosets: *Burkart & Heschl, 2007*, but see *Burkart & Heschl, 2006*) often fail to request food from the correct container when the human's gaze is the only cue. In another experiment (*Povinelli & Eddy, 1996*), chimpanzees that were trained to beg for food were confronted with two experimenters who could potentially give them food: one could see them and one could not. Because the chimpanzees did not solicit food from a human who could see them more than from one who could not see them, the authors concluded that chimpanzees do not have a mentalistic understanding of seeing (i.e. knowing that seeing is "about" something). Instead, according to *Povinelli & Eddy (1996)*, chimpanzees have a behaviorist appreciation of the behavior of others (i.e. "the chimpanzees' behavior is completely governed by observable entities and events without recourse to reasoning about unobservable mediating mental states," footnote 1 p 25).

Some researchers (*Johnson & Karim-D'Arcy, 2006* for review) have criticized the object-choice task as it diverges greatly from social conditions in which primates naturally use visual perspective taking; in other words it lacks ecological validity. Specifically, the object-choice task puts the subject in a cooperative situation with a human partner, an unusual context unlikely to occur in nonhuman primates' natural daily life. Therefore, acknowledging the importance of competition in primates' normal lives (*Byrne & Whiten, 1988*), researchers have developed alternative paradigms involving an intraspecific competitive context to test visual perspective taking in a more ecologically valid way (*Hare, 2001*). In the pioneering experiment by *Hare et al. (2000)*, two chimpanzees—a dominant and a subordinate—were tested in a food competition situation. The subjects were placed in opposite rooms with food pieces positioned in a room situated centrally between the dominant's room and the subordinate's room. In the test, one piece of food was visible to both individuals while the other, hidden behind a barrier, was visible only to one of the two subjects. *Hare et al. (2000)* hypothesized that when subordinates saw both pieces of food, they would head for the hidden food more often than the visible one, which would be evidence that they could take the visual perspective of their dominant conspecific. Subordinate chimpanzees did indeed preferentially go for the food that only they could see when released simultaneously with the dominant (*Hare et al., 2000*; *Bräuer, Call & Tomasello, 2007*). The same result was obtained when subordinates were released shortly before the dominant, forcing them to make a choice of direction towards one of the two pieces of food before the dominant that not depends on the dominant's intention movements towards food (*Hare et al., 2000*; *Hare, Call & Tomasello, 2001*; *Bräuer, Call & Tomasello, 2007*). However, these authors reported an alternative

hypothesis named the intimidation hypothesis: subordinates could choose the food the dominant was not looking at throughout the space under the trapdoor allowing subject to see the testing area. In order to rule out this hypothesis, Hare and collaborators assessed two controls. A first control was made nine months later in which the dominant's door was raised for some seconds after the baiting procedure and finally closed. Next, the subordinate's door was opened allowing the subordinate to enter in the testing area. The dominant was then released after the subordinate had adopted its first direction choice. Researchers reported that subordinates approached the hidden piece of food more often than the visible one. A second control placed the dominant in a situation in which it could see always a single piece of food hidden from the subordinate's view. In this control, two experimental conditions were performed: in one, both trapdoors were raised allowing both subjects to see the occluders but only the dominant could see the hidden piece of food. In this condition, the subordinate had the opportunity to read the dominant's behavior and locate food whereas in the second condition, only the subordinate's door was raised, so it could not read the dominant's behavior. Hare and collaborators reported that subordinates chose to head for one of the two occluders at random, so they did not use the dominant's behavior to locate food, which strengthen the hypothesis that chimpanzees know what conspecifics do and do not see.

Few comparable studies have been done on monkeys, with equivocal results regarding their visual perspective taking abilities. On one hand, subordinate capuchins (*Sapajus apella*) have been reported to prefer retrieving hidden food when released at the same time as dominants; however, they did not approach hidden food first when released with a short head start. Thus, capuchins appeared to base their choice on behavior reading rather than perspective taking (Hare et al., 2003). Marmosets reportedly behaved like chimpanzees (Burkart & Heschl, 2007) in conditions similar to those designed by Hare et al. (2000) and Hare et al. (2003) but the authors also acknowledged a possible behavior reading explanation. On the other hand, some lemur species (ring-tailed lemur, *Lemur catta*: Sandel, MacLean & Hare, 2011; MacLean et al., 2013; Bray, Krupenye & Hare, 2014; black lemur; brown lemur; Coquerel's sifaka, *Propithecus coquereli*: MacLean et al., 2013) and rhesus macaques (*Macaca mulatta*: Flombaum & Santos, 2005; Bray, Krupenye & Hare, 2014) have been shown to preferentially steal food from a human competitor who cannot see the food rather than one who can see it. In addition, Overduin-de Vries, Spruijt & Sterck (2014) reported that long-tailed macaques understood what a conspecific competitor could see; those authors ruled out a behavior reading explanation because only subordinates could see the dominants when making their choice, whereas dominants had no visual access to food or the subordinates either before or during the trial. In this situation dominants could not show special interest in one of the two pieces of food, and consequently they had no inhibiting effect on the subordinates. Social cognitive studies in macaques focused essentially on despotic species such as rhesus and long-tailed macaques, neglecting tolerant species as their Sulawesi cousins. How specific social dynamics affect cognitive abilities as Theory of Mind abilities is poorly understood and studies of socio-cognitive capacities tend to overlook the potential influence of social characteristics of the species. Studying socially tolerant species could thus provide insights

about the influence of sociocultural environment on perception reading abilities and can help to elucidate the ecological and social pressures that favoured the evolution of Theory of Mind. Social tolerance being one of the important factors for social complexity, we would expect more complex cognitive skills for a more socially tolerant species compared to a more despotic one. Testing a tolerant species in a competitive context also allows investigation of the contextual features that underlie such cognitive skills in species with different ecological and social characteristics.

In this context, we tested a tolerant macaque species that has not been extensively studied, the Tonkean macaque (*Macaca tonkeana*), in an experiment inspired by [Hare et al. \(2000\)](#) and [Hare et al. \(2003\)](#), to investigate their understanding of visual perception. For this, we used an equivalent of the “occluder test” from [Hare et al. \(2000\)](#) in four different experimental conditions. In conditions 1 and 2, the subordinate had visual access to two pieces of food: one positioned on the top of the visual barrier, visible to the subject and to the dominant, and one positioned under the barrier, thus only visible to the subject. The difference between conditions 1 and 2 was that in condition 1, both monkeys had access to the testing area at the same time, whereas in condition 2 the subordinate was released slightly earlier than the dominant. Thus, condition 2 was a control aimed at ruling out the possibility subordinates might simply react to the dominant’s intention movements towards the visible food. In conditions 3 and 4, the dominant had visual access to both pieces of food whereas the subordinate saw only one. Conditions 3 and 4 differed in that in condition 4, both monkeys had access to the testing area at the same time, whereas in condition 3, the dominant was released with a short head start on the subordinate. These two conditions were run to verify that macaques do not have a general preference for hidden food and that dominants do not exhibit specific behavioral strategies in the presence of subordinates. We expected that, as in long-tailed macaques, subordinate Tonkean macaques would move preferentially for the hidden food in conditions 1 and 2, whereas dominants would show no preference for either piece of food in conditions 3 and 4.

METHODS

Ethical note

The procedures used here adhere to the French legal requirements for the Use of Animals in Research. This experiment was approved by the Animal Experiment Committee of the Centre de Primatologie de l’Université de Strasbourg and by the CREMEAS Ethics Committee (Approval for conducting experiments on primates n° AL/46/53/02/13).

Subjects

The subjects were eleven Tonkean macaques (eight males aged two–11 years and three females aged four–17 years), tested in 21 dyads, all born and raised at the Centre de Primatologie de l’Université de Strasbourg, France. Four subjects were tested as dominant only, one as subordinate only and six as both dominant and subordinate (see [Table 1](#) for details). Subjects lived in a social group of 28 individuals in a one-acre wooded park with access to a 20 m² heated indoor housing area. The monkeys’ diet consisted of

Table 1 Sex, age, hierarchical rank, number of trials as dominant, number of trials as subordinate and total number of trials of subjects.

Subject	Sex	Age (years)	Hierarchical rank	Number of trials as dominant	Number of trials as subordinate	Total number of trials
Lady	Female	17	12	45	166	211
Yannick	Male	5	13	6	197	203
Nereis	Female	15	8	13	7	20
Nema	Female	3	14	45	11	56
Vishnu	Male	8	6	32	20	52
Uruk	Male	9	2	6	0	6
Wallace	Male	7	5	75	0	75
Wotan	Male	7	9	128	4	132
Walt	Male	7	10	54	0	51
Shan	Male	11	1	31	0	31
Nenno	Male	2	19	0	30	30

commercial pellets and water *ad libitum*, and fruits and vegetables twice a week, after experimental sessions.

Apparatus

Subjects were tested in dyads in an outdoor experimental enclosure adjacent to their park, which allowed individuals to participate voluntarily. The experimental enclosure consisted of three compartments interconnected by trapdoors (Fig. 1): an area “A” (430 × 290 cm and 190 cm high) directly connected to the park; a middle compartment “B” or testing area (290 × 290 cm and 190 cm high), and an area “C” (140 × 290 cm and 190 cm high). In compartment B two breeze blocks (49 × 38 cm and 15 cm high), served as visual barriers; they were placed in the middle of the area, equidistant to the trapdoors and separated by 80 cm. The three compartments were connected by double-layered trapdoors (42 × 52 cm) consisting of one transparent Plexiglas door doubled with an opaque metal door. The two layers of the trapdoors could be opened independently.

Establishment of dominance hierarchy within the group

The first step in this study was to determine dominance relationships between the subjects. This was done in two ways: firstly, by establishing the dominance hierarchy within the group, and secondly, verifying the dominance relationship within tested dyads.

The within-group dominance hierarchy was determined in 25 sessions of food competition tests. A bottle filled with diluted sweet syrup was attached to the wire mesh fencing inside the macaques’ park. This induced food competition for access to the syrup, and the experimenter recorded agonistic interactions in the vicinity of the bottle. At the end of each interaction, each participant was recorded as “winner” or “loser.” From the resulting global matrix the dominance hierarchy was obtained using Matman 1.1 (De Vries, Netto & Hanegraaf, 1993); it was significantly linear ($h' = 0.39$; $P = 0.00009$). Then we calculated hierarchical rank differences for each dyad to be tested

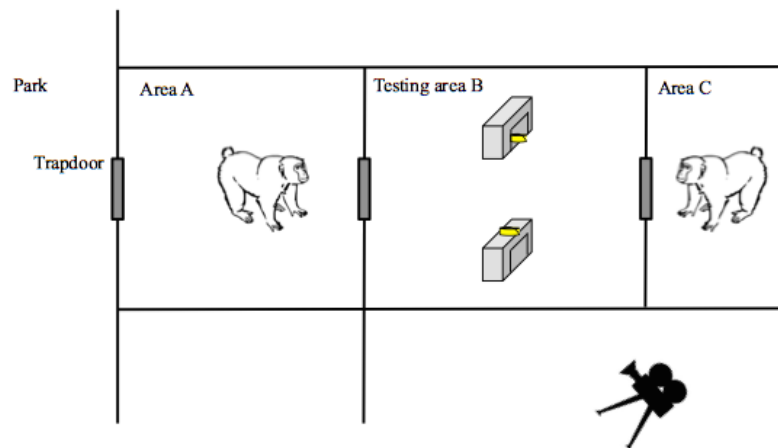


Figure 1 Schema of the experimental apparatus used in the visual perspective-taking experiment. Macaques in area A and C were given access to the testing area B where two pieces of food were placed. One piece was put on one of the two breeze blocks, i.e. visible by the two subjects (subjects in A and C), and another one was placed in and under the other breeze block, i.e. hidden from one of the two subject's view (subject in A).

by subtracting the rank of the subordinate from that of the dominant (see raw data for details).

Establishment of dominance relationship within dyads

Determination of the dominance relationship within dyads took place in the experimental area. Twenty-one dyads were tested between April and June 2014. One subject was placed in area A and the other in the area C (Fig. 1). The opaque trapdoors were lowered to hide the baiting procedure from each monkey. A slice of banana was placed centrally in the testing area, exactly half way between the two breeze blocks. The Experimenter (EP) then simultaneously raised the opaque layers of the two trapdoors to allow the subjects to see into the testing area through the transparent layers. Five seconds after the two subjects were in position behind the Plexiglas trapdoors and after having looked into the testing area, the experimenter simultaneously raised the transparent layers, allowing the monkeys to enter the testing area. Whichever monkey picked up the slice of banana was considered dominant in this trial. We performed 10 such tests per dyad and tested the significance of the difference in successes using a binomial test for each dyad.

Experimental procedure

The experiment took place in the three experimental areas described above (Fig. 1). For each trial, one slice of banana was placed on top of one of the two breeze blocks, and the other was put inside and near the back of the other breeze block, so that only one of the two subjects could see both banana pieces (subject in C in Fig. 1). Which piece of food

went in which location was randomized across trials. The experiment consisted of four experimental conditions as follows: In conditions 1 and 2, the subordinate could see both pieces of food, but in condition 1 both subordinate and dominant were released into the testing area simultaneously, whereas in condition 2 the subordinate was released slightly before the dominant (the dominant was released as soon as the subordinate's entire body was in the testing area). In conditions 3 and 4 the dominant could see both pieces of food, but in condition 3 the dominant was released slightly before the subordinate, whereas in condition 4 both individuals were released simultaneously. In cases when the individual released first (conditions 2 and 3) did not fully enter the testing area, the other individual was released 60 seconds after the first individual. Because subjects were tested opportunistically (i.e., they had free access to the experimental area and were never forced to participate), we ran between 1 and 22 trials of the four different experimental conditions following a same random list of trials per dyad (see data acquisition sheet on raw data for details), resulting in a total of 1 to 66 trials per dyad (total mean of trials per dyad = 20.7 ± 4.3 ; see Table 2 for details), with a maximum of twenty trials per condition in total (ten trials for each breeze block). Each trial started when at least one of the two transparent trapdoors was opened, and ended when the two pieces of food were picked up.

Data and reliability analyses

All experiments were recorded using a video camera HD (Canon, Legria HF S20) and data were later coded by CC using the software VLC 2.1.5. Two variables were measured: a) the first movement direction taken by individuals: (i) hidden: head and chest oriented towards the hidden banana; ii) visible: head and chest oriented towards the visible banana; iii) elsewhere: the subject did not enter in the testing area or entered and sat down in front of the trapdoor or entered and crossed the testing area between the two breeze blocks); b) the outcome of the test: (i) outcome 1: the dominant gets both pieces of food ii) outcome 2: the subordinate gets both pieces of food; iii) outcome 3: the dominant gets the visible piece of food and the subordinate gets the hidden one; iv) outcome 4: the subordinate gets the visible piece of food and the dominant gets the hidden one). In some cases, subjects behaved as if they understood that two pieces of food were present and began searching both locations, even on trials in which they only had visual access to one piece of food. In these trials, just after having retrieved the visible piece of food, some dominants systematically visited the other occluder on the subordinate's side to retrieve the hidden banana. We excluded these trials from the analysis. Twenty-nine trials were removed due to errors during experiments (e.g. one subject was released in the testing area too late). Ten additional trials were removed from the analysis due to the loss of two video clips (trial n°1 for the dyad Wotan-Yannick and trials 4 to 12 for the dyad Shan-Yannick). For reliability analysis, a random twenty percent of the videos were analysed by HM. Inter-observer agreements were excellent for both the first movement direction (Cohen's $\kappa = 0.94$) and the outcome of the test (Cohen's $\kappa = 0.99$).

Table 2 Hierarchical rank difference and number of trials per condition of tested dyads.

Tested dyad (dominant-subordinate)	Hierarchical rank difference	Number of trials condition 1	Number of trials condition 2	Number of trials condition 3	Number of trials condition 4
Wallace–Yannick	8	10	8	7	9
Wotan–Yannick	4	20	14	11	21
Walt–Yannick	3	3	5	4	2
Lady–Yannick	1	3	6	4	2
Nereis–Lady	4	3	3	3	2
Walt–Lady	2	9	11	9	11
Wotan–Lady	3	16	18	15	13
Nema–Lady	2	11	13	10	11
Vishnu–Yannick	7	7	8	10	7
Lady–Nenno	7	7	8	9	6
Shan–Yannick	12	8	7	6	10
Wallace–Wotan	4	0	2	0	0
Wallace–Vishnu	1	3	8	5	4
Uruk–Yannick	11	0	2	0	1
Wallace–Lady	7	0	3	2	2
Yannick–Nema	1	0	3	1	2
Uruk–Wotan	7	0	1	0	1
Nereis–Yannick	5	0	1	0	1
Wallace–Nereis	3	0	3	2	2
Wallace–Nema	9	0	1	2	2
Uruk–Lady	10	0	0	0	1

Statistical analysis

Analysis focused on experimental configurations where subjects chose between the two pieces of food, namely conditions 1 and 2 for subordinates and conditions 3 and 4 for dominants. In order to deal with pseudoreplication, we used several Generalized Linear Mixed Models (GLMMs) with identities of the dominant, the subordinate and the dyad as random effects. Each combination of the random variables was used in different models, and backward selection of the random effects based on Likelihood Ratio Test (LRT; *Lewis, Butler & Gilbert, 2011*) was performed for each model. In each model, experimental condition, trial number and hierarchical rank difference were assessed as fixed effects. We used these models to determine which factors most influenced the subjects' choice of direction and the outcome of the test.

Regarding subject choice, the analyses were divided into two sub-questions: 1) Which factors explain the choice of direction or no choice? 2) When subjects made a choice, which factors explain the direction chosen, i.e. hidden or visible? To answer these questions, GLMMs (GLMM1 to GLM4) for data following a binomial distribution with a logit link function were fitted. Additionally, to investigate potential learning effects on the

first movement direction and for a better comparison with results of previous studies on other species, we analysed only the two first trials per dyad using Wilcoxon signed rank tests.

Concerning the outcome of the test, we fitted a GLMM for each possible outcome (GLMM5 to GLMM8) to investigate whether the outcome depended on the experimental condition. Some outcomes did not occur for some conditions. Hence, we fitted: i) a model for outcome 1 on the basis of the four experimental conditions; ii) a model for outcome 2 on the basis of conditions 1 and 2; iii) a model for outcome 3 on the basis of conditions 1 and 2 and iv) a model for outcome 4 on the basis of conditions 3 and 4. Moreover, to investigate potential learning effects on outcome, and to better compare with the results of previous studies on other species, we analysed only the two first trials per dyad using Wilcoxon matched pairs tests.

To investigate whether subordinates obtained both pieces of food (outcome 2) significantly more often as a function of their first movement direction (i.e. towards the visible or the hidden food), we fitted a GLM (GLM9) including their first direction as a fixed effect.

Tukey corrections were applied when performing multiple comparison tests between experimental conditions. All models were performed using R 3.1.2's package lme4 (Bates *et al.*, 2014) and Wilcoxon tests were done with GraphPadInstat 3.1 with alpha set at 0.05.

RESULTS

First movement direction: towards food or not?

The best-fitting model on the basis of LRT was the one with the identity of the dominant as the only random effect (GLMM1; see details of each model in Table S1). According to this model, subordinates headed for food rather than elsewhere when they saw both pieces of food and were released at the same time as the dominants (condition 1; $z = 2.61$; $P = 0.009$), and with a head start (condition 2; $z = 5.44$; $P < 0.0001$) on the dominants (Fig. 2). In contrast, they mostly headed elsewhere instead of towards food when they saw only one piece of food and were released after the dominant (condition 3; $z = -2.72$; $P = 0.007$). When they saw only one piece of food and were released at the same time as the dominant, subordinates did not show any preference for approaching food or going elsewhere (condition 4; $z = -0.18$; $P > 0.05$). The probability that the subordinates would first go towards food increased significantly across trials ($z = 2.74$; $P = 0.006$).

We established another model (GLMM2) focusing only on conditions 1 and 2 to compare the behavior of subordinates in these two conditions. The best model on the basis of LRT was the one with only the dyad as random effect. According to this model, subordinates headed for food significantly more than elsewhere when they were released before the dominant than were released at the same time as the dominant ($z = 3.33$; $P = 0.0009$). The greater the hierarchical rank difference, the less likely subordinates headed towards food ($z = -2.26$; $P = 0.02$).

Dominants headed directly for food in all conditions (Fig. 2; see Table S2 for details).

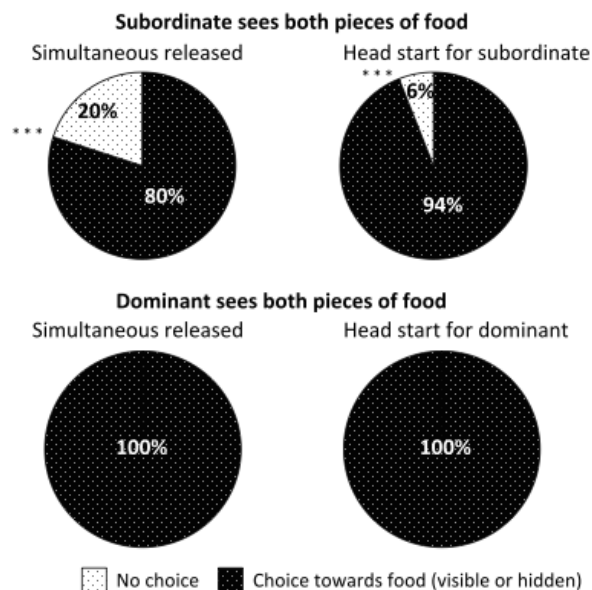


Figure 2 First direction choice taken by the subject able to see both pieces of food, i.e. the subordinate in the conditions 1 and 2 and the dominant in the conditions 3 and 4, in the different experimental conditions. “No choice” category corresponds to cases where the subject did not enter in the testing area or entered and sat down in front of the trapdoor or entered and crossed the testing area through the two breeze blocks. “Choice towards food” category corresponds to cases where the subject heads for hidden or visible food. *** $P < 0.0001$.

First direction choice: hidden or visible food?

The best-fitting model for when subordinates headed for food (hidden or visible) concerning conditions 1 and 2 was the one with the identity of the tested dyad as the only random effect (GLMM3). According to this model, subordinates headed for hidden food significantly more than visible food when they were released simultaneously (condition 1; $z = 4.64$; $P < 0.0001$) and with a head start on the dominant (condition 2; $z = 2.87$; $P = 0.004$) (Fig. 3). As the number of trials increased, the less subordinates headed for the hidden food first ($z = -2.91$; $P = 0.004$), and thus the more they headed for the visible food first. The hierarchical rank difference had no effect on whether the subject chose between hidden and visible food ($z = -0.27$; $P > 0.05$). Regarding only the two first trials per dyad, subordinates headed for hidden food significantly more than visible food in conditions 1 ($W = 54$; $T^+ = 60$; $T^- = -6$; $P = 0.01$) and 2 ($W = 104$; $T^+ = 112$; $T^- = -8$; $P = 0.002$). When they saw both pieces of food, subordinates headed significantly more frequently towards the hidden food when they were released at the same time than when they were released before the dominant (Fig. 3; $z = -4.11$; $P < 0.0001$). Regardless of random effects, all models assessed for dominants' first movement direction towards food reported a variance for the random effects equal to zero (i.e. each random parameter in each GLMM is equal to zero). As these parameters are meant to deal with dependence

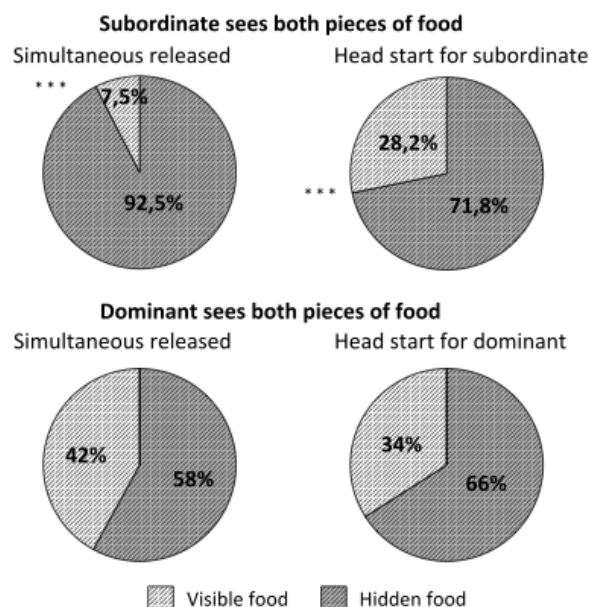


Figure 3 First direction choice taken by the subject able to see both pieces of food, i.e. the subordinate in the conditions 1 and 2 and the dominant in the conditions 3 and 4, towards food (hidden or visible) in the different experimental conditions. *** $P < 0.0001$.

among repeated measurements, dominants' data could be considered as independent, allowing us to perform a GLM and not a GLMM that fit our data better (GLM4). When fitting the GLM, none of the explanatory variables had a significant effect and none of the probabilities for both directions differed significantly from 0.5. Thus, dominants showed no significant preference for moving towards hidden or visible food in the two conditions in which they had visual access to the two pieces of food (conditions 3 and 4; Fig. 3; $P > 0.05$). Regarding only the two first trials per dyad, dominants again showed no preference for hidden or visible food in both conditions 3 ($W = 20$; $T+ = 24$; $T- = -4$; $P > 0.05$) and 4 ($W = 0$; $T+ = 52.5$; $T- = -52.5$; $P > 0.05$) in their two first trials per dyad.

Outcome of the test

The best models were those with the identity of the dominant as a random effect. Dominants obtained both pieces of food (outcome 1; GLMM5) significantly more when they saw both pieces of food and were released at the same time (condition 4: $z = 8.01$; $P < 0.001$) and also with a short head start on the subordinate (condition 3: $z = 8.60$; $P < 0.001$) than when they saw only one piece of food and were released at the same time as subordinates (condition 1; Fig. 4). Dominants obtained both pieces of food (outcome 1) significantly more when they saw both pieces of food and were released at the same time (condition 4: $z = 8.27$; $P < 0.001$) and also with a short head start on subordinates (condition 3: $z = 8.79$; $P < 0.001$) than when they saw only one piece of food

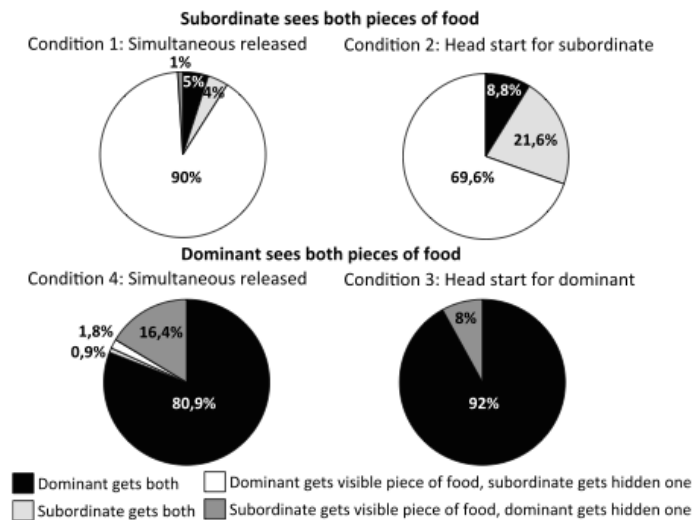


Figure 4 Outcome of encounters in the different experimental conditions.

and were released after a short head start for subordinates (condition 2). Moreover, dominants tended to obtain both pieces of food more often in condition 3 than in condition 4 ($z = -2.40$; $P = 0.073$). The number of trials and the hierarchical rank difference between the tested individuals had no significant effect on the probability of outcome 1 (Fig. 4; $P > 0.05$).

Subordinates were significantly more likely to obtain both pieces of food (outcome 2; GLMM6) when they were released before the dominant (condition 2) than when they were released at the same time as the dominant (condition 1; $z = 4.02$; $P < 0.0001$; Fig. 4). Moreover, subordinates obtained the two pieces of food significantly more often with increasing trials ($z = 2.64$; $P = 0.008$). The hierarchical rank difference between the two individuals had no significant effect on the probability of outcome 2 ($z = 0.95$; $P > 0.05$).

Dominants got the visible food and the subordinate the hidden one (outcome 3; GLMM7) significantly more often when the subordinate saw both pieces of food and was simultaneously released (condition 1; Fig. 4) than when released with a short head start on the dominant (condition 2; $z = -4.13$; $P < 0.0001$). As the number of trials ($z = -2.23$; $P = 0.03$) and the hierarchical rank difference increased ($z = -2.29$; $P = 0.02$), the more likely was the dominant to retrieve the visible food and the subordinate the hidden one.

Occurrences of the subordinate getting the visible food and the dominant the hidden one (outcome 4; GLMM8) were significantly more frequent when the dominant saw both pieces of food and was released at the same time (condition 4; $z = 2.23$; $P = 0.03$) than when released before the subordinate (condition 3; Fig. 4). Neither number of trials nor the hierarchical rank difference had a significant effect on the probability of outcome 4 ($P > 0.05$).

Table 3 Occurrences of first direction towards visible food item and occurrences of outcome 2 (Subordinate obtained two pieces of food) after subordinate chose to head for the visible piece of food in conditions 1 and 2.

	Lady	Nema	Nenno	Nereis	Vishnu	Wotan	Yannick
Subordinate headed for the visible food	15	1	8	0	1	0	15
Subordinate headed for the visible food and obtained both pieces of food (outcome 2)	9	0	6	0	0	0	8

Regarding the two first trials only, subordinates obtained the hidden piece of food rather than the visible one significantly more in conditions 1 ($W = 66$; $T^+ = 66$; $T^- = 0$; $P = 0.001$) and 2 ($W = 153$; $T^+ = 153$; $T^- = 0$; $P < 0.0001$). By contrast, dominants did not obtain one of the two pieces of food significantly more than the other in condition 3 ($W = 4$; $T^+ = 5$; $T^- = -1,0$; $P > 0.05$) or condition 4 ($W = 8$; $T^+ = 9$; $T^- = -1,0$; $P > 0.05$).

Effect of first direction on the outcome

Three subordinates (Lady, Nenno and Yannick) of the seven tested obtained both pieces of food when they first headed for the visible one (Table 3). The best model concerning outcome 2 for observations made when subordinates headed first for visible food in conditions 1 and 2 was the one with no random effect (GLM9). This model reported a significant effect of first movement direction by subordinates on the likelihood of outcome 2: when subordinates first headed for visible food they obtained the two pieces significantly more than when they first headed for the hidden one ($z = -6.72$; $P < 0.0001$).

DISCUSSION

We tested Tonkean macaques in an ecologically relevant competitive situation originally proposed by Hare *et al.* (2000) in which a subordinate subject could choose to retrieve a food item hidden from the view of a dominant conspecific and another one visible to both the dominant and itself. Our hypothesis was that if subordinates but not dominants preferentially went for the hidden food, this could be evidence of visual perspective taking in this macaque species. In agreement with previous studies on great apes (chimpanzees: Hare *et al.*, 2000; Hare, Call & Tomasello, 2001; Bräuer, Call & Tomasello, 2007) and monkeys (rhesus macaques: Flombaum & Santos, 2005; long-tailed macaques: Overduin-de Vries, Spruijt & Sterck, 2014), our results provide support for this hypothesis in a tolerant macaque species: the Tonkean macaque. However, we cannot completely rule out an alternative explanation, namely that subordinates just avoided visible food potentially looked at by dominants throughout the transparent trapdoor.

Subordinates preferentially headed for food (hidden or visible) when they saw both pieces of food and were released simultaneously or with a short head start on the dominant, whereas dominants always went for food. This result validates the naturalistic experimental paradigm used here: placing subordinates in a food competition situation with dominants. In previous studies with chimpanzees (Karin-D'Arcy & Povinelli, 2002;

Bräuer, Call & Tomasello, 2007), marmosets (*Burkart & Heschl, 2007*) and capuchins (*Hare et al., 2003*), limited space probably caused subjects to engage in scramble competition rather than use perspective taking skills. The size and spatial arrangement of our testing area clearly induced a competitive situation appropriate for revealing perspective taking by subordinate macaques. Moreover, the greater the hierarchical rank difference between the two members of each was, the less the subordinate headed for food, further supporting the validity of the competitive situation.

It seems reasonable to suggest that the experimental context—collaborative or competitive—might have a lesser impact on a species with a more fluid social organization than species demonstrating a more strict social system. However, the evidence for this is equivocal. On the one hand, we previously failed to demonstrate that Tonkean macaques distinguish between open and closed eyes in a cooperative interspecific context (*Canteloup, Boveé & Meunier, 2015*). On the other hand, *Costes-Thiré et al. (2015a)* and *Costes-Thiré et al. (2015b)* found no evidence of auditory perspective taking in Tonkean macaques tested in a food competition situation with a human experimenter, or intention reading abilities when they had to cooperate for food with a human partner.

In the present study, when they saw both pieces of food subordinates preferentially headed for the hidden food when they were released simultaneously with the dominant. The same result emerged when subordinates were released slightly before the dominant, allowing them to choose independently of the dominant's choice. Indeed, when released at the same time, the subordinate could head for the hidden food because at the same time the dominant headed for the only food it could see, namely the visible one.

For this reason we ran more trials than is usual in these kinds of studies (e.g. *Hare et al., 2000*). This could lead to the criticism that, in our study, subordinates simply learned the best way to get food, requiring no perspective-taking ability. To deal with this explanation, we ran the same statistical analyses as *Hare et al. (2000)* on only the two first trials for each dyad, and found exactly the same results as obtained using all the data. These results suggest that, like other primate species studied (*Hare et al., 2000; Hare, Call & Tomasello, 2001; Bräuer, Call & Tomasello, 2007; Overduin-de Vries, Spruijt & Sterck, 2014*), Tonkean macaques appear capable of understanding what a conspecific can and cannot see. This conclusion is strengthened by the fact that dominants showed no preference for either the hidden or visible food. This finding rules out the possibility that macaques have a general preference for hidden food. However, a final alternative explanation invoking behavior reading rather than perspective taking may be proposed. According to the “evil eye hypothesis” (*Kaminski, Call & Tomasello, 2008*) and other authors’ “behavioral rules” accounts (*Heyes, 1998; Povinelli & Vonk, 2003; Povinelli & Vonk, 2004*), the subordinates’ behavior could be influenced by what it sees the dominant doing through the transparent trapdoor. In other words, subordinates might prefer to head for the hidden food because the visible one will have been watched by the “evil eye” of the dominant, and thus considered as “contaminated.” They might also have learned that food coveted by the dominant is out of bounds. Unfortunately, our experimental design does not allow us to refute this alternative explanation; the use of

one-way mirrors as in *Overduin-de Vries, Spruijt & Sterck's (2014)* study on long-tailed macaques might be an appropriate procedure that would allow to rule out this low-level explanation.

Given that visual perspective taking has been demonstrated in a phylogenetically very close species, the long-tailed macaque (*Overduin-de Vries, Spruijt & Sterck, 2014*), we think it likely that this ability has evolved as common trait shared by macaque species. Some of the individual strategies that we observed further support our view that Tonkean macaques are capable of visual perspective taking. One such strategy used by subordinates consisted of traversing and leaving the testing area, and if followed by the dominant, rapidly doubling back to retrieve the hidden food (see [Video S3](#)). Another strategy was to head first for the visible food. Indeed, as the number of trials increased, the less the subordinates headed for the hidden food first. Moreover, when they saw both pieces of food, subordinates headed for hidden food significantly less often when released with a short head start on the dominant than when released simultaneously. Surprisingly, when released before the dominant, subordinates moved first to the visible food in almost thirty percent of cases. In terms of the outcome of the test, in this condition, subordinates often managed to obtain both pieces of food when they first headed for the visible food, and this occurred increasingly frequently over repeated trials. On the basis of these observations we conclude that three of the seven subordinates tested adopted this alternative strategy to get both pieces of food by taking into account what the dominant could and could not see. This kind of strategy was recently reported in a more despotic macaque species: the long-tailed macaque (*Overduin-de Vries, Spruijt & Sterck, 2014*), and similar behavior was reported in Tonkean macaques by *Ducoing & Thierry (2003)*. In the latter study, subordinates stopped approaching a hidden fruit, avoided being followed, or took a wrong direction when monitored by a dominant unaware of the location of the food. Together, these observations raise questions about the mechanisms underlying these strategies. Do they rely on relatively simple cognitive processes, such as withholding information due to behavioral inhibition caused by the presence of the dominant, or are more complex cognitive processes involved, such as tactical deception? In other words, do Tonkean macaques learn by operant conditioning to anticipate the consequences of their acts on the behaviors of others or/and do they intentionally attempt to manipulate the knowledge of others? Further investigations are necessary to be able to answer these unresolved questions.

To conclude, our experiment adds to the growing literature on components of Theory of Mind in nonhuman primates, especially in monkeys and notably in macaques (e.g. *Flombaum & Santos, 2005; Santos, Nissen & Ferrugia, 2006; Costes-Thiré et al., 2015a; Costes-Thiré et al., 2015b; Overduin-de Vries, Spruijt & Sterck, 2014*). Like chimpanzees (*Bräuer, Call & Tomasello, 2007; Hare et al., 2000; Hare, Call & Tomasello, 2001; Krachun & Call, 2009*) and despotic Old World monkeys as rhesus (*Flombaum & Santos, 2005*) and long-tailed macaques (*Overduin-de Vries, Spruijt & Sterck, 2014*), Tonkean macaques, socially more tolerant, seem capable of level 1 of visual perspective taking, although further experiments are needed to rule out a low level alternative explanation.

Additionally, we observed an alternative strategy developed by subordinates to obtain all

the available food. These findings show the advantages of a naturalistic experimental paradigm that recreates socio-cognitive problems that nonhuman primates face in their natural environment.

ACKNOWLEDGEMENTS

The authors are grateful to Nicolas Herrens Schmidt, Yves Larmet and the whole team of the Centre de Primatologie de l'Université de Strasbourg for allowing them to conduct this study. The authors are particularly thankful to Steve Lapp, Adrien Panter and Jean-Marc Woock for building the experimental apparatus and for their technical assistance. James R. Anderson and Nailah Ford Burrell are warmly thanked for editing the English of the manuscript. Finally we thank Juliane Kaminski, Academic Editor, and the two anonymous referees for their valuable comments on the manuscript.

ADDITIONAL INFORMATION AND DECLARATIONS

Funding

The research in this paper was supported by the Centre de Primatologie de l'Université de Strasbourg and the University of Strasbourg Institute for Advanced Study (USIAS) as part of a USIAS Fellowship. CC also received a grant "Expériences de jeunes" for innovative projects from the Alsace Region for her work. The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Competing Interests

The authors declare that they have no competing interests.

Author Contributions

- Charlotte Canteloup conceived and designed the experiments, analyzed the data, contributed reagents/materials/analysis tools, wrote the paper, prepared figures and/or tables, reviewed drafts of the paper.
- Emilie Piraux performed the experiments.
- Nicolas Poulin analyzed the data, contributed reagents/materials/analysis tools, reviewed drafts of the paper.
- Hélène Meunier conceived and designed the experiments, analyzed the data, contributed reagents/materials/analysis tools, reviewed drafts of the paper.

Animal Ethics

The following information was supplied relating to ethical approvals (i.e., approving body and any reference numbers):

The procedure adheres to the French legal requirements for the Use of Animals in Research. This experiment was approved by the Animal Experiment Committee of the Centre de Primatologie de l'Université de Strasbourg and by the CREMEAS ethics committee (approval for conducting experiments on primates n° AL/46/53/02/13).

Data Deposition

The following information was supplied regarding data availability:

Raw data are available in the [Supplemental Information](#).

Supplemental Information

Supplemental information for this article can be found online at <http://dx.doi.org/10.7717/peerj.1693#supplemental-information>.

REFERENCES

- Anderson JR, Sallaberry P, Barbier H. 1995. Use of experimenter-given cues during object-choice tasks by capuchin monkeys. *Animal Behaviour* 49(1):201–208 DOI 10.1016/0003-3472(95)80168-5.
- Anderson JR, Montant M, Schmitt D. 1996. Rhesus monkeys fail to use gaze direction as an experimenter-given cue in an object-choice task. *Behavioural Processes* 37(1):47–55 DOI 10.1016/0376-6357(95)00074-7.
- Anderson JR. 1998. Social stimuli and social rewards in primate learning and cognition. *Behavioural Processes* 42(2–3):159–175 DOI 10.1016/S0376-6357(97)00074-0.
- Anderson JR, Mitchell RW. 1999. Macaques but not lemurs co-orient visually with humans. *Folia Primatologica* 70(1):17–22 DOI 10.1159/000021670.
- Bates D, Maechler M, Bolker B, Walker S. 2014. lme4: Linear mixed-effects models using Eigen and S4. *Journal of Statistical Software Available at* <http://arxiv.org/abs/1406.5823>.
- Bräuer J, Call J, Tomasello M. 2005. All great apes species follow gaze to distant locations and around barriers. *Journal of Comparative Psychology* 119(2):145–154 DOI 10.1037/0735-7036.119.2.145.
- Bräuer J, Call J, Tomasello M. 2007. Chimpanzees really know what others can see in a competitive situation. *Animal Cognition* 10(4):439–448 DOI 10.1007/s10071-007-0088-1.
- Bray J, Krupenye C, Hare G. 2014. Ring-tailed lemurs (*Lemur catta*) exploit information about what others can see but not what they can hear. *Animal Cognition* 17(3):735–744 DOI 10.1007/s10071-013-0705-0.
- Burkart JM, Heschl A. 2006. Geometrical gaze following in common marmosets (*Callithrix jacchus*). *Journal of Comparative Psychology* 120(2):120–130 DOI 10.1037/0735-7036.120.2.120.
- Burkart JM, Heschl A. 2007. Understanding visual access in common marmosets, *Callithrix jacchus*: perspective taking or behaviour reading? *Animal Behaviour* 73(3):457–469 DOI 10.1016/j.anbehav.2006.05.019.
- Byrne RW, Bates LA. 2010. Primate social cognition: uniquely primate, uniquely social, or just unique? *Neuron* 65(6):815–830 DOI 10.1016/j.neuron.2010.03.010.
- Byrne RW, Whiten A. 1988. *Machiavellian Intelligence: Social Expertise and the Evolution of Intellect in Monkeys, Apes, and Humans*. Oxford, England: Clarendon Press.
- Call J, Hare BA, Tomasello M. 1998. Chimpanzee gaze following in an object-choice task. *Animal Cognition* 1(2):89–99 DOI 10.1007/s100710050013.
- Call J, Tomasello M. 1998. Distinguishing intentional from accidental actions in orangutans (*Pongypygmaeus*), chimpanzees (*Pan troglodytes*), and human children (*Homo sapiens*). *Journal of Comparative Psychology* 112(2):192–206 DOI 10.1037/0735-7036.112.2.192.
- Call J, Agnetta B, Tomasello M. 2000. Cues that chimpanzees do and do not use to find hidden objects. *Animal Cognition* 3(1):23–34 DOI 10.1007/s100710050047.

- Canteloup C, Bovet D, Meunier H. 2015. Do Tonkean macaques (*Macaca tonkeana*) tailor their gestural and visual signals to fit the attentional states of a human partner? *Animal Cognition* 18(2):451–461 DOI 10.1007/s10071-014-0814-4.
- Corkum V, Moore C. 1995. Development of joint visual attention in infants. In: Moore C, Dumham PJ, eds. *Joint Attention*. Hillsdale, NJ: Lawrence Erlbaum Associates, 61–84.
- Costes-Thiré M, Levé M, Uhlrich P, De Marco A, Thierry B. 2015a. Lack of evidence that Tonkean macaques understand what others can hear. *Animal Cognition* 18(1):251–258 DOI 10.1007/s10071-014-0795-3.
- Costes-Thiré M, Levé M, Uhlrich P, Pasquaretta C, De Marco A, Thierry B. 2015b. Evidence that monkeys (*Macaca tonkeana* and *Sapajus apella*) read moves, but no evidence that they read goals. Epub ahead of print August 2015. *Journal of Comparative Psychology* 129(3):304–310 DOI 10.1037/a0039294.
- De Vries H, Netto WJ, Hanegraaf PLH. 1993. Matman—a program for the analysis of sociometric matrices and behavioural transition matrices. *Behaviour* 125(3):157–175 DOI 10.1163/156853993X00218.
- Ducoing AM, Thierry B. 2003. Withholding information in semifree-ranging Tonkean macaques (*Macaca tonkeana*). *Journal of Comparative Psychology* 117(1):67–75 DOI 10.1037/0735-7036.117.1.67.
- Emery NJ, Lorincz EN, Perrett DI, Oram MW, Baker CI. 1997. Gaze following and joint attention in rhesus monkeys (*Macaca mulatta*). *Journal of Comparative Psychology* 111(3):286–293 DOI 10.1037/0735-7036.111.3.286.
- Emery NJ. 2000. The eyes have it: the neuroethology, function and evolution of social gaze. *Neuroscience and Biobehavioral Reviews* 24(6):581–604 DOI 10.1016/S0149-7634(00)00025-7.
- Flavell JH. 1992. Perspectives on perspective taking. In: Beilin H, Pufall P, eds. *Piaget's Theory: Prospects and Possibilities*. Hillsdale, NJ: Erlbaum, 107–139.
- Flombaum JI, Santos LR. 2005. Rhesus monkeys attribute perceptions to others. *Current Biology* 15(5):447–452 DOI 10.1016/j.cub.2004.12.076.
- Goossens BMA, Dekleva M, Reader SM, Sterck EHM, Bolhuis JJ. 2008. Gaze following in monkeys is modulated by observed facial expressions. *Animal Behaviour* 75(5):1673–1681 DOI 10.1016/j.anbehav.2007.10.020.
- Hare B, Call J, Agnetta B, Tomasello M. 2000. Chimpanzees know what conspecifics do and do not see. *Animal Behaviour* 59(4):771–785 DOI 10.1006/anbe.1999.1377.
- Hare B. 2001. Can competitive paradigms increase the validity of experiments on primate social cognition? *Animal Cognition* 4(3):269–280 DOI 10.1007/s100710100084.
- Hare B, Call J, Tomasello M. 2001. Do chimpanzees know what conspecifics know? *Animal Behaviour* 61(1):139–151 DOI 10.1006/anbe.2000.1518.
- Hare B, Addessi E, Call J, Tomasello M, Visalberghi E. 2003. Do capuchin monkeys, *Cebus apella*, know what conspecifics do and do not see? *Animal Behaviour* 65(1):131–142 DOI 10.1006/anbe.2002.2017.
- Heyes CM. 1998. Theory of mind in nonhuman primates. *Behavioral and Brain Sciences* 21(1):101–148 DOI 10.1017/S0140525X98000703.
- Itakura S. 2004. Gaze-following and joint visual attention in nonhuman primates. *Japanese Psychological Research* 46(3):216–226 DOI 10.1111/j.1468-5584.2004.00253.x.
- Johnson CM, Karin-D'Arcy MR. 2006. Social attention in nonhuman primates: a behavioral review. *Aquatic Mammals* 32(4):423–442 DOI 10.1578/AM.32.4.2006.423.

- Kaminski J, Call J, Tomasello M. 2008. Chimpanzees know what others know, but not what they believe. *Cognition* 109(2):224–234 DOI 10.1016/j.cognition.2008.08.010.
- Kano F, Call J. 2014. Cross-species variation in gaze following and conspecific preference among great apes, human infants and adults. *Animal Behaviour* 91:136–149 DOI 10.1016/j.anbehav.2014.03.011.
- Karin-D'Arcy MR, Povinelli DJ. 2002. Do chimpanzees know what each other see? A closer look. *International Journal of Comparative Psychology* 15:21–54.
- Krachun C, Call J. 2009. Chimpanzees (*Pan troglodytes*) know what can be seen from where. *Animal Cognition* 12:347–331 DOI 10.1007/s10071-008-0192-x.
- Lewis F, Butler A, Gilbert L. 2011. A unified approach to model selection using the likelihood ratio test. *Methods in Ecology and Evolution* 2(2):155–162 DOI 10.1111/j.2041-210X.2010.00063.x.
- Liebal K, Kaminski J. 2012. Gibbons (*Hylobates pileatus*, *H. moloch*, *H. lar*, *Symphalangus syndactylus*) follow human gaze, but do not take the visual perspective of others. *Animal Cognition* 15(6):1211–1216 DOI 10.1007/s10071-012-0543-5.
- MacLean EL, Sandel AA, Bray J, Oldenkamp RE, Reddy RB, Hare BA. 2013. Group size predicts social but non-social cognition in lemurs. *PLoS ONE* 8(6):e66359 DOI 10.1371/journal.pone.0066359.
- Micheletta J, Waller BM. 2012. Friendship affects gaze following in a tolerant species of macaque, *Macaca nigra*. *Animal Behaviour* 83(2):459–467 DOI 10.1016/j.anbehav.2011.11.018.
- Moll H, Meltzoff AN. 2011. How does it look? Level 2 perspective-taking at 36 months of age. *Child Development* 82(2):661–673 DOI 10.1111/j.1467-8624.2010.01571.x.
- Overduin-de Vries AM, Spruijt BM, Sterck EHM. 2014. Long-tailed macaques (*Macaca fascicularis*) understand what conspecifics can see in a competitive situation. *Animal Cognition* 17(1):77–84 DOI 10.1007/s10071-013-0639-6.
- Peignot P, Anderson JR. 1999. Use of experimenter-given manual and facial cues by gorillas (*Gorilla gorilla*) in an object-choice task. *Journal of Comparative Psychology* 113(3):253–260 DOI 10.1037/0735-7036.113.3.253.
- Povinelli DJ, Nelson KE, Boysen ST. 1990. Inferences about guessing and knowing by chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology* 104(3):203–210 DOI 10.1037/0735-7036.104.3.203.
- Povinelli DJ, Eddy TJ. 1996. What young chimpanzees know about seeing. *Monographs of the Society for Research in Child Development* 61(3):1–152 DOI 10.2307/1166159.
- Povinelli DJ, Vonk J. 2003. Chimpanzee minds: suspiciously human? *Trends on Cognitive Sciences* 7(4):157–160 DOI 10.1016/S1364-6613(03)00053-6.
- Povinelli DJ, Vonk J. 2004. We don't need a microscope to explore the chimpanzee's mind. *Mind & Language* 19(1):1–28 DOI 10.1111/j.1468-0017.2004.00244.x.
- Premack D, Woodruff G. 1978. Does the chimpanzee have a theory of mind? *Behavioural Brain Sciences* 1(4):515–526 DOI 10.1017/S0140525X00076512.
- Ruiz A, Gómez JC, Roeder JJ, Byrne RW. 2009. Gaze following and gaze priming in lemurs. *Animal Cognition* 12(3):427–434 DOI 10.1007/s10071-008-0202-z.
- Sandel AA, MacLean EL, Hare B. 2011. Evidence from four lemur species that ringtailed lemur social cognition converges with that of haplorhine primates. *Animal Behaviour* 81(5):925–931 DOI 10.1016/j.anbehav.2011.01.020.
- Shepherd SV. 2010. Following gaze: gaze-following behavior as a window into social cognition. *Frontiers in Integrative Neuroscience* 4(5):1–13 DOI 10.3389/fmint.2010.00005.

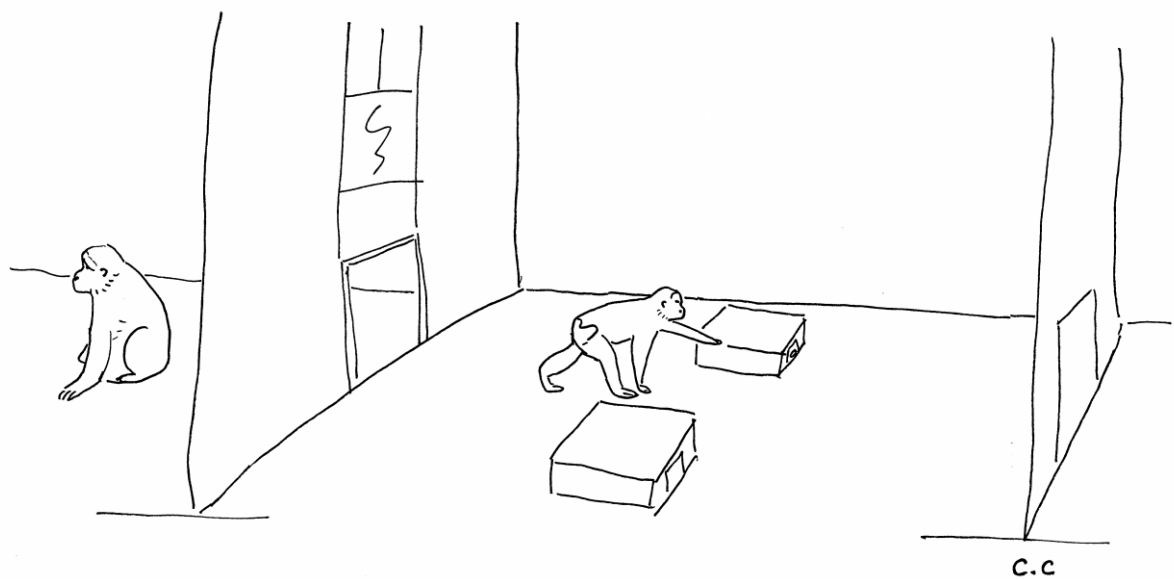
- Santos LR, Nissen AG, Ferrugia JA. 2006.** Rhesus monkeys, *Macaca mulatta*, know what others can and cannot hear. *Animal Behaviour* 71(5):1175–1181 DOI 10.1016/j.anbehav.2005.10.007.
- Tomasello M, Call J, Hare B. 1998.** Five primate species follow the visual gaze of conspecifics. *Animal Behaviour* 55(4):1063–1069 DOI 10.1006/anbe.1997.0636.
- Tomasello M, Hare B, Fogleman T. 2001.** The ontogeny of gaze following in chimpanzees, *Pan troglodytes*, and rhesus macaques, *Macaca mulatta*. *Animal Behaviour* 61(2):335–343 DOI 10.1006/anbe.2000.1598.
- Tomasello M, Carpenter M, Call J, Behne T, Moll H. 2005.** Understanding and sharing intentions: the origins of cultural cognition. *Behavioral and Brain Sciences* 28(5):675–735 DOI 10.1017/S0140525X05000129.

ARTICLE 4

Functionally deceptive behaviours in Tonkean macaques (*Macaca tonkeana*)

Canteloup C., Poitrasson I., Anderson J.R., Poulin N. & Meunier H.

Submitted to *Ethology*



Synthèse de l'article 4:

Functionally deceptive behaviours in Tonkean macaques (*M. tonkeana*)

Canteloup C., Poitrasson I., Anderson J.R., Poulin N. & Meunier H.

Submitted to *Ethology*

Questions

Dans notre étude précédente (Canteloup et al. 2016), nous avons rapporté que les subordonnés macaques de Tonkean utilisaient parfois des stratégies particulières face aux dominants pour obtenir le morceau de nourriture cachée. Ces stratégies peuvent-elles s'apparenter à de la tromperie tactique ? Si oui, quels facteurs influencent l'utilisation de telles stratégies ? Les subordonnés se comportent-ils selon le comportement du dominant ?

Méthode

Nous avons analysé les essais de l'étude de Canteloup et al. (2016) dans lesquels les subordonnés voyaient les deux morceaux de nourriture et étaient relâchés simultanément ou avant le dominant dans la zone de test. Les stratégies observées ont été décrites et classées selon la classification de Byrne & Whiten (1992) et les comportements des subordonnés ont été analysés finement et simultanément à ceux des dominants.

Résultats

Les macaques de Tonkean utilisent quatre catégories de tromperie tactique décrites par Byrne & Whiten (1992). L'utilisation de ces stratégies par les subordonnés est influencée par la différence de rang hiérarchique : plus celle-ci est grande, plus les subordonnés ont recours à de la tromperie. L'analyse fine des comportements révèle que les subordonnés se comportent en fonction du comportement des dominants et non de manière indépendante excepté pour un de ces comportements.

Conclusion

Quels que soient les mécanismes cognitifs impliqués dans ces comportements - apprentissage associatif ou représentation mentale - les subordonnés font preuve de comportements sociaux extrêmement complexes et sont, au moins, de remarquables lecteurs de comportement.

Functionally deceptive behaviours in Tonkean macaques (*Macaca tonkeana*)

Charlotte Canteloup^{1, 2, 3, 4}, Isis Poitrasson¹, James R. Anderson⁵, Nicolas Poulin⁶, H el ene Meunier^{1, 2, 3, 4}

¹ Centre de Primatologie de l'Universit e de Strasbourg, Fort Foch, 67207 Niederhausbergen, France

² Universit e de Strasbourg - Laboratoire de Neurosciences Cognitives et Adaptatives, 12 rue Goethe, 67000 Strasbourg, France

³ CNRS - Laboratoire de Neurosciences Cognitives et Adaptatives, UMR 7364, 12, rue Goethe, 67000 Strasbourg, France

⁴ University of Strasbourg Institute for Advanced Study, 5, all e du G en eral Rouvillois, 67083 Strasbourg, France

⁵ Department of Psychology, Kyoto University Graduate School of Letters, Yoshidahonmachi, Sakyo, Kyoto 606-8501, Japan

⁶ Centre Statistique de Strasbourg, IRMA, UMR 7501, 7, rue Ren e Descartes, 67084 Strasbourg Cedex, France

ABSTRACT

The complex social environments of primates create abundant opportunities for engaging in tactical and intentional deception. To examine such behaviours, we tested subordinate Tonkean macaques with dominant conspecifics in an experimental food competition context. The subordinate macaque could see two pieces of food whereas the dominant could only see one. The two individuals were released into the testing area at the same time or with the subordinate given a short head start on the dominant. Here, based on detailed video analysis of the behaviours of both individuals, we: i) describe and classify functionally deceptive strategies displayed by subordinates; ii) determine factors that influence the use of these strategies, and iii) investigate whether subordinates adjusted their behaviour as a function of the behaviour of the dominant. Subordinates used several types of tactical deception, including concealment and distraction, especially when paired with competitors of much higher social rank, and they obtained the hidden food more frequently when they used a combination of strategies rather than only one. The video analysis revealed significant interactions between subordinate and dominant's behaviours, suggesting that subordinates adjusted their behaviour to those of dominants, and are, at the least, highly skillful behaviour readers.

Keywords: Social cognition; Tactical deception; Monkeys; Strategies

INTRODUCTION

Group-living animals often provide honest behavioural cues that their social companions can use, for example to detect potential danger or food sources. However, group living also creates competition for resources, which results in individuals sometimes also withholding information or imparting dishonest cues (Dawkins & Krebs 1978; Hall & Brosnan 2016). These latter strategies, generally referred to as ‘deception’, are widespread among animals and plants (Krebs & Dawkins 1984). According to the ‘social brain’ and ‘Machiavellian intelligence’ hypotheses (Byrne & Whiten 1988; Dunbar 1998; Humphrey 1976; Jolly 1966), the complex social environments of primates create abundant opportunities for engaging in tactical and intentional deception.

The term ‘tactical deception’ was defined by Byrne and Whiten (1985, p. 672) as “(i) acts from the normal repertoire of an individual, (ii) used at low frequency, and in contexts different from those in which it uses the high frequency (honest) version of the act, (iii) such that another, familiar individual, (iv) is likely to misinterpret what the acts signify, (v) to the advantage of the actor.” Byrne and Whiten (1988; 1990; 1992) subsequently defined different functional categories of tactical deception in nonhuman primates (hereafter primates), including seven types of strategies: concealment, distraction, attraction, creating an image, deflection, using a social tool, and counter-deception. Those authors made no assumptions about underlying cognitive mechanisms. Indeed, according to Byrne (2003, p. 49): “it does not require that the primate agent planned its tactics, intended to deceive another individual, realized that its tactic worked by deception; not does it imply that the victim was capable of realizing that it had been deceived”.

Some authors have classified deceptive behaviours into different levels: of deception (de Waal 1992; Mitchell 1986), intentionality (Dennett 1988), and evidence (Byrne & Whiten 1990; 1992). De Waal (1992) hypothesized that group-living animals learn to deceive; he distinguished: i) conditioned deception, i.e., a particular communication signal is used outside its normal context because it has been positively reinforced in a similar past situation, and ii) intentional deception, involving an understanding of the meaning of actions. For Mitchell (1986), first-level deception is an appearance-related innate program, as seen in mimicry in plants. Second-level deception consists of a stimulus-response process, as in, for example, a plover feigning a broken wing to distract a predator (Ristau 1991). Third-level deception is the result of learned association, whereas in fourth-level deception one individual intentionally tries to create a false-belief in another’s mind, for example as in human lying

(Mitchell 1986). Regarding intentionality, Dennett (1988) proposed three degrees of deceptive behaviours as follows: i) zero-order intentionality occurs when the deception is the result of pre-programmed responses; ii) first-order intentionality occurs when the deceiver intends to affect the recipient's behaviour; and iii) second-order intentionality is involved when the recipient's mind is targeted by the deceiver. Finally, according to the evidence level scale of Byrne and Whiten (1990; 1992), at Level 0 competing explanations can be invoked so that what is perceived as tactical deception could arise simply from a favorable combination of circumstances or pre-programmed responses. At Level 1, evidence for tactical deception outweighs competing explanations. Level 1.5 is similar to level 1 but includes perspective-taking ability, i.e., understanding how the world appears from another's viewpoint. The highest level – Level 2 – implies that the individual represents mental states of others and understands the mechanism by which deceptive acts work.

Byrne and Whiten's (1990) catalog of anecdotal accounts of tactical deception by primates, mostly in the wild, stimulated new experimental studies in captive primates. Chimpanzees (*Pan troglodytes*) had already been shown to mislead a human competitor by withholding information or directing the competitor to an unbaited container rather than a baited one (Woodruff & Premack 1979). Studies on squirrel monkeys (*Saimiri sciureus*: Anderson et al. 2001), brown capuchins (*Sapajus apella*: Mitchell & Anderson 1997), black lemurs (*Eulemur macaco*: Genty & Roeder 2006) and brown lemurs (*Eulemur fulvus*: Genty et al. 2008) reported broadly similar outcomes. However, in view of the extensive training involved in these studies, deceptive behaviours might have reflected simple conditional discrimination without any higher-level deception.

Another experimental approach improved ecological validity by investigating tactical deception using competitive social contexts with conspecifics. In the 'informed forager' paradigm, a subordinate is informed about the location of food and then allowed to search for it the presence of a more dominant individual. Menzel (1971; 1974) reported that a subordinate chimpanzee knowledgeable about the location of hidden food withheld this information and actively led a dominant away from it (see also Hirata & Matsuzawa 2001; Hall et al. 2014). Similar behaviours were also reported in white-collared mangabeys (*Cercocebus torquatus torquatus*: Coussi-Korbel 1994) and Tonkean macaques (*Macaca tonkeana*: Ducoing & Thierry 2003). However, in these and similar studies (e.g. Fujita et al. 2002) subordinates might simply have learned that food near a more dominant individual is not accessible and they risk being attacked. Thus it remains unclear whether such cases represent intentional deception.

Although great apes and monkeys can infer what others can and cannot see (Bräuer et al. 2007; Flombaum & Santos 2005; Hare et al. 2000; Hare et al. 2001; Overduin-de-Vries et al. 2014), little is known about their use of this ability to actively manipulate others. Recently, based on a food competition paradigm originally used with chimpanzees (Hare et al. 2000), Canteloup et al. (2016) tested dominant-subordinate pairs of Tonkean macaques in four conditions of varying temporal and visual access to food. In each condition, each monkey started in an individual compartment, one on either side of a testing area. In the testing area, a slice of banana was placed on the top of one breezeblock so as to be visible to both individuals; a second slice was hidden inside a second breezeblock so that only one individual could see it. In the first two conditions, the subordinate could see both pieces of food. In condition 1 the two individuals were released simultaneously into the testing area; in condition 2 the dominant was released only after the subordinate had fully entered the testing area. In conditions 3 and 4 only the dominant could see the hidden food. In condition 3 the dominant was released with a short head start on the subordinate; in condition 4 both individuals were released simultaneously. Results showed that whereas dominants showed no preference, subordinates preferentially headed for the hidden food when released simultaneously with or before the dominant, suggesting visual perspective-taking (Canteloup et al. 2016). Strategies used by subordinates were also recorded, such as leaving the testing area and, if followed by the dominant, rapidly coming back to retrieve the food without being seen. What remains unanswered is whether and how subordinates adjusted their behaviour to those of the dominant.

The present study addresses the above question at the functional rather than the causal level (cf. Penn & Povinelli 2009), and provides new data on functionally deceptive behaviours in Tonkean macaques (*Macaca tonkeana*). We again focus on strategies used by subordinates in the presence of hidden food and a dominant conspecific. First, we classified for the first time in this species, all the strategies used by subordinates according to Byrne and Whiten's (1992) functional classification system. Second, we analyzed factors that influenced tactical deception by subordinates. Finally, we carried out a fine-grained analysis of their simultaneous behaviours to determine temporal relationships between the two individuals' behaviours; in other words whether subordinates adjusted their behaviours to those of dominant. To this aim, we tested the dependency between behavioural markers of deception by the subordinates and the proportion of time spent by dominants in different behavioural and spatiotemporal configurations conducive for deception (e.g. looks, head and/or body oriented towards the subordinate). In the case of dependency, we conclude that subordinates

adjust their behaviour those of dominants, indicating that they are highly skillful behaviour readers.

METHODS

Ethical note

The procedures reported here adhered to the French legal requirements for the Use of Animal in Research and to the EU Directive 2010/63/EU for animal experiments. The study was approved by the Animal Experiment Committee of the Centre de Primatologie de l'Université de Strasbourg and by the CREMEAS Ethics Committee (Approval for conducting experiments on primates n° AL/46/53/02/13).

Subjects

The subjects were eleven Tonkean macaques (*Macaca tonkeana*): eight males (2 to 11 years old) and three females (4 to 17 years old), all born and raised at the Centre de Primatologie de l'Université de Strasbourg, France. They lived in a group of 28 individuals in a 3,988 m² wooded park with permanent access to a 20 m² heated indoor housing area. Their diet consisted of commercial pellets and water ad libitum, with fresh fruits and vegetables distributed twice a week when no experiments were being conducted. The hierarchical rank of each subject was known from a recently conducted, related experiment (Canteloup et al. 2016).

Experimental procedure

The experiment took place in three experimental areas (Canteloup et al, 2016; Fig. 1). Each monkey started on opposite sides of the testing area, and both were given access to the testing area after an experimenter had placed two pieces of food there. One piece was placed on top of one of two breezeblocks so as to be visible to both individuals; the second piece was placed inside the other breezeblock, so as to be hidden from one of the monkeys. Subjects were already accustomed to these experimental areas, and no training was used in this experiment.

In the present study we focus on video recordings from trials in which only the subordinate could see both pieces of food and was released into the testing area at the same time as the dominant (condition 1), or with a short head start on the dominant (i.e. the dominant was released as soon as the subordinate's entire body was in the testing area: condition 2). On some trials dominants visited both food locations, indicating possible understanding that two pieces of food were present. We excluded these trials from the analyses, which therefore were done using a total of 360 trials concerning 20 dominant-subordinate dyads.

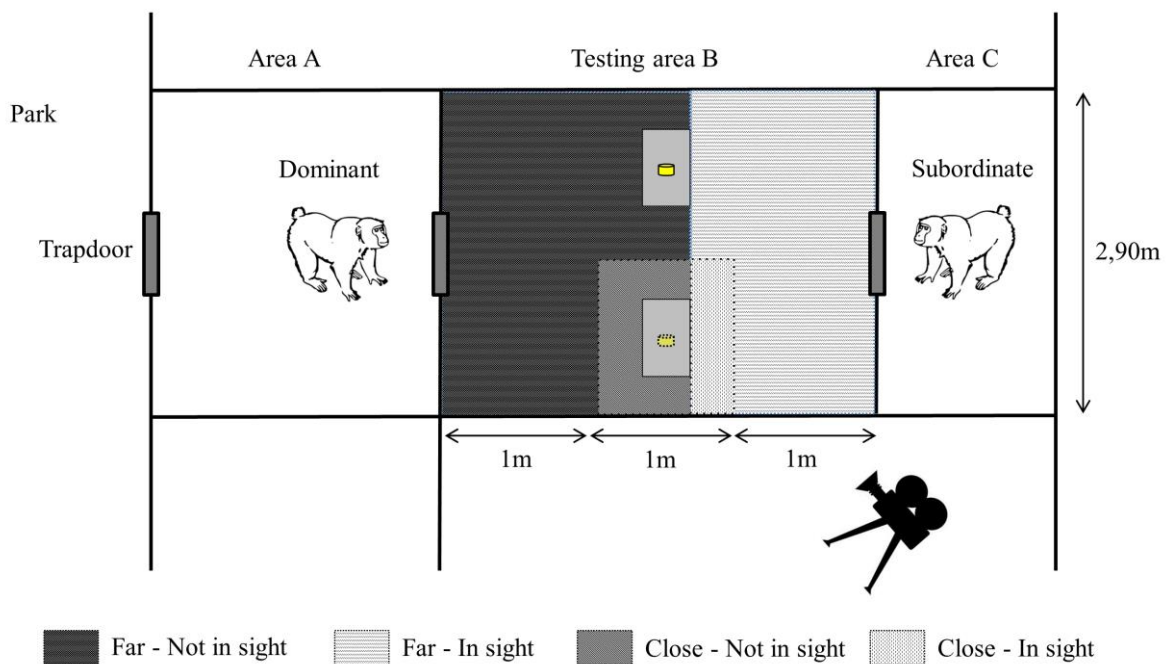


Figure 1. Schema of the experimental apparatus used in the visual perspective-taking experiment (Canteloup et al., 2016) seen from above. In this example, the dominant is in area A, the subordinate in area C. Both were given access to the testing area B where two pieces of food were placed. One slice of banana was put on one of the two breezeblocks and was visible to both subjects; another one was placed inside the other breezeblock and was thus hidden from the dominant's view. The four zones concerning the dominant's position regarding hidden food established for data coding are represented in the testing area B.

Data and reliability analyses

We used a two-step procedure for the video analysis: 1) a qualitative analysis of functionally deceptive strategies displayed by subordinates, and 2) quantitative analyses of those strategies and subordinates' behaviours in relation to those of the dominants.

Qualitative analysis

All 360 trials were viewed and classified as involving a deceptive strategy or not. Positive trials were defined as those in which the subordinate did something other than heading directly for the hidden food. For this, at least one of the following criteria had to be met: i) the subordinate did not enter the testing area, ii) the subordinate headed first for the hidden food but stopped short, iii) the subordinate headed first for food but then changed trajectory, iv) the subordinate headed first for any direction other than the food while it was still present. Trials that did not meet any of these criteria were classified as involving no deception.

To assess inter-observer agreement, a second observer (CC) analyzed a random sample (20%) of the trials; agreement concerning the classification of trials was excellent (Cohen's $\kappa = 0.97$). Trials involving deception were then described and categorized according to Byrne and Whiten's (1992) classification.

Quantitative analyses

Videos were analyzed frame by frame (one frame = 40 ms) by IP using Observer XT 10.1.5.548 software (Noldus). Each trial started when the two transparent trapdoors were opened, and ended when the hidden food was taken. The following information was recorded: who got food, duration of presence in testing area, inter-individual distance, locomotion, body orientation, gaze (head) orientation, self-directed behaviours and social behaviours for both individuals. We also recorded durations of the subordinate's visual monitoring of the dominant's head and body orientation, and the dominant's position with respect to hidden food (Table 1; Fig. 1). Given that each trial did not last the same length of time, we used proportions of trial time. Given the very low occurrence of self-directed and social behaviours, these were not analyzed statistically.

Categories of behaviours	Behaviours
Visibility	Visible Invisible
Presence in testing zone	Present Absent
Interindividual distance	More than 2m 1m to 2m Less than 1m
Displacement	Stop Towards hidden food Towards visible food Towards conspecific Towards elsewhere Climb on breezeblock
Body orientation	Towards hidden food Towards visible food Towards conspecific Towards elsewhere
Gaze-head orientation	Towards hidden food Towards visible food Towards conspecific Towards elsewhere Alternation conspecific/visible food Alternation conspecific/hidden food
Self centered behaviours	Scratch Shake
Social behaviours	Threat Lipsmack Sniff conspecific Yawn
Subordinate perception of dominant's head & body orientation (for subordinate only)	Head & body facing Head & body back Head & body side Head facing & body side Head side & body facing Head back & body side Head side & body back Not in sight
Dominant's position regarding hidden food (for dominant only)	Far - Not in sight Far - In sight Close - Not in sight Close - In sight

Table 1. List of categories of behaviours and behaviours recorded during video analysis.

Twenty percent of the trials were randomly selected and analysed by CC with a tolerance window of 400 ms, corresponding to ten frames. Inter-observer agreement was excellent (Cohen's $\kappa = 0.90$).

Statistical analyses

Analyses were aimed at answering two questions: 1) What factors influenced the use of tactical deception by subordinates? 2) Did subordinates adjust their behaviour to dominants' behaviours?

For the first question, we used a Generalized Linear Mixed Model (GLMM1) for data showing a binomial distribution. Experimental condition, trial-order for each subordinate, and hierarchical rank difference were assessed as fixed effects. To deal with pseudo-replication, the identities of the dominant, the subordinate and the nested effect between the dyad and the trial order of the dyad were considered as random effects. Each combination of random effects was used in different models that were compared and selected on the basis of the lowest AIC criteria (starting from the null model and going backward).

For the second question, we focused on four behaviours of the subordinate that could be markers of deception: a) move elsewhere (away from food or dominant); b) stop; c) body orientation elsewhere (away from food or dominant) and d) gaze (head) orientation elsewhere (away from food or dominant). We established Generalized Linear Mixed Models for data showing a binomial distribution to test for significant interactions between these four behaviours by subordinates and all behaviours by dominants taken two by two. As an example, we tested whether subordinates adjusted their behaviour "move elsewhere" according to distance from the dominant. In this example, six combinations of subordinate behaviour/dominant behaviour exist: one of each behaviour by subordinate (move elsewhere/move all but elsewhere) with one of each behaviour by dominant, here the distance (more than 2 m, 1 m to 2 m, less than 1 m). By establishing Generalized Linear Mixed Models, we aimed to find whether subordinates moved elsewhere differently as a function of distance from the dominant. If the interaction between the subordinate's "move elsewhere" and distance was significant, this implies that subordinates adjusted their locomotion as a function of distance from the dominant; a non-significant interaction indicates that subordinates behaved independently of distance from the dominant. We applied this method for each combination of subordinate/dominant behaviours. In the established models, interaction between the two individuals' behaviour was assessed as a fixed effect and the

identities of the dominant, the subordinate and the nested effect between the dyad and trial order were considered as random effects, the dependent variable being the proportion of time spent in each combined situation. For each model we first considered random effects, followed by model selection on the basis of the lowest AIC criteria similar to backward selection but on random effects (for more details see “the good approach” p.127 in Zuur et al. 2009). In the case of the best model having only one random effect, we compared it with a GLM (i.e., a model without random effect) with respect to the AIC. Models were fitted with R 3.1.2’s package lme4 (Bates et al. 2014), with alpha set at 0.05.

RESULTS

Quantification and classification of trials as tactical deception

Of the 360 trials involving 20 dyads (170 trials in condition 1, 190 trials in condition 2), 143 trials involving 17 dyads satisfied at least one criterion for a tactically deceptive strategy. For 17 of these trials, the observed strategy could not be classified following Byrne and Whiten (1992). For example, in some trials, the subordinate headed first for the visible food but rapidly diverted to the hidden food (Canteloup et al. 2016). We excluded these 17 trials, leaving a total of 126 trials involving 14 dyads (Table 2). These trials represented 36% of analyzed trials from condition 1 (N=62) and 34% of analyzed trials from condition 2 (N=64).

The breakdown of the 126 tactical deception trials according to Byrne and Whiten’s classification (1992) was as follows:

- Concealment by inhibiting interest in object (CIO): the subordinate refrained from showing interest in the object by avoiding looking at or moving towards it (Video 1). This strategy was observed in 100% of trials in condition 1 (N=62) and 97% in condition 2 (N=62).
- Concealment by hiding (CH): the subordinate acted so as to not be visually detected by the dominant (Video 2). This strategy was observed in 53% of trials in condition 1 (N=33) and 45% in condition 2 (N=29).
- Distraction by leading (DL): the subordinate moved away from the food and the dominant followed (Video 3). This strategy was observed in 13% of trials in condition 1 (N=8) and 16% in condition 2 (N=10).

- Distraction by close-range behaviour (DCRB): the subordinate engaged in close interaction with the dominant (Video 4). This strategy was observed only once, in condition 2.

Dyad (Dominant-Subordinate)	Hierarchical rank difference	Total analysed trials		Total TD trials		Occurrences of tactical deception categories							
						CIO		CH		DL		DCRB	
		C1	C2	C1	C2	C1	C2	C1	C2	C1	C2		
Lady-Nenno	7	7	8	0	0	0	0	0	0	0	0	0	0
Lady-Yannick	1	20	19	0	0	0	0	0	0	0	0	0	0
Nema-Lady	1	10	13	0	0	0	0	0	0	0	0	0	0
Nereis-Lady	4	4	8	4	6	4	6	3	1	0	0	0	0
Nereis-Yannick	5	10	10	8	8	8	8	1	1	0	0	0	0
Shan-Yannick	12	16	15	7	10	7	9	5	5	0	2	0	0
Uruk-Wotan	7	0	2	0	2	0	2	0	0	0	0	0	0
Uruk-Yannick	11	4	8	4	7	4	7	2	2	2	2	0	0
Vishnu-Yannick	7	10	8	8	5	8	5	4	3	0	1	0	0
Wallace-Lady	7	3	6	3	6	3	6	0	3	0	2	0	0
Wallace-Nema	9	1	1	1	0	1	0	0	0	0	0	0	0
Wallace-Nereis	3	0	3	0	0	0	0	0	0	0	0	0	0
Wallace-Vishnu	1	3	8	0	1	0	0	0	0	0	0	0	1
Wallace-Wotan	4	1	2	0	0	0	0	0	0	0	0	0	0
Wallace-Yannick	8	19	11	19	10	19	10	12	8	6	0	0	0
Walt-Lady	2	9	10	2	2	2	2	2	1	0	1	0	0
Walt-Yannick	3	7	7	2	6	2	6	2	4	0	1	0	0
Wotan-Lady	3	16	18	0	0	0	0	0	0	0	0	0	0
Wotan-Yannick	4	18	14	2	0	2	0	2	0	0	0	0	0
Yannick-Nema	1	12	19	2	1	2	1	0	1	0	1	0	0
Total per condition		170	190	62	64	62	62	33	29	8	10	0	1
Total		360		126		124		62		18		1	

Table 2. Dyad tested; hierarchical rank difference between subordinates and dominants; overall number of trials performed in condition 1 (C1) and in condition 2 (C2); number of trials containing tactical deception (TD) strategies; occurrences of each type of tactical deception per condition of tested dyads. CIO: concealment by inhibiting interest; CH: concealment by hiding; DL: distraction by leading; DCRB: distraction by close-range behaviour.

Frequently, the subordinate used more than one strategy within a single trial (Table 3). The CIO strategy was used alone in 40% of trials but was combined with CH in 44% of cases. The DL strategy was never observed alone, but was combined with either CIO (10% of trials), or more rarely with CIO plus CH (4%).

	CIO	CIO + CH	CIO + DL	CIO + CH + DL	CH	DCRB	Proportion of tactical deception depending on condition
Condition 1	24	30	5	3	0	0	49%
Condition 2	27	25	7	3	1	1	51%
Proportion of each combination	40%	44%	10%	4%	1%	1%	

Table 3. Occurrences of combinations of tactical deception strategies observed per condition in overall trials and proportion of use of each combination for both conditions and according to each condition.

Success of subordinates

In a “success”, the subordinate retrieved the hidden food. When using only concealment by inhibiting interest in object (CIO), the subordinate never retrieved the hidden food in condition 1 but did so in 4% of cases in condition 2. When combining CIO with concealment by hiding (CH), the subordinate succeeded in 93% of cases in condition 1 and 96% of cases in condition 2. CIO plus distraction by leading (DL) saw success in 100% of cases in condition 1 and 29% of cases in condition 2. Combining CIO, CH plus DL, the subordinate obtained the hidden food in 67% of cases in condition 1 and 100% of cases in condition 2. CH only and distraction by close range behaviour (DCRB) never resulted in success (Table 4).

	CIO	CIO + CH	CIO + DL	CIO + CH + DL	CH	DCRB
Condition 1	0%	93%	100%	67%	-	-
Condition 2	4%	96%	29%	100%	0%	0%

Table 4. Success rates of subordinates retrieving the hidden food in conditions 1 and 2 and in the trials displaying different categories of strategies and combinations of strategies: CIO: concealment by inhibiting interest; CH: concealment by hiding; DL: distraction by leading; DCRB: distraction by close-range behaviour; No TD: No tactical deception.

Factors influencing the use of tactical deception

The best fitting model on the basis of AIC was the one with identity of the dominant as a random effect (GLMM1). According to this model, neither experimental condition (AIC = 257.04; LRT = 0.153; Df = 1; $P > 0.05$) nor trial order for each subordinate (AIC = 257.23; LRT = 0.351; Df = 1; $P > 0.05$) had a significant effect on the probability of using tactical deception. However, the model reported that the greater the hierarchical rank difference between the individuals, the more likely was the subordinate to use tactical deception (AIC = 298.21; LRT = 41.33; Df = 1; $P < 0.001$; Table 5).

Dyad (Dominant - Subordinate)	Hierarchical rank difference	Number of trials in both conditions	Number of TD trials	Rate of TD use
Lady-Nenno	7	15	0	0%
Lady-Yannick	1	39	0	0%
Nema-Lady	1	23	0	0%
Nereis-Lady	4	12	10	77%
Nereis-Yannick	5	20	16	80%
Shan-Yannick	12	31	17	55%
Uruk-Wotan	7	2	2	100%
Uruk-Yannick	11	12	11	79%
Vishnu-Yannick	7	18	13	72%
Wallace-Lady	7	9	9	100%
Wallace-Nema	9	2	1	50%
Wallace-Nereis	3	3	0	0%
Wallace-Vishnu	1	11	1	9%
Wallace-Wotan	5	3	0	0%
Wallace-Yannick	8	30	29	91%
Walt-Lady	2	19	4	20%
Walt-Yannick	3	14	8	53%
Wotan-Lady	3	34	0	0%
Wotan-Yannick	4	32	2	6%
Yannick-Nema	1	31	3	8%

Table 5. Dyads tested; hierarchical rank difference between subordinates and dominants; overall number of trials in both conditions; number of tactically deceptive (TD) trials and rate of tactical deception (TD) use by subordinate.

Analyses of subordinates' behaviors in response to those of dominants

Subordinates "stop"

We found significant interactions between "stop" by the subordinates and behaviours displayed by the dominant ($P < 0.0001$; Table 6 for more statistical details about the final models obtained after selection): distance, body orientation, position with regard to the hidden food, visibility, presence, gaze orientation, movement and the subordinate's perception of the dominant's head and body orientation.

Subordinates' movement elsewhere

There were significant interactions between subordinates' moving elsewhere and behaviours displayed by the dominant ($P < 0.0001$; Table 6): distance, body orientation, position with regard to the hidden food, visibility, presence, gaze orientation, movement and the subordinate's perception of the dominant's head and body orientation.

Subordinates' body oriented elsewhere

Significant interactions were found between "body oriented elsewhere" and the following behaviours displayed by the dominant ($P < 0.0001$; Table 6): distance, body orientation, position with regard to the hidden food, presence, gaze orientation, movement, and the subordinate's perception of the dominant's head and body orientation. However, we found no significant interaction between this behaviour and visibility of the dominant ($P > 0.05$; Table 6).

Subordinates' gaze oriented elsewhere

There was a significant interaction between "gaze oriented elsewhere" for subordinates and behaviours displayed by the dominant ($P < 0.0001$; Table 6): distance, body orientation, position with regard to the hidden food, visibility, presence, gaze orientation, movement, and the subordinate's perception of the dominant's head and body orientation.

Subordinate behavior	Dominant behavior	Random effects	χ^2	P
Stop	Visibility	Trial number/dyade, Dom, Sub	10803.6	<0,0001
	Presence	Trial number/dyade, Dom, Sub	12899.4	<0,0001
	Distance	No random	3722.3	<0,0001
	Body Orientation	No random	4409.2	<0,0001
	Gaze-Head Orientation	Trial number/dyade	1638.92	<0,0001
	Displacement	Trial number/dyade	6275.5	<0,0001
	Position	Trial number/dyade, Dom	10803.6	<0,0001
	Perception	Trial number/dyade	5507.2	<0,0001
Displacement Elsewhere	Visibility	Trial number/dyade	1083.6	<0,0001
	Presence	Trial number/dyade	10005	<0,0001
	Distance	No random	587.68	<0,0001
	Body Orientation	Trial number/dyade	2508.20	<0,0001
	Gaze-Head Orientation	Trial number/dyade	1638.92	<0,0001
	Displacement	Trial number/dyade	8432.3	<0,0001
	Position	Trial number/dyade, Dom	5098.0	<0,0001
	Perception	Trial number/dyade	24434.6	<0,0001
Body Orientation Elsewhere	Visibility	Trial number/dyade, Dom, Sub	0.0570	0.81
	Presence	Trial number/dyade, Dom, Sub	4088.4	<0,0001
	Distance	No random	4088.4	<0,0001
	Body Orientation	No random	1864.5	<0,0001
	Gaze-Head Orientation	Trial number/dyade	1112.76	<0,0001
	Displacement	Trial number/dyade	4302.9	<0,0001
	Position	Trial number/dyade	2936.36	<0,0001
	Perception	Trial number/dyade	44967	<0,0001
Gaze-Head OrientationnElsewhere	Visibility	Trial number/dyade, Dom, Sub	36.04	<0,0001
	Presence	Trial number/dyade, Dom	5327.2	<0,0001
	Distance	No random	3862.1	<0,0001
	Body Orientation	No random	805.54	<0,0001
	Gaze-Head Orientation	No random	1245.8	<0,0001
	Displacement	Trial number/dyade	5842.6	<0,0001
	Position	Trial number/dyade	613.98	<0,0001
	Perception	Trial number/dyade	73685	<0,0001

Table 6. Best fitting models after selection on random effects for i) subordinates’ “stop” ; ii) subordinates’ movement elsewhere; iii) subordinates’ body oriented elsewhere and iv) subordinates’ gaze oriented elsewhere. Random effects considered were nested effects between dyad and trial number (Trial number/dyad); identity of dominant (Dom) and identity of subordinate (Sub). Best fitting models established with random effects are GLMM and those with no random are GLM. χ^2 and P value are those of interactions between subordinates’ and dominants’ behaviours on the proportions of time spent on these behaviours.

DISCUSSION

Our results show that subordinates Tonkean macaques used several types of tactical deception, especially when paired with a competitor of a much higher rank, and that they were more successful at obtaining the hidden food when they used a combination of strategies rather than only one. We found no evidence of learning during the experiment, or any influence of the subordinate’s identity or of the releasing condition. Finally, subordinates adjusted their behaviour to the dominant’s behaviour, confirming that subordinates are, at least, excellent behaviour readers.

Tactical deception was used in 126 out of the 360 observed trials. This high frequency can be explained by the experimental procedure, which was deliberately designed to create strong competition for food between the subordinate and the dominant. It is generally accepted that in the wild tactical deception should occur relatively rarely (Byrne & Whiten 1985; 1990; 1992).

Subordinate macaques displayed tactical deception regardless of whether they were released at the same time as the dominant or with a slight head start. This result is not surprising given that tactical deception could not result in subordinates being able to obtain both pieces of food. Nevertheless, Canteloup et al. (2016) described instances in which subordinates first rushed to and grasped the visible food, and then later retrieved the hidden food via tactical deception, e.g. concealing interest. This use of speed as a strategy raises interesting questions about alternative strategies to deception that might be used in competitive situations, and factors that influence the choice of the strategies.

Some subordinates did not use tactical deception at all. This could be due to intrinsic characteristics such as temperament, social tolerance, confidence, gender and aggressiveness. Moreover, dominants' identity appeared to be a factor influencing the use of tactical deception. As in previous studies (Ducoing & Thierry 2003; 2004), the difference in hierarchical rank between the dominant and the subordinate was influential: tactical deception was more common with a much higher-ranked competitor than with a closely ranked one. It therefore appears clear that specific aspects of the social situation influence the strategies of subordinates.

Subordinates often used a combination of strategies, notably concealment by inhibiting interest plus concealment by hiding. Although Byrne and Whiten (1990) requested their respondents to assign observed behaviours to only one category, it seems likely that many cases of deception involve more than one strategy being employed within a short time-span. Indeed, combining strategies seems inevitable: to lead dominants away from hidden food, subordinates first need to use concealment by inhibiting interest, followed by concealment by hiding to retrieve the food when not being watched. Interestingly, subordinates almost never obtained the hidden food when they used only concealment by inhibiting interest, whereas success rates increased when this strategy was combined with concealment by hiding and/or distraction by leading.

The most frequently used strategy was concealment by inhibiting interest in object, either by not going in the direction of the food, or "freezing" (video 1), sometimes avoiding looking at the food. In this kind of concealment, subordinates acted as if they were unaware of

the presence of food, for example by not entering the testing area, or entering and then stopping or sitting down. The most parsimonious interpretation of this strategy would be that the subordinate was simply inhibited by the dominant's presence and/or gaze (behaviour reading hypothesis; e.g. Povinelli & Vonk 2003), rather than actively refraining from approaching despite knowing that the dominant was unaware of the food (mindreading hypothesis; e.g. Call & Tomasello 2008). It is conceivable that most cases of simple concealment by inhibiting interest reflect simple behavioural inhibition induced by the presence of a dominant competitor.

Concealment by inhibiting interest was used on its own or combined with other strategies such as concealment by hiding. In concealment by hiding, subordinates behaved so as not to be seen by the dominant. For example, they refrained from immediately entering the testing area, or headed for the hidden food when the dominant's back was turned (video 2) or after the dominant left the testing area. Similar behaviour has been described in the context of sneaky mating in long-tailed macaques (*Macaca fascicularis*: Overduin-de Vries et al. 2015), and by geladas (*Theropithecus gelada*: le Roux et al. 2013) engaging in extra-pair copulations out of view of the alpha male. We previously reported that subordinate Tonkean macaques moved preferentially for hidden food when released simultaneously or slightly before a dominant, and proposed that they are capable of visual perspective-taking (Canteloup et al. 2016). In this context, concealment by hiding could reflect an active attempt by subordinates to be out of view of the dominant. However, we cannot exclude the lower-level explanation that subordinates merely reacted to the dominant's gaze without perspective-taking (Canteloup et al. 2016).

In 18 trials, subordinates used distraction by leading in addition to concealment by inhibiting interest and/or concealment by hiding, and in one trial a subordinate used distraction by close-range behaviour, interacting with the dominant. In this latter example, the subordinate first headed for the visible food and initiated a mouth contact with the dominant (video 4). Possibly the subordinate thus attempted to hold the dominant's attention, but this interpretation is weakened by the fact that it then went to the hidden food, followed closely by the dominant who usurped it. Of all the observed deceptive strategies, distraction by leading is the most active, requiring moving away from the food and then returning to the area after a delay (video 3). However, it remains an open question whether distraction by leading is an intentional strategy, as the subordinate might simply have been avoiding the dominant.

The goal of our fine-grained analysis was to closely examine the interplay between the actions of the two competitors, to establish whether subordinates tailored their behaviour to

that of the dominants. We found significant interactions between subordinates' stopping, moving, body orientation and gazing elsewhere, and dominants' visibility, presence, distance, body orientation, gaze orientation, movement, position and perception. However, the fact that subordinates moved elsewhere regardless of the dominants' visibility might be a mark of intentionality. Most of these results indicate that subordinates took into account dominants' behaviours, reminiscent of findings in domestic pigs (Held et al. 2002). Indeed, subordinate pigs reportedly changed direction towards a baited food bucket when the dominant was moving away from it, was out of sight, was further away, or was far from the subordinate. Held et al. (2002) suggested that subordinate pigs attempted to increase the time spent at the food source before the competitor arrived. Both subordinate pigs and macaques thus appear to be extraordinarily good behaviour readers; they precisely monitor the dominant's behaviour and adjust their own behaviour accordingly. In another "informed forager" paradigm, Hall et al. (2014) tested a subordinate chimpanzee that was given prior knowledge of a food location while a dominant conspecific was unaware. The authors reported that whereas dominant chimpanzees exploited informed subordinates' knowledge by following the latter's gaze direction, subordinates only occasionally followed dominants' movement and gaze.

To conclude, the present analyses provide new information on functionally deceptive behaviours in macaques (see Ducoing & Thierry 2003; Overduin-de Vries et al. 2015), notably in the little-studied species, the Tonkean macaque. The results reinforce the view that macaques behave as if they understand something about attentional states, perceptions and intentions of others (Canteloup et al. 2015a; 2015b; 2016; Flombaum & Santos 2005; Overduin-de Vries et al., 2014; Rochat et al. 2008; Santos et al. 2006; Wood et al. 2007). We suggest that some of the deceptive strategies observed here and in previous work correspond to third-level deception as described by Mitchell (1986), first-order intentionality as in Dennett (1988) and level 1.5 according to Byrne and Whiten (1990; 1992). Although we are as yet unable to conclude whether conditioned or intentional deception (de Waal 1992) underlies these strategies, the data show that Tonkean macaques have highly complex and flexible social skills that enable them to cope with challenges posed by conspecifics.

ACKNOWLEDGMENTS

The authors thank Yves Larmet and the whole teams of the Centre de Primatologie de l'Université de Strasbourg and SILABE-ADUEIS for allowing them to conduct this study.

The authors are particularly grateful to Steve Lapp, Adrien Panter and Jean-Marc Woock for building the experimental apparatus and to Emilie Piraux for conducting the experiments. This research was supported by the Centre de Primatologie de l'Université de Strasbourg and the University of Strasbourg Institute for Advanced Study (USIAS) as part of a USIAS fellowship.

REFERENCES

- Anderson, J.R., Kuroshima, H., Kuwahata, H., Fujita, K. & Vick, S.J. 2001: Training squirrel monkeys (*Saimiri sciureus*) to deceive: acquisition and analysis of behavior toward cooperative and competitive trainers. *Journal of Comparative Psychology* **15**, 282-293.
- Bates, D., Maechler, M., Bolker, B. & Walker, S. 2014: lme4: Linear mixed-effects models using Eigen and S4. *Journal of Statistical Software*. Available at <http://arxiv.org/abs/1406.5823>
- Bräuer, J., Call, J. & Tomasello, M. 2007: Chimpanzees really know what others can see in a competitive situation. *Animal Cognition* **10**, 439-448.
- Byrne, R.W. 2003: Tracing the evolutionary path of cognition. In: *The social brain: evolution and pathology* (Brüne, M., Ribbert, H. & Schiefenhövel W., eds). John Wiley & Sons, Ltd, pp. 43-60.
- Byrne, R.W. & Whiten, A. 1985: Tactical deception of familiar individuals in baboons (*Papio ursinus*). *Animal Behaviour* **33**, 669-673.
- Byrne, R.W. & Whiten, A. 1988: *Machiavellian intelligence: social expertise and the evolution of intellect in monkeys, apes and humans*. Oxford, UK: Oxford University Press.
- Byrne, R.W. & Whiten, A. 1990: Tactical deception in primates: the 1990 database. *Primate report* **27**, 1-101.
- Byrne, R.W. & Whiten, A. 1992: Cognitive evolution in primates: evidence from tactical deception. *Man, New Series* **27**, 609-627.
- Call, J. & Tomasello, M. 2008: Does the chimpanzee have a theory of mind? 30 years later. *Trends in Cognitive sciences* **12**, 187-192.
- Canteloup, C., Bovet, D. & Meunier, H. 2015a: Do Tonkean macaques (*Macaca tonkeana*) tailor their gestural and visual signals to fit the attentional states of a human partner? *Animal Cognition* **18**, 451-461.

- Canteloup, C., Bovet, D. & Meunier, H. 2015b: Intentional gestural communication and discrimination of human attentional states in rhesus macaques (*Macaca mulatta*). *Animal Cognition* **18**, 875-883.
- Canteloup, C., Piraux, E., Poulin, N. & Meunier, H. 2016: Do Tonkean macaques (*Macaca tonkeana*) perceive what conspecifics do and do not see? *PeerJ* 4:e1693; DOI 10.7717/peerj.1693
- Coussi-Korbel, S. 1994: Learning to outwit a competitor in mangabeys (*Cercocebus torquatus torquatus*). *Journal of Comparative Psychology* **108**, 164-171.
- Dawkins, R. & Krebs, J.R. 1978: Animal signals: information or manipulation? In: *Behavioral ecology: an evolutionary approach* (Krebs, J.R & Davies, N.B., eds). Blackwell, Oxford, pp. 282-309.
- Dennett, D.C. 1988: The intentional stance in theory and practice. In: *Machiavellian intelligence: Social expertise and the evolution of intellect in monkeys, apes and humans* (Byrne, R.W. & Whiten A., eds). Oxford, United Kingdom: Clarendon Press, pp. 180-202.
- de Waal, F.B.M. 1992: Intentional deception in primates. *Evolutionary Anthropology: Issues, News, and Reviews* **1**, 86-92.
- Ducoing, A.M. & Thierry, B. 2003: Withholding information in semifree-ranging tonkean macaques (*Macaca tonkeana*). *Journal of Comparative Psychology* **117**, 67-75.
- Ducoing, A.M. & Thierry, B. 2004: Following and joining the informed individual in semifree-ranging Tonkean macaques (*Macaca tonkeana*). *Journal of Comparative Psychology* **118**, 413-420.
- Dunbar, R.I.M. 1998: The social brain hypothesis. *Evolutionary Anthropology: Issues, News, and Reviews* **6**, 178-190.
- Flombaum, J.I. & Santos, L.R. 2005. Rhesus monkeys attribute perceptions to others. *Current Biology* **15**, 447-452.
- Fujita, K., Kuroshima, H. & Masuda, T. 2002: Do tufted capuchin monkeys (*Cebus apella*) spontaneously deceive opponents? A preliminary analysis of an experimental food-competition contest between monkeys. *Animal Cognition* **5**, 19-25.
- Genty, E. & Roeder, J.J. 2006: Can lemurs learn to deceive? A study in the black lemur (*Eulemur macaco*). *Journal of Experimental Psychology* **32**, 196-200.
- Genty, E., Foltz, J. & Roeder, J.J. 2008: Can brown lemurs (*Eulemur fulvus*) learn to deceive a human competitor? *Animal Cognition* **11**, 255-266.

- Hall, K., Oram, M.W., Campbell, M.W., Eppley, T.M., Byrne, R.W. & de Waal, F.B.M. 2014: Using Cross Correlations to Investigate How Chimpanzees (*Pan troglodytes*) Use Conspecific Gaze Cues to Extract and Exploit Information in a Foraging Competition. *American Journal of Primatology* **76**, 932-941.
- Hall, K. & Brosnan, S.F. 2016: Cooperation and deception in primates. *Infant Behavior and Development* DOI: 10.1016/j.infbeh.2016.11.007
- Hare, B., Call, J., Agnetta, B. & Tomasello, M. 2000: Chimpanzees know what conspecifics do and do not see. *Animal Behaviour* **59**, 771-785.
- Hare, B., Call, J. & Tomasello, M. 2001: Do chimpanzees know what conspecifics know? *Animal Behaviour* **61**, 139-151.
- Held, S., Mendl, M., Devereux, C. & Byrne, R.W. 2002: Foraging pigs alter their behaviour in response to exploitation. *Animal Behaviour* **64**, 157-166.
- Hirata, S. & Matsuzawa, T. 2001: Tactics to obtain a hidden food item in chimpanzee pairs (*Pan troglodytes*). *Animal Cognition* **4**, 285-295.
- Humphrey, N.K. 1976: The social function of intellect. In: *Growing Points in Ethology* (Bateson, P.P.G. & Hinde, R.A., eds). Cambridge University Press, pp. 303-317.
- Jolly, A. 1966: Lemur social behavior and primate intelligence. *Science* **153**, 501-506.
- Krebs, J.R. & Dawkins, R. 1984: Animal signals: mind reading and manipulation. In: *Behavioral ecology: an evolutionary approach*, 2nd edn. (Krebs, J.R. & Davies, N.B., eds). Oxford: Blackwell, pp. 380-401.
- le Roux, A., Snyder-Mackler, N., Roberts, E.K., Beehner, J.C. & Bergman, T.J. 2013: Evidence for tactical concealment in a wild primate. *Nature communications* **4**, 1462 doi: 10.1038/ncomms2468.
- Menzel, E.W. 1971: Communication about the environment in a group of young chimpanzees. *Folia Primatologica* **15**, 220-232.
- Menzel, E.W. 1974: A group of young chimpanzees in a one-acre field. In: *Behavior of nonhuman primates. Modern research trends*, volume 5 (Schrier, A.M. & Stollnitz, F. eds). New-York, NY: Academic Press, pp. 83-149.
- Mitchell, R.W. 1986: A framework for discussing deception. In: *Deception: perspectives on human and nonhuman deceit* (Mitchell, R.W. & Thompson, N.S. eds). State University of New-York Press, pp. 3-40.
- Mitchell, R.W. & Anderson, J.R. 1997: Pointing, withholding information, and deception in capuchin monkeys (*Cebus apella*). *Journal of Comparative Psychology* **111**, 351-361.

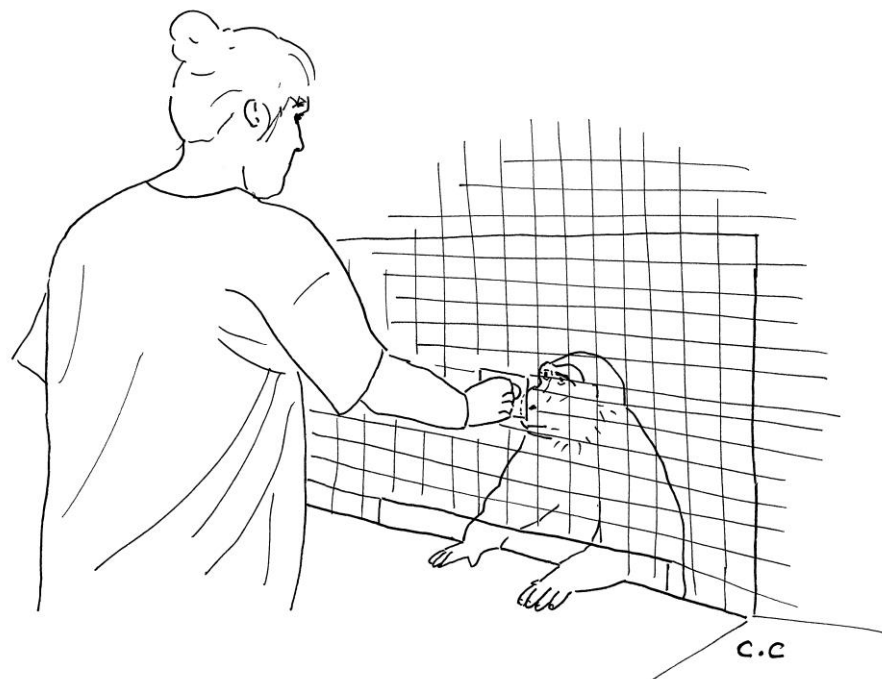
- Overduin-de-Vries, A.M., Spruijt, B.M. & Sterck, E.H.M. 2014: Long-tailed macaques (*Macaca fascicularis*) understand what conspecifics can see in a competitive situation. *Animal Cognition* **17**, 77-84.
- Overduin-de-Vries, A.M., Spruijt, B.M., de Vries, H. & Sterck, E.H.M. 2015: Tactical deception to hide sexual behaviour: macaques use distance, not visibility. *Behavioral Ecology Sociobiology* **69**, 1333-1342.
- Penn, D.C. & Povinelli, D.J. 2009: On becoming approximately rational: the relational reinterpretation hypothesis. In: *Rational animals, irrational humans* (Watanabe, S., Blaisdell, A.P., Huber, L. & Young, A. eds). Tokyo: Keio University Press, pp. 23-44.
- Povinelli, D.J. & Vonk, J. 2003: Chimpanzee minds: suspiciously human? *Trends in Cognitive Sciences* **7**, 157-160.
- Ristau, C.A. 1991: Aspects of the cognitive ethology of an injury-feigning bird, the piping plover. In: *Cognitive ethology: the minds of other animals* (Ristau, C.A. eds). Erlbaum, Hillsdale, N.J., pp. 91-126.
- Rochat, J., Serra, E., Fadiga, L. & Gallese, V. 2008: The evolution of social cognition: goal familiarity shapes monkeys' action understanding. *Current Biology* **18**, 227-232.
- Santos, L.R., Nissen, A.G. & Ferrugia, J.A. 2006: Rhesus monkeys, *Macaca mulatta*, know what others can and cannot hear. *Animal Behaviour* **71**, 1175-1181.
- Wood, J.N., Glynn, D.D., Phillips, B.C. & Hauser M.D. 2007: The perception of rational, goal-directed action in nonhuman primates. *Science* **317**, 1402-1405.
- Woodruff, G. & Premack, D. 1979: Intentional communication in the chimpanzee: the development of deception. *Cognition* **7**, 333-362.
- Zuur, A., Ieno, E.N., Walker, N., Saveliev, A.A. & Smith, G.M. 2009: *Mixed effects models and extensions in ecology with R*. Springer-Verlag, New-York, 574 pp.

ARTICLE 5

‘Unwilling’ *versus* ‘unable’: Tonkean macaques’ understanding of human goal-directed actions

Canteloup C. & Meunier H.

Submitted to *Cognition*



Synthèse de l'article 5:

'Unwilling' versus 'unable': Tonkean macaques' understanding of human goal-directed actions

Canteloup C. & Meunier H.

Submitted to *Cognition*

Questions

Etre capable de comprendre les actions intentionnelles d'autrui est considéré comme un composant de la Théorie de l'Esprit. Les macaques de Tonkean sont-ils capables de comprendre les actions d'une expérimentatrice comme dirigées vers un but?

Méthode

Quinze sujets ont été testés dans trois conditions expérimentales dans lesquelles l'expérimentatrice était soit i) distraite (elle manipulait un caillou au lieu de la nourriture) soit ii) incapable de leur donner de la nourriture (à cause d'une barrière physique) soit iii) réticente à le faire (elle pouvait mais ne le faisait pas) en effectuant exactement les mêmes mouvements dans chaque condition.

Résultats

Les macaques de Tonkean se comportent différemment selon les trois conditions expérimentales. Les sujets tentent d'attraper significativement plus souvent la nourriture dans la main de l'expérimentatrice, émettent plus de menaces et sont plus attentifs en présence d'une partenaire réticente qu'incapable ou distraite.

Conclusion

Les macaques semblent capables de percevoir les buts de l'expérimentatrice lorsque celle-ci va ou ne va pas leur donner la nourriture, ce qui correspond à la perception d'un premier niveau d'intention directement percevable à travers le comportement. En revanche, nos résultats ne nous permettent pas de conclure que les macaques sont capables de se représenter mentalement l'intention de l'expérimentatrice c'est-à-dire si elle veut ou ne veut pas leur donner la nourriture.

‘Unwilling’ versus ‘unable’: Tonkean macaques’ understanding of human goal-directed actions

Charlotte Canteloup^{1, 2, 3, 4}, H el ene Meunier^{1, 2, 3, 4}

¹ Centre de Primatologie de l’Universit e de Strasbourg, Fort Foch, 67207 Niederhausbergen, France

² Universit e de Strasbourg - Laboratoire de Neurosciences Cognitives et Adaptatives, 12, rue Goethe, 67000 Strasbourg, France

³ CNRS - Laboratoire de Neurosciences Cognitives et Adaptatives, UMR 7364, 12, rue Goethe, 67000 Strasbourg, France

⁴ University of Strasbourg Institute for Advanced Study, 5, all e du G en eral Rouvillois, 67083 Strasbourg, France

ABSTRACT

The present study investigated goal-directed actions understanding in Tonkean macaques (*Macaca tonkeana*) using the unwilling versus unable paradigm, previously used in several species. Subjects were tested in three experimental conditions that varied according to the goal-directed actions of a human actor. In the “unwilling” condition, the actor was capable of giving the subject food but unwilling to do it; in the “unable” condition, she was willing to give food but was unable to do it because of a physical barrier; and in the “distracted” condition, she was occupied by manipulating a pebble instead of food. We report for the first time that Tonkean macaques, like capuchins, chimpanzees and human infants, behaved differently across these experimental conditions. They attempted to grasp food in the actor’s hand significantly more and displayed more threats in the presence of an unwilling actor rather than an unable or a distracted one. Inversely, they begged significantly more and displayed more frustration behaviors facing a distracted and unable experimenter rather than an unwilling one. These results suggest that Tonkean macaques understand human goal-directed actions by predicting whether they were likely to obtain food merely based on movements, cue and motor intentions reading and understanding of physical constraints.

Keywords: goal-directed action; intentions; Theory of Mind; mindreading; behaviour-reading; monkeys; *Macaca tonkeana*

INTRODUCTION

The perception of others as intentional agents is essential in human daily life and development. We attribute thoughts, beliefs and intentions to other people, and this helps us to better understand them, especially why they behave in certain ways, and to assess who are the best social partners (Woodward, 2009). Being able to understand intentions thus has many advantages in social life. Gauging the goals of others allows individuals to extract information from the environment and to anticipate the future behavior of others, for example when facing a competitor in a novel situation (Call & Tomasello, 2008; Call, 2009). Are humans alone in being able to read the content of others' mind? Or do our closest relatives, the non-human primates, share this ability to represent other agents' mental states?

First, we need to define several terms such as 'goal-directed action', 'intentionality' and 'intention' that are commonly used in Theory of Mind research but rarely defined in the literature. On the one hand, a goal-directed behavior has been defined as "predominantly determined by endogenously generated (and internally represented) goals, rather than by external stimuli" (Pezzulo & Castelfranchi, 2009; p. 559). In this view, such action is expected to produce desired results – goals – and is guided toward these goals by the interplay of prediction, control and monitoring. A goal-directed action would thus imply knowledge of the causal relationships between actions and their consequences, and a desire for the expected consequences or goal (de Wit & Dickinson, 2009). On the other hand, some authors consider goal-directed action as a particular relationship that animate agents have with objects and environmental states without postulating the existence of internal goals (Penn & Povinelli, 2009). In this view, nonhuman animals reason on the basis of perceptual similarity between a given situation and a past one by simply matching them, without reasoning in terms of causal mechanisms involving unobservable mental states. Philosophers of mind have defined intentionality as the property that makes all mental states and events directed toward, or relative to, objects or situations in the world (Dennett, 1971; Searle, 1983; Brentano, 1995). Intention has been defined as the "mental process of steering and controlling actions until the intended goal is achieved" (Pezzulo & Castelfranchi, 2009; p. 562) and as "a plan of action the organism chooses and commits itself to in pursuit of a goal" (Tomasello, Carpenter, Call, Behne & Moll, 2005; p. 676). According to Buttelmann and collaborators (2008a), intentions comprised both a goal - what a person is doing - and a means chosen to achieve that goal - how she is doing it – and the rational choices of action plans – why she is doing it in that particular way. This is in accordance with the two levels of intentions proposed by

philosophers: a first, behavioral level named ‘intention in action’ (Searle, 1983) or ‘informative intention’ (Sperber & Wilson, 1995), corresponding to the expression “I am doing X” (goal), and a second, psychological level labeled ‘prior intention’ (Searle, 1983) or ‘communicative intention’ (Sperber & Wilson, 1995), corresponding to the expression “I will do X” (rational choice). In this view, the first level of intention that can be directly perceived through bodily movements causes a second level of intention that can only be inferred. The intention is thus embedded in action. Since it is commonly accepted that nonhuman animals are intentional agents, the question arises whether they understand that others are intentional subjects too (Penn & Povinelli, 2009).

Two main positions are found within the current, controversial debate about of human infants’ and other species’ abilities to perceive others’ actions as goal-directed and intentional. The ‘behavioral’ approach proposes that only representations of non-intentional actions are involved in the understanding of actions (Povinelli & Vonk, 2004; Vonk & Povinelli, 2006; Butterfill & Apperly, 2013). In the ‘behavioral abstraction hypothesis’ proposed by Povinelli and Vonk (2003), a goal-directed action is considered as an outcome to which an action is directed through bodily movements; it does not refer either to intentions or to representations of desires. This hypothesis suggests that individuals form abstract representations of the behavior of others; they form some concept (e.g. threat) and make separate associations between an observed behavior (e.g. open mouth) and the outcome (e.g. charging; Povinelli & Vonk, 2003). A chimpanzee thus acts as if it has learnt abstract rules about the general behavioral patterns of conspecifics (e.g. <a conspecific who stares at me with its mouth open is likely to threaten and charge me>). Only humans have an additional psychological system allowing them to form higher-order representations of unobservable mental states and their causal relations (e.g. <an individual who stares at me is feeling threatening toward me and is likely to behave badly toward me>). This latter view is what, by contrast, the ‘mentalistic’ approach proposes: representations of perceptions, knowledge and other unobservable mental states characterize this ability (Tomasello et al., 2005; Call & Tomasello, 2008). According to the ‘Theory of Mind-Without-Beliefs hypothesis’, understanding an action requires an ability to perceive not only what another individual is doing but also why, that is, what is the desired outcome (Call & Tomasello, 2008). According to these authors, chimpanzees and humans are able to go beyond the surface behavior to make causal inferences based on the actor’s feelings and intentions.

Because preverbal infants and nonhuman primates lack spoken language, a challenge for researchers is to evaluate their subjective understanding of unobservable internal states as

goals and perceptions of others by focusing on their behaviors. In their seminal paper, Premack and Woodruff (1978) asked whether a symbolic language-trained chimpanzee (*Pan troglodytes*) named Sarah understood others' intentions. Sarah was shown videotapes presenting several problem-solving situations, such as a human trying to escape from a locked cage. Then, she was shown two pictures, one of which depicted the solution (e.g. a key). Sarah chose the correct solutions significantly above chance, leading the authors to conclude that she understood the intentions of the human. However, an alternative, lower-level explanation has been proposed: Sarah could find the solution by associative learning and matching pictures and scenes on the basis of physical similarities (Savage-Rumbaugh & Rumbaugh, 1978). This study remains however pioneer and has incited numerous researchers to study Theory of Mind components both in human infants and in nonhuman primates through various methodologies (see Marsh & Legerstee, 2015 for review).

One method frequently used with human infants concerns imitation. In the Gergely et al. study (2002), 14-month-old children watched an adult turn on a light with her forehead. For half of the infants, the adult was forced to use this unusual action because her hands were occupied; the other half of the infants saw the adult displaying the same action despite her hands being free. When given the unconstrained possibility to act on the light themselves, 69% of infants re-enacted the head action after watching the hands-free condition whereas only 21% of infants reproduced the action after watching the hands-occupied condition. The authors proposed that infants inferred that the head action offered some advantage if it was used even if the adult's hands were free. Buttelmann et al. (2007) found a similar effect in chimpanzees (*Pan troglodytes*), suggesting that infants and great apes understand the rationality of actions (but see Buttelmann, Carpenter, Call, & Tomasello, 2013 for negative results concerning imitation in chimpanzees).

A second method often used to test infants and nonhuman primates' understanding of intentions is the accidental versus intentional protocol. Carpenter et al. (1998) showed 14 to 18-month-old infants an adult demonstrating either an intentional action in which the adult exclaimed: "There!" or an accidental action in which the adult said: "Whoops!". Following the demonstrations, infants were given the opportunity to make the action themselves. The authors reported that infants imitated significantly more intentional than accidental actions, and concluded that they understood something about people's intentions. Call and Tomasello (1998) compared discrimination between a human's intentional and accidental actions in 2- and 3 year-old children, and older chimpanzees and orangutans (*Pongo pygmaeus*). Subjects learned to use the marker shown by the experimenter as a reliable cue to the location of a food

reward in one of three boxes. In the experiment, the experimenter marked one box intentionally – by deliberately placing the marker - and one box accidentally – by accidentally dropping the marker. The subjects were then allowed to select one box. The results showed that the three species significantly selected the intentionally marked box more often than the accidentally marked one, suggesting shared sensitivity to the intentional nature of the experimenter’s actions (Call & Tomasello, 1998). By contrast, Povinelli et al. (1998) found negative results using a similar paradigm in chimpanzees. Using a slightly different protocol, Wood et al. (2007) reported that chimpanzees, cotton-top tamarins (*Saguinus oedipus*) and rhesus macaques choose an intentionally targeted container more frequently than an accidentally one, and concluded that these species were able to infer rational and goal-directed actions of a human. Recently, the same paradigm has been applied to Tonkean macaques (*Macaca tonkeana*) and tufted capuchin monkeys (*Sapajus apella*) but with no evidence that these monkeys recognized others’ goals (Costes-Thiré et al., 2015).

A third method used to test the attribution of intentions is the unwilling versus unable paradigm. In the original study using this paradigm (Call, Hare, Carpenter, & Tomasello, 2004), after habitually feeding chimpanzees through a hole in a Plexiglass wall, the experimenter suddenly stopped feeding them because either i) he did not want to though he still could (unwilling), or ii) he wanted to but could not (unable). The authors reported more spontaneous begging and auditory behaviors, and shorter latencies to leave by the chimpanzees when confronted with an unwilling compared with an unable experimenter, leading the authors to conclude that chimpanzees interpreted human actions as goal-directed. Similar results have been found in human infants from 9 months of age (Behne, Carpenter, Call, & Tomasello, 2005), and in capuchin monkeys for actions displayed by a human but not those performed by inanimate rods (Phillips, Barnes, Mahajan, Yamaguchi, & Santos, 2009).

Despite differing views (Lurz & Krachun, 2011; Povinelli & Vonk, 2003), numerous researchers concluded that great apes can read below surface behavior to understand something about the goals, perceptions and intentions of others (Tomasello & Carpenter, 2005; Tomasello et al., 2005; Call & Tomasello, 2008; Buttelmann, Call, & Tomasello, 2008b; Buttelmann, Schütte, Carpenter, Call, & Tomasello, 2012). Studies on monkeys are fewer and evidence of Theory of Mind abilities as intention-reading abilities in these species remains scarce (e.g. Barnes, Hill, Langer, Martinez, & Santos, 2008; Phillips et al., 2009; Drayton & Santos, 2014; see Cheney & Seyfarth, 1990; Povinelli, Parks, & Novak, 1991; Kummer, Anzenberger, & Hemelrijk, 1996 for negative results in macaques and Drayton, Varman, & Santos, 2016 for negative results in capuchins). From this perspective, we

investigated understanding of goal-directed actions by adapting a protocol previously used with human infants (Behne et al. 2005), chimpanzees (Call et al., 2004), capuchins (Phillips et al., 2009) and African grey parrots (*Psittacus erithacus*: Péron, Rat-Fischer, Nagle & Bovet, 2010) in a little known old world monkey species, the Tonkean macaque. The literature on this species, and notably on its social cognition, is indeed still scarce, in spite of its known very tolerant sociality. On the one hand, by testing a non-ape species, we aim at tracing back the evolutionary history of such characteristics in the primate lineage by filling the gap between chimpanzees and capuchins. On the other hand, and in a more general way, studying a tolerant species could bring new light on the effects of sociocultural environment on cognitive abilities. We tested macaques in three experimental conditions: i) Unwilling: the experimenter did not want to give food to the subject; ii) Unable: the experimenter could not give food to the subject because of a physical barrier and iii) Distracted: the experimenter was manipulating a pebble instead of food. Hypothesizing that they understand goal-directed actions and that this ability is a formerly shared trait with at least the common ancestor we have with macaques, we predicted that the macaques would behave differently toward a human who was distracted, unwilling or unable to give them food. More precisely, we expected that they would display more gaze alternation between the human and the food and more agonistic behaviors especially in the ‘Unwilling’ condition compared to the ‘Unable’ and ‘Distracted’ ones. Conversely, we hypothesized that macaques would be less attentive by looking more elsewhere facing a distracted or unable experimenter than an unwilling one.

MATERIALS AND METHODS

Ethical note

The procedures used here adhered to the French legal requirements for the Use of Animals in Research. This experiment was approved by the Animal Experiment Committee of the Centre de Primatologie de l’Université de Strasbourg and by the CREMEAS Ethics Committee (Approval for conducting experiments on primates n° AL/46/53/02/13).

Subjects

The subjects were fifteen Tonkean macaques (thirteen males aged 3 – 12 years and two females aged 6 and 16 years), all born and raised at the Centre de Primatologie de l'Université de Strasbourg, France. They lived in one of two groups: group A was composed of five adult males living in multi cage complex of two outdoor areas (14.40 + 16.00 m²) connected to two indoor areas (23.78 + 8.73 m²), and group B contained 26 individuals living in a 2694 m² wooded park with access to a 20 m² indoor housing area. Subjects were tested between July and August 2015. Their daily diet consisted of commercial pellets and water ad libitum, and fruits and vegetables twice a week, out of experimental sessions.

Apparatus

Subjects were tested within their social group in an outdoor area situated alongside their indoor area for group A and alongside their park for group B. A concrete block (58 X 19 cm) was placed inside the test area perpendicularly to the mesh, about 1 m from the ground, to be used as a seat by the subject (Fig. 1). In the experimenter area, a table (85 X 50 cm) was placed in front of the subject. A horizontal opening (64 X 5 cm) in the mesh allowed subjects to beg for food by extending their hand through the opening. Above the table, a Plexiglass panel (100 X 60 cm) drilled with a feeding hole (3 cm in diameter, 22.5 cm above the horizontal opening) doubled the mesh on the experimenter's side. This small hole could be easily closed by a pivoting shutter (10 X 6 cm).



Figure 1. Picture of the experimental apparatus during a trial of the ‘Unwilling’ condition

Experimental procedure

The experiment required one assistant and one experimenter (CC). Each subject participated in three different experimental conditions that varied according to the intentional action of the experimenter:

- Unwilling: the experimenter held a raisin and placed it near the edge of the table out of the subject’s reach. She then grasped the raisin in one hand and made five explicit back and forth movements with this hand between her and the feeding hole. Each time her hand was close the hole she made five small back and forth movements, preventing the subject from grabbing the raisin through the hole. The experimenter alternated her gaze between the raisin and the monkey’s face.
- Unable: the experimenter held a raisin and placed it near the edge of the table out of the subject’s reach. She then grasped the raisin in one hand and made five explicit back and forth movements with this hand between her and the feeding hole. However, prior to the trial, the assistant blocked the hole with the pivoting

shutter. The experimenter's hand made the same back and forth movements as in Unwilling trials, but striking each time against the Plexiglass shutter. The experimenter alternated her gaze between the raisin and the monkey's face.

- Distracted: The experimenter held a raisin and a pebble and placed both on the table out of the subject's reach. She then grasped only the pebble in one hand, leaving the raisin on the table, and made five explicit back and forth movements with this between her and the feeding hole. Each time her hand was close to the hole she made five small back and forth movements. The experimenter alternated her gaze between the pebble and the monkey's face.

Six sessions per subject were conducted on a minimum six different days. One session was composed of 12 trials including three experimental trials - one for each experimental condition - and nine motivational trials in which the food was placed on the table and then given to the subject through the feeding hole when the subject begged. Each experimental trial lasted about 30 sec and no food was given to the subject at the end of the trial. All subjects were tested using the same series of motivational and test trials and the order of presentation of experimental trials was pseudo-randomized across sessions, involving a session to always begin with two motivational trials in order to motivate the subject to stay for participating to the experiment. Experimental trials were separated by two or three motivational trials. The inter-trial interval was about 10 sec during which the experimenter briefly left the experimenter area. Subject participation was voluntary; they were free to leave the apparatus and testing area at any time.

Data and reliability analyses

Experiments were recorded by a high-definition video camera (Canon, Legria HF S20). Videos were analyzed frame by frame (1 frame = 0.04s) by CC using the software *The Observer XT 10.1.548*. For the analysis, we recorded the following behaviours:

- Duration of presence of the subject on the seat
- Duration of gaze elsewhere
- Frequency of gaze alternations between the experimenter and the raisin on the table and between the experimenter and the item (raisin or pebble) in the hand
- Frequency of begging gestures, i.e., the subject extends an arm through the horizontal opening of the wire mesh. This was recorded when the extension of the gesture was at its peak just before the subject began to retract or lower his arm

- Duration of attempting to grasp the item
- Duration of threat towards the experimenter
- Duration of yawn and self- scratch

For reliability analysis, a random 20% of trials were analyzed by a naïve observer using The Observer, with a tolerance window of 120 ms corresponding to 3 frames. Inter-observer agreement was excellent for the all the behaviors recorded: presence (Cohen's $\kappa = 0.86$), grasping attempt (Cohen's $\kappa = 0.90$), gaze elsewhere (Cohen's $\kappa = 0.89$), begging (Cohen's $\kappa = 0.90$), gaze alternation (Cohen's $\kappa = 0.88$), threat (Cohen's $\kappa = 0.94$) and yawn and self-scratch (Cohen's $\kappa = 0.92$).

Statistical analysis

Two types of mathematical models were used to determine whether experimental conditions influenced behavioral measures. First, Generalized Linear Mixed Models (GLMMs) for count data (i.e. with a Poisson law distribution) were fitted to test which experimental condition influenced variables including begging gestures and gaze alternations between the experimenter and the item in the hand. Second, because experimental trials did not last exactly 30 sec, we established GLMMs for proportional data (by considering a binomial distribution) in order to test which experimental conditions influenced continuous variables as the proportion of time spent in the following behaviors: item grasp attempt, gaze elsewhere, threat, yawn and self-scratch.

In each model, to deal with repeated measures, experimental condition ('unwilling'; 'unable'; 'distracted') was considered a fixed effect and subject identity was assessed as a random effect. Tukey corrections were applied when performing multiple comparison tests between experimental conditions. All models were performed with R 3.1.2's package lme4 (Bates, Maechler, Bolker, & Walker, 2014), with alpha set at 0.050.

RESULTS

Presence of the subject

Macaques spent more than 95 % of time on the seat in the three experimental conditions ('unwilling' condition: Mean proportion of presence time per trial = 95.79% \pm

Standard error of the mean = 1.30; ‘distracted’ condition: $95.36\% \pm 1.65$; ‘unable’ condition: $95.92\% \pm 1.79$).

Gaze

The frequency of gaze alternations between the experimenter and the item in the experimenter’s hand (Fig. 2A) was significantly influenced by the experimental condition (LRT = 25.45; Df = 2; $P < 0.0001$). GLMM revealed that macaques displayed significantly more gaze alternation in the ‘unable’ condition (Mean frequency per trial = 5.08 ± 0.39) than the ‘distracted’ condition (4.22 ± 0.40 ; $P = 0.02$); in the ‘unwilling’ (5.91 ± 0.49) compared with the ‘distracted’ condition ($P < 0.001$), and in the ‘unwilling’ compared with the ‘unable’ condition ($P = 0.04$).

The proportion of looking time elsewhere (Fig. 2B) was significantly influenced by the experimental condition (LRT = 14535; Df = 2; $P < 0.0001$). According to GLMM, macaques looked elsewhere for significantly longer in the ‘unable’ condition ($46.79\% \pm 2.04$) than the ‘distracted’ condition ($45.52\% \pm 2.41$; $P < 0.0001$); in ‘distracted’ compared with the ‘unwilling’ condition ($32.06\% \pm 2.37$; $P < 0.0001$), and in the ‘unable’ condition compared with the ‘unwilling’ condition ($P < 0.0001$).

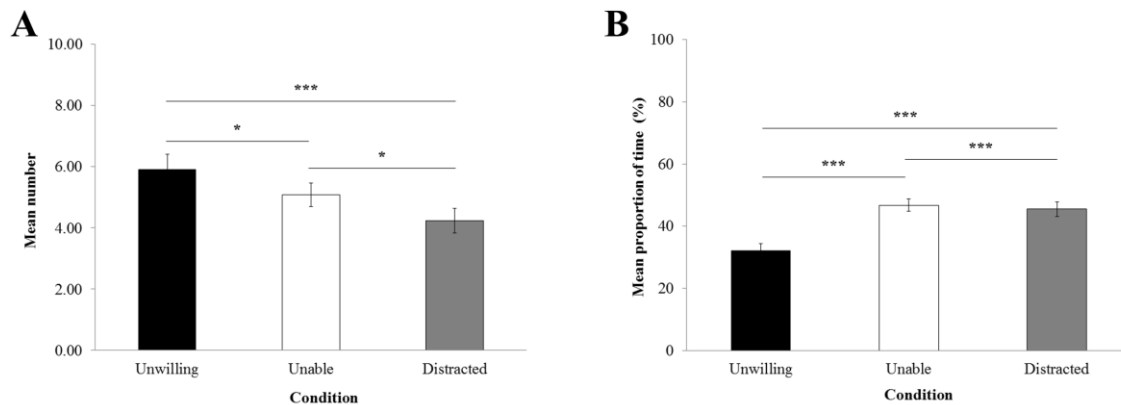


Figure 2. A) Mean number of gaze alternations between the experimenter and her hand holding the item per trial. B) Mean proportion of time (\pm standard error of the mean) macaques looked elsewhere per trial.

Gestures

The frequency of begging (Fig. 3A) was significantly influenced by the experimental condition (LRT = 129.15; Df = 2; $P < 0.0001$). GLMM reported that macaques begged significantly more in the ‘distracted’ (4.36 ± 0.38) than in the ‘unable’ (2.43 ± 0.26) and ‘unwilling’ conditions (1.57 ± 0.22 ; $P < 0.0001$), and more in the ‘unable’ than the ‘unwilling’ condition ($P = 0.0002$).

The proportion of time trying to grasp the item through the hole (Fig. 3B) was significantly influenced by the experimental condition (LRT = 78888; Df = 2; $P < 0.0001$). According to GLMM, macaques spent significantly more time attempting to grasp the item in the ‘unable’ ($13.94\% \pm 1.81$) than the ‘distracted’ condition ($5.69\% \pm 1.41$; $P < 0.0001$), and in the ‘unwilling’ condition ($34.78\% \pm 2.26$) compared with ‘distracted’ and ‘unable’ conditions ($P < 0.0001$).

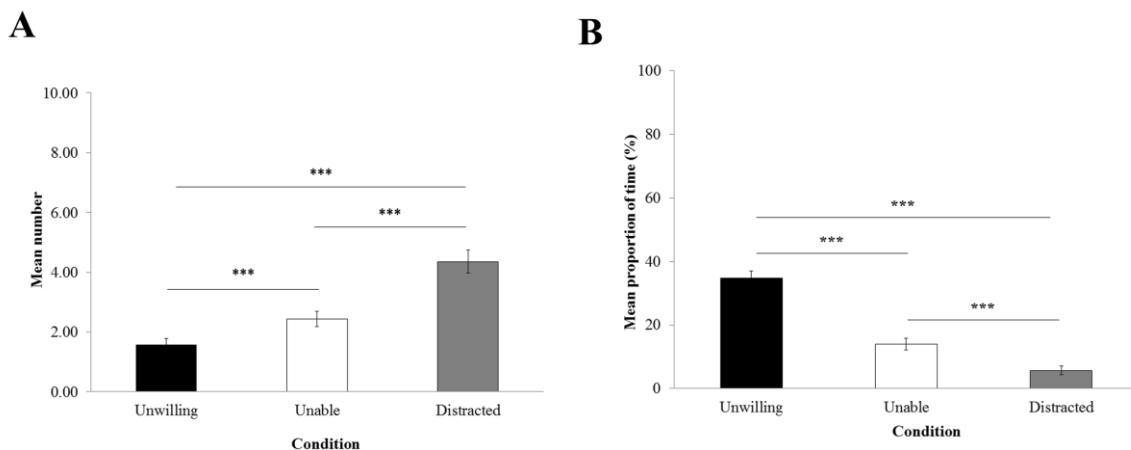


Figure 3. Mean proportion of time (\pm standard error of the mean) macaques A) spent begging and B) attempted to grasp the item in her hand per trial

Threat, yawn and self-scratch

The proportion of time threatening (Fig. 4A) was significantly influenced by the experimental condition (LRT = 1607; Df = 2; $P < 0.0001$). GLMM reported more threat behavior towards the experimenter in the ‘unable’ ($0.09\% \pm 0.09$) than the ‘distracted’ condition ($0.02\% \pm 0.02$; $P < 0.0001$) and in the ‘unwilling’ condition ($0.48\% \pm 0.17$) compared with the ‘distracted’ and ‘unable’ conditions ($P < 0.0001$).

The proportion of time yawning and self-scratching (Fig. 4B) was significantly influenced by the experimental condition (LRT = 3173.7; Df = 2; $P < 0.0001$). GLMM revealed significantly more time in these behaviors in the ‘distracted’ ($4.95\% \pm 1.01$) than the ‘unable’ ($2.78\% \pm 0.72$) and ‘unwilling’ conditions ($2.33\% \pm 0.61$; $P < 0.0001$), and in the ‘unable’ condition compared with the ‘unwilling’ condition ($P < 0.0001$).

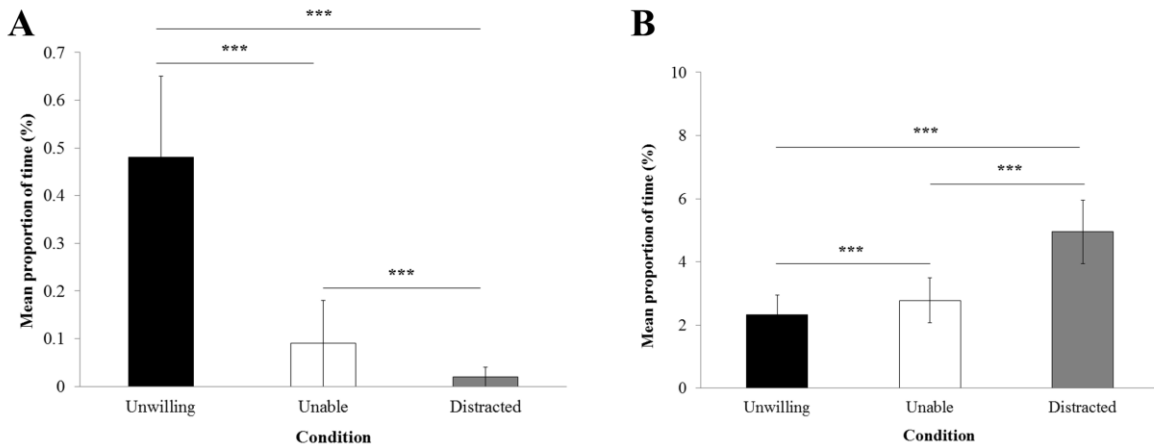


Figure 4. Mean proportion of time macaques (\pm standard error of the mean) spent displaying A) threat towards the experimenter per trial and B) yawn and self-scratch per trial

DISCUSSION

We tested Tonkean macaques in the unwilling versus unable paradigm previously used in parrots (Péron et al., 2010), capuchins (Phillips et al., 2009), chimpanzees (Call et al., 2004) and human infants (Behne et al., 2005; Marsh, Stavropoulos, Nienhuis, & Legerstee, 2010). Like these species, Tonkean macaques behaved as if they understood the intentions of the experimenter, i.e., willing to give them food or not, as they attempted to grasp the raisin in the experimenter’s hand significantly more, threatened more and were more attentive when she was unwilling rather than unable to give them food, or was distracted. We report for the first time that Tonkean macaques act differently according to the goal-directed actions of a human experimenter. Given that the experimenter displayed exactly the same gestural and visual behaviors in each experimental condition, our results cannot be explained by a low-level behavior reading. Moreover, we observed that Tonkean macaques displayed more frustration behaviors when facing an unable experimenter than an unwilling one which makes the explanation that Tonkean macaques simply discriminate environmental variations

unlikely. Tonkean macaques appear thus able to perceive the goals of the experimenter – she is going to give them food or not. However, we cannot conclude from our experiment that Tonkean macaques truly understand all aspects of the underlying intentions of the human in a mentalistic way.

Tonkean macaques displayed significantly more gaze alternation between the experimenter's face and hand, threatened more, and tried to grasp the item significantly more in the 'unwilling' than the 'unable' and 'distracted' conditions, and in the 'unable' than the 'distracted' condition. Moreover, Tonkean macaques spent more time looking elsewhere facing a distracted or unable experimenter than an unwilling one showing a disinterest for the experiment in these conditions. Together, these results indicate that, in accordance with results in human infants (Behne et al., 2005), chimpanzees (Call et al., 2004) and rhesus macaques (Wood, Glynn, Phillips, & Hauser, 2007), but in contradiction to a recent study in Tonkean macaques (Costes-Thiré et al., 2015), our subjects behaved differently according to experimental conditions corresponding to different goal-directed actions by a human experimenter. Notably, our Tonkean macaques had received no training prior to the experiment, as in other studies reporting positive results (Behne et al., 2005; Call et al., 2004; Marsh et al., 2010; Phillips et al., 2009; Wood et al., 2007), and unlike the study reporting negative results (Costes-Thiré et al., 2015). Moreover, it would be necessary to test our subjects in many more trials to observe a learning effect; chimpanzees needed hundreds of trials to discriminate between a human that could and could not see them (Povinelli & Eddy, 1996). It is important to stress that, the experimenter acted in exactly the same way in the three experimental conditions in terms of gaze alternation and manual movements. From this perspective our results cannot be explained by recourse to low-level behavior-reading based on the topography of the experimenter's motoric and visual behavior. By contrast, skeptics could propose that the macaques' aggressive and gestural behaviors might simply reflect frustration at not receiving food. Indeed, we reported that Tonkean macaques threatened significantly more the human experimenter when she was unwilling to give them food than when she was unable or distracted to do so. This result can be interpreted as a result of frustration of not obtaining the raisin that is close to reach but also as an understanding of experimenter's goal-directed actions. To rule out this explanation in their study of chimpanzees, Call et al. (2004) ran a non-social control condition in which the experimenter left the testing area after placing the food on the platform. In this condition chimpanzees produced fewer behaviors and left the testing area earlier compared to conditions in which he remained. On the one hand, we recognize that we did not run such a non-social control, but

we previously reported in a comparable non-social condition that Tonkean macaques and rhesus macaques produced gestures intentionally towards a human experimenter and pointed significantly less towards food when the experimenter was absent (Canteloup, Bovet, & Meunier, 2015a; 2015b) that makes then this explanation unlikely. On the other hand, another way to test for the frustration hypothesis is to analyze results of frustration behaviors displayed by macaques as yawning and self-scratching (Maestriperi, Schino, Aureli, & Troisi, 1992). If we observe the same pattern throughout the experimental conditions concerning frustration and agonistic behaviors, then the frustration explanation could be valuable: macaques could simply perceive that they are not going to obtain food because of the physical barrier instead of understanding the underlying goal of the human experimenter. It is interesting to observe completely reverse results between threats and yawning and self-scratching: Tonkean macaques displayed then more frustration behaviors when facing an unable experimenter than an unwilling one which strengthen the explanation that Tonkean macaques perceive the goals of the human actions.

The Tonkean macaques begged significantly more through the horizontal opening when the experimenter was distracted rather than when she was unwilling or unable to give them food, and more when she was unable than unwilling to give them food. The greater incidence of begging in the ‘distracted’ condition compared with the others might be related to the raisin being out of reach on the table in this condition, eliciting attempts to grasp it or to attract the experimenter’s attention towards the food. It appears thus clear that the macaques understood that the Plexiglass panel was a physical barrier in the ‘unable’ condition, making the transfer of food impossible. Begging would thus be an alternative way to attempt to obtain food from a well-intentioned experimenter. These results support the idea that Tonkean macaques understood that the physical barrier impeded the transfer of food in the ‘unable’ condition, and that they tried to solve the problem by raising their arm above the opening.

Contrary to capuchin monkeys (Phillips et al., 2009) and chimpanzees (Call et al., 2004), Tonkean macaques did not leave the testing area earlier when faced with an unwilling experimenter. According to those authors, capuchins and chimpanzees appear sensitive to the experimenter’s intentions when determining how long to wait for food. However, Tonkean macaques remained present for more than 95 percent of time in the three experimental conditions. The fact that Tonkean macaques are a highly tolerant macaque species (Thierry, 2000) could explain why they were so patient, quiet and peaceful throughout the experiment, in comparison with species more despotic as chimpanzees. Simple “presence” thus does not

appear to be a useful measure of discrimination of intentional actions in this species. Their social tolerance could also explain the low rates of threat in the ‘unwilling’ condition.

To sum up, our results suggest that Tonkean macaques understand goal-directed actions by perceiving a first level of intention labeled ‘intention in action’ (Searle, 1983) or ‘informative intention’ (Sperber & Wilson, 1995) in the literature, concepts that are directly perceivable through bodily movements. Indeed, intention is not a unitary concept but a multi-level one, and evaluation of an individual’s action differs from the understanding of the individual’s intentions (Call & Tomasello, 2008). Tonkean macaques seem thus able to understand intentional actions as pursuing goals persistently. According to Povinelli and Vonk (2003) and their ‘behavioral abstraction hypothesis’, macaques would form an association between the experimenter’s behavior (food in hand close to me versus food far from me) and the outcome (obtaining food probable versus obtaining food improbable). They may learn the rule: <when there is a physical barrier between me and food, I cannot have access to food>, and not have mentalized: <the experimenter is well intentioned when trying to give me food but unable because of the physical barrier>. Phillips et al. (2009) proposed another explanation of their results with capuchins: the monkeys might have a set of mechanical principles in mind construing that animate agents can move on their own, contrary to inanimate objects. This proposition is quite different from the ‘teleological stance’ adopted by Gergely and Csibra (2003), in which interpreting goal-directed actions relies on the understanding of efficient action and physical efficiency of actions of both animate and inanimate agents. Our results fit with several theories as embodied social cognition proposing that cognitive processes operate on perceptual input and involve motor representations rather than representation of unobservable mental states (e.g. Fenici, 2012; Gómez, 1999).

CONCLUSION

To conclude, we reported that Tonkean macaques behaved *as if* they understood the actions and the underlying intentions of an experimenter. Despite the existence of high-level mindreading explanations (Call & Tomasello, 2008; Dennett, 1971; 1987), all the existing findings and ours can also be explained by lower-level explanations whose behavior-reading hypotheses (Butterfill & Apperly, 2013; Fenici, 2012; Gergely & Csibra, 2003; Heyes, 2014; Povinelli & Vonk, 2003; see also Meunier, 2016 for a review). However, it may be worth re-evaluating the dichotomy between high *versus* low mental levels. For example, following

Grandin (1995; 2002; 2004; 2009), it might be proposed that nonhuman animals can develop internal representation of what others see, do etc. not in a language-based way, as humans do, but rather in a sensory-based way. From this perspective, animals develop a large visual or other sensory-based data bank in their brain that enables them to project their own experience to others, to take the visual perspective of others or to discriminate their intentions, not by thinking in words like normal humans do but rather by thinking in images, similar to what some autistic persons do (Grandin, 1995; 2009). We should reconsider what “mentalistic” means: is it only linked to human language? Or does a different way of mentalizing exist, especially for creatures that have no spoken language? These questions may be valuable for framing future projects by researchers from the Humanities and Biological Sciences.

ACKNOWLEDGMENTS

The authors are grateful to Yves Larmet and the whole team of the Centre de Primatologie de l’Université de Strasbourg for allowing them to run this study. The authors are particularly thankful to Steve Lapp and Adrien Panter for their help in building the experimental apparatus. Lucie Hoornaert, Justine Guillaumont and Lena Buscara are greatly thanked for their assistance during the experiment. The authors would also like to especially thank Gaël Raimbault who served as a second coder for the reliability analysis and to Nicolas Poulin for his precious statistical assistance. James R. Anderson is warmly thanked for insightful discussions and for editing the English of the manuscript. This study was funded by the University of Strasbourg Institute for Advanced Study (USIAS) that had no role in study design, data collection, interpretation of data, writing the article, and in the decision to submit the article for publication.

REFERENCES

- Barnes, J. L., Hill, T., Langer, M., Martinez, M., & Santos, L. R. (2008). Helping behaviour and regard for others in capuchin monkeys (*Cebus apella*). *Biology Letters*, *4*, 638–640.
- Bates, D., Maechler, M., Bolker, B., & Walker, S. (2014). lme4: Linear mixed-effects models using Eigen and S4. ArXiv e-print; submitted to *Journal of Statistical Software*: <http://arxiv.org/abs/1406.5823>

- Behne, T., Carpenter, M., Call, J., & Tomasello, M. (2005). Unwilling versus unable: infants' understanding of intentional action. *Developmental Psychology, 41*(2), 328-337.
- Brentano, F. (1995). Psychology from an empirical standpoint. Trans. A. C. Rancurello, D. B. Terrell, & L. L. McAlister, 2nd edition. New introduction by P. Simons. London: Routledge.
- Buttelmann, D., Carpenter, M., Call, J., & Tomasello, M. (2007). Enculturated chimpanzees imitate rationally. *Developmental Science, 10*(4), F31-F38.
- Buttelmann, D., Call, J., & Tomasello, M. (2008a). Rational tool use and tool choice in human infants and great apes. *Child Development, 79*, 609-626.
- Buttelmann, D., Call, J., & Tomasello, M. (2008b). Behavioral cues that great apes use to forage for hidden food. *Animal Cognition, 11*, 117-128.
- Buttelmann, D., Schütte, S., Carpenter, M., Call, J., & Tomasello, M. (2012). Great apes infer others' goals based on context. *Animal Cognition, 15*(6), 1037-1053.
- Buttelmann, D., Carpenter, M., Call, J., & Tomasello, M. (2013). Chimpanzees, *Pan troglodytes*, recognize successful actions, but fail to imitate them. *Animal Behaviour, 86*(4), 755-761.
- Butterfill, S.A., & Apperly, I.A. (2013). How to construct a minimal theory of mind. *Mind & Language, 28*(5), 606-637.
- Call, J., & Tomasello, M. (1998). Distinguishing intentional from accidental actions in orangutans (*Pongo pygmaeus*), chimpanzees (*Pan troglodytes*), and human children (*Homo sapiens*). *Journal of Comparative Psychology, 112*(2), 192-206.
- Call, J., Hare, B., Carpenter, M., & Tomasello, M. (2004). 'Unwilling' versus 'unable': chimpanzees' understanding of human intentional action. *Developmental Science, 7*(4), 488-498.
- Call, J., & Tomasello, M. (2008). Does the chimpanzee have a theory of mind? 30 years later. *Trends in Cognitive Sciences, 12*(5), 187-192.
- Call, J. (2009). Contrasting the social cognition of humans and nonhuman apes: the shared intentionality hypothesis. *Topics in Cognitive Science, 1*, 368-379.
- Canteloup, C., Bovet, D., & Meunier, H. (2015a). Do Tonkean macaques (*Macaca tonkeana*) tailor their gestural and visual signals to fit the attentional states of a human partner? *Animal Cognition, 18*(2), 451-461.
- Canteloup, C., Bovet, D., & Meunier, H. (2015b). Intentional gestural communication and discrimination of human attentional states in rhesus macaques (*Macaca mulatta*). *Animal Cognition, 18*(4), 875-883.

- Carpenter, M., Akhtar, N., & Tomasello, M. (1998). Fourteen-through 18-month-old infants differentially imitate intentional and accidental actions. *Infant Behavior & Development, 21*(2), 315-330.
- Cheney, D., & Seyfarth, R. (1990). Attending to behaviour versus attending to knowledge: examining monkeys' attribution of mental states. *Animal Behaviour, 40*, 742-753.
- Costes-Thiré, M., Levé, M., Uhlrich, P., Pasquaretta, C., De Marco A., & Thierry, B. (2015). Evidence that monkeys (*Macaca tonkeana* and *Sapajus apella*) read moves, but no evidence that they read goals. *Journal of Comparative Psychology, 129*(3), 304-310.
- Dennett, D.C. (1971). Intentional systems. *The Journal of Philosophy, 68*(4), 87-106.
- Dennett, D.C. (1987). *The intentional stance*. The MIT Press, Cambridge, Massachusetts, London, England. 400pp
- de Wit, S., & Dickinson, A. (2009). Associative theories of goal-directed behaviour: a case for animal-human translational models. *Psychological Research, 73*, 463-476.
- Drayton, L.A., & Santos, L.R. (2014). Capuchins' (*Cebus apella*) sensitivity to others' goal-directed actions in a helping context. *Animal Cognition, 17*, 689-700.
- Fenici, M. (2012). Embodied social cognition and embedded Theory of Mind. *Biolinguistics, 6*, 3-4, 276-307.
- Gergely, G., Bekkering, H., & Király, I. (2002). Rational imitation in preverbal infants. *Nature, 415*, 755.
- Gergely, G., & Csibra, G. (2003). Teleological reasoning in infancy: the naïve theory of rational action. *Trends in Cognitive Sciences, 7*(7), 287-292.
- Gómez, J.C. (1999). Théories des primates sur l'esprit des primates: objectifs conceptuels et méthodologiques. *Enfance, 3*, 336-344.
- Grandin, T. (1995). How people with autism think. *Learning and cognition in autism*. Edited by Eric Schopler and Gary B. Mesibov. Plenum Press, New-York. 137-156
- Grandin, T. (2002). Do animals and people with autism have true consciousness? *Evolution and Cognition, 8*, 241-248.
- Grandin, T., & Johnson, C. (2004). *Animals in translation*. Scribner, New-York. 356pp
- Grandin, T. (2009). How does visual thinking work in the mind of a person with autism? A personal account. *Philosophical Transactions of the Royal Society, 364*, 1437-1442.
- Heyes, C. (2014). Submentalizing: I'm not really reading your mind. *Perspectives on Psychological Science, 9*, 131-143.

- Kummer, H., Anzenberger, G., & Hemelrijk, C.K. (1996). Hiding and perspective taking in long-tailed macaques (*Macaca fascicularis*). *Journal of Comparative Psychology*, *110*, 97-102.
- Lurz, R.W., & Krachun, C. (2011). How could we know whether nonhuman primates understand others' internal goals and intentions? Solving Povinelli's problem. *Review of Philosophy and Psychology*, *2*, 449-481.
- Maestriperi, D., Schino, G., Aureli, F., & Troisi, A. (1992). A modest proposal: displacement activities as an indicator of emotions in primates. *Animal Behaviour*, *44*, 967-979.
- Marsh, H.L., Stavropoulos, J., Nienhuis, T., & Legerstee, M. (2010). Six-and 9-month-old infants discriminate between goals despite similar action patterns. *Infancy*, *15*(1), 94-106.
- Marsh, H.L., & Legerstee, M. (2015). Goal-oriented behaviour among human and non-human primates. *International Encyclopedia of the Social & Behavioral Sciences, Second Edition*, 268-274.
- Meunier, H. (2016). Do monkeys have a theory of mind? How to answer the question? *Neuroscience and Biobehavioral Reviews*
- Penn, D.C., & Povinelli, D.J. (2009). On becoming approximately rational: the relational reinterpretation hypothesis. In S. watanabe, AP. Blaisdell, L. Huber & A. Young (Eds.), *Rational animals, irrational humans* (pp. 23-44). Tokyo: Keio University Press.
- Pezzulo, G., & Castelfranchi, C. (2009). Thinking as the control of imagination: a conceptual framework for goal-directed systems. *Psychological Research*, *73*, 559-577.
- Phillips, W., Barnes, J.L., Mahajan, N., Yamaguchi, M., & Santos, L.R. (2009). 'Unwilling' versus 'unable': capuchin monkeys' (*Cebus apella*) understanding of human intentional action. *Developmental Science*, *12*(6), 938-945.
- Péron, F., Rat-Fischer, L., Nagle, L., & Bovet, D. (2010). 'Unwilling' versus 'unable': do grey parrots understand human intentional actions? *Interaction Studies*, *11*(3), 428-441.
- Povinelli, D.J., Parks, K.A., & Novak, M.A. (1991). Do rhesus monkeys (*Macaca mulatta*) attribute knowledge and ignorance to others? *Journal of Comparative Psychology*, *105*, 318-325.
- Povinelli, D.J., & Eddy, T.J. (1996). What young chimpanzees know about seeing. *Monographs of the Society for Research in Child Development*, *247*, (61(3), 5-152.
- Povinelli, D.J., Perilloux, H.K., Reaux, J.E., & Bierschwale, D.T. (1998). Young and juvenile chimpanzees' (*Pan troglodytes*) reactions to intentional versus accidental and inadvertent actions. *Behavioural Processes*, *42*, 205-218.

- Povinelli, D.J., & Vonk, J. (2003). Chimpanzee minds: suspiciously human? *Trends in Cognitive Sciences*, 7(4), 157-160.
- Premack, D., & Woodruff, G. (1978). Does the chimpanzee have a theory of mind? *Behavioral and Brain Sciences*, 1, 515-526.
- Savage-Rumbaugh, S.E., & Rumbaugh, D.M. (1979). Chimpanzee problem comprehension: insufficient evidence. *Science*, 206(7), 1201-1202.
- Searle, J. (1983). *Intentionality*. Cambridge, England: Cambridge University Press
- Sperber, D., & Wilson, D. (1995). *Relevance: communication and cognition*. Second Edition. Oxford: Blackwell
- Thierry, B. (2000). Covariation of conflict management patterns across macaque species. In F. Aureli, & F. B. M. de Waal (Eds.) *Natural Conflict resolution*. University of California Press, Berkeley. Pp. 106-128.
- Tomasello, M., & Carpenter, M. 2005. The emergence of social cognition in three young chimpanzees. *Monographs of the Society for Research in Child Development*, 70(1), 1-152.
- Tomasello, M., Carpenter, M., Call, J., Behne, T., & Moll, H. (2005). Understanding and sharing intentions: the origins of cultural cognition. *Behavioral and Brain Sciences*, 28, 675-735.
- Vonk, J., & Povinelli, D.J. (2006). Similarity and difference in the conceptual systems of primates: the unobservability hypothesis. In E. Wasserman & T. Zentall (Eds.) *Comparative Cognition: Experimental explorations of Animal Intelligence*. Oxford University Press, England. Pp. 363-387.
- Wood, J.N., Glynn, D.D., Phillips, B.C., & Hauser M.D. (2007). The perception of rational, goal-directed action in nonhuman primates. *Science*, 317, 1402-1405.
- Woodward, A.L. (2009). Infants' grasp of others' intentions. *Current Directions in Psychological Science*, 18(1), 53-57.

DISCUSSION GENERALE

Ma thèse a consisté en l'étude de prérequis et composants de la Théorie de l'Esprit tels que la discrimination de l'attention, des perceptions et des intentions d'autrui, chez des singes de l'Ancien Monde, plus particulièrement des macaques. Le premier objectif de mon projet doctoral était ainsi de déterminer si les macaques rhésus (*Macaca mulatta*) et les macaques de Tonkean (*Macaca tonkeana*) étaient capables de discriminer différents états attentionnels d'un partenaire humain (**Articles 1 & 2**). Le deuxième objectif était de savoir si les macaques de Tonkean se comportaient en fonction de la perspective visuelle de leurs congénères (**Article 3**). Le troisième objectif était d'étudier les comportements de manipulation sociale émis par des subordonnés face à des compétiteurs dominants (**Article 4**). Enfin, le quatrième et dernier objectif de ma thèse était d'évaluer si les macaques de Tonkean discernaient les intentions d'un expérimentateur humain (**Article 5**).

J'exposerai et discuterai les résultats de chacune des expériences menées à l'aune des différentes interprétations possibles. Cela m'amènera ensuite à développer la controverse à la fois méthodologique et théorique se situant au cœur du débat sur la Théorie de l'Esprit. Puis, je présenterai quelles sont les solutions et perspectives qui sont proposées afin de faire progresser la recherche dans ce domaine. Je terminerai enfin par une conclusion générale concernant mon travail doctoral.

1. Discrimination de l'attention

Les expériences que j'ai menées chez les macaques rhésus et les macaques de Tonkean ont permis de mettre en évidence que ces singes sont capables, d'une part, d'utiliser intentionnellement un geste de pointage préalablement appris et, d'autre part, de discriminer l'état d'attention d'un humain sur la base d'indices attentionnels « grossiers » tels que l'orientation de son corps et de son visage plutôt que sur la base d'indices plus subtils comme l'état de ses yeux (**Articles 1 & 2**).

Nos résultats montrent qu'à l'instar des grands singes (orangs-outans : Poss et al. 2006 ; Cartmill & Byrne 2007 ; 2010 ; gorilles : Pika et al. 2003 ; Genty et al. 2009 ; chimpanzé : Pika et al. 2005 ; Hobaiter & Byrne 2011 ; Roberts et al. 2013 ; bonobo : Pika et al. 2005) et de certaines espèces de singes (capucin : Hattori et al. 2007 ; 2010 ; mangabey :

Maille et al. 2012 ; babouin : Bourjade et al. 2013 ; Meunier et al. 2013), macaques rhésus et macaques de Tonkean font preuve de communication gestuelle intentionnelle. En effet, nous avons mis en évidence que ces macaques émettaient davantage de gestes de pointage en présence d'une expérimentatrice se tenant face à eux, qu'ils étaient sensibles à son état attentionnel et émettaient des alternances de regard entre son visage et la nourriture cachée, validant ainsi trois des critères considérant un acte communicatif comme intentionnel (Leavens et al. 2005 ; Townsend et al. 2016).

Macaques rhésus et macaques de Tonkean qu'émandaient ainsi plus de nourriture face à une expérimentatrice se tenant face à eux les yeux ouverts que lorsque celle-ci avait la tête et les yeux orientés vers le haut ou de côté ou encore lorsqu'elle leur tournait le dos. En accord avec de précédentes études menées chez les grands singes (Kaminski et al. 2004 ; Liebal et al. 2004 ; Pika et al. 2005 ; Tempelmann et al. 2011) et les singes (Maille et al. 2012 ; Bourjade et al. 2013 ; Meunier et al. 2013), les macaques sont ainsi capables de discriminer des indices attentionnels « grossiers » tels que l'orientation du corps et du visage d'un humain. La distinction de tels indices corporels est aussi perceptible à travers leur comportement visuel: ils alternaient davantage leurs regards entre le visage de la partenaire et la nourriture cachée lorsque celle-ci était entièrement tournée vers eux. En revanche, les macaques ne qu'émandaient pas différemment face à une expérimentatrice ayant les yeux ouverts ou les yeux fermés, suggérant ainsi qu'ils ne discernent pas d'indices plus fins comme l'état des yeux. Il semblerait donc que, contrairement aux chimpanzés (Hostetter et al. 2007), babouins (Bourjade et al. 2013) et capucins (Hattori et al. 2010), les macaques rhésus et les macaques de Tonkean ne distinguent pas l'état des yeux dans leur appréciation de l'attention (**Articles 1 & 2**).

Nous avons néanmoins rapporté que les macaques rhésus émettaient moins d'alternances de regard lorsque l'expérimentatrice les regardait fixement que lorsqu'elle suivait leur propre regard, signalant ainsi une sensibilité accrue à une situation d'attention conjointe (**Article 2**). Il se pourrait donc que, comme pour les humains (Langton 2000 ; Langton & Bruce 2000), une combinaison d'indices - tête et yeux mobiles – plutôt qu'un seul, soit particulièrement efficace et signifiante afin d'estimer l'état attentionnel d'autrui. De plus, Hattori, Kuroshima et Fujita (2007) ont mis en lumière une sensibilité aux yeux chez des singes capucins, et cela uniquement à travers leurs comportements visuels et non gestuels. Cela nous amène à proposer que les alternances de regard, comportement spontané non entraîné (voir aussi Bourjade et al. 2014), sont peut-être une meilleure mesure de la sensibilité aux états attentionnels qu'un geste de qu'émande appris par conditionnement.

D'autres explications d'ordre méthodologique peuvent également expliquer nos résultats. En ce sens, les études précédentes ayant rapporté une faculté de discrimination de l'état des yeux chez les chimpanzés (Hostetter et al. 2007), capucins (Hattori et al. 2010) et babouins (Bourjade et al. 2013), diffèrent d'un point de vue méthodologique de la nôtre. En effet, le paradigme expérimental utilisé par ces auteurs plaçait les primates dans un contexte dyadique, par conséquent plus compétitif car ils devaient attirer l'attention de l'humain tenant la nourriture directement dans sa main alors que notre situation était triadique et requérait que les sujets attirent et dirigent l'attention de l'expérimentatrice vers une récompense alimentaire cachée se situant sur une table. Ainsi, la configuration triadique de notre expérience, plus coopérative qu'une situation dyadique aurait pu être trop artificielle pour des primates dont les capacités cognitives auraient été mieux révélées dans un contexte de compétition, écologiquement plus valide pour eux (Hare 2001). D'autre part, selon l'« hypothèse du choix d'objet abject » proposée par Mulcahy et Hedge (2012), la vue de plusieurs récipients spatialement proches et potentiellement remplis de nourriture aurait pu distraire le singe qui aurait détourné son attention de l'expérimentateur. La configuration de notre tâche, alors cognitivement plus exigeante, pourrait expliquer ces résultats divergents.

Pour conclure quant à cette première partie, nous avons montré que les macaques rhésus et les macaques de Tonkean étaient sensibles aux états attentionnels d'un humain, et plus particulièrement à l'orientation de son corps et de son visage mais pas à l'état de ses yeux (ouverts *versus* fermés). Nous avons aussi mis en évidence une sensibilité particulière des macaques rhésus à une combinaison d'indices « yeux et tête mobiles » correspondant à une situation d'attention conjointe. Ce résultat peut être mis en lien avec leur type de sociabilité qui se situe à l'opposé de celui des macaques de Tonkean. Les macaques de Tonkean font preuve d'une grande tolérance sociale, ponctués leurs conflits par de nombreuses protestations bidirectionnelles et dont l'issue résulte souvent en des réconciliations. En revanche, les macaques rhésus ont une vie sociale gouvernée par une hiérarchie stricte et leurs interactions, à l'instar des sociétés despotiques, sont très dépendantes de leurs relations hiérarchiques. Ainsi, chez les macaques rhésus, les membres du groupe surveillent sans cesse leurs congénères, sont à l'affût et réagissent au moindre changement de leur comportement. Ainsi, nous pouvons faire l'hypothèse que ce comportement de surveillance visuelle est plus développé chez les macaques rhésus en raison des particularités de leur système social. Ces résultats nous permettent-ils pour autant d'affirmer que les macaques *comprennent* que lorsque l'expérimentatrice est de dos ou de profil, elle est inattentive et ne *peut pas* les voir ? Car une explication de bas niveau cognitif

selon laquelle les macaques auraient appris au cours de leur vie un ensemble de règles comportementales simples telle que *<ne pas tenter de communiquer avec un individu qui ne me fait pas face>* est tout à fait plausible. Cette question reste ainsi ouverte et a motivé le second questionnement de ma thèse, à savoir : les macaques perçoivent-ils ce que leurs congénères peuvent et ne peuvent pas voir ?

2. Prise de perspective

Nous avons testé des macaques de Tonkean cette fois dans une situation de compétition écologiquement signifiante, originellement proposée par Hare, Call, Agnetta et Tomasello (2000) à des chimpanzés, dans laquelle un subordonné avait le choix entre récupérer un morceau de nourriture visible par un dominant ou en récupérer un caché à la vue de ce dernier. Nous avons également mis en place un contrôle en testant les dominants dans les mêmes conditions afin de vérifier que ces derniers n'avaient pas une préférence pour de la nourriture cachée, indépendamment d'un contexte de compétition alimentaire. Notre hypothèse était la suivante : si les subordonnés, et non les dominants, préfèrent se diriger vers le morceau de nourriture hors de la vue de leur congénère, cela pourrait alors vouloir dire que les macaques sont capables de prendre en compte la perspective visuelle de leurs congénères.

Nos résultats ont tout d'abord permis de valider la pertinence du contexte compétitif par différentes observations. En effet, tandis que les dominants choisissaient de se diriger vers de la nourriture quelque soit la condition expérimentale, les subordonnés préféraient, quant à eux, se diriger vers un des deux morceaux de banane uniquement lorsqu'ils avaient un accès visuel aux deux fruits et non à un seul. Et, plus la différence de rang existant entre les deux sujets testés était grande, moins les subordonnés se dirigeaient vers un morceau de nourriture (**Article 3**). Nos résultats confirment ainsi la pertinence du paradigme expérimental naturaliste utilisé consistant à placer un subordonné dans une situation de compétition alimentaire avec un congénère dominant. En effet, la configuration spatiale et la dimension de notre zone de test furent adéquates pour créer une situation de compétition appropriée, à la différence d'études précédentes dont la taille de la pièce expérimentale était réduite et qui rapportèrent des résultats négatifs pour la prise de perspective visuelle (Karin-D'Arcy & Povinelli 2002 ; Hare et al. 2003 ; Bräuer et al. 2007 ; Burkart & Heschl 2007).

De plus, nos subordonnés ne choisissaient pas aléatoirement le morceau de nourriture, montrant une préférence significative pour le morceau de banane caché à la vue du dominant, et ce, lorsqu'ils étaient relâchés simultanément mais aussi avant le dominant dans la zone de

test. Ainsi, les subordonnés faisaient un choix de direction indépendamment de celui du dominant et non comme une conséquence du comportement de ce dernier. Les dominants, placés dans les mêmes conditions, n'exprimaient quant à eux, aucune préférence et semblaient choisir un des deux morceaux de nourriture aléatoirement, rendant l'hypothèse d'une préférence spontanée des macaques pour de la nourriture dissimulée peu probable (**Article 3**). Fidèles à notre hypothèse de départ, nos résultats suggèrent donc que les macaques de Tonkean se comportent selon ce que les autres peuvent et ne peuvent pas voir, comme cela fut proposé pour les chimpanzés (Hare et al. 2000 ; 2001 ; Bräuer et al. 2007), les macaques rhésus (Flombaum & Santos 2005) et les macaques à longue-queue (Overduin-de Vries et al. 2014).

Toutefois, cette conclusion peut être remise en question : une explication de plus bas niveau cognitif comme une lecture de comportement pourrait être invoquée à la place d'une prise de perspective visuelle. Selon l'« hypothèse de l'œil maléfique » (Kaminski et al. 2008) et autres règles de lecture comportementale (Heyes 1998 ; Povinelli & Vonk 2003 ; 2004), les subordonnés auraient pu être influencés par la vue du dominant à travers la trappe transparente. Ainsi, les subordonnés se seraient préférentiellement dirigés vers le morceau de nourriture caché et auraient évité le fruit visible, non pas parce qu'ils comprenaient que le morceau caché était hors de la vue du dominant mais parce que le morceau de banane visible était considéré comme « contaminé » par le regard persistant du dominant. La pose de miroirs sans tain sur les trappes, adoptée par Overduin-de Vries, Spruijt et Sterck (2014), est une bonne solution afin d'exclure cette hypothèse alternative. Ces auteurs ayant rapporté des preuves de prise de perspective visuelle malgré l'utilisation de ces miroirs chez les macaques à longue-queue, proches cousins des macaques de Tonkean, notre hypothèse reste plausible : cette capacité pourrait être un trait cognitif partagé par les grands singes et les singes de l'Ancien Monde au sein de l'arbre phylogénétique.

Un autre résultat renforce l'hypothèse de la prise de perspective visuelle par les macaques de Tonkean: certains subordonnés utilisaient des stratégies particulières face au dominant pour obtenir la nourriture. Au fil de l'expérience, les subordonnés se dirigeaient moins souvent en premier lieu vers la nourriture cachée notamment lorsqu'ils avaient accès à la zone de test un peu avant et non au même moment que le dominant. Comme rapporté chez les macaques à longue-queue (Overduin-de Vries et al. 2014), une des stratégies employée par certains subordonnés était alors de se diriger d'abord et rapidement vers le morceau de nourriture visible ce qui leur permettait de récupérer ainsi les deux morceaux de banane. Une autre stratégie utilisée par quelques subordonnés était de traverser et de quitter la zone de test,

suivi de près par le dominant, puis d'y revenir ensuite rapidement pour saisir le morceau de nourriture caché lorsque le dominant n'y était plus (**Article 3**). Ce comportement, précédemment décrit comme de la rétention d'information par certains auteurs (Ducoing & Thierry 2003) pose question quant aux mécanismes sous-jacents impliqués. Ces stratégies comportementales suggérant de la tromperie dépendent-elles de mécanismes cognitifs simples de lecture et d'inhibition comportementale ou bien de processus cognitifs plus complexes impliquant une intention de manipuler le savoir ou les perceptions d'autrui ? Cela constitua le questionnement de la troisième partie de ma thèse.

3. Manipulation sociale

Placés dans un contexte de compétition alimentaire, nous avons rapporté que les subordonnés macaques de Tonkean utilisaient plusieurs catégories de tromperie tactique décrites par Byrne et Whiten (1992), et ce, sans apprentissage au cours de l'expérience car observé dès les premiers essais. Comme cela a déjà été décrit dans de précédentes études (Ducoing & Thierry 2003 ; 2004), les subordonnés mettaient en place de telles stratégies plus particulièrement face à un dominant haut placé par rapport à eux dans la hiérarchie que face à un congénère leur étant hiérarchiquement plus proche. La stratégie la plus fréquemment utilisée était la « dissimulation d'intérêt pour un objet » consistant pour le subordonné à réfréner son intérêt pour la nourriture cachée en évitant de se diriger et de regarder vers le morceau de banane dissimulé ou encore en se figeant. Cette tactique, inefficace lorsque utilisée seule, était souvent combinée à de la « dissimulation en se cachant » dans laquelle les subordonnés agissaient de telle façon qu'ils ne pouvaient être visuellement détectés par le dominant : ils restaient hors de sa vue ou se dirigeaient vers le morceau de fruit caché une fois que ce dernier avait le dos tourné. Ce type de dissimulation a déjà été décrit dans le contexte de copulations hors de la vue du mâle alpha chez des geladas (le Roux et al. 2013) et des macaques à longue-queue (Overduin-de Vries et al. 2015). En complément d'un ou de ces deux types de stratégies, certains subordonnés utilisaient une tactique plus active appelée « distraction par déplacement » : les subordonnés quittaient d'emblée la zone de test puis y revenaient rapidement pour récupérer le morceau de nourriture caché après que le dominant l'ait quittée. Une seule occurrence de « distraction par interaction directe » au cours de laquelle le subordonné se dirigea d'abord vers la nourriture visible puis interagit avec le dominant en lui reniflant le museau avant de se diriger vers la nourriture cachée fut enregistrée (**Article 4**).

La classification des stratégies de tromperie tactique proposée par Byrne et Whiten (1990 ; 1992) étant purement fonctionnelle, aucune supposition quant à leurs mécanismes cognitifs sous-jacents n'a été émise par ces auteurs. Deux types d'interprétation peuvent à chaque fois être invoqués pour expliquer le comportement des subordonnés (voir Meunier *in press*). D'une part, le subordonné pourrait être uniquement inhibé par la vue, le regard et la présence du dominant et aurait appris au cours de sa vie des règles comportementales simples l'amenant à éviter un objet convoité par un dominant sans inférer ce que l'autre peut et ne peut pas voir ou savoir (lecture de comportement : *e.g.* Povinelli & Vonk 2003). D'autre part, le subordonné pourrait être capable d'adopter la perspective visuelle du dominant et comprendre que celui-ci ne voit ou ne sait pas qu'il y a un morceau de nourriture caché à sa vue, et pourrait par conséquent tenter de le duper intentionnellement (lecture mentale : *e.g.* Call & Tomasello 2008). Notre étude ne nous permet toutefois malheureusement pas d'investiguer plus précisément les mécanismes cognitifs sous-jacents impliqués dans les stratégies émises par les subordonnés.

Nous avons voulu savoir si les subordonnés se comportaient en fonction du comportement du dominant et quels indices comportementaux de ce dernier ils utilisaient. L'analyse fine des comportements des subordonnés simultanément à ceux des dominants a révélé des interactions significatives entre tous les comportements d'intérêt quant à la tromperie tactique du subordonné (*e.g.* comportement d'arrêt ; déplacement, orientation du corps et du visage ailleurs que vers la nourriture et le dominant) et tous les comportements du dominant (*e.g.* visibilité ; présence ; distance ; déplacement ; orientation du corps et du visage ; position et perception) excepté pour le déplacement ailleurs du subordonné selon l'état de visibilité du dominant (**Article 4**). Cela veut dire que les subordonnés, remarquables lecteurs de comportements, prirent en compte le comportement du dominant et ajustèrent le leur en conséquence. Le fait que les subordonnés se déplacèrent ailleurs quelque soit la visibilité du dominant et non les autres comportements peut être une marque d'intentionnalité mais ce résultat doit toutefois être pris avec prudence. En effet, c'est le seul comportement émis par les subordonnés de manière indépendante à un des comportements du dominant ; il serait alors intéressant de vérifier ce résultat dans de futures études et d'approfondir nos connaissances sur les indices comportementaux qui sont pris en compte par ces animaux dans un contexte intraspécifique. La forte dépendance existante entre le comportement des subordonnés et des dominants pour la grande majorité des comportements étudiés peut donner lieu aux deux interprétations possibles que sont la lecture de comportement et la lecture mentale. Ainsi, l'ajustement des subordonnés au comportement du dominant pourrait indiquer

aussi bien de la rétention d'information que de la manipulation active d'information (Cheney & Seyfarth 1990 ; Kirkpatrick 2007). Cette question ouverte amène le quatrième questionnement de ma thèse : les macaques de Tonkean sont-ils capables de discriminer les intentions d'autrui ?

4. Compréhension des intentions

L'expérience menée chez les macaques de Tonkean a permis de tester leur capacité de discrimination des actions intentionnelles émises par une expérimentatrice qui était réticente ou incapable de leur donner une récompense alimentaire ou encore distraite. Nos résultats montrent qu'à l'image des jeunes enfants (Behne et al. 2005 ; Marsh et al. 2010), chimpanzés (Call et al. 2004), capucins (Phillips et al. 2009) et macaques rhésus (Wood et al. 2007), les macaques de Tonkean se comportaient *comme s'ils* comprenaient les intentions de l'expérimentatrice-réticente à leur donner une récompense alimentaire ou de l'expérimentatrice incapable de le faire. En effet, ils émettaient plus d'alternances de regard entre son visage et sa main, la menaçaient davantage et tentaient d'attraper l'objet qu'elle tenait dans sa main (raisin sec ou caillou) significativement plus souvent lorsque celle-ci était « mal » intentionnée (réticente) que « bien » intentionnée (mais incapable) ou distraite. Ils se montraient de la même manière plus actifs en condition « expérimentatrice incapable » qu'en condition « expérimentatrice distraite ». De plus, quand l'expérimentatrice était distraite, les macaques de Tonkean quémendaient davantage à travers la fente et regardaient plus longtemps ailleurs que dans sa direction ou dans celle du dispositif que lorsqu'elle était incapable ou réticente à leur donner la nourriture. Face à un humain incapable de leur donner le raisin, ils tentaient plus souvent d'attraper le fruit en relevant leur bras au-dessus de la fente, montrant ainsi qu'ils comprenaient que la barrière physique les empêchait de recevoir la récompense (**Article 5**). Les macaques se comportaient de la sorte sans avoir reçu d'entraînement au préalable, contrairement à une étude précédente rapportant des résultats négatifs chez des individus de la même espèce (Costes-Thiré et al. 2015). D'autre part, l'expérimentatrice effectuait exactement les mêmes mouvements et alternances de regard dans les trois conditions, éliminant ainsi la possibilité que les macaques se basent sur la topographie de ses comportements moteurs et visuels pour discriminer les situations.

Ces résultats peuvent à nouveau être interprétés à la lumière des deux hypothèses que sont la lecture mentale et la lecture comportementale. D'une part, selon l'hypothèse de mentalisation (Dennett 1987, Call & Tomasello 2008 ; Caron 2009), les macaques de

Tonkean comprendraient pourquoi l'assistante se comporte différemment dans les trois situations en inférant ses intentions sous-jacentes. Ainsi, ils n'auraient pas uniquement perçu son comportement mais l'auraient interprété comme une volonté ou non de sa part de leur donner la nourriture. L'utilisation ici de notions de « volonté » et de « bonnes » ou « mauvaises » intentions est toutefois discutable : ces concepts ont-ils un sens pour des primates ? D'autre part, en accord avec l'hypothèse de lecture de comportement, les macaques de Tonkean comprendraient les actions dirigées vers un but sans avoir recours à la représentation d'états mentaux comme les intentions mais plutôt en faisant appel à des associations rapides, simples et automatiques (Butterfill & Apperly 2013 ; Heyes 2014). L'« hypothèse d'abstraction comportementale », proposée par Povinelli et Vonk (2003), suggère que les macaques pourraient associer les actions (nourriture proche *versus* nourriture éloignée) avec leur résultat (probabilité forte d'obtenir la nourriture *versus* probabilité faible d'obtenir la nourriture). Transcrite en mots, ils auraient pu suivre la règle suivante : *<lorsqu'il y a une barrière physique entre la nourriture et moi, je ne peux pas y accéder>* au lieu de mentaliser : *<l'expérimentatrice est disposée à me donner la nourriture mais elle en est incapable à cause de la barrière physique>*.

La notion d'intention n'est pas un concept unitaire et peut se décliner selon plusieurs niveaux allant de la compréhension du but d'une action au raisonnement d'états mentaux abstraits (Chiavarino et al. 2013). Si l'on se fie à certaines définitions selon lesquelles il s'agit d'un plan d'action émis dans un but précis (Tomasello et al. 2005), ou encore à la notion d'« intention dans l'action » qui, selon Searle (1983), est directement percevable à travers les mouvements corporels, nous pouvons alors suggérer que les macaques de Tonkean en sont capables. Cette proposition est renforcée par l'existence d'un système de neurones miroirs dans le cortex pré-moteur et le sillon intra-pariétal antérieur des primates leur permettant d'avoir une compréhension, dite basique, des buts d'une action physique *via* des relations comportementales (Gallese 2007 ; Rizzolatti & Sinigaglia 2010 ; Tramacere & Ferrari 2016). En revanche, si l'on adopte une définition plus riche des intentions à travers les termes d'« intention préalable » (Searle 1983) ou d'« intention informative » (Sperber & Wilson 1995) requérant une représentation mentale et conceptuelle des propriétés logiques et sémantiques des intentions, il est alors plus difficile de se prononcer (**Article 5**).

Cette conception d'intention, dont aucune définition n'est communément acceptée dans la littérature, pose question et il se pourrait que les enfants préverbaux et les primates ne comprennent pas les intentions d'autrui à la manière des humains adultes. Après tout, comment savons-nous, nous humains, ce que c'est qu'avoir une intention ? N'avons-nous pas

été capables un jour de poser ce mot – intention – sur quelque chose qui nous était alors visuellement perceptible et compréhensible avant même que nous ne puissions le verbaliser ? L'hypothèse qu'il existerait alors une autre façon de comprendre les intentions - et peut-être de les « mentaliser » - pour les êtres sans langage ne paraît alors pas si saugrenue. En ce sens, nous pouvons suivre la proposition de Grandin (1995 ; 2002 ; 2004 ; 2009) pour qui les animaux seraient capables de naviguer dans une large banque mentale de données sensorielles leur permettant d'accéder aux perceptions et intentions d'autrui en « pensant en images » plutôt qu'en « pensant en mots ».

L'analyse des résultats de ma thèse montre que les macaques font preuve de comportements extrêmement complexes *comme s'ils* étaient capables de discriminer et comprendre les états attentionnels, la perspective visuelle et les intentions d'autrui. Il est alors tentant de conclure que, comme leurs cousins humains, ils peuvent se représenter mentalement ces états mentaux, suggérant une faculté cognitive anciennement acquise au cours de l'évolution. Toutefois, des hypothèses de plus bas niveau cognitif considérant des associations simples d'indices comportementaux peuvent être invoquées. Ces deux visions divergentes sont au cœur du débat bouillonnant à la fois méthodologique et théorique qui stimule la recherche sur la Théorie de l'Esprit.

5. Lecture de comportement ou lecture d'esprit ?

5.1. Casse-tête méthodologique

Outre le fait que de nombreuses études aient nécessité un grand nombre d'essais pouvant aboutir à des apprentissages, aient manqué de contrôles et aient testé des primates dans des contextes de coopération pouvant être peu significatifs pour eux (cf. introduction ; Byrnie 2006 ; van der Vaart & Hemelrijk 2014), le problème méthodologique majeur de la recherche sur la Théorie de l'Esprit réside en la difficulté de mettre au point un paradigme expérimental permettant d'expliquer les comportements observés par de réelles capacités de lecture mentale et non par des mécanismes plus simples. Ce problème, connu sous le nom de « problème logique » ou « problème de Povinelli » (Povinelli & Vonk 2004) a amené de nombreux biologistes, psychologues et philosophes à douter de la validité des résultats positifs jusqu'alors rapportés chez les enfants et chez plusieurs espèces animales (Heyes 1998 ; Penn & Povinelli 2007 ; Lurz 2009 ; Shettleworth 2010 ; Lurz & Krachun 2011). Pour

illustrer cela, si l'on tente de verbaliser ce que pourrait être la pensée d'un singe regardant un expérimentateur saisir un grain de raisin, nous pourrions l'interpréter simplement de la façon suivante *<lorsque je saisis un raisin, je le mange ; un expérimentateur saisissant un raisin devrait aussi le manger>* à la place de *<lorsque je saisis un raisin, j'ai l'intention de le manger ; un expérimentateur saisissant un raisin devrait aussi avoir l'intention de le manger>*. La différence réside en ce que dans la première proposition, une simple relation entre l'action et son issue peut être invoquée tandis que la seconde version requiert l'attribution du concept d'intention.

5.2. Casse-tête théorique

La recherche dans ce domaine chez les primates est par conséquent habitée par deux clans principaux : les « sceptiques » et les « partisans » de la Théorie de l'Esprit (voir Meunier *in press* pour une révision bibliographique). Tandis que les premiers clament que les animaux prédisent le comportement des autres uniquement grâce au décryptage de caractéristiques environnementales telles que couleurs, formes et mouvements (sous-mentalisation : Heyes 2014 ; 2015) ou de relations et associations d'indices comportementaux (lecture de comportement : Povinelli & Vonk 2003 ; 2004 ; Gallagher & Povinelli 2012 ; variables intermédiaires : Whiten 2013), les seconds soutiennent que les primates interprètent les comportements en termes d'états mentaux tels que 'voir' et 'savoir' (lecture mentale : Call et al. 2004 ; Hare et al. 2000 ; 2001 ; Buttelmann et al. 2007 ; Call & Tomasello 2008 ; Schmelz et al. 2010 ; Overduin-de Vries et al. 2014). D'autres auteurs préfèrent adopter quant à eux un « agnosticisme optimiste » leur évitant de juger si les animaux sont capables ou pas de mentalisation tant qu'une solution méthodologique au problème de Povinelli n'est pas trouvée (Fitzpatrick 2008 ; Lurz et al. 2014).

La recherche sur la Théorie de l'Esprit se confronte à un autre problème substantiel et théorique : il n'existe pas de définition déposée, claire et précise de ce qu'est qu'avoir une Théorie de l'Esprit ou de faire preuve de lecture mentale ou mentalisation (Heyes 2015). Il est communément admis que la compréhension des états mentaux d'autrui repose sur un système d'inférences (Premack & Woodruff 1978) mais le type et le contenu de ces inférences, chaudement débattus, restent obscurs. La controverse théorique touchant la Théorie de l'Esprit est en réalité plus complexe que la vision dichotomique 'lecture de comportement' *versus* 'lecture d'esprit'. En effet, certains auteurs ont une vision quelque peu différente et considèrent que la Théorie de l'Esprit consiste en un système à deux niveaux (Frith & Frith

2008 ; Apperly & Butterfill 2009 ; Baillargeon et al. 2010 ; Butterfill & Apperly 2013 ; Christensen & Michael 2016). Ces chercheurs se basent sur des études rapportant que les jeunes enfants seraient capables de discriminer les fausses croyances dès leur première année de vie (Woodward 1998 ; Gergely et al. 2002 ; Behne et al. 2005 ; Onishi & Baillargeon 2005) et que les adultes seraient capables d'attribuer des états mentaux aux autres parfois de manière implicite, rapide et cognitivement efficace (Sebanz et al. 2003 ; Kovacs et al. 2010 ; Samson et al. 2010 ; Santiesteban et al. 2014). Certains auteurs distinguent ainsi i) un premier système dit de 'mentalisation implicite' consistant en des processus cognitifs rapides, inflexibles, automatiques et inconscients, ii) d'un second système appelé 'mentalisation explicite', requérant des mécanismes lents, flexibles, conscients et mentalement plus exigeants (Frith & Frith 2008 ; 2012 ; van Overwalle & Vandekerckhove 2013). Les jeunes enfants et animaux seraient dotés du premier système tandis que seuls les adultes seraient pourvus des deux processus fonctionnant en parallèle. Selon Gómez (1999), une « Théorie implicite de l'esprit » reposerait non pas sur des représentations d'états mentaux inobservables mais sur des représentations de comportements observables.

Selon Butterfill et Apperly (2013), les enfants et les animaux seraient dotés d'un premier système appelé « Théorie de l'Esprit minimale » impliquant la représentation de relations entre agents, objets et localisations mais pas celle des états mentaux en tant que tels. Enfants et animaux seraient capables de se représenter la *causalité* d'actions comme *dirigées vers un but* après les avoir *rencontrées* et *enregistrées* sans avoir recours à des concepts psychologiques comme les intentions ou les croyances. Un second système dépendant du langage et des fonctions exécutives se développant plus tard au cours de l'ontogénie, et pouvant être facilité par un apprentissage, existerait uniquement chez les adultes (Apperly & Butterfill 2009).

D'autres auteurs suggèrent que les primates sont capables d'un premier niveau de mentalisation leur permettant d'attribuer des états mentaux à autrui congruents à la réalité tels que voir, savoir et ignorer ainsi que des états motivationnels comme désirer et avoir un but. En revanche, les primates seraient dépourvus de la capacité à attribuer des états mentaux non conformes à la réalité comme les fausses croyances ou les perceptions erronées (Fletcher & Carruthers 2013 ; Martin & Santos 2016). Selon Martin et Santos (2016), les résultats positifs rapportés jusqu'à présent chez des espèces de singes et de grands singes pourraient être interprétés comme des preuves de « relation de connaissance » leur permettant de se représenter les relations entre agents et les informations qui sont vraies de leur point de vue (cf. « Théorie de l'Esprit Brentanienne » : Gómez 2009). Les résultats négatifs quant à la

compréhension des fausses croyances rapportés chez les primates (Kaminski et al. 2008 ; Martcorena et al. 2011 ; Martin & Santos 2014 mais voir Krupenye et al. 2016 pour un avis divergent concernant la compréhension des fausses-croyances chez les grands singes) pourraient s'expliquer par l'absence de « relation représentationnelle » au sein de ces espèces, postulant qu'ils sont capables de se représenter le fait que certains états du monde sont différents ou découplés de leurs propres perceptions de la réalité (cf. « Théorie de l'Esprit Représentationnelle » : Gómez 2009).

6. Quelles solutions à ce puzzle ?

Comment déterminer quels processus cognitifs sous-jacents aux comportements complexes des primates sont en jeu lorsqu'un grand nombre d'explications allant des plus bas aux plus hauts niveaux cognitifs peut être proposé ? Quelles hypothèses doivent être préférées et pour quelles raisons ? En psychologie animale, un principe de parcimonie appelé « canon de Morgan » (Morgan 1894) selon lequel un comportement ne doit en aucun cas être interprété comme la conséquence d'une faculté mentale élaborée si ce même comportement peut être considéré comme le fruit d'une activité mentale moins élevée est communément accepté par les scientifiques. La controverse concernant la Théorie de l'Esprit est construite sur ce postulat qui est de plus en plus remis en question par de nombreux philosophes (Fitzpatrick 2008 ; Clatterbuck 2015 ; Halina 2015 ; Fagan 2016). En effet, le débat porte sur ce que signifie être l'explication la plus parcimonieuse. Selon ces auteurs, de nombreux principes de parcimonie peuvent être émis, et l'hypothèse de lecture comportementale n'est pas forcément plus parcimonieuse que celle de lecture mentale si l'on s'intéresse par exemple au nombre de connections nécessaires qu'un individu doit former entre un agent et un objet dans une situation donnée (Fagan 2016). Afin de tenter de résoudre cette antinomie entre lecture de comportement et lecture mentale, il est désormais nécessaire de définir clairement ce que l'on entend par mécanismes cognitifs impliqués et de construire des protocoles expérimentaux permettant d'éliminer le problème de Povinelli.

Heyes (1998) a proposé le paradigme expérimental dit des « visières opaques » repris par Povinelli et Vonk (2003 ; 2004) sous l'appellation d'« expérience des lunettes noires » permettant de résoudre ce problème. L'idée est que les primates fassent l'expérience de deux paires de lunettes noires au cours d'une phase d'apprentissage. Vues de l'extérieur, les deux paires de lunettes diffèrent uniquement par la couleur de leurs montures. En revanche, lorsqu'ils les portent, les sujets se rendent compte qu'une des paires est opaque alors que

l'autre est transparente. Lors de la phase de test, les sujets sont testés dans une variante de la « tâche de choix d'objet » dans laquelle ils peuvent quémander de la nourriture envers deux expérimentateurs portant chacun une des paires de lunettes noires, un pouvant voir à travers, l'autre pas. L'hypothèse est alors la suivante : si les singes sont capables de mentalisation, ils devraient utiliser leur propre expérience et la projeter aux autres pour inférer leurs états mentaux. En d'autres termes, les individus devraient préférer quémander de la nourriture à l'expérimentateur qui porte les lunettes lui permettant de voir. Les sujets n'ayant précédemment jamais observé les expérimentateurs interagir avec les lunettes, un effet d'apprentissage par observation est exclu. Tandis que Vonk et Povinelli (2011) rapportèrent des résultats négatifs dans une étude pilote chez trois chimpanzés, Karg, Schmelz, Call et Tomasello (2015) ont récemment montré pour la première fois que les chimpanzés étaient capables d'utiliser leur propre expérience pour inférer ce qu'un compétiteur humain pouvait voir ou ne pas voir (mais pas dans une tâche de suivi de regard). Toutefois, selon certains sceptiques, les chimpanzés ne feraient pas l'expérience de « voir » à travers les lunettes transparentes en se représentant un tel concept mais plutôt l'expérience d'avoir une « ligne de vue dégagée » en utilisant des concepts de transparence et d'opacité (Lurz 2009 ; Perner 2012). Aucune expérience de ce type n'a en revanche été menée à ce jour chez des singes.

D'autres protocoles, basés sur la discrimination entre l'apparence et la réalité, permettant de surmonter le problème logique ont été proposés par Lurz (2009 ; 2011) et Lurz et Krachun (2011). Le principe général de ce type d'expérience implique des écrans déformant la taille des images dans un contexte de compétition alimentaire entre un subordonné et un dominant. Lors d'une phase d'entraînement, les subordonnés apprennent que lorsque le dominant est autorisé à choisir en premier entre un raisin de petite taille et un raisin de grosse taille situés derrière des écrans transparents, celui-ci choisit toujours le gros raisin. Ils apprennent aussi qu'afin de recevoir le grain de raisin restant, ils doivent toucher une cible devant l'item convoité avant que le compétiteur ne fasse son choix. Lors de la phase de test, les écrans transparents sont remplacés par des écrans d'aspect semblable sauf que l'un distord l'image du raisin le rendant artificiellement plus gros, l'autre le faisant apparaître faussement plus petit. Contrairement au dominant qui n'assiste pas à la scène, le subordonné observe le placement de deux raisins de tailles identiques derrière chaque écran. Le compétiteur arrive ensuite et peut faire son choix entre les deux raisins placés derrière les écrans déformants. Avant cela, et pour obtenir le raisin non choisi par le dominant, le subordonné doit anticiper quel sera le choix de son congénère. Une prédiction correcte consiste à reconnaître que le dominant percevra le raisin illusoirement plus gros que sa taille

réelle et choisira celui-ci. Un tel résultat indiquerait ainsi une capacité à attribuer de fausses perceptions à autrui (Lurz et al. 2014). Quatre études utilisant des protocoles plus ou moins similaires ont été menées chez des chimpanzés (Krachun et al. 2009 ; Karg et al. 2014 ; Karg et al. 2016 ; Krachun et al. 2016) et aucune chez des singes. Alors que certaines études rapportèrent des résultats peu concluants quant à l'attribution de fausses perceptions à autrui (Krachun et al. 2009 ; Karg et al. 2016), d'autres fournirent des résultats prometteurs suggérant que les chimpanzés sont capables de faire la distinction entre les propriétés apparentes des objets et leurs réelles particularités (Karg et al. 2014 ; Krachun et al. 2016).

7. Conclusion générale

Ma thèse a démontré que les macaques se comportaient *comme s'ils* comprenaient les états attentionnels, les intentions et les perceptions d'autrui. De nombreuses interprétations quant aux mécanismes cognitifs impliqués dans ces comportements – lecture comportementale à lecture mentale – pouvant être invoquées, mon travail doctoral apporte des connaissances au niveau *fonctionnel* plutôt qu'au niveau *causal* (cf. Penn & Povinelli 2009). Ainsi, quels que soient les mécanismes sous-jacents en cause, les macaques font preuve de comportements extrêmement complexes qui leur permettent de faire face aux défis sociaux de leur espèce. Tant que les processus cognitifs restent indéterminés, il est difficile de retracer l'apparition de ces capacités cognitives au cours de l'évolution. Il semblerait toutefois qu'humains, grands singes et singes, partagent au moins certaines capacités sociocognitives. Il pourrait s'agir d'une « mentalisation implicite » (Frith & Frith 2008) ou d'une « Théorie de l'Esprit minimale » (Butterfill & Apperly 2013) partagée avec leur ancêtre commun il y a environ 30 à 40 millions d'années. Par ailleurs, les primates, et peut-être d'autres espèces animales, auraient pu développer indépendamment un autre type de mentalisation différent de celui de l'espèce humaine requérant des représentations non basées sur le langage articulé.

Les primates ne perçoivent probablement pas les états mentaux d'autrui comme les êtres langagiers que nous sommes. Tout simplement parce que nous avons posé des mots et créé des concepts qui ne sont certainement pas accessibles en tant que tels à des êtres sans parole. Toutefois, une partie du contenu de ces notions ne semble pas étrangère aux enfants préverbaux ni aux animaux. Une représentation mentale basée autrement que sur les mots existerait-elle ? Dans cette optique et afin d'outrepasser la dichotomie lecture de comportement *versus* lecture d'esprit, je suggérerais, en accord avec Grandin (2002 ; 2004), qu'il puisse exister une autre forme de mentalisation c'est-à-dire de représentation mentale

basée sur différentes modalités sensorielles plutôt que sur les mots. Ainsi, des animaux ayant le sens de la vue bien développé, comme les macaques par exemple, pourraient se représenter visuellement la perception visuelle d'autrui en naviguant au sein d'une représentation mentale graphique de l'environnement leur permettant de se mettre picturalement à la place des autres. Le concept « voir » que nous, humains, avons nommé de la sorte pourrait alors être accessible aux animaux d'une façon différente et non verbalisée.

Ma thèse apportant plus de questions que de réponses, ce débat fascinant reste ouvert. La nécessité de définir plus clairement les termes utilisés de représentation, mentalisation et lecture mentale ainsi que l'emploi de protocoles plus contrôlés sont essentiels. En ce sens, je propose d'adopter l'« agnosticisme optimiste » de Lurz, Kanet et Krachun (2014) en refusant de dénier trop rapidement des capacités de mentalisation aux animaux sans clamer pour autant qu'ils en sont capables. La difficulté majeure de ce challenge est de s'adresser aux animaux autrement qu'à travers nos propres termes et concepts mais plutôt en prenant en compte leur *umwelt* ou monde vécu (von Uexküll 1965), différent du nôtre et certainement à l'origine de multiples formes d'intelligence.

REFERENCES BIBLIOGRAPHIQUES

- Amici F., Aureli F. & Call J. 2010. Monkeys and apes: Are their cognitive skills really so different? *American Journal of Physical Anthropology*, 143: 188-197.
- Anderson J.R., Sallaberry P. & Barbier H. 1995. Use of experimenter-given cues during object-choice tasks by capuchin monkeys. *Animal Behaviour*, 49(1): 201–208.
- Anderson J.R., Montant M. & Schmitt D. 1996. Rhesus monkeys fail to use gaze direction as an experimenter-given cue in an object-choice task. *Behavioural Processes*, 37(1): 47–55.
- Anderson J.R., Kuroshima H., Kuwahata H., Fujita K. & Vick S.J. 2001. Training squirrel monkeys (*Saimiri sciureus*) to deceive: acquisition and analysis of behavior toward cooperative and competitive trainers. *Journal of Comparative Psychology*, 15(3): 282-293.
- Anderson J.R., Kuroshima H., Hattori Y. & Fujita K. 2010. Flexibility in the use of requesting gestures in squirrel monkeys (*Saimiri sciureus*). *American Journal of Primatology*, 72: 707–714.
- Apperly I.A. & Butterfill S.A. 2009. Do humans have two systems to track beliefs and belief-like states? *Psychological Review*, 116(4): 953-970.
- Baillargeon R., Scott R.M. & He Z. 2010. False-belief understanding in infants. *Trends in Cognitive Sciences*, 14(3): 110-118.
- Bania A.E. & Stromberg E.E. 2013. The effect of body orientation on judgments of human visual attention in western lowland gorillas (*Gorilla gorilla gorilla*). *Journal of Comparative Psychology*, 127(1): 82–90.
- Baron-Cohen S. 1995. *Mindblindness: an essay on autism and theory of mind*. MIT Press, Cambridge, MA.
- Baron-Cohen S., Leslie A.M. & Frith U. 1985. Does the autistic child have a “theory of mind”? *Cognition*, 21: 37-46.
- Barth J., Reaux J.E. & Povinelli D.J. 2005. Chimpanzees’ (*Pan troglodytes*) use of gaze cues in object-choice tasks: different methods yield different results. *Animal Cognition*, 8: 84–92.
- Barton R.A. 2006. Primate brain evolution: integrating comparative, neuro-physiological, and ethological data. *Evolutionary Anthropology: Issues, News, and Reviews*, 15: 224-236.

- Beck B.B. 1982. Chimpocentrism: Bias in cognitive ethology. *Journal of Human Evolution*, 11: 3-17.
- Behne T., Carpenter M., Call J. & Tomasello M. 2005. Unwilling versus unable: infants' understanding of intentional action. *Developmental Psychology*, 41(2): 328-337.
- Boesch C. 2012. The ecology and evolution of social behavior and cognition in primates. In: J. Vonk & T. Shackelford (Eds.), *The Oxford Handbook of Comparative Evolutionary Psychology*. (pp. 486-503). Oxford: Oxford University Press.
- Bolhuis J.J. & Wynne C.D.L. 2009. Can evolution explain how minds work? *Nature*, 458: 832-833.
- Bourjade M., Meguerditchian A., Maille A., Gaunet F. & Vauclair J. 2013. Olive baboons, *Papio anubis*, adjust their visual and auditory intentional gestures to the visual attention of others. *Animal Behaviour*, 87: 121–128.
- Bourjade M., Canteloup C., Meguerditchian A., Vauclair J. & Gaunet F. 2014. Training experience in gestures affects the display of social gaze in baboons' communication with a human. *Animal Cognition*, 18(1): 239-250.
- Brandone A.C. & Wellman H.M. 2009. You can't always get what you want: infants understand failed goal-directed actions. *Psychological Science*, 20: 85-91.
- Bräuer J., Call J. & Tomasello M. 2007. Chimpanzees really know what others can see in a competitive situation. *Animal Cognition*, 10(4): 439–448.
- Bray J., Krupenye C. & Hare G. 2014. Ring-tailed lemurs (*Lemur catta*) exploit information about what others can see but not what they can hear. *Animal Cognition*, 17(3): 735–744.
- Brentano F. 1995. *Psychology from an empirical standpoint*. O. Kraus & L.L. McAlister (Eds.), Translated by A.C. Rancurello, D.B. Terrell, & L. L. McAlister, 2nd edition. New introduction by P. Simons. London & New-York: Routledge.
- Bulloch M.J., Boysen S.T. & Furlong E.E. 2008. Visual attention and its relation to knowledge states in chimpanzees, *Pan troglodytes*. *Animal Behaviour*, 76: 1147-1155.
- Burkart J.M. & Heschl A. 2007. Understanding visual access in common marmosets, *Callithrix jacchus*: perspective taking or behaviour reading? *Animal Behaviour*, 73(3): 457–469.
- Burkart J.M., Schubiger M.N. & van Schaik C.P. 2016. The evolution of general intelligence. *Behavioral and Brain Sciences*, 1: 1-65.
- Butler A.B. 2009. Homology and homoplasy. In: L.R. Squire (Ed.), *Encyclopedia of Neuroscience*, 4:1-5. Oxford Academic Press.

- Buttelmann D., Carpenter M., Call J. & Tomasello M. 2007. Enculturated chimpanzees imitate rationally. *Developmental Science*, 10(4): F31-F38.
- Butterfill S.A. & Apperly I.A. 2013. How to construct a minimal theory of mind. *Mind & Language*, 28(5): 606-637.
- Byrne R.W. 1995. Primate cognition: comparing problems and skills. *American Journal of Primatology*, 37: 127-141.
- Byrne R.W. 2000. Evolution of primate cognition. *Cognitive Sciences* 24(3): 543-570.
- Byrne R.W. 2003. Tracing the evolutionary path of cognition. In M. Brüne, H. Ribbert, & W. Schiefenhövel (Eds.), *The social brain: evolution and pathology* (pp. 43-60). John Wiley & Sons, Ltd.
- Byrne R.W. 2013. Primate intelligence. In: W. Henke, H. Rothe & I. Tattersall (Eds.), *Handbook of palaeoanthropology, vol. 2. Primate evolution and human origin*. Springer-Verlag: Heidelberg.
- Byrne R.W. & Whiten A. 1985. Tactical deception of familiar individuals in baboons (*Papio ursinus*). *Animal Behaviour*, 33(2): 669-673.
- Byrne R.W. & Whiten A. 1988. *Machiavellian Intelligence: Social expertise and the evolution of intellect in monkeys, apes, and humans*. Oxford: Oxford University Press.
- Byrne R.W. & Whiten A. 1990. Tactical deception in primates: the 1990 database. *Primate report*, 27: 1-101.
- Byrne R.W. & Whiten A. 1992. Cognitive evolution in primates: evidence from tactical deception. *Man, New Series*, 27: 609-627.
- Byrnie J. 2006. Primate theory of mind: a state-of-the-art review. *Journal of Anthropological Psychology*, 17: 2-21.
- Call J. 2009. Contrasting the social cognition of humans and nonhuman apes: the shared intentionality hypothesis. *Topics in Cognitive Science*, 1: 368-379.
- Call J. & Tomasello M. 1994. Production and comprehension of referential pointing by orangutans (*Pongo pygmaeus*). *Journal of Comparative Psychology*, 108: 307-317.
- Call J. & Tomasello M. 1998. Distinguishing intentional from accidental actions in orangutans (*Pongo pygmaeus*), chimpanzees (*Pan troglodytes*), and human children (*Homo sapiens*). *Journal of Comparative Psychology*, 112: 192-206.
- Call J., Agnetta B. & Tomasello M. 2000. Cues that chimpanzees do and do not use to find hidden objects. *Animal Cognition*, 3(1): 23-34.

- Call J., Hare B., Carpenter M. & Tomasello M. 2004. 'Unwilling' versus 'unable': chimpanzees' understanding of human intentional action. *Developmental Science*, 7(4): 488-498.
- Call J. & Tomasello M. 2008. Does the chimpanzee have a theory of mind? 30 years later. *Trends in Cognitive Sciences*, 12: 187–192.
- Caron A.J. 2009. Comprehension of the representational mind in infancy. *Developmental Review*, 29: 69-95.
- Carpenter M., Akhtar N. & Tomasello M. 1998. Fourteen-through 18-month-old infants differentially imitate intentional and accidental actions. *Infant Behavior & Development*, 21(2): 315-330.
- Cartmill E.A. & Byrne R.W. 2007. Orangutans modify their gestural signaling according to their audience's comprehension. *Current Biology*, 17: 1345–1348.
- Cartmill E.A. & Byrne R.W. 2010. Semantics of primate gestures: intentional meaning of orangutan gestures. *Animal Cognition*, 13: 193–804.
- Chance M.R.A. 1967. Attention structure as the basis of primate rank orders. *Man*, 2(4): 503–518.
- Cheney D.L. & Seyfarth R.M. 1990. *How monkeys see the world: inside the mind of another species*. Illinois: University of Chicago Press, 377pp.
- Chiavarino C., Apperly I.A. & Humphreys G.W. 2013. Understanding intentions: distinct processes for mirroring, representing, and conceptualizing. *Current Directions in Psychological Science*, 21(5): 284-289.
- Christensen W. & Michael J. 2016. From two systems to a multi-systems architecture for mindreading. *New Ideas in Psychology*, 40: 48-64.
- Clatterbuck H. 2015. Chimpanzee mindreading and the value of parsimonious mental models. *Mind & Language*, 30(4): 414-436.
- Corballis M.C. & Lea S. 2000. *The descent of mind: psychological perspectives on hominid evolution*. Oxford University Press.
- Costes-Thiré M., Levé M., Uhlrich P., Pasquaretta C., De Marco A. & Thierry B. 2015. Evidence that monkeys (*Macaca tonkeana* and *Sapajus apella*) read moves, but no evidence that they read goals. *Journal of Comparative Psychology*, 129(3): 304-310.
- Coussi-Korbel S. 1994. Learning to outwit a competitor in mangabeys (*Cercocebus torquatus torquatus*). *Journal of Comparative Psychology*, 108: 164-171.
- Darwin C. 1871. *The decent of man and selection in relation to sex*. London: John Murray.

- Deaner R.O., van Schaik C.P. & Johnson V. 2006. Do some taxa have better domain-general cognition than others? A meta-analysis of nonhuman primate studies. *Evolutionary Psychology*, 4: 149-196.
- Defolie C., Malassis R., Serre M; & Meunier H. 2015. Tufted capuchins (*Cebus apella*) adapt their communicative behaviour to human's attentional states. *Animal Cognition*, 18: 747-755.
- Dennett D.C. 1971. Intentional systems. *The Journal of Philosophy*, 68(4): 87-106.
- Dennett D.C. 1987. *The intentional stance*. The MIT Press, Cambridge, Massachusetts, London, England.
- Descartes R. 1637. *Discours de la méthode*. V^{ème} partie. Œuvres et lettres. La Pléiade.
- de Waal F.B.M. 1992. Intentional deception in primates. *Evolutionary Anthropology: Issues, News, and Reviews*, 1(3): 86-92.
- de Wit S. & Dickinson A. 2009. Associative theories of goal-directed behaviour: a case for animal-human translational models. *Psychological Research*, 73: 463-476.
- Ducoing A.M. & Thierry B. 2003. Withholding information in semifree-ranging tonkean macaques (*Macaca tonkeana*). *Journal of Comparative Psychology*, 117: 67-75.
- Ducoing A.M. & Thierry B. 2004. Following and joining the informed individual in semifree-ranging Tonkean macaques (*Macaca tonkeana*). *Journal of Comparative Psychology*, 118: 413-420.
- Dunbar R.I.M. 1998. The social brain hypothesis. *Evolutionary Anthropology*, 6(5): 178-190.
- Dunbar R.I.M. 2003. The social brain: mind, language, and society in evolutionary perspective. *Annual Review of Anthropology*, 32: 163-181.
- Dunbar R.I.M. 2009. The social brain hypothesis and its implications for social evolution. *Annals of Human Biology*, 36(5): 562-572.
- Dunbar R.I.M. & Schultz S. 2007. Evolution in the social brain. *Science*, 317: 1344-1347.
- Emery N.J. 2000. The eyes have it: the neuroethology, function and evolution of social gaze. *Neuroscience and Biobehavioral Reviews*, 24(6): 581-604.
- Fagan T.K. 2016. Animal mindreading and the principle of conservatism. *The Southern Journal of Philosophy*, 54(2): 189-208.
- Fitzpatrick S. 2008. Doing away with Morgan's canon. *Mind & Language*, 23(2): 224-246.
- Flavell J.H. 1992. Perspectives on perspective taking. In: H. Beilin & P. Pufall (Eds.), *Piaget's Theory: Prospects and Possibilities*. (pp. 107-139). Hillsdale, N.J: Erlbaum.

- Fletcher L. & Carruthers P. 2013. Behavior-reading versus mentalizing in animals. In J. Metcalfe and H. Terrace (Eds.), *Agency and Joint Attention*. Oxford: Oxford University Press.
- Flombaum J.I. & Santos L.R. 2005. Rhesus monkeys attribute perceptions to others. *Current Biology*, 15(5): 447–452.
- Fragaszy D.M. & Perry S. 2003 *The biology of traditions: models and evidence*. Cambridge, UK; New York, NY: Cambridge University Press.
- Frith C.D. & Frith U. 2008. Implicit and explicit processes in social cognition. *Neuron*, 60 : 503-510.
- Frith C.D. & Frith U. 2012. Mechanisms of social cognition. *Annual Review of Psychology*, 63 : 287-313.
- Gallagher S. & Povinelli D.J. 2012. Enactive and behavioral abstraction accounts of social understanding in chimpanzees, infants, and adults. *Review of Philosophy and Psychology*, 3 : 14-169.
- Gallese V.H. 2007. Before and below « theory of mind » : embodied simulation and the neural correlates of social cognition. *Philosophical Transactions of the Royal Society of London, Series B*, 362 : 659-669.
- Genty E. & Roeder J.J. 2006. Can lemurs learn to deceive? A study in the black lemur (*Eulemur macaco*). *Journal of Experimental Psychology*, 32(2): 196-200.
- Genty E., Foltz J. & Roeder J.J. 2008. Can brown lemurs (*Eulemur fulvus*) learn to deceive a human competitor? *Animal Cognition*, 11: 255-266.
- Genty E., Breuer T., Hobaiter C. & Byrne R.W. 2009. Gestural communication of the gorilla (*Gorilla gorilla*): repertoire, intentionality and possible origins. *Animal Cognition*, 12: 527–546.
- Genty E., Neumann C. & Zuberbühler K. 2015. Bonobos modify communication signals to recipient familiarity. *Scientific Reports*, 5 : 16442
- Gergely G., Bekkering H. & Kiraly I. 2002. Rational imitation in preverbal infants. *Nature*, 415(6873) : 755.
- Gibson K.R. 1986. Cognition, brain size, and the extraction of embedded food resources. In : J. Else & P.C. Lee (Eds.), *Primate ontogeny, cognition and social behaviour*. (pp. 93-104). Cambridge : Cambridge University Press.
- Gillot P. 2007. *L'esprit, figures classiques et contemporaines*. CNRS Editions.
- Gómez J.C. 1999. Théories des primates sur l'esprit des primates: objectifs conceptuels et méthodologiques. *Enfance*, 3 : 336-344.

- Gómez J.C. 2009. Embodying meaning : insights from primates, autism, and Brentano. *Neural Networks*, 22 : 190-196.
- Goodall J. 1986. *The chimpanzees of Gombe: Patterns of Behaviour*. Harvard University Press, Boston MA.
- Grandin T. 1995. How people with autism think. In: E. Schopler & G.B. Mesibov (Eds.), *Learning and cognition in autism*. (pp. 137-156). Plenum Press, New-York.
- Grandin T. 2002. Do animals and people with autism have true consciousness? *Evolution and Cognition*, 8: 241-248.
- Grandin T. & Johnson C. 2004. *Animals in translation*. Scribner, New-York.
- Grandin T. 2009. How does visual thinking work in the mind of a person with autism? A personal account. *Philosophical Transactions of the Royal Society*, 364: 1437-1442.
- Halina M. 2015. There is no special problem of mindreading in nonhuman animals. *Philosophy of Science*, 82: 473-490.
- Hare B. 2001. Can competitive paradigms increase the validity of experiments on primate social cognition ? *Animal Cognition*, 4(3) : 269-280.
- Hare B., Call J., Agnetta B. & Tomasello M. 2000. Chimpanzees know what conspecifics do and do not see. *Animal Behaviour*, 59: 771-785.
- Hare B., Call J. & Tomasello M. 2001. Do chimpanzees know what conspecifics know? *Animal Behaviour*, 61: 139-151.
- Hare B., Addessi E., Call J., Tomasello M. & Visalberghi E. 2003. Do capuchin monkeys, *Cebus apella*, know what conspecifics do and do not see? *Animal Behaviour*, 65(1): 131-142.
- Hare B. & Tomasello M. 2004. Chimpanzees are more skillful in competitive than in cooperative cognitive tasks. *Animal Behaviour*, 68: 571-581.
- Hare B., Call J. & Tomasello M. 2006. Chimpanzees deceive a human competitor by hiding. *Cognition*, 101: 495-514.
- Hattori Y., Kuroshima H. & Fujita K. 2007. I know you are not looking at me: capuchin monkeys' (*Cebus apella*) sensitivity to human attentional states. *Animal Cognition*, 10: 141-148.
- Hattori Y., Kuroshima H. & Fujita K. 2010. Tufted capuchin monkeys (*Cebus apella*) show understanding of human attentional states when requesting food held by a human. *Animal Cognition*, 13: 87-92.

- Hauser M.D. 1997. Minding the behaviour of deception. In A. Whiten & R.W. Byrne (Eds.), *Machiavellian intelligence II, extensions and evaluations* (pp. 112-143). Cambridge: Cambridge University Press.
- Herlyn H. 2016. The phylogenetic system of primates – character evolution in the light of a consolidated tree. *Organisms, Diversity & Evolution*, doi:10.1007/s13127-016-0279-1.
- Herrmann E., Call J., Hernández-Lloreda M.V., Hare B. & Tomasello M. 2007. Humans have evolved specialized skills of social cognition : the cultural intelligence hypothesis. *Science*, 317 : 1360-1366.
- Heyes C.M. 1993. Anecdotes, training, trapping and triangulating: do animals attribute mental states? *Animal Behaviour*, 46: 177–188.
- Heyes C.M. 1998. Theory of mind in nonhuman primates. *Behavioral and Brain Sciences*, 21: 101-148.
- Heyes C.M. 2014. Submentalizing: I'm not really reading your mind. *Perspectives on Psychological Science*, 9: 131–143.
- Heyes C.M. 2015. Animal mindreading : what's the problem ? *Psychonomic Bulletin and Review*, 22 : 313-327.
- Hirata S. & Matsuzawa T. 2001. Tactics to obtain a hidden food item in chimpanzee pairs (*Pan troglodytes*). *Animal Cognition*, 4: 285-295.
- Hobaiter C. & Byrne R.W. 2011. Serial gesturing by wild chimpanzees: its nature and function for communication. *Animal Cognition*, 14: 827–838.
- Hostetter A.B., Cantero M. & Hopkins W.D. 2001. Differential use of vocal and gestural communication by chimpanzees (*Pan troglodytes*) in response to the attentional status of a human (*Homo sapiens*). *Journal of Comparative Psychology*, 115(4): 337–343.
- Hostetter A.B., Russell J.L, Freeman H. & Hopkins W.D. 2007. Now you see me, now you don't: evidence that chimpanzees understand the role of the eyes in attention. *Animal Cognition*, 10: 55–62.
- Humphrey N.K. 1976. The social function of intellect. In: G. Bateson & R. Hinde (Eds.), *Growing Points in Ethology*. (pp. 303-317). Cambridge University Press.
- Johnson C.M. & Karin-D'Arcy M.R. 2006. Social attention in nonhuman primates: a behavioral review. *Aquatic Mammals*, 32(4): 423-442.
- Jolly A. 1966. Lemur social behavior and primate intelligence. *Science*, 153: 501-506.
- Kaminski J., Call J. & Tomasello M. 2004. Body orientation and face orientation: two factors controlling apes' begging behaviour from humans. *Animal Cognition*, 7: 216–223.

- Kaminski J., Call J. & Tomasello M. 2008. Chimpanzees know what others know, but not what they believe. *Cognition*, 109(2): 224–234.
- Karg K., Schmelz M., Call J. & Tomasello M. 2014. All great apes species (*Gorilla gorilla*, *Pan paniscus*, *Pan troglodytes*, *Pongo abelii*) and two-and-half-year-old children (*Homo sapiens*) discriminate appearance from reality. *Journal of Comparative Psychology*, 128: 431-439.
- Karg K., Schmelz M., Call J. & Tomasello M. 2015. The goggles experiment: can chimpanzees use self-experience to infer what a competitor can see? *Animal Behaviour*, 105: 211-221.
- Karg K., Schmelz M., Call J. & Tomasello M. 2016. Differing views: can chimpanzees do level 2 perspective-taking? *Animal Cognition*, 19: 555-564.
- Karin-D'Arcy M.R. & Povinelli D.J. 2002. Do chimpanzees know what each other see? A closer look. *International Journal of Comparative Psychology*, 15: 21–54.
- Kirkpatrick C. 2007. Tactical deception and the great apes: insight to the question of theory of mind. *Totem: The University of Western Ontario Journal of Anthropology*, 15: 31-37.
- Kovács Á.M., Téglás E. & Endress A.D. 2010. The social sense: susceptibility to others' beliefs in human infants and adults. *Science*, 330: 1830–1834.
- Krachun C., Call J. & Tomasello M. 2009. Can chimpanzees (*Pan troglodytes*) discriminate appearance from reality? *Cognition*, 112: 435-450.
- Krachun C., Lurz R., Russell J.L. & Hopkins W.D. 2016. Smoke and mirrors: testing the scope of chimpanzees' appearance-reality understanding. *Cognition*, 150: 53-67.
- Krause M.A. & Fouts R.S. 1997. Chimpanzee (*Pan troglodytes*) begging: hand shapes, accuracy, and the role of eye gaze. *Journal of Comparative Psychology*, 111: 330–336.
- Krupenye C., Kano F., Hirata S., Call J. & Tomasello M. 2016. Great apes anticipate that other individuals will act according to false beliefs. *Science*, 354(6308): 110-113.
- Langton S.R.H. 2000. The mutual influence of gaze and head orientation in the analysis of social attention direction. *The Quarterly Journal of Experimental Psychology*, 53(3): 825–845.
- Langton S.R.H. & Bruce V. 2000. You must see the beg: automatic processing of cues to the direction of social attention. *Journal of Experimental Psychology: Human Perception & Performance*, 26(2): 747–757.
- le Roux A., Snyder-Mackler N., Roberts E.K., Beehner J.C. & Bergman T.J. 2013. Evidence for tactical concealment in a wild primate. *Nature communications*, 4: 1462, doi: 10.1038/ncomms2468.

- Leavens D.A., Russell J.A. & Hopkins W.D. 2005. Intentionality as measured in the persistence and elaboration of communication by chimpanzees (*Pan troglodytes*). *Child Development*, 76(1): 296–306.
- Leslie A.M. 1994. ToMM, ToBy, and Agency: Core architecture and domain specificity. In: L.A. Hirschfeld & S.A. Gelman (Eds.), *Mapping the mind: Domain specificity in cognition and culture*. (pp. 119-148). Cambridge University Press.
- Lestel D. 2007. *L'animalité. Essai sur le statut de l'humain*. Editions de l'Herne.
- Liebal K., Pika S., Call J. & Tomasello M. 2004. To move or not to move: how apes alter the attentional state of humans when begging for food. *Interaction Studies*, 5: 199–219.
- Liebal K., Waller B.M., Burrows A.M. & Slocombe K.E. 2013. *Primate communication. A multimodal approach*. Cambridge University Press, Cambridge.
- Lurz R.W. 2009. If chimpanzees are mindreaders, could behavioral science tell? Toward a solution to the logical problem. *Philosophical Psychology*, 22, 305–28.
- Lurz R.W. 2011. Belief attribution in animals : on how to move forward conceptually and empirically. *Review of Philosophy and Psychology*, 2 : 19-59.
- Lurz R.W. & Krachun C. 2011. How could we know whether nonhuman primates understand others' internal goals and intentions? Solving Povinelli's problem. *Review of Philosophy and Psychology*, 2(3): 449-481.
- Lurz R.W., Kanet S. & Krachun C. 2014. Animal mindreading: a defense of optimistic agnosticism. *Mind & Language*, 29(4): 428-454.
- MacLean E.L., Matthews L.J., Hare B.A., Nunn C.L., Anderson R.C., Aureli F., Brannon E.M., Call J., Drea C.M., Emery N.J., Haun D.B.M., Herrmann E., Jacobs L.F.J., Platt M.L., Rosati A.G., Sandel A.A., Schroepfer K.K., Seed A.M., Tan J., van Schaik C. & Wobber V. 2012. How does cognition evolve ? Phylogenetic comparative psychology. *Animal Cognition*, 15: 223-238.
- MacLean E.L., Sandel A.A., Bray J., Oldenkamp R.E., Reddy R.B. & Hare B.A. 2013. Group size predicts social but non-social cognition in lemurs. *PLoS ONE*, 8(6): e66359.
- MacLean E.L. 2016. Unravelling the evolution of uniquely human cognition. *Proceedings of the National Academic of Sciences*, 113(23): 6348-6354.
- Maille A., Engelhart L., Bourjade M. & Blois-Heulin C. 2012. To beg, or not to beg? That is the question: mangabeys modify their production of requesting gestures in response to human's attentional states. *PLoS ONE*, 7(7): e41197.
- Marsh H.L., Stavropoulos J., Nienhuis T. & Legerstee M. 2010. Six- and 9-month-old infants discriminate between goals despite similar action patterns. *Infancy*, 15(1): 94-106.

- Martcorena D.C.W., Ruiz A.M., Mukerji C., Goddu A. & Santos L.R. 2011. Monkeys represent others' knowledge but not their beliefs. *Developmental Science*, 14: 1406–1416.
- Martin A. & Santos L.R. 2014. The origins of belief representation: monkeys fail to automatically represent others' beliefs. *Cognition*, 130: 300–308.
- Martin A. & Santos L.R. 2016. What cognitive representations support primate theory of mind? *Trends in Cognitive Sciences*, 20(5): 375-382.
- McFarland D. 1989. *Problems of animal behaviour*. New-York: John Wiley & Sons.
- Melis A.P., Call J. & Tomasello M. 2006. Chimpanzees (*Pan troglodytes*) conceal visual and auditory information from others. *Journal of Comparative Psychology*, 120(2): 154-162.
- Menzel E.W. 1971. Communication about the environment in a group of young chimpanzees. *Folia Primatologica*, 15: 220-232.
- Menzel E.W. 1974. A group of young chimpanzees in a one-acre field. In A.M. Schrier & F. Stollnitz (Eds.) *Behavior of nonhuman primates. Modern research trends*, volume 5 (pp. 83-149). New-York, NY: Academic Press.
- Meunier H., Prieur J. & Vauclair J. 2013. Olive baboons communicate intentionally by pointing. *Animal Cognition*, 16(2): 155-163.
- Meunier H. *In press*. Do the monkeys have a theory of mind ? How to answer the question ? *Neuroscience & Biobehavioral Reviews*.
- Michaud Y. 2000. *Qu'est-ce que l'humain?* Vol. 2. Edition Odile Jacob.
- Miklósi Á. 2002. Can dancing replace scientific approach: Lost (again) in chimpancentrism. *Behavioral and Brain Sciences*, 25 : 633-634.
- Milton K. 1988. Foraging behaviour and the evolution of primate cognition. In: A. Whiten & R.W. Byrne (Eds.), *Machiavellian intelligence*. (pp. 285-305). Oxford: Oxford University Press.
- Mitchell R.W. 1993. Animals as liars: the human face and the nonhuman duplicity. In M. Lewis & C. Saarni (Eds.), *Lying and deception in everyday life* (pp. 59-89). The Guilford Press. New-York: London.
- Mitchell R.W. & Anderson J.R. (1997). Pointing, withholding information, and deception in capuchin monkeys (*Cebus apella*). *Journal of Comparative Psychology*, 111(4): 351-361.
- Moll H. & Meltzoff A.N. 2011. How does it look? Level 2 perspective-taking at 36 months of age. *Child Development*, 82(2): 661–673.

- Montgomery S., Capellini I., Barton R. & Mundy N. 2010. Reconstructing the ups and downs of primate brain evolution: implications for adaptive hypotheses and *Homo floresiensis*. *BMC Biology*, 8: 9.
- Morgan C.L. 1894. *An introduction to comparative psychology*. London: Walter Scott.
- Mulcahy N.J. & Hedge V. 2012. Are great apes tested with an object-choice task? *Animal Behaviour*, 83: 313–321.
- Onishi K.H. & Baillargeon R. 2005. Do 15-month-old infants understand false beliefs? *Science*, 308: 255-258.
- Overduin-de Vries A.M., Spruijt B.M. & Sterck E.H.M. 2014. Long-tailed macaques (*Macaca fascicularis*) understand what conspecifics can see in a competitive situation. *Animal Cognition*, 17(1): 77–84.
- Overduin-de Vries A.M., Spruijt B.M., de Vries H. & Sterck E.H.M. 2015. Tactical deception to hide sexual behaviour: macaques use distance, not visibility. *Behavioral Ecology Sociobiology*, 69: 1333-1342.
- Panksepp J. 2007. Neuroevolutionary sources of laughter and social joy: modelling primate human laughter in laboratory rats. *Behavioral Brain Research*, 182(2): 131-244.
- Parker S.T. & Gibson K.R. 1977. Object manipulation, tool use and sensorimotor intelligence as feeding adaptations in cebus monkeys and great apes. *Journal of Human Evolution*, 6: 623-641.
- Passingham R.E. 1981. Primate specializations in brain and intelligence. *Symposium of the Zoological Society of London*, 46: 361-388.
- Peignot P. & Anderson J.R. 1999. Use of experimenter-given manual and facial cues by gorillas (*Gorilla gorilla*) in an object-choice task. *Journal of Comparative Psychology*, 113(3): 253–260.
- Penn D.C., Holyoak K.J. & Povinelli D.J. 2008. Darwin’s mistake: explaining the discontinuity between human and nonhuman minds. *Behavioral and Brain Sciences*, 31: 109-178.
- Penn D.C. & Povinelli, D.J. 2007. On the lack of evidence that non-human animals possess anything remotely resembling a ‘theory of mind’. *Philosophical Transactions of The Royal Society of Biological Sciences*, 362: 731-744.
- Penn D.C. & Povinelli, D.J. 2009. On becoming approximately rational: the relational reinterpretation hypothesis. In S. Watanabe, AP. Blaisdell, L. Huber & A. Young (Eds.), *Rational animals, irrational humans* (pp. 23-44). Tokyo: Keio University Press.

- Perner J., Leekam S.R. & Wimmer H. 1987. Three-year-olds' difficulty with false-belief: the case for a conceptual deficit. *British Journal of Developmental Psychology*, 5: 125-137.
- Perner J. 2012. MiniMeta : in search of minimal criteria for metacognition. In M. Beran, J. Brandl, J. Perner & J. Proust (Eds.), *The Foundations of Metacognition* (pp. 94-116). Oxford University Press.
- Pezzulo G. & Castelfranchi C. 2009. Thinking as the control of imagination: a conceptual framework for goal-directed systems. *Psychological Research*, 73: 559-577.
- Phillips A.T. & Wellman H.M. 2005. Infant's understanding of object-directed reaching; *Cognition*, 98: 137-155.
- Phillips W., Barnes J.L., Mahajan N., Yamaguchi M. & Santos L.R. 2009. 'Unwilling' versus 'unable': capuchin monkeys' (*Cebus apella*) understanding of human intentional action. *Developmental Science*, 12(6): 938-945.
- Picq P., Serres M. & Vincent J-D. 2003. *Qu'est-ce que l'humain ?* Editions Le Pommier.
- Pika S., Liebal K. & Tomasello M. 2003. Gestural communication in young gorillas (*Gorilla gorilla*): gestural repertoire, learning and use. *American Journal of Primatology*, 60: 95-111.
- Pika S., Liebal K. & Tomasello M. 2005. Gestural communication in subadults bonobos (*Pan paniscus*): repertoire and use. *American Journal of Primatology*, 65: 39-61.
- Poss S., Kuhar C., Stoinski T.S. & Hopkins W.D. 2006. Differential use of attentional and visual communicative signaling by orangutans (*Pongo pygmaeus*) and gorillas (*Gorilla gorilla*) in response to the attentional status of a human. *American Journal of Primatology*, 68(10): 978-992.
- Povinelli D.J. 1994. Comparative studies of animal mental state attribution: a reply to Heyes. *Animal Behaviour*, 48: 239-241.
- Povinelli D.J., Nelson K.E. & Boysen S.T. 1990. Inferences about guessing and knowing by chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology*, 104: 203-210.
- Povinelli D.J. & Eddy T.J. 1996. What young chimpanzees know about seeing. *Monographs of the Society for Research on Child Development*, 61: 1-152.
- Povinelli D.J., Perilloux H.K., Reaux J.E. & Bierschwale D.T. 1998. Young and juvenile chimpanzees' (*Pan troglodytes*) reactions to intentional versus accidental and inadvertent actions. *Behavioural Processes*, 42: 205-218.
- Povinelli D.J. & Vonk J. 2003. Chimpanzee minds: suspiciously human? *Trends in Cognitive Sciences*, 7(4): 157-160.

- Povinelli D.J. & Vonk J. 2004. We don't need a microscope to explore the chimpanzee's mind. *Mind & Language*, 19(1): 1-28.
- Premack D. 1990. The infant's theory of self-propelled objects. *Cognition*, 36(1): 1-16.
- Premack D. & Woodruff G. 1978. Does the chimpanzee have a theory of mind? *The Behavioral and Brain Sciences*, 4: 515-526.
- Reader S.M. & Laland K. 2002. Social intelligence, innovation, and enhanced brain size in primates. *Proceedings of the National Academy of Sciences*, 99(7): 4436-4441.
- Reader S.M., Hager Y. & Laland K. 2011. The evolution of primate general and cultural intelligence. *Philosophical Transactions of The Royal Society of Biological Sciences*, 366: 1017-1027.
- Rizzolatti G. & Sinigaglia C. 2010. The functional role of the parieto-frontal mirror circuit: interpretations and misinterpretations. *Nature Reviews Neuroscience*, 11: 264-274.
- Roberts A.I., Vick S.J. & Buchanan-Smith H.M. 2013. Communicative intentions in wild chimpanzees: persistence and elaboration in gestural signaling. *Animal Cognition*, 16: 187-196.
- Rochat J., Serra E., Fadiga L. & Gallese, V. 2008. The evolution of social cognition: goal familiarity shapes monkeys' action understanding. *Current Biology*, 18: 227-232.
- Samson D., Apperly I.A., Braithwaite J.J. Andrews B.J. & Bodley Scott S.E. 2010. Seeing it their way: Evidence for rapid and involuntary computation of what other people see. *Journal of Experimental Psychology: Human Perception and Performance*, 36: 1255-1266.
- Sandel A.A., MacLean E.L. & Hare B. 2011. Evidence from four lemur species that ringtailed lemur social cognition converges with that of haplorhine primates. *Animal Behaviour*, 81(5): 925-931.
- Santesteban I., Catmur C., Hopkins S., Bird G. & Heyes, C.M. 2014. Avatars and arrows: Implicit mentalizing or domain general processing? *Journal of Experimental Psychology: Human Perception and Performance*, 40: 929-937.
- Santos L.R., Nissen A.G. & Ferrugia J.A. 2006. Rhesus monkeys, *Macaca mulatta*, know what others can and cannot hear. *Animal Behaviour*, 71(5): 1175-1181.
- Savage-Rumbaugh E.S. & Rumbaugh D.M. 1979. Chimpanzee problem comprehension: insufficient evidence. *Science*, 206: 1201-1202.
- Schmelz M., Call J. & Tomasello M. 2010. Chimpanzees know that others make inferences. *Proceedings of the National Academy of Sciences*, 108: 3077-3079.

- Schmitt V., Pankau B. & Fischer J. 2012. Old World monkeys compare to apes in the PCTB. *Plos One*, 7: e32024.
- Schmitt V., Kröger I., Zinner D., Call J. & Fischer J. 2013. Monkeys perform as well as apes and humans in a size discrimination task. *Animal Cognition*, 16(5): 829-838.
- Scott-Phillips T.C. 2015. Nonhuman primate communication, pragmatics, and the origins of language. *Current Anthropology*, 56(1): 56-80.
- Searle J. 1983. *Intentionality*. Cambridge, England: Cambridge University Press.
- Sebanz N., Knoblich G. & Prinz W. 2003. Representing others' actions: Just like one's own? *Cognition*, 88(3): B11–B21.
- Semple S. & McComb, K. 1996. Behavioural deception. *TREE*, 11(10): 434-437.
- Shettleworth S. 2010. *Cognition, Evolution and Behavior*. New-York: Oxford University Press.
- Southgate V., Senju A. & Csibra G. 2007. Action anticipation through attribution of false belief by 2-year-olds. *Psychological Science*, 18: 587–592.
- Sperber D. & Wilson D. 1995. *Relevance: communication and cognition*. Second Edition. Oxford: Blackwell.
- Tempelmann S., Kaminski J. & Liebal K. 2011. Focus on the essential: all great apes know when others are being attentive. *Animal Cognition*, 14: 433–439.
- Thierry B., Singh M., & Kaumanns W. 2004. *Macaque societies: A Model for the Study of Social Organization*. Cambridge: Cambridge University Press.
- Tomasello M. 1999. *The cultural origins of human cognition*. Cambridge, MA: Harvard University Press.
- Tomasello M. & Call J. 1997. *Primate cognition*. New-York: Oxford University press.
- Tomasello M. & Rakoczy H. 2003. What makes human cognition unique? From individual to shared cognitive intentionality. *Mind & Language*, 18(2): 121-147.
- Tomasello M., Carpenter M., Call J., Behne T. & Moll H. 2005. Understanding and sharing intentions: the origins of cultural cognition. *Behavioral and Brain Sciences*, 28: 675-735.
- Tomasello M. 2014. *A Natural History of Human Thinking*. Harvard University Press.
- Townsend S.W., Kosli S.E., Byrne R.W., Slocombe K.E., Bickel B., Boeckle M., Gonçalves I.B., Burkart J.M., flower T., Gaunet F., Glock H.J., Gruber T., Jansen D.A.W.A.M., Liebal K., Linke A., Miklósi Á., Moore A., van Schaik C.P., Stoll S., Vail A., Waller B.M., Wild M., Zuberbühler K. & Manser M.B. 2016. Exorcising Grice's ghost : an

- empirical approach to studying intentional communication in animals. *Biological Reviews of the Cambridge Philosophical Society* : doi: 10.1111/brv.12289.
- Tramacere A. & Ferrari P.F. 2016. Faces in the mirror, from the neuroscience of mimicry to the emergence of mentalizing. *Journal of Anthropological Sciences*, 94 : 1-14.
- van der Vaart E. & Hemelrijk C.K. 2014. ‘Theory of mind’ in animals : ways to make progress. *Synthese*, 191 : 335-354.
- van Overwalle F. & Vandekerckhove M. 2013. Implicit and explicit social mentalizing : dual processes driven by a shared neural network. *Frontiers in Human Neuroscience*, 7 : 560 : doi: 10.3389/fnhum.2013.00560.
- van Schaik C.P. & Deaner R.O. 2003. Life history and cognitive evolution in primates. In: F.B.M. de Waal & Tyack P.L. (Eds.), *Animal social complexity: intelligence, culture, and individualized societies*. (pp. 5-25). Harvard University Press.
- van Schaik C.P. & Burkart J.M. 2011. Social learning and evolution: the cultural intelligence hypothesis. *Philosophical Transactions of the Royal Society of Biological Sciences*, 366: 1008-1016.
- Vauclair J. 1992. *L’intelligence de l’animal*. Edition Seuil.
- Vauclair J. 1996. *La cognition animale*. Que sais je ? Presses universitaires de France.
- Vauclair J. 2016. *Psychologie comparée: cognition, communication et langage*. Presses Universitaires de Paris Ouest.
- Vick S.J. & Anderson J.R 2003. Use of human visual attention cues by olive baboons (*Papio anubis*) in a competitive task. *Journal of Comparative Psychology*, 117(2): 209–216.
- Vonk J. & Povinelli D.J. 2011. Social and physical reasoning in human-reared chimpanzees: preliminary studies. In: N. Eilan, H. Lerman, & J. Roessler (Eds.), *Perception, causation, and objectivity. Issues in philosophy and psychology*. (pp. 342-352). Oxford, U.K.: Oxford University Press.
- von Uexküll J. 1965. *Mondes animaux et monde humain*. Editions Denoël.
- Watson J.B. 1913. Psychology as the behaviorist views it. *Psychological Review*, 20(2): 158-177.
- Whiten A. & Byrne R. W. 1997. *Machiavellian intelligence II: extensions and evaluations*. Cambridge, UK: Cambridge University Press.
- Whiten A. 2013. Humans are not alone in computing how others see the world. *Animal Behaviour*, 86: 213–221.

- Wimmer H. & Perner J. 1983. Beliefs about beliefs: representation and constraining function of wrong beliefs in young children's understanding of deception. *Cognition*, 13: 103-128.
- Wood J.N., Glynn D.D., Phillips B.C. & Hauser M.D. 2007. The perception of rational, goal-directed action in nonhuman primates. *Science*, 317: 1402-1405.
- Woodruff G. & Premack D. 1979. Intentional communication in the chimpanzee: the development of deception. *Cognition*, 7: 333-362.
- Woodward A.L. 1998. Infants selectively encode the goal object of an actor's reach. *Cognition*, 69: 1-34.
- Woodward A.L. 2009. Infants' grasp of others' intentions. *Current Directions in Psychological Science*, 18(1): 53-57.
- Zimmermann F., Zemke F., Call J. & Gomez J.C. 2009. Orangutans (*Pongo pygmaeus*) and bonobos (*Pan paniscus*) point to inform a human about the location of a tool. *Animal Cognition*, 12: 347-358.

Sur les traces de la Théorie de l'Esprit chez les singes : compréhension de l'attention, des perceptions et des intentions d'autrui

La Théorie de l'Esprit est l'ensemble des capacités cognitives permettant à un individu de se mettre à la place d'autrui. Longtemps considérée comme spécifiquement humaine, de plus en plus de comportements sociaux complexes sont rapportés chez les grands singes et plus récemment chez certaines espèces de singes, rendant son existence au sein d'autres espèces hautement débattue. Ce travail s'intéresse aux capacités de macaques à discriminer l'attention, la perception et les intentions d'autrui en situation de coopération ou de compétition, intraspécifique ou interspécifique. Dans ces expériences, les macaques se comportaient différemment selon les états d'attention, la perception visuelle et les intentions de leurs partenaires. Toutefois, les mécanismes sous-jacents à ces comportements complexes restent incertains. Les primates non humains peuvent en effet être de très bons lecteurs de comportements, capables de déchiffrer les comportements des autres sur la base d'apprentissages associatifs, mais pourraient également faire usage de représentations mentales.

Mots-clés : Cognition sociale ; Attention ; Intention ; Perception ; Théorie de l'Esprit ; Primate ; *Macaca spp.*

Theory of Mind is the set of cognitive abilities allowing an individual to put himself in the place of others. Considered as specifically human for a long time, more and more complex social behaviours are reported in great apes, and more recently in some monkeys' species. This work focuses on attention, perception and intention reading abilities in macaques in cooperative or competitive experiments and in interspecific and intraspecific situations. In these experiment, macaques behaved differently according to the attentional state, visual perception and intentions of their partners. However, the underlying mechanisms of these complex behaviours remain uncertain. Nonhuman primates would thus be very good behaviour readers, capable of decoding others behaviours via associative learning but could also use mental representations.

Key-words : Social cognition ; Attention ; Intention ; Perception ; Theory of Mind ; Primate ; *Macaca spp.*