THESE

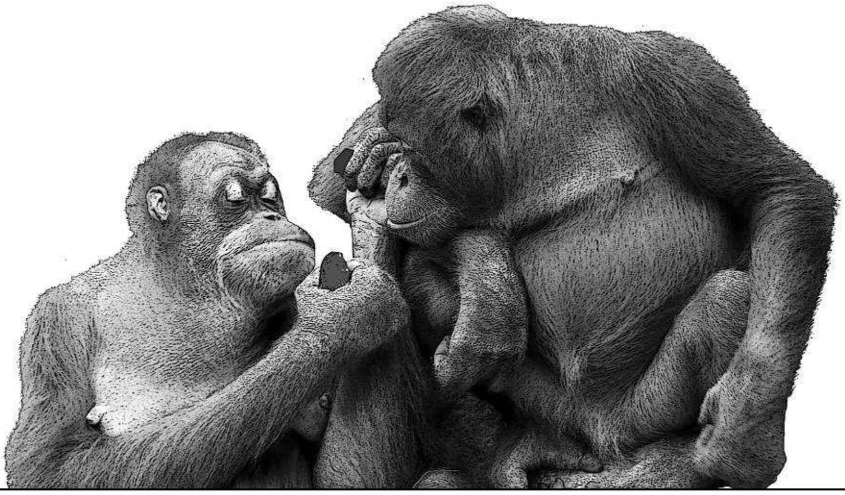
Présentée devant l'Université de Strasbourg

Pour l'obtention du

DOCTORAT DE L'UNIVERSITE DE STRASBOURG

Discipline : Physiologie et Biologie des Organismes et des Populations
Spécialité : Ethologie

par **Marie PELE**



Etude comparative des facultés d'échange chez les primates non humains

Soutenue le 29 Janvier 2010 devant la commission d'examen :

Dr. Bernard Thierry	Directeur de thèse
Pr. Ronald Noë	Rapporteur interne
Dr. Elsa Addessi	Rapporteur externe
Pr. Jean-Michel Lassalle	Rapporteur externe
Dr.Valérie Dufour	Examinateur externe

A ma petite mamie de moi,

à mes parents.

Remerciements

Tout d’abord, je souhaite adresser mes sincères remerciements à l’ensemble des personnes qui ont co-dirigé ce travail de thèse de manière officielle mais aussi officieuse. Bernard Thierry, pour m’avoir fait partager sa grande connaissance de la science, de l’éthologie et des primates. Valérie Dufour, pour sa confiance, son soutien et m’avoir donné l’opportunité de travailler sur ce projet. Josep Call, pour m’avoir acceuillie avec tant d’enthousiasme en Allemagne.

Je remercie les membres de mon jury de thèse : Mme Elsa Addessi, Mr Jean-Michel Lassalle et Mr Ronald Noë qui ont accepté de relire et de commenter ce manuscrit.

Je remercie également Stéphane Blanc et René Groscolas pour m’avoir accueillie au sein de leur département de recherche.

J’adresse ma gratitude à Odile Petit pour m’avoir permis de réaliser mon tout premier stage en éthologie. Sans ton soutien et tes encouragements, je n’en serais certainement pas là.

Ce travail n’aurait pu se faire sans l’aide et le savoir-faire des techniciens animaliers : P. Uhlrich à Strasbourg ; D. Gessler, M. Hacker, R. “Mozart” Herrman, E. Kanzler, S. Leideritz, M. Lohse, F. Maxis, D. Rogge, N. Romanowsky, N. Schenk, S. Schorr, K. Schuldei et M. Tischmeyer à Leipzig et Ruth à Rijswijk.

Un grand merci à tous les étudiants et à tous les stagiaires qui m’ont aidé à récolter les données : C. Arnaud, M. Arnaud, L. Bahans, S. Bauer, A. Boniface, M. Bordaberry, N. Bourbia, A. Coulon, A. Delabouglise, M. Demontfaucon, J. Devillechabrolle, C. Dilger, P. Gayet, V. Grondin, PY. Hell, A. Jacquemin, A. Leroy, C. Morin, A. Navarre, M. Neumann, A. Ouvrard, A. Racca, L. Sainz, M. Schmelz, E. Suarez, H. Viciana, F. Vogelweith, F. Voinot, C. Wagner, F. Wehrle. J’espère que notre rencontre aura été aussi enrichissante pour vous que pour moi.

Je tiens à saluer mes colocataires de bureau, Jérôme Micheletta et Sophie Steelandt qui ont fait preuve de patience en supportant au fil des mois mes sinusites à répétition et mes petites chansons à tutette.

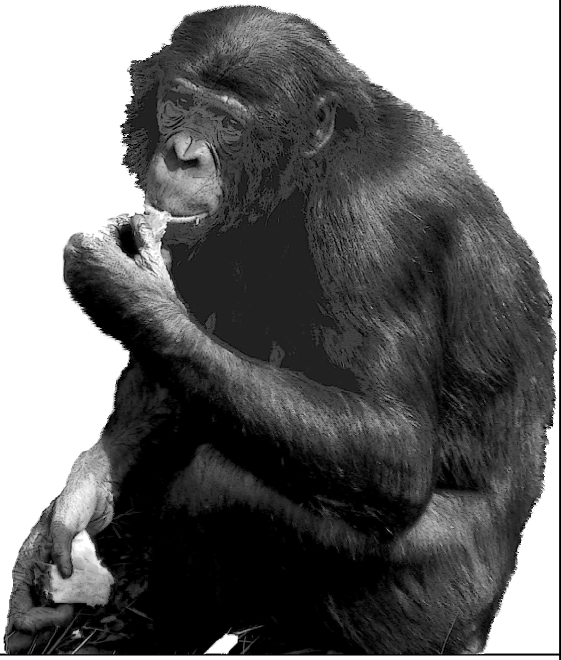
Un grand merci également à vous tous, Cécile, Hélène, Laureline, Marie, Alex, Armand et Cédric pour avoir été présents, dans les bons comme dans les mauvais moments. Auprès de vous je me suis enrichie de mille et une façons.

Un message tout particulier à mes parents et à ma grand-mère. Vous avez été présents à chaque étape. Vous m'avez toujours encouragée et soutenue et contrairement à moi, vous n'avez jamais douté. Merci.

Enfin, je souhaiterai exprimer toute ma reconnaissance, et plus encore à Cédric. Ton soutien durant ces quatres dernières années a rendu l'achèvement de cette thèse possible.

Bien évidemment, ce travail n'aurait pu se faire sans la participation des animaux, 57 au total. Autant de personnalités auxquelles j'ai eu plaisir à me frotter ! Un dernier clin d'oeil donc à Kinika, Kolette, Pétula, Rosy, Pistou, Asson, Accroc, Kloklo, Arnaud, Alila, Raven, Paola, Samir, Velvet, Popeye, Lady, Olga, Shan, Gaëtan, Milos, Janek, Rimbaud, Sybille, Sherlock, Simbad, Thomas, Juus, Willy, Ton, Noah, Castor, Donald, Jack, Joe, Ramis, Saddam, Zébulon, Zorro, Loukkoum, Dokana, Padana, Kila, Dunja, Pini, Bimbo, Joey, Limbuko, Kuno, Ulindi, Yasa, N'Diki, Bebe, Viringika, Unyoro, Jahaga, Gertrudia alias « Trudie » et Fifi.

SOMMAIRE



Chapitre I: Introduction générale 1

- **1. Coopération et réciprocité 3**
  - 1.1. Les déterminants de la coopération 3
    - 1.1.1. La théorie de la sélection de parentèle 4
    - 1.1.2. La théorie de l’altruisme réciproque 4
    - 1.1.3. La théorie du marché biologique 5
  - 1.2. Les interactions réciproques chez les primates non humains 6
    - 1.2.1. Le toilettage social 6
    - 1.2.2. Les coalitions 7
    - 1.2.3. Le partage de nourriture 7
  - 1.3. La question de la valeur des services 8
  - 1.4. Les mécanismes sous-jacents aux interactions réciproques 9
    - 1.4.1. La réciprocité de symétrie 9
    - 1.4.2. La réciprocité d’émotion 9
    - 1.4.3. La réciprocité d’attitude 10
    - 1.4.4. La réciprocité calculée 10
- **2. Les compétences requises par la réciprocité calculée 10**
  - 2.1. La tolérance sociale 11
  - 2.2. L'estimation de la valeur des biens 12
  - 2.3. Les dons et transferts de biens 13
  - 2.4. L'attente d'un retour 14
  - 2.5. Le calcul du risque 16
  - 2.6. La reconnaissance du partenaire 16
  - 2.7. La mémoire et l'anticipation 17
  - 2.8. La détection et la prévention de la tricherie 17
- **3. Vers une économie expérimentale des primates 18**
  - 3.1. L’échange comme modèle expérimental 18
  - 3.2. Les biais de jugement 19
    - 3.2.1. L'effet de dotation 19
    - 3.2.2. L'aversion pour la perte 20
  - 3.3. Le sens de l'équité 21

3.3.1. L’aversion pour l’iniquité ... 21
3.3.2. Le jeu de l’ultimatum ... 22

4. Objectifs de l’étude ... 23

Chapitre II: Méthodes générales 25

1. Les groupes d’étude et les conditions d’élevage ... 26
1.1. Les capucins bruns ... 26
1.2. Les macaques à longue queue ... 26
1.3. Les macaques de Tonkean ... 26
1.4. Les chimpanzés ... 27
1.5. Les orangs-outangs ... 27
1.6. Les bonobos ... 28
1.7. Les gorilles ... 28

2. Les procédures d’entraînement à l’échange ... 29
2.1. L’échange d’un objet pour de la nourriture ... 29
2.2. L’échange d’items alimentaires ... 29

Chapitre III: La dimension temporelle de l’échange 31

1. L’estimation de la valeur et l’anticipation de l’attente chez les chimpanzés ... 32
Résumé de l’article 1 ... 33
Article 1 : Chimpanzee anticipation of food return: coping with waiting time in exchange task ... 34

2. L’estimation de la valeur et l’anticipation de l’attente chez les macaques à longue queue ... 45
Résumé de l’article 2 ... 46
Article 2 : Long-tailed macaques display unexpected waiting abilities in exchange tasks ... 48

3. L’estimation de la valeur et l’anticipation de l’attente chez les macaques de Tonkean et les capucins **60**

Résumé de l’article 3 61

Article 3 : Delay maintenance in Tonkean macaques and brown capuchin monkeys 63

Chapitre IV: La prise de risque dans l’échange 85

La prise de risque chez trois espèces de primates **86**

Résumé de l’article 4 87

Article 4 : Non-human primates take their chance in a food-gambling game 89

Chapitre V: Les échanges réciproques entre congénères 105

1. Les quémandes et les transferts de biens chez les grands singes **106**

Résumé de l’article 5 107

Article 5 : Token transfers among great apes: species differences, gestural requests and reciprocal exchange 109

2. La réciprocité calculée chez deux orangs-outangs **119**

Résumé de l’article 6 120

Article 6 : Calculated reciprocity after all: computation behind token transfers in orangutans 122

3. L’absence de quémande et de don chez les macaques de Tonkean et les capucins **128**

Résumé de l’article 7 129

Article 7 : Monkeys fail to reciprocate in an exchange task 130

Chapitre VI: Discussion générale 142

1. La décision face à une période d’attente **143**

2. L’aptitude à accepter un risque **144**

3. L’échange avec un congénère 146

4. Perspectives 149

Références 150

CHAPITRE I

INTRODUCTION GENERALE

L’être humain se distingue des autres espèces animales – y compris des autres espèces d’hominidés – par son aptitude à effectuer des transactions et à faire du commerce. Depuis l’*Essai sur le don* de Marcel Mauss (1924), nous savons que le don et l’échange représentent une pierre angulaire des sociétés humaines telles que nous les connaissons aujourd’hui. La distribution et l’échange de biens et de services sont les bases de ce qui apparaît comme l’une des principales activités humaines, l’économie. On a décrit différents systèmes économiques en fonction des systèmes de distribution entre les individus. Dans les sociétés de chasseurs-cueilleurs, par exemple, les membres du groupe prélèvent des ressources et les redistribuent de manière égalitaire au sein de la communauté, et ils en retirent une reconnaissance sociale (Sahlins, 1965). Entre des individus ou des groupes d’individus, des réseaux d’échange peuvent également apparaître sous forme de trocs, c’est-à-dire d'échanges de biens de différentes natures. En constituant un bien échangeable contre tous, la monnaie a permis le développement de réseaux d’échange et l’émergence d’un commerce à grande échelle. L’offre et la demande, et les relations qu’entretiennent ces deux notions, constituent le cœur des économies modernes.

La réciprocité est à la base de l’économie. Elle est par définition bilatérale et contingente, c'est-à-dire que l'action de chaque partenaire dépend de celle de l'autre. En revanche, la réciprocité n'est pas nécessairement symétrique : les coûts et bénéfices des deux partenaires peuvent être inégaux. On peut observer des interactions réciproques chez les animaux et on peut les interpréter en termes d’échange. Cependant, l’existence de corrélations entre les services donnés et reçus ne suffit pas pour conclure à l'intentionnalité ou à un calcul des coûts et bénéfices potentiels de la part des individus qui s’y engagent. Comme l’écrivait Adam Smith (1776) :

« *On n'a jamais vu de chien faire, de propos délibéré, l’échange d’un os avec un autre chien. On n’a jamais vu d’animal chercher à faire entendre à un autre, par la voix ou les gestes : “Ceci est à moi, ceci est à toi, je te donnerai l’un pour l’autre”.* »

Adam Smith posait implicitement la question des compétences cognitives nécessaires à la réciprocité. Comprendre quelles sont les compétences des animaux nous permettrait de mieux appréhender l’apparition d’une activité aussi complexe que le commerce. Ceci demande d'étudier les facultés cognitives qui interviennent dans les interactions réciproques chez les animaux.

La réciprocité des dons entre deux individus n’étant pas toujours immédiate, l'individu doit être capable de soutenir l'écart temporel entre le don et le retour. Considéré comme un facteur crucial pour l’évolution des actes altruistes (Trivers, 1971), ce délai représente une contrainte dans la mise en place des échanges de type calculé. En premier lieu, en imposant au sujet de tolérer un temps d’attente significatif durant lequel l’individu doit faire preuve de contrôle de soi pour être en mesure de tenir compte des conséquences positives ou négatives de ses actes. En second lieu, en amenant le sujet à prendre le risque de perdre son investissement initial ;

l’individu doit être capable d’accepter l’éventualité d’une perte et de mesurer celle-ci en fonction des bénéfices potentiellement retirés à la fin de l’échange.

Ce travail de thèse a pour objectif d’étudier les conditions de la réciprocité calculée (1) en testant si les primates non humains intègrent le coût temporel associé à un échange, (2) en étudiant leur aptitude à prendre en compte le risque inhérent à la situation d’échange et (3) en recherchant s'ils peuvent s’engager dans des échanges de type calculé sous des conditions expérimentales contrôlées.

Dans cette introduction, je rappellerai tout d'abord les différents faits et hypothèses concernant la coopération et les interactions réciproques chez les primates non humains. Je poserai ensuite la question des compétences nécessaires à la réciprocité calculée. Enfin, avant d'exposer les objectifs de cette thèse, je détaillerai dans une troisième partie le modèle d'échange expérimental qui permet d'étudier ces compétences.

1. COOPERATION ET RECIPROCITE

1.1. Les déterminants de la coopération

Selon la théorie de l’évolution, la sélection naturelle favorise les organismes possédant le meilleur succès reproducteur, c’est-à-dire la meilleure valeur adaptative ou *fitness*, mesurée par le nombre de descendants fertiles capables de se reproduire à leur tour. Chez les espèces vivant en groupes sociaux, les individus peuvent intervenir sur la fitness des autres membres du groupe. Lorsque deux individus entrent en interaction, le comportement de l’un peut directement affecter la fitness du second. On peut reconnaître quatre catégories d’interactions en fonction du bilan des coûts et bénéfices entre individu qui donne et individu qui reçoit (Tableau 1): (1) dans l’*égoïsme*, l'interaction est au bénéfice du donneur et au détriment du récepteur ; (2) dans la *coopération*, les deux individus sont bénéficiaires ; (3) dans la *malveillance*, l'action de l'un engendre un coût pour l'autre sans que le premier en retire un bénéfice ; (4) dans l’*altruisme* le coût est pour le donneur et le bénéfice pour le récepteur (Hamilton, 1964, 1970).

Tableau 1. Catégories d’interaction en fonction des coûts et bénéfices des partenaires.

		Récepteur	
		Gains (+)	Pertes (-)
Donneur	Gains (+)	Coopération (+,+)	Egoïsme (+,-)
	Pertes (-)	Altruisme (-,+)	Malveillance (-,-)

Les mécanismes de la sélection naturelle favorisent les individus qui tendent à optimiser leur succès reproducteur. Il apparaît cependant que certains comportements ne bénéficient pas directement à l'individu qui l'accomplit. C'est par exemple le cas pour le toilettage au cours duquel un individu consacre du temps à nettoyer la fourrure ou le plumage d'un congénère, l’émission de cris d’alarme qui peut entraîner la localisation de l'émetteur par le prédateur, le soutien lors d’un conflit qui est susceptible d'occasionner des blessures ou encore le partage de nourriture qui réduit les ressources du donneur. Plusieurs théories ont été proposées pour rendre compte de la sélection des individus produisant de tels comportements « altruistes ».

1.1.1. La théorie de la sélection de parentèle

En 1964, Hamilton propose l’une des premières solutions théoriques au paradoxe de l’altruisme : la sélection de parentèle. Il émet l’hypothèse que les animaux sont susceptibles de se comporter de façon altruiste envers des individus qui leur sont apparentés, favorisant ainsi la transmission de leurs propres gènes. La règle d’Hamilton établit que la transmission d’un caractère sera favorisée lorsque : $r \times b > c$ où r représente le coefficient d’apparentement du donneur et du récepteur, b l’augmentation de la fitness du récepteur, et c la réduction de la fitness du donneur. Les comportements altruistes apparaissent quand le coût de production du comportement est moindre que le bénéfice retiré.

1.1.2. La théorie de l’altruisme réciproque

Les comportements altruistes qui surviennent entre individus non apparentés ne peuvent s’expliquer par la sélection de parentèle. En 1971, Trivers propose la théorie de l’altruisme réciproque pour expliquer la production de comportements altruistes entre non apparentés. Il définit l’altruisme réciproque comme un échange de biens ou services entre deux partenaires dans lequel le donneur produit un acte coûteux bénéficiaire pour le récepteur. La réciprocité se produit lorsqu’après avoir reçu le récepteur donne à son tour. L’altruisme réciproque permet l’émergence du phénomène de coopération entre deux partenaires dont les bénéfices peuvent être asynchrones.

L’altruisme réciproque requiert trois conditions (Trivers, 1971) : (1) plusieurs interactions doivent avoir lieu entre les partenaires impliqués, (2) les partenaires doivent être capables de se reconnaître afin de pouvoir de nouveau interagir dans le futur, (3) le bénéfice ultérieurement retiré doit être plus important que le coût immédiat.

La sélection d’individus altruistes au cours de l’évolution n’a pu se faire qu’à la condition que les individus tricheurs – qui ne retournent pas le don – soient eux éliminés. Chez l’être humain, les actes altruistes et les actes de tricherie reposeraient sur des mécanismes psychologiques (Trivers, 1971). Cela suppose que les individus détectent les tricheurs, calculent le ratio coût/bénéfice, reconnaissent leur partenaire et mémorisent les interactions passées. Chez les animaux, on illustre fréquemment l’altruisme réciproque par les dons de nourriture observés chez les chauves-souris vampires (*Desmodus rotondus*), au cours desquels des individus régurgitent du sang afin d’alimenter ceux dont la chasse a été infructueuse et qui risquent de mourir après trois jours de privation de nourriture (Wilkinson, 1984). Toutefois, cet exemple reste contesté car il reste à démontrer que ce sont les mêmes partenaires qui jouent régulièrement les rôles de donneur et récepteur au cours d'une succession d'interactions. De même, Packer (1977) proposa d'expliquer par l’altruisme réciproque la formation de coalitions chez les babouins (*Papio anubis*) cherchant à accéder aux femelles en œstrus monopolisées par un concurrent. Mais d'autres études ont ensuite montré qu'il n'y a pas de réciprocité entre les alliés vainqueurs d'un mâle dominant, seul l'un d'entre eux s'accouple avec la femelle (Bercovitch, 1988 ; Noë, 1990).

L’altruisme réciproque, de par les compétences psychologiques qu’il requiert pourrait être le mécanisme évolutif à la base des transactions économiques chez l’être humain : « si tu me donnes ceci, je te donne cela » (Trivers, 1971). Clutton-Brock (2009) suggère que de nombreux exemples de coopération chez l’animal s'expliquent par des motivations égoïstes. Les coûts supportés par le donneur seraient selon lui peu élevés, contrairement à ce que l'on observe chez l’être humain. Bien qu’il soit possible qu’il existe dans la nature des échanges basés sur des facultés cognitives comparables à celles mises en jeu chez l’être humain, il reste qu'aucun exemple avéré d’altruisme réciproque n’a été à ce jour mis en évidence chez les animaux.

1.1.3. La théorie du marché biologique

Noë et Hammerstein (1994, 1995) ont proposé une alternative à la théorie de l’altruisme réciproque pour expliquer les comportements coopératifs observés chez les animaux : la théorie du marché biologique. Contrairement à l’altruisme réciproque, le marché biologique intègre le choix du partenaire de coopération. Les individus ayant le choix entre plusieurs partenaires, peuvent décider à tout moment de ne plus coopérer avec un partenaire et d’en choisir un autre. Ainsi, les individus se comporteraient comme des « vendeurs » et des « acheteurs », et les interactions entre les individus seraient comparables à des transactions (Noë & Hammerstein, 1994, 1995). En conséquence, les individus négocieraient certains de leurs comportements en fonction de l’offre et de la demande (Noë & Hammerstein, 1994, 1995). A remarquer, cependant, que la théorie du marché biologique ne fait aucune hypothèse sur les processus cognitifs mis en œuvre.

On a établi que les poissons labres (*Labroides dimidiatus*) qui se nourrissent des ectoparasites présents sur des poissons de coraux, modulent leur comportement de nettoyage en fonction de différentes caractéristiques de leurs « clients » telles que leur lieu de résidence (Bshary & Grutter, 2002). Il apparaît que les « clients » prennent en compte la qualité d'un service antérieur avant de retourner vers un poisson nettoyeur donné (Bshary & Schäffer, 2002). On a également appliqué la théorie du marché biologique aux comportements des primates non humains. Par exemple, plus le nombre de jeunes non sevrés dans un groupe est faible, plus les femelles sans jeune sont enclines à toiletter (babouin, *Papio c. ursinus* : Henzi & Barrett, 2002) ou étreindre (singe-araignée, *Ateles geoffroyi* : Slater et al., 2007) les mères pour avoir accès à leur bébé. Enfin, une récente étude a montré expérimentalement que des singes vervets (*Chlorocebus aethiops*) modulent leur comportement de toilettage envers des partenaires susceptibles de leur apporter un avantage – en l'occurrence l'accès à des ressources alimentaires – en fonction du nombre de ces partenaires au sein du groupe (Fruteau et al., 2009).

1.2. Les interactions réciproques chez les primates non humains

La sélection de parentèle s'exerce sans que les individus fassent nécessairement preuve de réciprocité. Le marché biologique n'exige pas non plus la réciprocité des comportements. A l'inverse, l'altruisme réciproque repose sur une réciprocité différée où, par définition, le don initial est coûteux. Que ce soit à long terme ou à court terme, les êtres humains possèdent les compétences psychologiques pour évaluer les coûts potentiels et décider ou non de s’engager dans des interactions réciproques. Il n’existe aucune certitude que tel soit le cas chez l’animal. Dans de nombreux cas, c'est l'intérêt individuel qui est responsable de la coopération entre congénères (Clutton-Brock, 2009) et le niveau de calcul mis en jeu est mal connu. On peut donc s'attendre à ce que la sélection naturelle favorise l'aptitude des individus à s'engager dans des actions réciproques qui ne font pas appel à l'altruisme mais qui ont pour résultat de bénéficier aux deux individus.

La majorité des primates non humains vivent en groupes sociaux ou familiaux. Chez ces espèces, le recouvrement des générations grâce notamment à une espérance de vie élevée (Austad & Fischer, 1992) et à l'association d’individus d’âge, de sexe et de liens de parenté différents permettent la mise en place de relations sociales stables entre les individus. Chez les primates, une grande diversité d’interactions réciproques est rapportée, en particulier dans le toilettage social, le soutien dans les conflits et le partage de la nourriture (Dugatkin, 1997).

1.2.1. Le toilettage social

Le toilettage d’un individu par un autre – *social grooming* – est le comportement coopératif le plus fréquemment observé chez les primates non humains. Pour l’individu toiletté, ce comportement peut réduire le nombre d’ectoparasites (Hutchins & Barash, 1976) mais également diminuer la tension (Schino et al., 1988 ; Terry, 1970) grâce notamment à la libération de béta-endorphines (Keverne et al., 1989). Pour l’individu toiletteur, ce comportement engendre un coût en temps mais produirait *a posteriori* certains bénéfices à l’individu. D’abord, toiletter permettrait d’être toiletté en retour. Récemment, Schino et Aureli (2008) ont montré le caractère réciproque du comportement de toilettage entre femelles chez 22 espèces de primates. Des mâles chimpanzés (*Pan troglodytes*) peuvent également se toiletter de manière réciproque en terme de durée (Gomes et al., 2009 ; Watts, 2002). Par ailleurs, chez plusieurs espèces, le toilettage augmenterait la tolérance des congénères envers le toiletteur (Henzi & Barrett, 1999) et diminuerait le nombre d'interactions agonistiques envers lui (Fairbanks, 1980 ; Silk, 1982 ; Silk et al. 1981). En toilettant, le toiletteur accèderait parfois plus facilement aux ressources alimentaires (de Waal, 1989 ; de Waal, 1997a ; Ventura et al., 2006) ; les femelles obtiendraient l'accès au nouveau-né de leurs congénères (Gumert, 2007a ; Henzi & Barrett, 2002) et les mâles accèderaient plus facilement aux femelles en œstrus (Gumert 2007b). Les interactions de toilettage sont également corrélées avec le soutien dans les conflits (Hemelrijk, 1994 ; Hemelrijk & Ek, 1991 ; Koyama et al., 2006 ; Seyfarth & Cheney, 1984 ; Watts, 2002). Chez les vervets, les individus répondent plus fréquemment aux sollicitations de soutien dans les conflits impliquant des congénères qui viennent de les toiletter (Seyfarth & Cheney, 1984).

1.2.2. Les coalitions

Une coalition est une interaction triadique qui se forme lorsqu'un individu intervient dans un conflit entre deux congénères, soutenant l'un d'eux contre l'autre. On reconnaît alors trois types de protagonistes : l'intervenant, le récepteur soutenu par l'intervenant et l'individu cible. On parle d'alliance lorsque les mêmes individus forment la même coalition de manière régulière. Chez les primates, les coalitions sont fréquentes chez de nombreuses espèces et elles peuvent associer des partenaires non apparentés. Or, intervenir dans un conflit peut engendrer des blessures et se révéler coûteux pour l'intervenant. Différentes hypothèses ont été proposées pour expliquer un tel comportement. Soutenir un individu dans un conflit pourrait améliorer (de Waal, 1982) ou stabiliser (Widdig et al., 2000) le rang hiérarchique de l'intervenant. Intervenir dans un conflit pourrait permettre d'être soutenu en retour lors de futurs conflits, auquel cas les alliés se soutiendraient de manière réciproque dans les conflits (de Waal & Luttrell, 1988 ; Silk, 1992 ; Watts, 1997). Il est également possible que l'individu cible "se venge" en intervenant à son tour dans une coalition établie contre un précédent adversaire (Aureli et al., 1992; de Waal & Luttrell, 1988 ; Silk, 1992 ; Watts, 1997).

1.2.3. Le partage de nourriture

Le partage de nourriture est un comportement que l'on observe chez diverses espèces de primates (Brown, 2004). Il peut être facilité par le possesseur, forcé par le récepteur ou précédé de comportements de quémande (Feistner & McGrew, 1989). Le partage de nourriture peut engendrer des dons de nourriture entre les membres du groupe même si dans la grande majorité des cas ils se limitent à des dons des parents vers leur progéniture (Brown, 2004 ; Feistner & McGrew, 1989).

Chez les chimpanzés, plusieurs auteurs ont rapporté le partage de viande, de plantes ou de fruits entre des individus non apparentés (Goodall, 1986 ; Teleki, 1973 ; Slocombe et al., 2005). Pour un individu, partager entraîne une diminution de sa propre ressource et apparaît désavantageux. Différentes hypothèses ont été proposées pour expliquer un tel comportement. Tout d'abord le partage aurait pour effet de diminuer les comportements d'agression envers le possesseur de nourriture. D'un point de vue énergétique, il apparaît plus avantageux de perdre une partie de la ressource que d'être harcelé par des quémandeurs (*harassment* ou *sharing-under-pressure hypothesis*) (Goodall, 1986 ; Stevens, 2004 ; Wrangham, 1975). Partager les ressources avec ses congénères permettrait également à l'individu d'améliorer son statut social au sein du groupe, notamment en consolidant ses relations sociales avec des individus plus haut dans la hiérarchie (*share-to-enhance-status hypothesis*) (de Waal, 1982 ; Moore, 1984). On a aussi proposé que la viande issue des chasses collectives serait un « outil social » permettant aux mâles de consolider leurs alliances (Mitani & Watts, 2001 ; Nishida et al., 1992). Certaines études suggèrent que le partage de la viande favorise l'acceptation des accouplements par les femelles (*meat-for-sex hypothesis*) (Gomes & Boesch, 2009 ; Stanford et al., 1994 ; Teleki, 1973), mais d'autres ne confirment pas cette hypothèse (Gilby, 2006 ; Mitani & Watts, 2001).

1.3. La question de la valeur des services

Affirmer que les animaux obtiennent un service contre un bien ou un autre service suppose que l'on puisse estimer la valeur des services. Certains auteurs emploient des termes tels que « contrepartie » (*interchange*) (Hemelrijk, 1990) ou « économie de service » (*service economy*) (de Waal, 1982, 1997a) pour désigner des interactions réciproques de différente nature. De tels qualificatifs rappellent des termes employés en économie humaine et suggèrent l'existence de comportements interchangeables. Cependant, on ne trouve aucun équivalent de la monnaie chez les animaux. Prouver l'existence d'un calcul lors d'échanges entre deux individus exige d'établir une relation de contingence entre le don et le retour observés, ce qui est particulièrement difficile dans le contexte social. La valeur des biens ou des services peut varier d'une interaction à l'autre, et mesurer les coûts et les bénéfices de chacun des partenaires est souvent impossible (Seyfarth & Cheney, 1988). Cela est particulièrement vrai dans le cas de services de nature différente tels que du toilettage contre un soutien dans les conflits ou de la viande pour l'accès à des femelles. Déterminer le niveau de satisfaction des individus dans l'échange s'avère délicat sinon impossible. En outre, la valeur des biens peut varier en fonction de facteurs intrinsèques aux individus tels que le rang hiérarchique, l'âge ou le sexe (Seyfarth & Cheney, 1988). Par exemple, un individu dominé pourra se satisfaire d'une durée moindre de toilettage de la part d'un individu dominant que ce qu'il aura lui même donné à ce dernier.

Il est difficile d'estimer la valeur des biens ou services transférés dans un contexte social. Etablir des corrélations entre ce qui est donné et reçu ne permet pas de conclure à un échange calculé de la part des individus. Il est nécessaire de passer à l'approche expérimentale pour contrôler la valeur des biens ou services transférés entre les partenaires et démontrer l'existence d'une relation de contingence entre les comportements de l'un et l'autre. Alors seulement, nous serons en mesure de conclure à un véritable échange de biens ou services entre deux individus.

1.4. Les mécanismes sous-jacents aux interactions réciproques

Différents mécanismes ont été proposés pour expliquer la réciprocité des comportements observée chez les primates non humains. On peut les distinguer en fonction de la complexité des capacités cognitives qu'ils supposent.

1.4.1. La réciprocité de symétrie

Dans sa forme la plus simple, la réciprocité est qualifiée de symétrique (*symmetry-based reciprocity*) car basée sur le degré d'association des individus (de Waal & Luttrell, 1988). Deux partenaires auront d'autant plus tendance à agir de manière réciproque qu'ils passeront plus de temps à proximité l'un de l'autre. Les relations de proximité reflétant les relations d'affiliation entre deux membres d'un groupe, un individu agira vis-à-vis d'un congénère en fonction de l'identité de celui-ci et de l'attraction ou de l'aversion qu'il aura pour ce dernier. Un tel mécanisme a été proposé pour expliquer le toilettage réciproque chez les macaques rhésus (*Macaca mulatta*) (Colvin & Tissier, 1985 ; de Waal & Luttrell, 1986) ou la formation de coalitions chez les geladas (*Theropithecus gelada*) (Dunbar, 1980). On doit remarquer que la réciprocité de symétrie ne requiert pas de réelle contingence entre les comportements des partenaires en interaction. En ce cens, il ne s'agit pas d'une réciprocité au sens strict mais plutôt d'un mécanisme de coopération du type mutualisme. Il est préférable de réserver le terme de réciprocité aux actions bilatérales et contingentes.

1.4.2. La réciprocité d'émotion

Un second mécanisme s'appuie sur la capacité des individus à associer un état émotionnel à un partenaire potentiel. L'émotion est ici considérée comme une variable intervenant entre la réception de stimuli internes et externes et la mise en place des réponses physiologiques et comportementales de l'individu (Aureli & Schaffner, 2002). Cette « comptabilité émotionnelle » (*emotional bookkeeping*) permettrait des interactions réciproques à long terme avec un partenaire de son choix sans qu'il soit fait recours à des facultés cognitives élaborées (Aureli & Schaffner, 2002). Un tel mécanisme a été proposé pour expliquer les séquences de toilettage réciproques observées chez le capucin brun (*Cebus apella*) (Schino et al., 2009) et le mandrill (*Mandrillus sphinx*) (Schino & Pellegrini, 2009) et le toilettage donné pour le soutien rendu lors des coalitions chez le macaque japonais (*Macaca fuscata*) (Schino et al., 2007).

1.4.3. La réciprocité d'attitude

De Waal (2000) propose un troisième mécanisme lié au comportement du partenaire : la réciprocité d'attitude (*attitudinal reciprocity*) par laquelle les individus agissent en miroir par rapport à leur partenaire. Si un individu agit favorablement envers son partenaire, celui-ci se comportera de manière favorable envers le premier. Au contraire, si un individu agit de manière défavorable, le partenaire se comportera de manière défavorable. Un tel mécanisme n'implique que la capacité cognitive des individus à mémoriser des évènements passés (de Waal, 2000). La réciprocité d'attitude a été proposée en particulier pour expliquer les transferts passifs de nourriture observés chez les capucins bruns lors d'expériences de coopération (de Waal, 2000 ; de Waal & Berger, 2000).

1.4.4. La réciprocité calculée

La réciprocité est dite calculée (*calculated reciprocity*) lorsqu'elle est basée sur la capacité des individus à mémoriser les services donnés et reçus et à en tenir compte dans leurs futurs échanges. De Waal & Luttrell (1988) ont proposé ce mécanisme pour expliquer les soutiens observés lors de conflits chez le chimpanzé, le macaque rhésus et le macaque ours (*Macaca arctoïdes*) (de Waal & Luttrell, 1988). Après avoir éliminé l'influence de facteurs tels que le sexe, la parenté ou les relations de proximité des individus, ces auteurs ont suggéré par défaut que la réciprocité observée chez ces espèces pouvait être basée sur des processus cognitifs complexes. Un tel mécanisme a également été proposé pour rendre compte des corrélations constatées entre les interactions de toilettage et les transferts de nourriture chez le chimpanzé (de Waal, 1997a).

Sur le plan des facultés cognitives, ce mécanisme suppose l'estimation des biens ou services transférés, la mémorisation des dons et des retours, la capacité à attendre le retour ou encore la détection de tricherie de la part du partenaire (Stevens et al., 2005a). Ainsi en termes cognitifs, le mécanisme de réciprocité calculée pourrait permettre la mise en place d'interactions réciproques du type de ce que l'on observe chez l'homme. Alors que l'existence de certaines des facultés cognitives nécessaires à la réciprocité calculée ont pu être mises en évidence chez plusieurs espèces animales, d'autres restent à déterminer avant de conclure à l'existence de la réciprocité calculée chez les primates non humains.

2. LES COMPETENCES REQUISES PAR LA RECIPROCITE CALCULEE

Si l'on considère la réciprocité comme calculée, mener à terme un échange de biens ou services avec un partenaire implique de multiples compétences notamment cognitives. Pour les énumérer, je prendrai l'exemple de deux individus non apparentés A et B qui s'échangent de manière différée deux objets. Au cours de leur première interaction, A et B devront tout d'abord être capables de (1) se tolérer mutuellement pour (2) estimer la valeur des biens de chacun. L’individu A devra (3) donner son bien à l’individu B et, l’échange étant différé, (4) attendre avant de recevoir le retour de la part de B. Ce temps d’attente engendre pour l’individu A (5) le risque que le don ne soit pas rendu. Au cours de leur seconde interaction, les individus devront (6) mutuellement se reconnaître et (7) se remémorer ce qui a déjà été donné. Enfin, au moment d’obtenir le retour de B, l’individu A devra être capable de (8) détecter de la part de son partenaire d’éventuels comportements de tromperie ou de tricherie.

La liste que je viens de citer n’est évidemment pas exhaustive mais elle regroupe les compétences nécessaires à deux individus pour achever un échange de type économique comparable à ceux qui sont observés chez l’homme. Mettre en évidence ces compétences chez les animaux apparaît alors comme la première étape dans l’étude de leur faculté à échanger de manière calculée.

2.1. La tolérance sociale

Pour s’engager dans un échange de type calculé, les individus A et B doivent être capables de se tolérer mutuellement. La tolérance sociale d’un individu se définit par sa capacité à accepter un autre individu ou un groupe d’individus dans son proche environnement physique et/ou social. Chez des espèces vivant en groupes sociaux, la tolérance sociale va conditionner le type d’interaction entre les individus, les comportements des individus envers les autres membres du groupe et donc influer sur leurs relations sociales. Ils existent parfois de fortes différences dans les niveaux de tolérance sociale entre des espèces même proches phylogénétiquement. Par exemple, dans une tâche consistant à soulever de lourdes pierres appâtées, des macaques de Tonkean (*Macaca tonkeana*) décrits comme socialement tolérants co-agissent plus que des macaques rhésus décrits *a contrario* comme peu tolérants (Petit et al., 1992). Chez les grands singes, les bonobos (*Pan paniscus*) montrent également plus d'aptitude à coopérer que des chimpanzés dans une tâche requérant que deux individus tirent chacun sur un des bouts d’une corde pour attirer à eux un plateau de nourriture (Hare et al., 2007). Des espèces dites tolérantes montrent ainsi de meilleurs résultats dans des tâches de coopération que des espèces présentant une tolérance sociale moindre (Anderson, 2007).

Au sein d’une même espèce, il n’est pas rare que seules les paires d’individus les plus tolérantes parviennent à accomplir des tâches coopératives. La tolérance sociale a ainsi été proposée pour expliquer certains actes coopératifs observés chez des capucins bruns (Chalmeau et al., 1997). Testés par paires, les sujets devaient tirer simultanément sur deux barres pour rapprocher un plateau sur lequel était disposée de la nourriture. L’analyse des résultats montre que les individus tiraient chacun de leur côté sans comprendre le rôle du partenaire ; on peut attribuer leurs actes coopératifs à une importante tolérance interindividuelle qui permettrait aux sujets de se rapprocher physiquement pour tirer le plateau (Chalmeau et al., 1997). L’effet facilitateur de la tolérance sociale a également été montré dans une tâche similaire, chez des marmousets (*Callithrix jacchus*) (Werdenich & Huber, 2002). Chez des chimpanzés, la tolérance sociale influence l’apparition d'actes coopératifs : les sujets sont plus enclins à coopérer avec des partenaires socialement tolérés plutôt qu’avec des partenaires peu tolérés à l’extérieur du cadre expérimental (Melis et al., 2006a).

2.2. L'estimation de la valeur des biens

Afin de maximiser leur profit, les individus A et B doivent être capables d’estimer la valeur des biens de chacun avant de s’engager dans un échange. La valeur d’un bien peut s'estimer selon deux critères, la qualité et la quantité. On a pu montrer que des capucins bruns entraînés à réaliser des échanges d'aliments avec un expérimentateur sont capables de tenir compte de leur qualité (Drapier et al., 2005). Lorsque la différence de qualité des aliments échangés est faible, toutefois, les capucins montrent plus de difficulté à les distinguer (Drapier et al., 2005).

Les primates non humains sont également capables de reconnaître des volumes et d’estimer des quantités continues ou discrètes. Par exemple, face à deux quantités continues, des chimpanzés, des bonobos (Suda & Call, 2004, 2005) et des capucins bruns (van Marle et al., 2006) sont capables de discriminer le volume le plus important. Des orangs-outangs (*Pongo pygmaeus*) sont également capables de discriminer deux volumes alors même que la dimension et la forme du récipient varient (Call & Rochat, 1996, 1997). Face à deux quantités discrètes, des chimpanzés (Boysen & Berntson, 1995 ; Boysen et al., 1996 ; Hanus & Call, 2007), des bonobos (Hanus & Call, 2007), des orangs-outangs (Call, 2000 ; Hanus & Call, 2007), des gorilles (*Gorilla gorilla*) (Hanus & Call, 2007), des macaques japonais (*Macaca fuscata*) (Silberberg & Fujita, 1996), des capucins bruns (Addessi et al., 2007 ; Beran, 2008 ; Beran et al., 2007) et des singes écureuils (*Saimiri sciureus*) (Anderson et al., 2000) sont capables de comparer et de discriminer la plus grande ou la plus petite des deux quantités lorsque le total ne dépasse pas l'ordre de la dizaine. On a enfin montré que des capucins bruns sont capables de discriminer deux collections d’items variant à la fois en quantité et en qualité suivant le principe de transitivité (Addessi et al., 2008a ; Padoa-Schioppa et al., 2006).

Les primates sont également capables de combiner des quantités discrètes. Face à deux collections d’items divisées chacune en deux sous-groupes, des chimpanzés sont capables de sélectionner la plus élevée indiquant qu’ils tiennent compte du total des deux sous-groupes (Rumbaugh et al., 1987; Rumbaugh et al., 1988). Lorsqu'un expérimentateur présente deux collections d’items, couvre celles-ci et ajoute ou retire des items, des chimpanzés (Beran, 2001, 2004), des orangs-outangs (Call, 2000), des macaques rhésus (Hauser et al., 2000) et des singes capucins (Beran et al., 2008) s'avèrent capables de choisir la plus élevée.

Chez les singes, la capacité de macaques rhésus à reconnaître des additions et des soustractions a également été étudiée par Hauser et collaborateurs (1996) suivant la technique utilisée chez l’enfant humain par Wynn (1992). Cette technique repose sur le principe que les individus vont réagir plus fortement à des événements qui semblent en violation avec leur connaissance du monde physique. Des situations d'addition et de soustraction vraies (par exemple, 1+1=2) et fausses (par exemple, 1+1=1) sont présentées à des macaques rhésus. L'expérimentateur place l'une après l'autre deux récompenses dans une boîte à la vue du sujet. Après 10 s, le contenu de la boîte est présenté à l'individu : deux récompenses dans le cas d'une addition vraie, une seule dans le cas d'une addition fausse. Dans le cas d'opérations impossibles, les sujets passent plus de temps à scruter le contenu de la boîte, indiquant leur surprise devant la violation des règles additives ou soustractives (Hauser et al., 1996). Addessi et collaborateurs (2007) ont également montré que des capucins bruns somment la valeur de jetons représentant de petites quantités. Enfin, une femelle chimpanzé entraînée à compter fut capable d'indiquer en chiffre arabe la somme d'items de nourriture placés en trois endroits différents (Boysen & Berntson, 1989).

En situation expérimentale, les primates montrent d'importantes capacités à comparer deux biens selon leur qualité et leur quantité. Cependant chez la plupart des espèces, plus la différence entre la valeur des biens est faible, plus les sujets montrent des difficultés à les discriminer. Le ratio entre deux quantités apparaît comme un facteur susceptible de limiter la capacité des primates à estimer correctement des biens. Une telle limite pourrait affecter la compréhension d'un échange équilibré entre partenaires.

2.3. Les dons et transferts de biens

Après avoir estimé la valeur des biens mis en jeu, l'individu A doit être capable de s'engager dans la relation d'échange en donnant un bien à l'individu B. Dans le milieu naturel, les dons sont relativement rares chez les primates non humains, hormis le cas entre apparentés (Brown, 2004 ; Feistner & McGrew, 1989). Dans le cadre d'études expérimentales, certains auteurs ont cependant observé des transferts entre individus non apparentés. Dans la majorité des cas, ces transferts sont de type passif : un individu laisse un congénère prendre en partie ou en totalité un de ses biens. Chez des capucins bruns par exemple, des individus qui ont reçu de la nourriture permettent à des congénères de se saisir d'éventuels morceaux (de Waal, 1997b ; de Waal, 2000). Chez des marmousets, on a également observé des individus laissant des congénères leur ouvrir la bouche pour y récupérer de la nourriture (Kasper et al., 2008).

Dans le cas de transferts actifs, c'est le donneur qui initie le transfert. Les transferts actifs sont parfois qualifiés d'indirects lorsqu'un individu place un objet dans la cage de son partenaire. Ils sont qualifiés de directs lorsqu'un sujet donne un objet de la main à la main à son partenaire (de Waal, 1997b ; de Waal et al., 1993). En ce qui concerne les transferts actifs indirects, on a pu voir des capucins bruns placer des outils ou de la nourriture dans le compartiment d'un congénère (Westergaard & Suomi, 1997 ; Westergaard et al., 2007). Des transferts indirects d'outils ont également été rapportés chez des babouins hamadryas (*Papio hamadryas*) entre un mâle et une femelle (Beck, 1973). En ce qui concerne les transferts actifs directs, on a observé des chimpanzés et des capucins entraînés à échanger avec un être humain placer à travers un grillage des outils dans la main d'un congénère afin que celui-ci puisse accéder à de la nourriture (Westergaard et al., 2007 ; Yamamoto et al., 2009). Concernant des transferts actifs directs et réciproques, un seul cas spontané a pu être rapporté entre deux jeunes mâles chimpanzés entraînés au langage des signes : un premier individu devait fournir un outil au second afin qu'il puisse accéder à de la nourriture, celle-ci était ensuite partagée entre les individus (Savage-Rumbaugh et al., 1978). En revanche, on a dû entraîner des chimpanzés adultes de manière intensive pour qu'ils se montrent capables d'échanger des objets avec un congénère ; ils n'ont maintenu ce comportement d'échange que par le biais d'un renforcement positif de la part d'un expérimentateur humain (Brosnan & Beran, 2009).

La nature passive des transferts ne permet pas de conclure à l'intentionnalité des dons. Seuls les transferts actifs, et notamment ceux qui sont de nature directe, permettent d'interpréter le geste de l'individu comme un acte de don. La rareté de tels comportements même en conditions expérimentales souligne la difficulté des individus à donner à un congénère et met en évidence l'existence de facteurs limitant la mise en place de la réciprocité calculée chez les primates non humains. On est droit de se demander si les exemples de réciprocité calculée décrits dans la littérature (de Waal, 1997a ; de Waal & Luttrell, 1988) sont effectivement basés sur une intention de donner de la part des individus. Il apparaît nécessaire de mener des études approfondies sur ce sujet.

2.4. L'attente d'un retour

Après avoir donné un bien à l'individu B, l'individu A doit attendre un délai avant de recevoir un retour. Un moyen de déterminer la capacité d'un individu à attendre est de mesurer son aptitude à retarder l'accès à une récompense. Chez l'être humain, Mischel (1974) a proposé deux options à de jeunes enfants: une récompense immédiatement disponible ou bien deux mais seulement après un temps d'attente. Les enfants ayant obtenu les deux récompenses ont fait preuve de patience tandis que les enfants n'ayant reçu qu'une seule récompense se montrent plus impulsifs (Mischel, 1974). Ce test permet de mettre en évidence deux phases dans le processus d'attente. Dans la première phase, l'individu fait le choix d'attendre (ou pas) en fonction de variables telles que la durée du temps d'attente ou la dimension de la récompense : c'est la prise de décision (*delay-choice*) (Toner & Smith, 1977 ; Toner et al., 1979). Dans la seconde phase, l'individu doit maintenir sa décision d'attendre tout au long du délai : c'est le maintien de la décision d'attendre (*delay-maintenance*) (Toner & Smith, 1977 ; Toner et al., 1979).

La capacité des animaux à attendre un délai a été étudiée suivant différentes procédures expérimentales, souvent semblables à celles utilisées chez l'être humain. Lors de tests de choix par exemple, deux options sont proposées au sujet : une récompense de base immédiate ou une récompense préférée – car de meilleure qualité ou de plus grande quantité – mais retardée. Si les sujets optent pour la récompense retardée, ils n'ont plus la possibilité de revenir à la récompense immédiate durant le délai. Dans ce type de tests, des bonobos, des chimpanzés et des singes araignées se montrent capables de refuser la récompense immédiate et d'attendre une à deux minutes pour recevoir une récompense triple (Amici et al., 2008 ; Rosati et al., 2007). Testés dans des conditions identiques, des marmousets, des macaques à longue queue (*Macaca fascicularis*) et des singes capucins peuvent différer de 20 s l'accès à la plus grande récompense tandis que des tamarins (*Saguinus oedipus*) ne tolèrent qu'un délai de 10 s (Amici et al., 2008 ; Stevens et al. 2005b).

Lors de tests du maintien de la décision, la récompense immédiate reste à portée de l'individu tout au long du temps d'attente, laissant aux sujets la possibilité de changer leur décision. Ce type de procédure permet à l'expérimentateur de mesurer avec exactitude le délai que peuvent supporter les sujets avant de saisir la récompense. Face à un morceau de céleri immédiatement accessible et un raisin dont l'accès est retardé, des macaques rhésus sont capables d'attendre 2 mn pour obtenir le raisin même si le cèleri reste à portée de main (Evans & Beran, 2007a). Testés selon la procédure de Mischel (1974), des chimpanzés retardent la prise de la récompense préférée entre 3 et 5 mn (Beran et al., 1999). Des chimpanzés entraînés au langage des signes sont également capables de retarder de 3 mn la prise d'une récompense représentée sous forme de photographies et de lexigrammes (Beran et al., 1999). Si l'accès à une distraction est autorisée durant le temps d'attente, des chimpanzés tolèrent un délai allant jusqu'à 18 mn (Evans & Beran, 2007b).

Un dernier type d'expérience consiste à présenter au sujet une accumulation d'items alimentaires au fur et à mesure du temps d'attente. Les sujets doivent inhiber la prise immédiate de nourriture afin de maximiser leur gain. Dans ce test d'accumulation, des macaques rhésus sont capables d'attendre 30 s avant de saisir la récompense (Evans & Beran 2007a) tandis que des chimpanzés et un orang-outang sont capables d'attendre jusqu'à 3 mn (Beran, 2002).

Les études expérimentales visant à mesurer l'aptitude des primates à attendre un délai ont permis de mettre en évidence des différences interspécifiques significatives. Elles ont également permis de souligner l'influence de la procédure expérimentale employée sur les performances des individus. Cependant, même si les résultats obtenus nous permettent de circonscrire la tolérance au délai, ils ne nous permettent pas de conclure quant à la capacité des primates à attendre au cours d'un échange. Jusqu'ici, une seule étude a permis de déterminer la tolérance au délai de capucins bruns au cours d'échanges d'items alimentaires avec un expérimentateur. Ramseyer et collaborateurs (2006) ont ainsi mis en évidence que des singes capucins attendent 10 s pour une récompense différée huit fois supérieure à la récompense immédiate et 20 s pour une récompense différée quarante fois supérieure à la récompense immédiate. Si au cours d'un échange, les capacités d'attente des individus ne dépassent pas quelques dizaines de secondes, il est peu probable que les interactions réciproques observées chez d'autres espèces que l'être humain, soient basées sur l'attente d'un retour. Tester la capacité de primates non humains à attendre lors d'un échange est crucial pour évaluer leur capacité à échanger de manière calculée.

2.5. Le calcul du risque

Le délai entre le don et le retour n'engendre pas seulement un temps d'attente pour l'individu A mais également une prise de risque. En s'engageant dans un échange différé, l'individu A prend le risque qu'au cours de l'attente le bien à retourner soit détérioré, dérobé par un tiers ou encore qu'il ne soit jamais rendu. L'individu A doit donc être capable de juger les risques liés à la situation d'échange.

En économie, la notion de risque se distingue de la notion d'incertitude (Knight, 1921). Le risque se définit comme une situation dans laquelle les issues possibles sont affectées de probabilités connues. Dans une situation d'incertitude, les probabilités des issues restent inconnues.

Plusieurs études ont porté sur la sensibilité au risque chez les animaux. Le protocole type utilisé consiste à présenter deux options de récompenses alimentaires aux individus : une option constante et une option dite « risquée ». En choisissant la première option, les individus reçoivent toujours la même quantité de nourriture à des intervalles de temps fixes. En choisissant la deuxième option, les individus reçoivent une récompense qui varie soit en quantité, soit en temps nécessaire pour y accéder. Face à des choix variant en délai, les animaux favorisent l'option « risquée » tandis que, face à des choix variant en quantité, les animaux favorisent l'option constante (Kacelnik & Bateson, 1996). Chez les primates non humains, on a montré que face à des choix variant en quantité, des chimpanzés se montrent plus enclins à choisir l'option « risquée » que des bonobos (Heilbronner et al., 2008). Les auteurs ont conclu à une influence des pressions écologiques sur la prise de décision des individus (Heilbronner et al., 2008). Même si une telle procédure nous donne des indications sur les facteurs influençant la prise de décision des individus face à une situation risquée, elle ne nous permet pas d'étudier la réponse des individus face à un risque de perdre. En effet, dans la procédure décrite précédemment, les sujets obtiennent à la fin des essais la même quantité de récompense, qu'ils choisissent l'une ou l'autre des options. Or, dans un échange, le risque potentiellement pris par l'individu est que leur partenaire ne retourne pas le don et donc de réellement perdre. Il est nécessaire de mesurer le degré de tolérance au risque des individus lorsqu'ils s'engagent dans un échange.

2.6. La reconnaissance du partenaire

Pour recevoir le retour, l'individu A doit être capable de reconnaître l'individu B et inversement. La reconnaissance des membres du groupe est une condition de l'établissement de relations sociales durables. Par l'utilisation d'images photographiques, plusieurs études ont montré que les primates non humains pouvaient utiliser le visage pour reconnaître des congénères. Cette faculté a été mise en évidence par exemple chez les chimpanzés (Parr et al., 1998), les macaques japonais (Tomonaga, 1994), les macaques rhésus (Parr et al., 1999), les macaques à longue queue (Dasser, 1987), les macaques de Tonkean (Dufour et al., 2006) et les capucins bruns (Dufour et al., 2006). Les primates sont également capables de reconnaître les relations sociales qui les lient à leurs congénères (Tomasello & Call, 1997). On a enfin montré que les individus pouvaient reconnaitre les relations sociales qui lient deux de leurs congénères entre eux. Par exemple, Dasser (1988) a montré que des macaques à longues queue sont capables de discriminer à partir de photographies entre des partenaires apparentés et non apparentés, ce qui signifie qu'il leur est possible de reconnaître les relations sociales qui unissent les membres de leur groupe. Ces différents résultats indiquent que la connaissance du partenaire ne devrait pas représenter un facteur limitant des échanges chez les primates.

2.7. La mémoire et l'anticipation

Au cours d'un échange, mémoriser ce qui est donné et anticiper ce qui va l'être sont deux facultés indispensables. La capacité des animaux à se remémorer des événements passés – mémoire épisodique – et à se projeter dans le futur – planification – a fait l'objet de nombreuses études. Cependant, l'aptitude des animaux à se déplacer mentalement dans le temps reste un sujet controversé (Clayton et al., 2003 ; Roberts, 2002 ; Suddendorf & Busby, 2003). Certains auteurs affirment que les animaux sont incapables de se rappeler d'événements qui leur seraient propres et qu'ils seraient par conséquent incapables de planifier des besoins futurs (Roberts, 2002 ; Suddendorf & Busby, 2003).

Une étude a montré que des chimpanzés sont incapables de stocker des fruits par avance, conduisant les auteurs à conclure à une « myopie temporelle », c'est-à-dire à une incapacité à anticiper un besoin futur (Silberberg et al., 1998). Cependant, différents travaux indiquent que des primates non humains sont capables de comportements orientés vers le futur. On a montré que des capucins bruns se déplaçant vers des sites de nourritures éloignés choisissent avec quelques minutes d'avance la route la plus appropriée (Janson, 1998). Chez les grands singes, on a observé des chimpanzés élevés en captivité en train de stocker spontanément des jetons en vu de les échanger dans un futur proche contre de la nourriture (Sousa & Matsuzawa, 2001). Des orangs-outangs et des bonobos peuvent également collecter, garder et transporter des outils afin de les utiliser jusque 12 heures plus tard (Mulcahy & Call, 2006). Des chimpanzés se sont également montrés capables de discriminer, garder et transporter des outils pour les utiliser dans un futur proche, mais lorsqu'ils ont du planifier le transport et l'utilisation d'un objet dans une tâche d'échange, ils ont été incapables de résoudre cette tâche (Dufour & Sterck, 2008). Il est possible que la dimension sociale de l'échange rende la planification d'un échange particulièrement complexe.

2.8. La détection et la prévention de la tricherie

L'individu A doit détecter et prévenir l'abus de comportement de tricherie de la part de l'individu B. Chez l'être humain, Trivers (1971) distingue une forme de tricherie flagrante (*gross cheating*) où le tricheur ne donne rien d'une forme plus subtile (*subtle cheating*) où le tricheur donne moins que ce qui a été donné tout en maintenant un comportement apparemment coopératif.

Chez les primates, on a rapporté de façon anecdotique de nombreux cas de dissimulation ou tromperie (Byrne & Whiten, 1990). Des individus subordonnés ayant localisé une ressource alimentaire peuvent s’abstenir d’émettre des vocalisations (*food calls*) pour éviter d’attirer des individus dominants qui viendraient monopoliser la ressource (Hauser, 1992, 1997 ; Hauser et al., 1993). Des individus dominés peuvent également pousser de faux cris d’alarme pour éloigner des individus dominants d’une ressource de nourriture (Wheeler, 2009). Ils sont également capables de cacher leur présence à d’éventuels compétiteurs (de Waal, 1998 ; Gygax, 2000 ; Kummer et al., 1996) et arrivent parfois à éloigner un individu dominant d’une source cachée de nourriture (Coussi-Korbel, 1994 ; Goodall, 1986 ; Hirata & Matsuzawa, 2001). Si l'on a aujourd'hui peu de doutes que des primates soient capables de dissimuler une information (e.g., Amici et al., 2009 ; Coussi-Korbel, 1994 ; Ducoing & Thierry, 2003 ; Hare et al., 2001), il reste à démontrer expérimentalement qu'ils peuvent donner une information fausse. Savoir s'ils peuvent anticiper une tricherie est *a fortiori* plus problématique encore, en particulier si cela requiert d'attribuer des états mentaux à autrui.

3. VERS UNE ECONOMIE EXPERIMENTALE DES PRIMATES

Comme il a déjà été dit, l’approche expérimentale est nécessaire pour déterminer dans quelle mesure les primates non humains sont capables d’échanger avec leurs congénères. En économie humaine, l’approche expérimentale consiste à créer un environnement contrôlé afin de reproduire artificiellement une situation reflétant les conditions des transactions économiques. L’économie expérimentale teste les prédictions de théories ou de modèles économiques en les confrontant à des données obtenues dans un environnement contrôlé (Eber & Willinger, 2005). Chez les primates non humains, une approche similaire par le biais du modèle expérimental de l’échange a déjà permis de reconnaître et mesurer quelques unes de leurs compétences.

3.1. L’échange comme modèle expérimental

Plusieurs études en captivité ont mis en évidence la propension des primates à donner des objets à des êtres humains (Bertrand, 1976 ; Coussi-Korbel, 1993 ; Hyatt & Hopkins, 1998 ; Lefevbre, 1982). Le renforcement de ce comportement par l’obtention d’une récompense alimentaire est à la base de la tâche que représente l’échange avec un expérimentateur. L’avantage d’un tel modèle est qu’il ne requiert de la part de l’animal que le geste de donner, impliquant un minimum d’entraînement, comparé à des tâches plus complexes comme celles faisant intervenir l’utilisation d’outils.

Des capucins bruns et des chimpanzés s’avèrent aptes à échanger avec un expérimentateur humain des items de nourriture qui diffèrent en qualité (Drapier et al., 2005 ; Lefebvre, 1982 ; Ramseyer et al., 2006 ; Westergaard et al., 2004) ou en quantité (Drapier et al., 2005 ; Ramseyer et al., 2006). Ils sont capables de discriminer parmi plusieurs objets celui qui leur donne accès à une récompense alimentaire (Brosnan & de Waal, 2004ab, 2005 ; de Waal et al., 2008) ou à un outil nécessaire pour accéder à un item alimentaire (Westergaard et al., 1998). Les sujets en viennent ainsi à attribuer une valeur symbolique aux objets qui leur permettent d'acquérir de la nourriture (Addessi et al., 2007, 2008ab). Des capucins bruns et des gorilles peuvent également réaliser des échanges successifs d’items alimentaires et d’objets avec un expérimentateur humain (Chalmeau & Peignot, 1998 ; Drapier et al., 2005), par exemple des capucins sont capables de donner une pierre pour recevoir un granulé alimentaire qu’ils échangent ensuite pour un morceau de pomme.

3.2. Les biais de jugement

En économie, la théorie sur les choix individuels s’appuie en particulier sur le modèle de la maximisation d’utilité, c’est-à-dire la maximisation de la satisfaction par l’obtention de biens ou services. En situation de certitude, cette théorie est qualifiée de théorie de l’utilité (*Utility Theory*) tandis qu’en condition d’incertitude elle est qualifiée de théorie de l’espérance d’utilité (*Expected Utility Theory*, von Neumann & Morgenstern, 1944). Les préférences des agents humains sont supposées respecter un certain nombre de propriétés. On les représente par une fonction d’utilité que l’individu maximise pour déterminer son choix. En maximisant l'utilité, on suppose que celui qu'on qualifie d’*Homo oeconomicus* agit de manière rationnelle. Les travaux des dernières décennies ont montré qu'il s'agit en réalité d'une approximation. Les décisions économiques humaines sont souvent faussées par des biais de jugement d'origine psychologique (Tversky & Kahneman, 1981). L’économie expérimentale a montré qu'en de nombreuses circonstances les êtres humains ne maximisent pas l'utilité, ce qui les conduit à des décisions moins rationnelles que celles prédites par les modèles. Quelques études ont cherché des biais de jugement chez les primates.

3.2.1. L'effet de dotation

En situation de certitude, l’une des anomalies comportementales les plus significatives chez l’être humain est l’effet de dotation (*endowment effect*) qui traduit le fait que les personnes exigent plus pour céder un objet qu’elles ne sont prêts à payer pour l’acquérir (Knetsch, 1989). L’effet de dotation pour le choix entre deux biens a pour la première fois été mis en évidence dans une expérience effectuée par Knetsch (1989) au cours de laquelle participaient trois groupes de sujets humains répartis aléatoirement. Les sujets du groupe 1 se voyaient offrir une tasse à café qu’ils pouvaient échanger contre une barre en chocolat. Les sujets du groupe 2, au contraire, se voyaient offrir une barre de chocolat qu’ils pouvaient échanger contre une tasse à café. Les sujets du groupe 3 quant à eux n'avaient pas de dotation initiale et devaient simplement choisir entre la tasse à café et la barre en chocolat. Les résultats obtenus sont les suivants : 89% des sujets du groupe 1 ont choisi de conserver leur tasse à café, 90% des sujets du groupe 2 ont choisi de conserver leur barre de chocolat, et 56% des sujets du groupe 3 ont opté pour la tasse à café. La tasse à café a ainsi été valorisée par rapport à la barre de chocolat par les sujets détenant la tasse à café, alors que c'est la barre de chocolat qui a été davantage valorisée par rapport à la tasse à café par les sujets détenant le chocolat. Les préférences des individus pour des biens apparaissent ainsi sensibles à leur dotation initiale. Des travaux ultérieurs ont confirmé la généralité de ces résultats (Kahneman et al., 1990 ; Knetsch, 1992).

L'effet de dotation a récemment été testé chez les primates non humains. Chez les grands singes, des chimpanzés se sont vus attribuer un item alimentaire ou un jouet et ont ensuite été autorisés à les échanger avec un expérimentateur humain pour différents items de même nature (alimentaire/non alimentaire) mais préférés. La majorité des chimpanzés ont échangé leur jouet initial pour le second jouet mais ont refusé d'échanger leur item alimentaire (Brosnan et al., 2007). Une autre expérience chez des capucins bruns entraînés à l'échange a montré qu'ils refusent d'échanger des items alimentaires pour des items de nature équivalente avec un expérimentateur humain (Lakshminaryanan et al., 2008). Les auteurs concluent à l'existence d'un effet de dotation chez les primates. Même si des similitudes apparaissent dans les comportements observés chez les différentes espèces, il reste nécessaire d'approfondir l'étude des mécanismes sous-jacents à un tel phénomène pour pouvoir conclure avec certitude à un effet de dotation chez les primates non humains.

3.2.2. L'aversion pour la perte

En situation d'incertitude ou de risque, l'une des anomalies comportementales les plus importantes observées chez l'être humain est l'aversion pour la perte (*loss aversion*) par laquelle les individus perçoivent les pertes plus intensément que les gains (Tversky & Kahneman, 1986). Chen et al. (2006) ont testé l'existence d'une aversion pour la perte chez des capucins bruns au cours de tests d'échange. Les sujets pouvaient choisir d'échanger un jeton avec un expérimentateur E1 qui leur présentait et leur donnait une récompense, et un expérimentateur E2 qui leur présentait deux récompenses mais ne leur en donnait qu'une. Les échanges avec les deux expérimentateurs étaient donc équivalents – une seule récompense. Cependant, dans la majorité des cas, les capucins ont préféré l'alternative fixe et ont échangé leurs jetons avec l'expérimentateur E1, ce qui a été interprété par les auteurs comme résultant d'un effet d'aversion pour la perte (Chen et al., 2006). D'autres hypothèses cependant pourraient expliquer les résultats obtenus chez les capucins. Par exemple, le délai dû au fait de retirer l'une des deux récompenses chez l'expérimentateur E2 dans l'étude de Chen et al. (2006) pourrait entraîner le choix par les sujets de l'expérimentateur E1 qui rend aussitôt la récompense (Silberberg et al., 2008). Un effet de frustration dû au fait de voir mais de ne pas obtenir les deux récompenses pourrait également expliquer la préférence pour l’expérimentateur E1 par les sujets. Conclure à un véritable effet d’aversion pour la perte chez les singes capucins là encore demande des travaux supplémentaires.

3.3. Le sens de l'équité

La théorie des jeux est une approche mathématique des problèmes liés aux interactions stratégiques entre deux protagonistes ou plus. De même que la théorie de l’utilité le fait en conditions de choix individuel, la théorie des jeux prédit un comportement rationnel des individus à partir de la maximisation de l'utilité. L’économie expérimentale a permis de confronter les prédictions de la théorie des jeux à des expérimentations en environnement contrôlé. Les résultats mettent en évidence des comportements altruistes réciproques chez l'être humain, basés sur la confiance et le désir d’équité dans les comportements stratégiques des individus (voir Eber & Willinger, 2005). De tels résultats ne correspondent à la théorie de la maximisation de l’utilité par les individus que si le modèle de l’utilité prend en compte la satisfaction basée sur les préférences sociales des individus.

Des travaux récents ont étudié les décisions économiques de primates non humains dans des situations qui mettent en jeu deux partenaires. Je développerai ici l’exemple de l’aversion pour l’iniquité (*inequity aversion*) (Fehr & Schmidt, 1999) et du jeu de l’ultimatum (*ultimatum game*) (Güth et al., 1982).

3.3.1. L’aversion pour l’iniquité

Dans le modèle d’aversion pour l’iniquité de Fehr et Schmidt (1999), les individus ont une satisfaction qui augmente avec leurs propres gains mais qui diminue lorsque l’iniquité entre les joueurs croît. Cette aversion pour l’iniquité mise en évidence chez l’homme dans le jeu de l’ultimatum, a été étudié chez le capucin brun (Brosnan & de Waal, 2003) et le chimpanzé (Brosnan et al., 2005) suivant des protocoles similaires. Deux sujets placés dans des compartiments de test adjacents ont la possibilité d’échanger l’un après l’autre des jetons contre de la nourriture avec un expérimentateur. Dans une première condition, les récompenses obtenues par les deux sujets sont identiques et de nombreux échanges sont observés chez les deux sujets. Dans une seconde condition, le premier sujet reçoit une récompense d'une grande valeur tandis que le second reçoit une récompense de moindre valeur. Dans une troisième condition, le premier sujet reçoit une récompense sans avoir à échanger tandis que le second sujet doit échanger pour recevoir la récompense de valeur inférieure. Dans ces deux dernières conditions, on constate une augmentation des refus d'échanger avec l'expérimentateur de la part du second individu, ou même de consommer la récompense lorsque l'échange a eu lieu. Ces résultats amènent les auteurs à conclure à une aversion pour l’iniquité chez les singes capucins (Brosnan & de Waal, 2003) et les chimpanzés (Brosnan et al., 2005).

Toutefois, plusieurs études ont remis en question ces conclusions (Henrich, 2004 ; Wynne, 2004). En particulier, on peut expliquer les comportement des sujets par des effets de frustration – voir sans obtenir une récompense convoitée – chez les capucins (Dubreuil et al., 2006 ; Roma et al., 2006) ou d'attente de la récompense chez les chimpanzés (Bräuer et al., 2006) sans avoir recours à l'hypothèse de l'aversion pour l'iniquité. Une autre étude montre que l'estimation de la valeur relative des récompenses et l'effort lié à la tâche d'échange entre les deux sujets se révèle difficile pour les singes capucins, or celle-ci s'avère nécessaire dans l'aversion pour l'iniquité (Fontenot et al., 2007). Les capucins et les chimpanzés paraissent réagir sans directement tenir compte de la perspective de l'autre. L'existence d'une intolérance à l'iniquité reste donc à démontrer chez ces espèces.

3.3.2. Le jeu de l'ultimatum

Le jeu de l'ultimatum consiste en une négociation entre deux individus dans laquelle le joueur 1 fait une seule et unique offre au joueur 2. Le joueur 1 dispose du pouvoir de répartir et le joueur 2 celui d'émettre un veto (Güth et al., 1982). Prenons l'exemple d'une somme d'argent de 100 euros qui doit être répartie entre les deux joueurs. La solution théorique de ce jeu est que le joueur 1 fasse la plus petite offre au joueur 2 (1 euro) et que celui-ci l'accepte. En effet, aussi faible soit-il un gain est toujours préférable à 0. Les résultats expérimentaux cependant montrent une tendance des individus à s'éloigner de la solution théorique : les joueurs 1 faisant des offres comprises entre 40 et 50%, et les joueurs 2 refusant les offres inférieures à 20% de la somme (Eber & Willinger, 2005). Récemment, Jensen et collaborateurs (2007) ont testé des chimpanzés dans une version simplifiée du jeu de l'ultimatum où l'argent est remplacé par des raisins. Un premier individu fait face à deux offres possibles : par exemple, 8 raisins pour lui et 2 raisins pour son partenaire, ou bien 5 raisins pour chacun. Une fois le choix effectué, le partenaire peut accepter ou refuser l'offre. Les résultats montrent que les chimpanzés ne font pas toujours d'offres dites honnêtes à leurs partenaires mais que ceux-ci acceptent la quasi totalité des offres non nulles (Jensen et al., 2007). Du point de vue de la théorie économique classique, on peut dire que la stratégie égoïste des chimpanzés fait d'eux des joueurs rationnels dans le sens où ils maximisent leurs gains dans le contexte expérimental.

La différence entre le chimpanzé et l'homme dans le jeu de l'ultimatum réside dans le fait que les joueurs humains prennent en compte les normes collectives de leur société alors que les chimpanzés n'en sont probablement pas capables. Celui qui ne respecterait pas la justice dans les sociétés humaines serait puni ou exclu. A l'échelon collectif, il devient alors rationnel pour l'individu de renoncer à une partie de ses gains et de faire preuve d'équité. Les résultats du jeu de l'ultimatum chez le chimpanzé renforcent les conclusions actuelles quant à l'absence d'un sens de l'équité chez les primates non humains.

4. OBJECTIFS DE L’ETUDE

Le présent travail a eu pour but de comprendre dans quelle mesure des primates non humains peuvent s'engager dans des transactions de type économique. En étudiant les facultés nécessaires à l'échange d'objet ou de nourriture, il s'agit de déterminer les conditions favorisant l'émergence de la réciprocité calculée et de préciser les compétences susceptibles d'intervenir dans les relations sociales des primates.

J’ai étudié sept espèces de primates appartenant à six genres différents : capucins bruns, macaques de Tonkean et macaques à longue queue au *Centre de Primatologie* de Strasbourg ; chimpanzés, orangs-outangs, gorilles et bonobos au *Wolfgang Köhler Primate Centre* de Leipzig. Ces espèces se distinguent par leurs organisations sociales mais également par des niveaux différents de tolérance sociale. Chez les singes, les capucins et les macaques vivent en groupes multimâles multifemelles dont l’organisation se caractérise par une structure en – lignées maternelles – sous-groupes d’individus apparentés issus d’une même femelle (Fragaszy et al., 2004). Les relations sociales des macaques varient en fonction des espèces : le macaque à longue queue présente une hiérarchie de dominance stricte et une forte intensité d’agression en comparaison avec le macaque de Tonkean où le gradient de dominance est moins fort et le degré de tolérance sociale plus élevé, ces différences sociales correspondent à des tempéraments différents chez les individus (Thierry et al., 2004). Chez les grands singes, les chimpanzés et les bonobos forment des groupes sociaux multimâles multifemelles selon un système de fission-fusion : celui-ci consiste en une communauté d’individus fractionnée sous-groupes de composition variable (Goodall, 1986 ; Nishida, 1968 ; White, 1988). Les gorilles de plaine se caractérisent par un groupe social constitué d’un mâle adulte, d’un ou deux mâles sub-adultes et de plusieurs femelles accompagnées de leur progéniture (Harcourt et al., 1981). Enfin, les orangs-outangs se distinguent des autres espèces de grands singes par leur organisation sociale dispersée sur un large territoire (Mitra Setia et al., 2009). Ces espèces diffèrent également des unes des autres par leurs facultés cognitives. Les grands singes présentent généralement de meilleures performances que les espèces de singes dans les tâches d’imitation, les tests d’inférence, les tests de reconnaissance dans le miroir ou encore les situations expérimentales requérant que les sujets tiennent compte des perceptions d'autrui (Tomasello & Call, 1997). L’étude d'espèces différentes doit permettre de faire apparaître des variations dans le phénomène étudié et de repérer ainsi les facteurs susceptibles d'affecter la réponse des individus.

Dans une première partie (Chapitre III), j’ai cherché à déterminer les mécanismes de la prise de décision lorsque les individus doivent soutenir une période d'attente au cours d’un échange. J'ai étudié des chimpanzés, des singes capucins, des macaques de Tonkean et des macaques à longue queue. Pour cela, les sujets ont été testés dans deux tâches d’échange de nourriture avec un expérimentateur au cours desquels des délais croissants étaient imposés avant l'obtention de la récompense finale (articles 1, 2 et 3). J'ai employé différentes quantités de récompense pour déterminer si la valeur quantitative de la récompense influence la décision d'attendre. J’ai étudié l'influence de deux facteurs susceptibles d'influencer la tolérance au délai : l’inhibition de la consommation et la dépréciation au cours du temps de la récompense.

Dans une seconde partie (Chapitre IV), j’ai étudié les facteurs qui déterminent les décisions des individus lorsqu'ils s'engagent dans une transaction comportant un risque de perte. J’ai étudié la capacité d’orangs-outangs, de singes capucins et de macaques à longue queue à calculer un risque au cours d’un échange de nourriture avec un expérimentateur (article 4). Au cours de la phase de test, je présentais une combinaison de récompenses de différentes dimensions au sujet. Ces récompenses pouvaient être de dimension supérieure, inférieure ou équivalente à l'item de nourriture qu'il devait rendre. Lorsque le sujet acceptait l'échange, il recevait une récompense choisie de manière aléatoire dans cette combinaison. J'ai testé différents modèles de décision de manière à identifier les stratégie suivies par les individus face au risque : (1) miser aussi longtemps que les chances de gain sont plus fortes que les chances de perte, (2) miser aussi longtemps qu'il y a des chances de gain et cela quelles que soient les pertes potentielles, (3) cesser de miser dès qu'une perte survient et cela quels que soient les gains potentiels.

Dans une troisième partie (Chapitre V), l'objectif fut de déterminer dans quelle mesure les sujets peuvent s’engager dans des échanges de biens avec un congénère. J’ai étudié les quatre espèces de grands singes (articles 5 et 6), les singes capucins et les macaques de Tonkean (article 7) dans une procédure visant à faciliter l’émergence de transferts réciproques. J'ai placé les sujets par paire dans une situation où il leur fallait échanger des objets afin d’obtenir de la nourriture auprès d’un expérimentateur humain. Il s'est agi de tester la réciprocité des quémandes et des dons susceptible de survenir entre les partenaires. On s'attend à ce que les espèces présentant la propension la plus élevée à attendre ou à prendre un risque montrent plus de facilité à s’engager dans un échange avec un congénère.

CHAPITRE II

METHODES GENERALES

1. LES GROUPES D'ETUDE ET LES CONDITIONS D'ELEVAGE

1.1. Les capucins bruns

Fig. 1. Capucins bruns.

Les capucins bruns (*Cebus apella*) sont élevés au *Centre de Primatologie* de l'Université de Strasbourg (Fig. 1). Ils sont issus d'un même groupe social comprenant entre 19 individus en 2006 (5 mâles adultes et 11 femelles adultes) et 17 individus en 2009 (5 mâles adultes et 8 femelles adultes). Ils évoluent dans un environnement composé de deux animaleries intérieures (33m^2 de surface au total) et de deux volières extérieures (30 m^2). Ces différents compartiments communiquent par des tunnels que l'on peut fermer par des portes coulissantes. Des granulés et de l'eau sont disponibles *ad libitum* dans les animaleries intérieures et des fruits sont distribués une fois par semaine.

1.2. Les macaques à longue queue

Fig. 2. Macaques à longue queue.

Les macaques à longue queue (*Macaca fascicularis*) sont élevés au *Centre de Primatologie* de l'Université de Strasbourg (Fig. 2). Un premier groupe de trois mâles adultes évolue dans une animalerie intérieure de 10 m^2. Un second groupe de cinq mâles adultes évolue dans une animalerie intérieure de 15 m^2 donnant accès à une volière extérieure de 20 m^2. Quatre autres mâles adultes disposent de cages individuelles (2 cages de 125 x 80 x 60 cm). De l'eau et des granulés sont disponibles *ad libitum* et des fruits sont distribués une fois par semaine.

1.3. Les macaques de Tonkean

Fig. 3. Macaques de Tonkean.

Les macaques de Tonkean (*Macaca tonkeana*) sont élevés au *Centre de Primatologie* de l'Université de Strasbourg (Fig. 3). Un premier groupe comprend entre 4 individus en 2006 (3 mâles sub-adultes et 1 femelle sub-adulte) et 7 individus en 2009 (3 mâles adultes et 1 femelle adulte). Il évolue dans un environnement composé de deux animaleries intérieures (15 m^2 de surface au total) donnant accès à deux volières extérieures (30 m^2). Ces différents compartiments communiquent par des tunnels que l'on peut fermer par des portes coulissantes. Un second groupe comprend entre 11 individus en 2006 (1 mâle adulte et 5 femelles adultes) et 16 individus en 2009 (2 mâles adultes et 5 femelles adultes). Ce groupe évolue en semi-liberté dans un parc boisé de 0,5 ha. Il a accès à une animalerie intérieure de 15 m^2. De l'eau et des granulés sont disponibles *ad libitum* et des fruits sont distribués une fois par semaine.

1.4. Les chimpanzés

Fig. 4. Un chimpanzé.

Deux groupes de 5 et 6 chimpanzés adultes (*Pan troglodytes verus*) comprenant respectivement 3 et 2 femelles sont entretenus au *Biomedical Primate Research Centre* de Rijswik (Pays-Bas). Chacun des groupes évolue dans une animalerie intérieure de 40 m^2. Dans le même centre, un troisième groupe est constitué de deux mâles chimpanzés adultes (*Pan troglodytes schweinfurthii*). Ces deux individus évoluent dans une animalerie intérieure de 15 m^2. Les animaux reçoivent deux fois par jour des fruits et des légumes de nature variée. De l'eau est également fournie *ad libitum*. Toutes les deux heures, des compléments nutritionnels tels que des graines, du miel ou de la glace sont distribués aux animaux.

Un autre groupe social de 4 chimpanzés (*Pan troglodytes verus*) comprenant 1 mâle et 3 femelles adultes est élevé au *Wolfgang Köhler Research Primate Center* du Zoo de Leipzig (Allemagne) (Fig. 4). Les individus évoluent dans un espace comprenant un enclos intérieur de 175 m^2 et un enclos extérieur de 1400 m^2. Pendant la nuit, les chimpanzés sont isolés dans une salle de repos de 32 m^2. Lors des tests, les individus sont isolés dans une salle de 19 m^2 de surface totale comprenant deux compartiments. De l'eau est disponible *ad libitum* dans ces différents espaces. De la nourriture constituée de fruits, légumes et céréales est distribuée quatre fois par jour.

1.5. Les orangs-outangs

Fig. 5. Orangs-outangs.

Un groupe de 8 orangs-outangs (*Pongo pygmaeus abelii*) comprenant 1 mâle et 3 femelles adultes est entretenu au *Wolfgang Köhler Research Primate Center* du Zoo de Leipzig (Fig. 5). Les animaux évoluent dans un espace comprenant un enclos intérieur de 230 m^2 et un enclos extérieur de 1680 m^2. Les orangs-outangs passent la nuit dans une salle de repos de 36 m^2. Lors des tests, les sujets sont isolés dans une salle de test de 25 m^2 composée de trois compartiments.

De l’eau est fournie *ad libitum* aux animaux et des repas constitués de fruits, légumes, céréales et yaourts leur sont distribués quatre fois par jour.

1.6. Les bonobos

Fig. 6. Un bonobo.

Un groupe de 6 bonobos (*Pan paniscus*) comprenant 3 mâles et 2 femelles adultes est élevé au *Wolfgang Köhler Research Primate Center* du Zoo de Leipzig en Allemagne (Fig. 6). Les animaux évoluent dans un espace comprenant un enclos intérieur de 256 m^2 et d'un enclos extérieur de 2300 m^2. Les bonobos passent la nuit dans une salle de repos de 36 m^2. Lors des tests, les sujets sont isolés dans une salle de test de 25 m^2 composée de trois compartiments. De l’eau est fournie *ad libitum* et des repas constitués de fruits, légumes, céréales et yaourts sont distribués quatre fois par jour.

1.7. Les gorilles

Fig. 7. Gorilles.

Un groupe de 5 gorilles (*Gorilla gorilla*) comprenant 1 mâle et 3 femelles adultes est élevé au *Wolfgang Köhler Research Primate Center* du Zoo de Leipzig en Allemagne. Les animaux évoluent dans un espace comprenant un enclos intérieur de 264 m^2 et un enclos extérieur de 2300 m^2. Les gorilles passent la nuit dans une salle de repos de 36 m^2. Lors des tests, les sujets sont isolés dans une salle de test de 25 m^2 composée de trois compartiments. De l’eau est fournie *ad libitum* et des repas constitués de fruits, légumes, céréales et yaourts sont distribués quatre fois par jour.

On trouvera dans le tableau qui suit un récapitulatif des caractéristiques des sujets et les études auxquelles chacun a participé.

Tableau 2. Caractéristiques individuelles des sujets

Nom	Espèce	Sexe	Naissance	Périodes de test pour les études auxquelles chaque sujet a participé		
				Etude 1 : délai	Etude 2 : risque	Etude 3 : réciprocité
Accroc	*C. apella*	mâle	1996	mars – septembre 2007	juillet 2006 – février 2007	non testé
Alila	*C. apella*	femelle	1999	non testée	août 2007 à mars 2008	non testé
Arnaud	*C. apella*	mâle	1998	mars – septembre 2007	juillet 2006 à février 2007	mars – mai 2008
Asson	*C. apella*	femelle	1989	mai – septembre 2007	non testée	non testée
Kinika	*C. apella*	femelle	1992	non testée	non testée	mai – juin 2009
Paola	*C. apella*	femelle	2001	non testée	novembre 2007 à mars 2008	non testée
Pétula	*C. apella*	femelle	2001	juillet 2007 à juillet 2008	avril – juin 2007	non testée
Pistou	*C. apella*	mâle	2001	mars – septembre 2007	juillet 2006 – février 2007	mars – mai 2008/mai – juin 2009
Popeye	*C. apella*	mâle	2001	août 2007 – février 2008	avril – juillet 2007	mars à mai 2008
Raven	*C. apella*	mâle	2002	mai 2007 – février 2008	décembre 2006 à avril 2007	non testé
Gaëtan	*M. tonkeana*	mâle	1996	avril 2007 à février 2008	non testé	non testé
Janek	*M. tonkeana*	mâle	1997	janvier – juin 2007	non testé	non testé
Lady	*M. tonkeana*	femelle	1997	mai 2007 – juin 2008	non testée	non testée
Milos	*M. tonkeana*	mâle	1997	janvier – juin 2007	non testé	non testé
Olga	*M. tonkeana*	femelle	2000	août 2007 – septembre 2008	non testée	non testée
Rimbaud	*M. tonkeana*	mâle	2002	avril 2006 – août 2007	non testé	mars – avril 2009
Shan	*M. tonkeana*	mâle	2003	avril 2007 – janvier 2008	non testé	non testé
Sherlock	*M. tonkeana*	mâle	2003	février 2007 – janvier 2008	non testé	mars – avril 2009
Simbad	*M. tonkeana*	mâle	2003	février – novembre 2007	non testé	non testé
Sybille	*M. tonkeana*	femelle	2003	mai 2006 – octobre 2007	non testée	mars – avril 2009
Castor	*M. fascicularis*	mâle	1996	août 2006 – août 2007	juillet 2007 – octobre 2008	non testé
Donald	*M. fascicularis*	mâle	1992	août 2006 – septembre 2007	juillet 2007 – octobre 2008	non testé
Jack	*M. fascicularis*	mâle	1992	août 2006 – septembre 2007	juillet 2007 – octobre 2008	non testé
Joe	*M. fascicularis*	mâle	1997	août 2006 – août 2007	juillet 2007 – octobre 2008	non testé
Loukkoum	*M. fascicularis*	mâle	1997	septembre 2006 à août 2007	non testé	non testé
Ramis	*M. fascicularis*	mâle	1992	août 2006 – août 2007	juillet 2007 – octobre 2008	non testé
Saddam	*M. fascicularis*	mâle	1996	septembre 2006 – août 2007	non testé	non testé

Tableau 2. Caractéristiques individuelles des sujets (suite)

Nom	Espèce	Sexe	Naissance	Périodes de test pour les études auxquelles chaque sujet a participé		
				Etude 1 : délai	Etude 2 : risque	Etude 3 : réciprocité
Zébulon	*M. fascicularis*	mâle	2003	juillet 2007 – mars 2008	non testé	non testé
Zorro	*M. fascicularis*	mâle	2003	septembre 2007 – février 2008	non testé	non testé
Fifi	*P. troglodytes*	femelle	1993	non testée	non testée	décembre 2006 – mars 2007
Gertrudia	*P. troglodytes*	femelle	1993	non testée	non testée	décembre 2006 – mars 2007
Jahaga	*P. troglodytes*	femelle	1993	non testée	non testée	décembre 2006 – mars 2007
Juus	*P. troglodytes*	mâle	1990	août – septembre 2005	non testé	non testé
Noah	*P. troglodytes*	mâle	1989	août – septembre 2005	non testé	non testé
Thomas	*P. troglodytes*	mâle	1990	août – septembre 2005	non testé	non testé
Ton	*P. troglodytes*	mâle	1981	août – septembre 2005	non testé	non testé
Unyoro	*P. troglodytes*	mâle	1997	non testé	non testé	décembre 2006 – mars 2007
Willy	*P. troglodytes*	femelle	1990	août – septembre 2005	non testée	non testé
Bimbo	*P. pygmaeus*	mâle	1980	non testé	non testé	mars – mai 2006
Dokana	*P. pygmaeus*	femelle	1989	non testée	juin – juillet 2008	mars – mai 2006
Dunja	*P. pygmaeus*	femelle	1973	non testée	non testée	mars – mai 2006
Kila	*P. pygmaeus*	femelle	2000	non testée	juin – juillet 2008	non testée
Padana	*P. pygmaeus*	femelle	1997	non testée	juin – juillet 2008	mars – mai 2006
Pini	*P. pygmaeus*	femelle	1988	non testée	juin – juillet 2008	mars – mai 2006
Joey	*P. paniscus*	mâle	1982	non testé	non testé	avril – août 2006
Kuno	*P. paniscus*	mâle	1996	non testé	non testé	avril – août 2006
Limbuko	*P. paniscus*	mâle	1995	non testé	non testé	avril – août 2006
Ulindi	*P. paniscus*	femelle	1993	non testée	non testée	avril – août 2006
Yasa	*P. paniscus*	femelle	1997	non testée	non testée	avril – août 2006
Bébé	*G. gorilla*	femelle	1979	non testée	non testée	mars – avril 2006
N'Diki	*G. gorilla*	femelle	1979	non testée	non testée	mars – avril 2006
Viringika	*G. gorilla*	femelle	1995	non testée	non testée	mars – avril 2006

2. LES PROCEDURES D’ENTRAINEMENT A L’ECHANGE

2.1. L’échange d’un objet pour de la nourriture

Les grands singes avaient été entraînés à échanger des objets avec un expérimentateur au cours de séances d’enrichissement antérieures à mon travail de thèse. Seuls les macaques et les singes capucins ont été entraînés à échanger un objet (un bouchon en plastique ou un caillou) avec un expérimentateur au cours de ce doctorat.

L'apprentissage s’est effectué en plusieurs étapes successives :

1. L’expérimentateur donne un objet au sujet. Le sujet est récompensé par un raisin sec lorsqu’il lâche ou jette l’objet.
2. Le sujet obtient la récompense uniquement lorsqu’il lâche ou jette l’objet hors de son enclos.
3. L’individu est récompensé lorsqu’il lâche l’objet au-dessus de la main de l’expérimentateur.
4. L’individu reçoit la récompense lorsqu’il place l’objet dans la main de l’expérimentateur.

Pour arriver à cette dernière étape, entre 27 et 37 jours d’entraînement (20 à 30 essais par jour, deux fois par jour maximum) ont été nécessaires pour que les macaques échangent un objet avec l’expérimentateur. L’entraînement des macaques à l’échange a donc nécessité entre 675 et 925 essais. En ce qui concerne les capucins bruns, certains individus avaient été entraînés à rendre un objet ou un item alimentaire à un expérimentateur au cours de précédentes études (Drapier et al., 2005 ; Ramseyer et al., 2006). L’entraînement des nouveaux individus à l’échange a nécessité entre 3 et 101 essais.

2.2. L’échange d’items alimentaires

Des capucins, des macaques de Tonkean, des macaques à longue queue, des chimpanzés et des orangs-outangs ont été entraînés à échanger des items de nourriture avec un expérimentateur humain. Les stades d’entraînement ont suivi le même protocole que précédemment, seule la nature des items variait. Les individus ont d’abord été entraînés à échanger des items de faible appétence (endive, carotte) contre des items de plus grande appétence (pomme, banane). Le but de l’entraînement était ensuite d’amener progressivement les sujets à échanger deux morceaux de biscuits de même nature mais de dimension différente (Tableau 3).

La procédure d’entraînement s’est effectuée en plusieurs étapes successives (Fig. 8) :

1. L’expérimentateur se tient devant le sujet avec deux morceaux de biscuit de dimension différente dans les mains. L’item à échanger est le biscuit de petite dimension, la récompense est le biscuit de grande dimension.
2. Les deux biscuits sont présentés au sujet pendant 3 secondes, sur la paume de la main, puis le plus petit des deux est donné à l’individu.

3. L'expérimentateur retire la main qui présente le premier biscuit et la maintient fermée ou tournée vers le bas pour éviter sa restitution par le sujet. La main contenant la récompense reste toujours à la vue du sujet.
4. L'expérimentateur avance la main vide, paume ouverte. Si le sujet pose le premier biscuit dans la main, il obtient la récompense. Si le premier biscuit est jeté, consommé ou porté à la bouche, l'échange est considéré comme un échec. La main choisie pour présenter la récompense est randomisée entre la gauche et la droite.

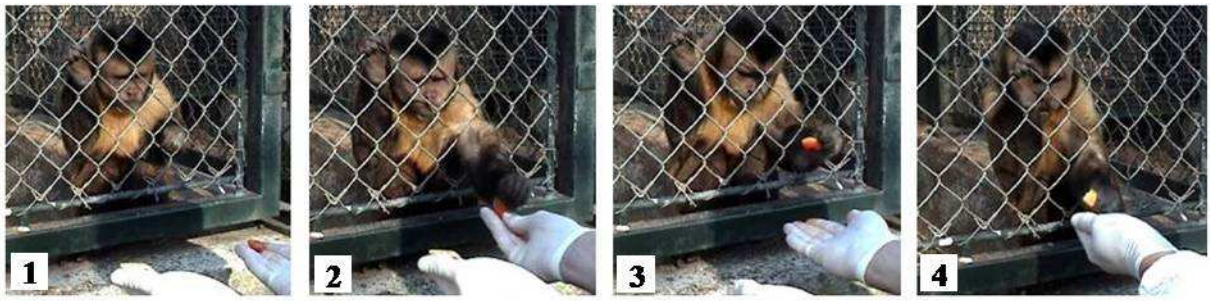


Figure 8. Séquence d'échange entre un singe capucin et l'expérimentateur.

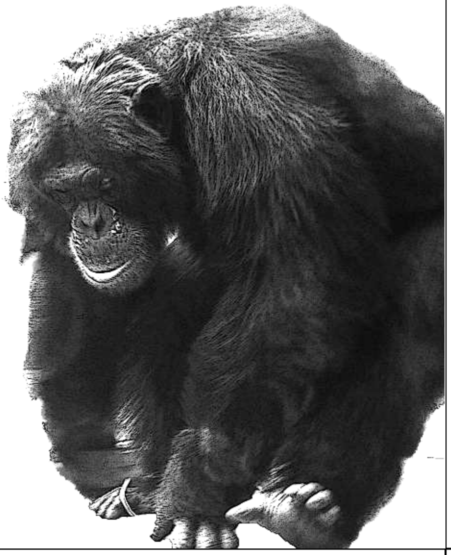
Des critères d'entraînement ont été définis pour chaque espèce. Les sujets ont pu être testés une fois qu'ils avaient atteint ce critère. Le Tableau 3 présente pour chaque espèce le critère d'entraînement et le nombre de séances (composées de 12 essais) nécessaires pour atteindre le critère. Les modalités et critères d'entraînement peuvent varier d'une espèce à l'autre en fonction de la première expérience réalisée chez ces groupes.

Tableau 3. Modalités d'entraînement.

Espèces	Dimensions biscuits (cm)	Critère d'entraînement	Nombre de séances nécessaires pour atteindre le critère
Capucins	1 x 1 x 0,5 contre 2 x 2 x 0,5	100% de réussite sur 1 session	2 à 4
Macaques de Tonkean	1 x 2 x 0,5 contre 2 x 4 x 0,5	80% de réussite sur 2 sessions consécutives	3 à 13
Macaques à longue queue	1 x 2 x 0,5 contre 2 x 4 x 0,5	80% de réussite sur 2 sessions consécutives	3 à 13
Chimpanzés	1 x 2 x 0,5 contre 2 x 4 x 0,5	80% de réussite sur 1 session	7 à 12
Orangs-outangs	1 x 2 x 0,5 contre 2 x 4 x 0,5	100% de réussite sur 1 session	2 à 4

CHAPITRE III

LA DIMENSION TEMPORELLE DE L’ECHANGE



Article 1

L'estimation de la valeur et l'anticipation de l'attente chez les chimpanzés

Article publié dans *Journal of Comparative Psychology*

RESUME DE L'ARTICLE 1

Introduction

L'étude a pour but de déterminer la capacité d'anticipation de chimpanzés au cours d'un échange. Pour cela, j'ai mesuré l'attente de chimpanzés au cours d'un échange avec un expérimentateur. Des chimpanzés sont-ils capables de différer le retour d'une récompense au cours d'un échange de nourriture ? Leurs performances sont-elles fonction de la quantité de la récompense ?

Méthodes

J'ai mesuré la capacité à attendre de cinq chimpanzés adultes au cours d'une tâche d'échange de nourriture. Les sujets devaient rendre un morceau de biscuit à un expérimentateur pour obtenir un plus gros morceau de biscuit dont la dimension pouvait être égale à deux, quatre, huit ou quarante fois la dimension du premier. Le délai imposé entre le don du plus petit morceau de biscuit et le retour de la récompense variait de 2 s à 16 mn.

Résultats

Pour une récompense égale à deux, quatre ou huit fois le premier morceau de biscuit, trois des cinq sujets ont réussi à attendre 4 mn. Pour une récompense quarante fois plus importante, quatre des cinq sujets ont toléré un délai de 8 mn. Les chimpanzés ont su estimer la dimension de la récompense et adapter leur comportement d'attente en fonction de celle-ci. L'analyse du temps de renoncement a permis de mettre en évidence la capacité des individus à anticiper le délai d'attente et à accepter l'échange en conséquence.

Conclusion

Des chimpanzés se montrent capables de différer le retour d'une récompense alimentaire sur plusieurs minutes. Ils peuvent de plus anticiper la durée de l'attente et ajuster leur décision en fonction de sa durée et de la quantité de la récompense. Cependant, même si les temps d'attente tolérés par les chimpanzés sont de l'ordre de plusieurs minutes, ils apparaissent insuffisants pour aboutir à la mise en place d'échanges calculés sur des périodes de temps plus longues telles que des jours ou des semaines.

Journal of Comparative Psychology
2007, Vol. 121, No. 2, 145–155

Copyright 2007 by the American Psychological Association
0735-7036/07/$12.00 DOI: 10.1037/0735-7036.121.2.145

Chimpanzee (*Pan troglodytes*) Anticipation of Food Return: Coping With Waiting Time in an Exchange Task

V. Dufour
Biomedical Primate Research Centre

M. Pelé
Université Louis Pasteur

E. H. M. Sterck
Biomedical Primate Research Centre and Utrecht University

B. Thierry
Université Louis Pasteur

Despite controversial expectations that animals achieve reciprocal altruism, it is unclear if nonhuman species possess the necessary cognitive abilities. For reciprocal altruism, individuals must anticipate the loss of a commodity and accept a delay before some return. The authors investigated the abilities of 5 chimpanzees (*Pan troglodytes*) to cope with increasing waiting duration in exchange tasks. Subjects had to keep a small cookie before returning it to a human partner to obtain a larger piece. For a piece 2, 4, or 8 times the size of the small piece, 3 of the 5 subjects waited for up to 4 min. For a piece 40 times larger, 4 of the 5 subjects waited up to 8 min. At long time lag, renouncement to wait occurred earlier than predicted by subjects' general waiting capacity, suggesting that the decision to wait was based on a trade-off between reward quantity and expected costs of the waiting duration. Chimpanzees could anticipate a delayed reward at a time scale of several minutes. If this reflects a cognitive limit in chimpanzees' anticipation capacity, reciprocal altruism by keeping track of costs and benefits over extended periods may be unlikely in chimpanzees.

Keywords: reciprocal altruism, delayed gratification, exchange, anticipation, chimpanzee

Reciprocal altruism has been proposed to be a mechanism that can support cooperation (Trivers, 1971). A donor who performs a costly behavior and a recipient who benefits from this behavior alternate their roles, producing delayed reciprocity. Although several studies have shown that unrelated animals may benefit from each other's behavior (Milinski, 1987; Packer, 1977; Seyfarth & Cheney, 1984; Wilkinson, 1984), research on the mechanisms involved is still scarce (Stevens, Cushman, & Hauser, 2005). In its simplest form, reciprocity is *symmetry based*. If individuals mostly direct positive behavior to close associates, reciprocal turn taking occurs in relation to the time spent in association (de Waal, 2000; de Waal & Luttrell, 1988). Another process, *attitudinal reciprocity*, has been proposed to explain some occurrences of food transfers between unrelated capuchin monkeys (*Cebus apella*). In this context, reciprocity would emerge from monkeys mirroring the behavior of the others (de Waal, 2000). The most demanding mechanism would require that partners take into account the costs and benefits of reciprocated behaviors. This *calculated reciprocity* was suggested to account for the exchanges of goods and services in chimpanzees (*Pan troglodytes*; Brosnan & de Waal, 2002). For instance, males may groom females to increase their chances of mating, or they may share meat according to the amount of help provided in hunting the prey (de Waal, 1989; Mitani & Watts, 2001), which would be in line with the reciprocal altruism hypothesis as originally formulated by Trivers (1971). Although some authors have maintained that chimpanzees keep a record of social credits and debits (Brosnan & de Waal, 2002), others argue that the correlations observed in the reciprocity of the positive behavior are not sufficient to draw conclusions about the calculation that would underlie this reciprocity (Hemelrijk, 1996).

In view of the lack of evidence for the occurrence of reciprocal altruism in nature, the cognitive prerequisites for the occurrence of calculated reciprocity have been reevaluated (Stevens & Hauser, 2005). Reciprocal altruism supposes estimating the values of goods, memorizing what has been given and received, anticipating the return of goods, and displaying a sufficient degree of self-control to accept in advance the loss of some goods. Both the ability to estimate the value of goods and memory capacities have been assessed in primates. Chimpanzees may select the largest quantity from two options when bananas had been accumulated in opaque containers over a 20-min period (Beran & Beran, 2004). A number of other experiments also point at an ability of capuchin monkeys and chimpanzees to recognize food quantity and quality; they may also attribute value to tokens and exchange goods with

---

V. Dufour, Ethology Research, Animal Science Department, Biomedical Primate Research Centre, Rijswijk, the Netherlands; M. Pelé and B. Thierry, Département d'Ecologie, Physiologie et Ethologie, Centre National pour la Recherche Scientifique, Université Louis Pasteur, Strasbourg, France; E. H. M. Sterck, Ethology Research, Animal Science Department, Biomedical Primate Research Centre, and Behavioral Biology, Utrecht University, Utrecht, the Netherlands.

We are grateful to Han de Vries for guidance and collaboration in statistical analysis of the results and to the keepers for their help and assistance in working with the chimpanzees.

Correspondence concerning this article should be addressed to V. Dufour, who is now at the Département d'Ecologie, Physiologie et Ethologie, UMR 7178, IPHC, Centre National pour la Recherche Scientifique, 23, rue Becquerel, 67087 Strasbourg Cedex 2, France. E-mail: valerie.dufour@c-strasbourg.fr

humans in bartering tasks (Brosnan & de Waal, 2004, 2005; Drapier, Chauvin, Dufour, Uhlrich, & Thierry, 2005; Hyatt & Hopkins, 1998; Lefebvre, 1982; Padoa-Schioppa, Jandolo, & Visalberghi, 2006; Sousa & Matsuzawa, 2001; Westergaard, Liv, Rocca, Cleveland, & Suomi, 1998, 2004). With regard to memory performances, a study showed that a chimpanzee remembered the location of food over 3 days (Menzel, 1999). In another investigation chimpanzees remembered the value of Arabic numerals over periods longer than 3 years (Beran, 2004). Melis, Hare, and Tomasello (2006) further reported that chimpanzees could choose the best partner between two, based on previous experience and success with this partner in a cooperative task. Thus, the cognitive prerequisite for calculated reciprocity such as accurate memory for food or partner quality has been described in nonhuman species.

Much less is known of the temporal dimension involved in anticipation and self-control, which are other capacities reciprocal altruism is thought to require. When bartering about food, for instance, individuals have both to anticipate an expected gain and to inhibit food consumption while waiting. In general, animals prefer immediacy of reward, as shown in studies on self-control. When given a choice between a small immediate reward and a larger delayed reward, pigeons (Mazur, 1987), domestic fowl (Abeyesinghe, Nicol, Hartnell, & Wathes, 2005), and rats (Richards, Mitchell, de Wit, & Seiden, 1997) opt for the small immediate reward when the delay surpasses a length of a few seconds. Long-tailed macaques (*Macaca fascicularis*; Tobin, Logue, Chelonis, Ackerman, & May, 1996), rhesus macaques (*M. mulatta*; Szalda-Petree, Craft, Martin, & Deditius-Island, 2004), marmosets (*Callithrix jacchus*), and tamarins (*Saguinus oedipus*; Stevens, Hallinan, & Hauser, 2005) reach an indifference point of 50% of preference for one or the other option for delays shorter than a half a minute with a similar paradigm. Other studies have explored the duration that subjects can delay gratification when they can choose the initial smaller reward at any time during the delay. Children, for example, can delay the retrieval of cookies for 5 min when the reward is visible and can wait for 18 min when the expected reward is not visible (Mischel, Shoda, & Rodriguez, 1989). In a variant of this delay-of-gratification task, chimpanzees could inhibit themselves to access preferred food for 3 to 5 min when the quantity to gain increased regularly with time (Beran, 2002; Beran, Savage-Rumbaugh, Pate, & Rumbaugh, 1999). However, in Beran's paradigm, chimpanzees did not experience costs other than refraining from accessing a favored food and they did not experience a loss. These aspects can be assessed in a context in which animals have to barter for food.

The ability to delay gratification in an exchange task was recently addressed in brown capuchin monkeys (Ramseyer, Pelé, Dufour, Chauvin, & Thierry, 2005). The subjects had to return a small piece of a cookie after a certain time lag to obtain a larger one. These capuchins did not wait for over 20 s before returning food (although 1 subject waited for 40 s in 25% of the trials), pointing at limited self-control abilities and tolerance to loss in this species. In view of chimpanzees' excellent performances in exchange and cognition tasks (Beran et al., 1999; de Waal, 1989; Hyatt & Hopkins, 1998; Mitani & Watts, 2001; Mulcahy & Call, 2006; Savage-Rumbaugh, Rumbaugh, & Boysen, 1978), we expect that chimpanzees will postpone returns on a longer time scale than capuchin monkeys. We lack evidence about chimpanzees' understanding of time when anticipating an expected valuable reward, however. To get an insight into their ability to calculate reciprocity, we need to investigate at which time scale they can anticipate the return of some food. The aim of the present study was to assess how long a chimpanzee can wait for varying amounts of returns and decide to engage in an exchange with a human partner.

In a variant of a delayed-gratification paradigm (Beran, 2002; Mischel et al., 1989), we offered 5 chimpanzees the opportunity to exchange small pieces of cookie for larger pieces. Upon receiving the initial cookie, the chimpanzee had to keep it for a given time before returning it to the human partner in order to obtain the larger one. The larger pieces of cookie remained visible from the chimpanzees throughout the trial. In a first phase, various amounts of reward were offered in exchange for the initial piece of cookie to assess the mean duration of waiting chimpanzees could reach. In a second phase, we offered a reward 40 times the size of the initial piece to assess for the maximum waiting duration.

Method

Subjects and Breeding Conditions

Five chimpanzees (*Pan troglodytes*) of the Biomedical Primate Research Centre's colony were tested: 2 male and 1 female chimpanzee age 15 years from Group A (Tho, Juu, and Wil); a 24-year-old male chimpanzee from Group B (Ton); and a pair- and, because of the natural death of his companion, temporarily single-housed 16-year-old male (Noa). He obtained as soon as possible a new partner. Groups A and B were composed of chimpanzees from the subspecies *Pan troglodytes verus*. The 5th subject, Noa, belonged to the subspecies *Pan troglodyte schweinfurthii*. Groups A and B lived in similar conditions and were housed in a 40-m^2 indoor main room connected with individual compartments. Noa was also housed in a 40-m^2 indoor room. The study was part of a program designed to provide daily enrichment for the chimpanzees. Two prerequisites were strictly followed during this study: Only subjects willing to participate were included, and the entire study was conducted using positive reinforcement only. Subjects showed a constant willingness to participate, indicating that the tasks indeed improved the well-being of the chimpanzees.

Training Procedure

Prior to the study, Groups A and B had been involved in a cognitive task aimed at assessing their planning abilities in an exchange procedure (Dufour & Sterck, 2007). As this task relied on the immediate exchange of one nonedible token for a favored food (a peanut), both groups were familiar with immediate exchange procedures. In the current task, however, subjects had to learn to barter one food for another. In a first training phase, they were given a small piece of lettuce that they had to give back to the partner, when instructed so, to obtain a small piece of cookie held in front of them in the partner's hand. The instruction given was the word *terug* (the Dutch equivalent for *back*) that was uttered by the partner, who also showed her empty hand, palm open, in front of the chimpanzee. The other hand was holding the reward. This phase was run until chimpanzees reached a criterion of 100% of success. This training required a mean of 3 sessions (range = 1 to 5) of 12 trials each per subject. In this phase, there was no delay between the moment when subjects were given the initial item and the moment they were instructed to give it back. In a second training phase, they were required to dispose of the food they gave back in a plastic cup, but only when the cup was presented in its normal orientation in front of them by the human partner. Reverting the cup never took more than 2 s, but as long as the cup was presented upside down, chimpanzees could not give the initial food item back—they received no reward if they dropped the food item too fast out or on top of the cup. If they did so, they were given back their initial item, and the partner stepped back and waited for 30 s before starting a new trial. The same procedure was followed if chimpanzees broke, nibbled, or just touched with their lips the initial item before returning it. For this second training phase, a first step consisted in training the chimpanzees to exchange a small piece of lettuce for a piece of cookie of 2 × 4 × 0.5 cm, until they reached 80% successful returns. This step required a mean of 3.2 sessions (range = 1 to 4) of 12 trials each per chimpanzee. A second step consisted in training them to exchange a piece of cookie measuring 1 × 2 × 0.5 cm to obtain a piece 4 times the size of the initial item (2 × 4 × 0.5 cm). This second step required a mean of 3.2 sessions (range = 2 to 5) of 12 trials each. Once they reached 80% success, they entered the testing phase. In total, the chimpanzees required a mean of 9.5 sessions (range = 7 to 12) of 12 trials each to successfully master the entire procedure.

Procedure for Phase 1

Chimpanzees were separated in their familiar individual compartment. The human partner (V. Dufour and M. Pelé) gave the initial piece of cookie (1 × 2 × 0.5 cm in size) to the chimpanzee and stood in front of the cage. The partner was holding in one hand the inverted plastic cup while showing in the other hand the exchange reward that was visible during the whole delay for the chimpanzee. After a given time period, the human reversed the cup and asked *terug* to the chimpanzee. If the latter dropped the cookie in the cup, the chimpanzee received the exchange reward. The chimpanzee was required to return the first item intact; whenever the chimpanzee consumed part of it, the human partner refused the exchange and stepped back. If the chimpanzees dropped the initial small item out of the compartment, it was given back to them. During the task, the human partner looked at the timer and remained still, avoiding the gaze of the chimpanzee. If ever a subject displayed signs of excitement, the human softly said *rustig* (the Dutch equivalent for *calm down*) to quiet the chimpanzees and avoid any attempt to engage in an interaction with the human. This instruction was familiar to the chimpanzees because it was used by keepers during daily routine, for example, during feeding and/or conflicts. All chimpanzees were tested by both V. Dufour and M. Pelé, except for Juu and Noa. When tested by M. Pelé, Noa only attempted to play and did not focus on the task. Therefore, Noa was tested by V. Dufour only, and M. Pelé tested Juu instead. Other chimpanzees were tested by both human partners. The two partners each worked at the same time with 1 chimpanzee from a different group. No other people were present in the room.

We ran the tests in a succession of stages, each stage corresponding to a specific time lag. All chimpanzees followed seven stages with increasing time lag: The first stage tested their capacity to wait for 2 s, the second stage for 7 s, and the following stages tested for 15 s, 30 s, 1 min, 2 min, and 4 min. Chimpanzees who succeeded in waiting at least once at 4 min were also tested at 8 min. Each stage was composed of four identical sessions of 12 consecutive trials. In each session, three possible sizes of cookie were presented four times, in a predetermined random order. In each trial, a chimpanzee was first given a small piece of cookie (1 × 2 × 0.5 cm), while the human partner held a cookie of a larger size—2 × 2 × 0.5 cm (2 times the initial item), 4 × 2 × 0.5 cm (4 times), or 4 × 4 × 0.5 cm (8 times)—that was visible during the whole trial. The experimenter waited for 30 s after the subject ended food consumption before starting another trial. To "inform" chimpanzees about the duration of the time lag, the human partner always maintained the cup inverted for the whole time lag in the first 3 trials of a session, even if the chimpanzee dropped or ate the cookie before the whole delay had elapsed. Failure to return the initial cookie, as well as its timing and the type of error, was recorded. Chimpanzees were tested daily during weekdays. For the first series with a relatively short time lag, it was possible to run two sessions per day and per chimpanzee, with a minimum delay of 1 hr between two sessions (mean delay between two sessions: 2.64 hr, range = 1 to 4 hr). With time lags longer than 1 min, however, only one session could be run per day and per chimpanzee. Trials were not filmed, so that no behavioral data other than success, error type, and timing of error were available for the analysis.

Procedure for Phase 2

The procedure was identical to that of Phase 1 except that chimpanzees were offered a reward 40 times the size of the initial food item: five pieces of cookie, each measuring 4 × 4 × 0.5 cm. Testing started at a 7-s time lag, and longer time lags were successively tested until the individual performance dropped to 0% of return. Because this reward represented a large quantity, sessions were reduced to 4 daily trials (2 in the morning, 2 in the afternoon), with each trial being followed by, minimally, a 15-min interval before the start of the following one. The last morning trial was separated from the 1st afternoon trial by a duration of 3 hr minimum. In the previous phase, testing long delays sometimes led to the extinction of the exchange behavior. At the end of Phase 1, some subjects (such as Ton or Tho) immediately ate the initial cookie without waiting when tested at the 2- or 4-min time lag. These time lags being the most recently tested, exchange behavior had to be refreshed before starting Phase 2. To do so, chimpanzees were asked to exchange a small piece of cookie for a cookie 4 times its size with a time lag of 2 s, and then of 7 s. This required a mean of five sessions of 12 trials per chimpanzee (two sessions minimum were given at each time lag; an additional session was given if the score of 80% successful return was not reached). Because all chimpanzees succeeded in delaying the reward for 7 s in Phase 1, this time lag was chosen as the starting delay in Phase 2.

Each subject was run in 12 trials for each time lag: 7 s, 15 s, 30 s, 1 min, 2 min, 4 min, 8 min, and 16 min. A trial ended as soon as the chimpanzee dropped, broke, or ate the cookie. If a chimpanzee succeeded in waiting at least once in the time lag, it was tested at the next longer time lag. Testing was performed by V. Dufour, who recorded, as in Phase 1, the success, timing, and type of error made by the chimpanzees. Trials were not videotaped.

Data Analysis

The results of this study were analyzed following three different steps. First, for both phases, we report the longest waiting duration observed in the chimpanzees. In addition, for Phase 1, we used a nonparametric Friedman analysis of variance (ANOVA), two-tailed test (Siegel & Castellan, 1988), to compare the percentages of successful returns for the sizes of 2, 4, and 8 times the size of the initial cookie, at each of the time lags separately. Average values are given as means and standard error of the mean. This analysis was not performed for Phase 2, because only one size of reward was tested (40 times the initial size).

Second, we analyzed for both phases the type of errors made. The various error types were analyzed by comparing their relative proportion of occurrence at each time lag using a Friedman ANOVA, two-tailed test (Siegel & Castellan, 1988).

Third, we conducted an analysis on the timing of errors, that is, the time at which chimpanzees gave up waiting before the end of the trial. We compared the distribution of observed error times with the distribution of times to be expected under the null hypothesis of a constant giving up chance during the trial. If the chimpanzees could anticipate from the start of the trial the length of the delay that remained to be waited for, they may have decided early on whether to wait or not. To test this hypothesis, we calculated the estimated (observed) probability to keep on waiting at each point of time that the chimpanzee gave up waiting by using the Kaplan Meier survival analysis. This analysis includes both the failure times and the times of successful return at the end of the trial (as censored data). In this analysis, the survival probability is expressed as percentage of chance to wait longer than the time already elapsed in the trial. Against this observed survival function, we calculated the expected (exponential) distribution of giving up times under the null hypothesis of a constant giving up chance. The two distributions, the expected and the observed one, were compared using an adjusted Kolmogorov–Smirnov test (Haccou & Meelis, 1992). A statistically significant difference between both distributions leads to the rejection of the null hypothesis that a subject has a constant chance to fail (to give up) independent of the time elapsed in the trial. We ran the analysis on Phase 1 by combining all cookie sizes: 2, 4, and 8 times the original size (N = 48). In Phase 2, only one size of reward was tested; therefore, the analysis was run on a smaller number of events ($N = 12$). For all analyses, the significance level was set at .05.

Results

Percentage of Success in Delaying Gratification

In Phase 1, the results showed that the chimpanzees failed to return the initial cookie at the time lag of 8 min but that they succeeded for shorter time lags (see Figure 1). At the 15-s time lag, 1 chimpanzee (Tho) stopped to exchange, then systematically consumed or discarded the initial item when tested at longer time lags. The success percentage of a 2nd chimpanzee (Ton) dropped to 0% at the 30-s time lag. The last 3 chimpanzees still delayed rewards at the 4-min time lag, albeit at very low rates. The longest time lag before renouncing was displayed by chimpanzee Wil, who waited once for 5 min before consuming the initial item.

The time lag sustained by the subjects did not exceed 4 min in this first phase of tests. It could be that the subjects estimated that the payoff was not worth the wait. In Phase 2, we dramatically increased the subjects' gains to 40 times the size of the initial cookie. The results showed that all subjects reached high levels of success at the 4-min time lag (see Figure 1). Performances decreased at 8 min, but 4 of the 5 chimpanzees still returned food at low rates for this delay. Of interest, the chimpanzee (Tho) who could not wait for more than 15 s in the previous phase was 1 of these subjects. None of the subjects reached the time lag of 16 min. It is worth mentioning, however, that Wil (after 14 consecutive failures) and Noa (after 4 consecutive failures) once waited for 11 min 48 s and 10 min 25 s, respectively, which were the longest waiting times observed in this study (see the Appendix).

In Phase 1, chimpanzees could receive three different amounts of cookie that were either 2, 4, or 8 times the size of the initial item. We observed that the cookie had an effect on the success rate at both the 1- and the 4-min time lag (see Figure 2). For these time lags, a Friedman ANOVA, two-tailed test (Siegel & Castellan, 1988), revealed that the percentage of return for larger cookies is significantly higher than for cookies of smaller size. (For the 1-min time lag, for the cookie size that was 2 times the initial size the percentage of return was 26.25%, for the cookie size that was 4 times the initial size it was 32.5%, and for the cookie size that was 8 times the initial size it was 38.75%, $p < .05$, $N = 5$. For the 4-min time lag, for the cookie size that was 2 times the initial size the percentage of return was 0%, for the cookie size that was 4 times the initial size it was 3.75%, and for the cookie size that was 8 times the initial size it was 13.75%, $p < .05$, $N = 5$.) Despite a

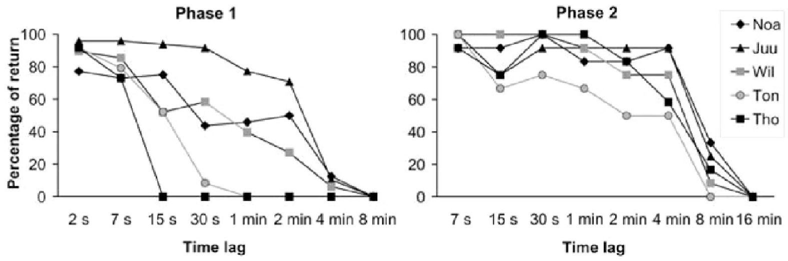


Figure 1. Percentage of successful returns for the 5 chimpanzees in Phase 1 (all sizes of cookies combined) at each time lag (from 2 s to 8 min; left panel). Percentage of successful returns for the 5 chimpanzees in Phase 2 when the reward was 40 times the size of the initial item at each time lag (from 7 s to 16 min; right panel).

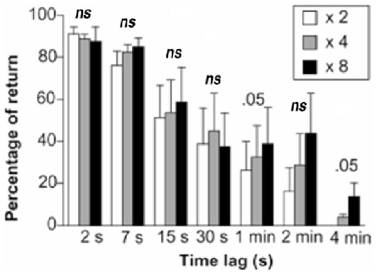


Figure 2. Percentage of successful returns for each size of cookie (2, 4, and 8 times the size of the original cookie) at each time lag (from 2 s to 4 min) in Phase 1. The percentage of return increased significantly with the size of the cookies for the time lag of 1 and 4 min (Friedman test for each time lag, $N = 5$, $^{*}p < .05$, $^{**}p < .01$). Error bars represent standard errors of the mean.

similar pattern for the 2-min time lag, the effect of size on the proportion of returns did not reach significance. (For the cookie size that was 2 times the initial size the percentage of return was 16.25%, for the cookie size that was 4 times the initial size it was 28.75%, for the cookie size that was 8 times the initial size it was 43.75%, *ns*, $N = 5$.) Together, these data indicate that chimpanzees match waits to expected gains at long time lags. No such effects were found for shorter time lags.

Error Type

An analysis of the type of error revealed four different categories of error: "Eat directly" the initial cookie (Ed), "Eat" the initial cookie after some time had elapsed (Et; this category includes error due to contact between the cookie and the lips of the subjects even if the subject further attempted to give the cookie back), "Drop, Break, or Give back" the initial cookie before the end of the delay (Db), and refuse to take the initial cookie (R). Figure 3 shows the mean of error type (on a maximum of 48 trials) per time lag observed in Phases 1 and 2. A Friedman ANOVA, two-tailed test (Siegel & Castellan, 1988), was used to compare the mean of error type occurring at each time lag. As the last type of error, R, occurred only four times in the course of Phase 1 (two times for Tho and 1 time for Noa and Ton), it was not included in the analysis. In Phase 1, no significant differences were observed between the means of error type at the 2-, 7-, 15-, and 30-s time lags (Friedman test; at 2 s, mean Et = 3.6, mean Ed = 0.6, mean Db = 1, *ns*; at 7s, mean Et = 4.2, mean Ed = 1.6, mean Db = 3.2, *ns*; at 15 s, mean Et = 7.8, mean Ed = 8.8, mean Db = 4.8, *ns*; at 30 s, mean Et = 6.6, mean Ed = 14.8, mean Db = 7, *ns*). At the 1-min time lag, there was a nonsignificant trend that error type Ed occurred more frequently than other error types (Friedman test; mean Et = 7.4, mean Ed = 21.8, mean Db = 3.2, $p < .07$, $df = 2$). At the 2- and 4-min time lags, error type Ed occurred significantly more often than other error types (Friedman test; at 2-min time lag, mean Et = 7.8, mean Ed = 24.2, mean Db = 1.8, $p < .05$, $df = 2$; at 4-min time lag, mean Et = 3.8, mean Ed = 39.8, mean Db = 1.6, $p < .01$, $df = 2$). For this phase, chimpanzees ate the initial piece of cookie at the start of the trial more often when they had to wait for long time lags (over 1 min) than when they had to wait for shorter time lags.

In Phase 2, error types encountered were Ed, Et, and Db (see Figure 3). None of the chimpanzees refused to take the initial item. A Friedman ANOVA, two-tailed test (Siegel & Castellan, 1988), conducted on the mean of occurrence for each error type reveals that error type Db was encountered significantly more often than other error types at the 2-min time lag and had a trend to be more frequent than other error types at the 4-min time lag (Friedman test; at 2 min, mean Et = 0.6, mean Ed = 0.2, mean Db = 2.2, $p < .05$, $df = 2$; at 4 min, mean Et = 0.4, mean Ed = 0.4, mean Db = 2.4, $p < .05$, $df = 2$). Contrary to Phase 1, chimpanzees' main errors in longer time lag were not caused by early renouncement but by failures to keep the initial cookie intact without dropping it until the end of the trial.

Timing of Error

The amount of food and the duration of the delay affected the waiting time of subjects. Chimpanzees might consider that a rather small food item is not worth waiting for. If they anticipated the time duration before they could exchange and receive the second cookie, they may have decided early on whether to wait or to give up. Such a hypothesis is suggested by the results of the errors analysis. In the current analysis, we compared the distribution of observed error times with the distribution of times to be expected under the null hypothesis of a constant giving up chance during the

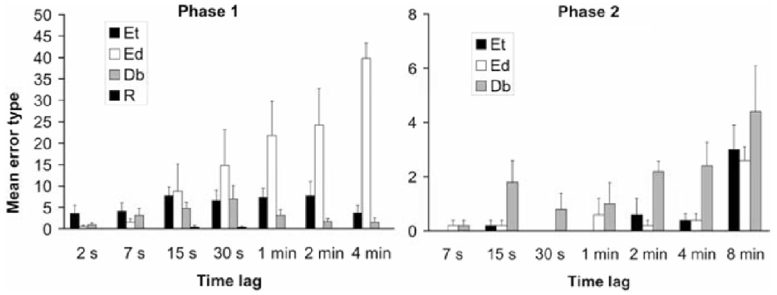


Figure 3. Mean occurrences and standard error of each error type for Phase 1 (left) and Phase 2 (right). Et = eat the initial item after waiting for some time; Ed = eat the initial item directly; Db = drop or break the initial item; R = refuse to take the initial item. Error bars represent standard errors of the mean.

trial. Figures 4 and 5 present for Phase 1 and 2, respectively, the difference in percentage between the observed and expected distribution at each tested time lag. A positive value indicates that the expected chance to keep on waiting is higher than the observed percentage of trials where chimpanzees waited longer than the time already elapsed. Therefore, it indicates that the chimpanzees renounced earlier than predicted, whereas a negative value indicates that chimpanzees waited longer than expected. In Phase 1, the adjusted Kolmogorov–Smirnov test was used to assess whether the difference between both distributions (expected and observed) was significant (see Table 1). The results show that at the 15-s time lag Noa and Tho renounced earlier than predicted (see Figure 4). These 2 chimpanzees also renounced earlier than expected when tested at the longer time lags. At the 30-s time lag, an additional chimpanzee, Ton, renounced significantly earlier than predicted, and this was also the case when he was tested at the 1-, 2-, and 4-min time lag. For the 2- and 4-min time lag, 5 chimpanzees renounced waiting earlier than expected. Renouncement for Tho at the 4-min time lag could not be assessed statistically because he ate the cookie from the start of the trials.

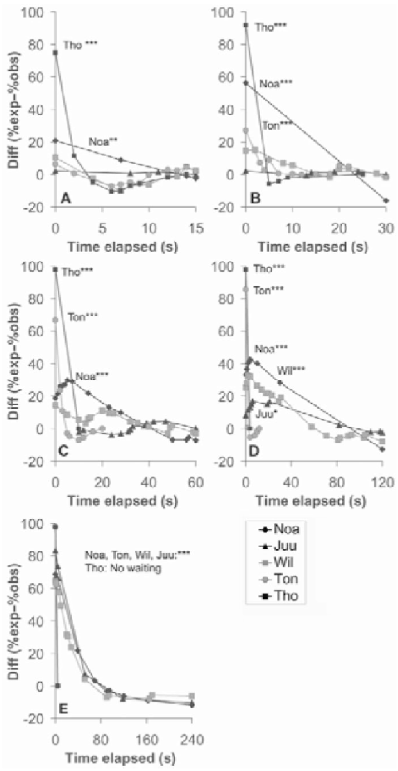


Figure 4. Phase 1: Difference between the distribution (in percentages) of expected and observed error time at each tested time lag. A: 15-s time lag; B: 30-s time lag; C: 1-min time lag; D: 2-min time lag; E: 4-min time lag. A positive value means that the expected chance to keep on waiting is higher than the actual percentage of trials where chimpanzees waited longer than the time already elapsed. It indicates that renouncement occurred earlier than predicted by a constant chance to give up through the trial. A negative value means that chimpanzees waited longer than expected, considering the time already elapsed in the trial. The statistics indicate whether the difference was statistically significant for a given chimpanzee as estimated by the adjusted Kolmogorov–Smirnov test. $^{*}p < .05$. $^{**}p < .01$. $^{***}p < .001$.

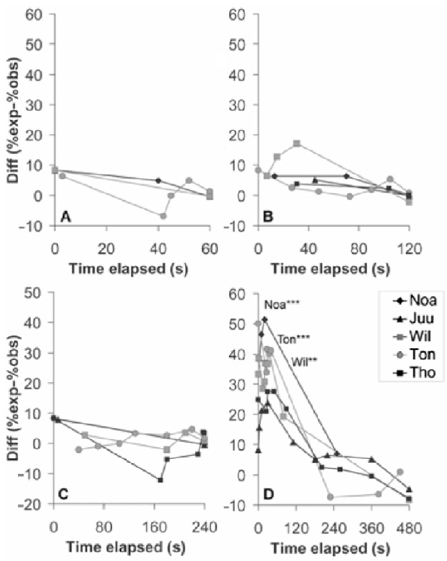


Figure 5. Phase 2: Difference between the distribution (in percentages) of expected and observed error time at each tested time lag. A: 1-min time lag; B: 2-min time lag; C: 4-min time lag; and D: 8-min time lag. Earlier time lags are not represented because of the very low percentage of failures. A positive value means that renouncement occurred earlier than predicted by a constant chance to give up through the trial. A negative value means that chimpanzees waited longer than expected considering the time already elapsed in the trial. The statistics indicate whether the difference was statistically significant for a given chimpanzee as estimated by the adjusted Kolmogorov–Smirnov test. $^{*}p < .05$. $^{**}p < .01$. $^{***}p < .001$.

In Phase 2, when the reward was 40 times the size of the initial item, we conducted a similar analysis. For all time lags between 15 s and 4 min, none of the chimpanzees renounced significantly differently from the expected error times (see Table 1; see Figure 5 for an illustration at the 1-, 2-, and 4-min time lags). At the 8-min time lag, however, Noa, Wil, and Ton renounced significantly earlier than expected.

The early renouncement suggests that chimpanzees estimated early whether the reward was worth waiting for and decided accordingly whether to wait or to give up. This effect was more pronounced in Phase 1, where cookies were of smaller size than in Phase 2.

Discussion

We found that chimpanzees can wait for up to 4 min when the delayed reward is 2 to 8 times the size of the original item and that they can wait for up to 8 min when the delayed reward is 40 times its size. By offering rewards 40 times the size of the initial item, we aimed at testing the maximum duration for which chimpanzees delayed reward. Indeed, this seemed to increase the chimpanzees' motivation in the task and thereby increased their capacity to wait.

Table 1

Maximum Values Obtained From the Kolmogorov–Smirnov Statistical Test Used To Compare the Expected and Observed Distribution of Giving Up Times

Subject–variable	15 s	30 s	1 min	2 min	4 min	8 min	16 min
Phase 1							
Noa	1.44^{**}	3.9^{***}	2.07^{***}	2.95^{***}	4.76^{***}	6.95^{***}	
Juu	0.14	0.14	0.32	1.17^{*}	5.77^{***}	6.78^{***}	
Wil	0.72	1.04	1.01	2.26^{***}	4.47^{***}	5.62^{***}	
Ton	0.49	1.88^{***}	4.61^{***}	5.91^{***}	NW	NT	
Tho	5.2^{***}	6.35^{***}	6.78^{***}	6.78^{***}	6.78^{***}	NT	
Mean no. of errors per subject	22.6	28.8	32.4	33.8	44.5	48	
Range	0–48	5–48	11–48	14–48	42–48	48	
Phase 2							
Noa	0.29	S	0.29	0.22	0.29	1.78^{***}	3.17^{***}
Juu	0.18	0.24	0.29	0.18	0.29	0.83	2.31^{***}
Wil	S	S	0.29	0.59	0.12	1.4^{**}	2.6^{***}
Ton	0.76	0.28	0.24	0.29	0.16	1.73^{***}	NT
Tho	0.31	S	S	0.13	0.42	0.96	0.74
Mean number of errors per subject	3	2	2.5	2.8	3	10	12
Range	1–5	1–3	2–4	1–6	1–6	8–12	12

Note. A statistically significant effect was observed when maximum values surpassed the critical values as follows. Phase 1, $N = 48$: Critical value = 1.07 for $p < .05$, critical value = 1.26 for $p < .01$, critical value = 1.45 for $p < .001$. Phase 2, $N = 12$: Critical value = 1.03 for $p < .05$, critical value = 1.22 for $p < .01$, critical value = 1.43 for $p < .001$. NW = no waiting; NT = not tested; S = 100% success. Mean no. of errors does not include NW individuals nor S individuals.

$^{*}p < .05$. $^{**}p < .01$. $^{***}p < .001$.

Brown capuchin monkeys tested using the same task were able to sustain 10 to 20 s to receive a larger reward, and only one monkey managed to wait for 40 s, that is, the next duration interval, to obtain a food amount 40 times the size of the initial one (Ramseyer et al., 2005). Similar tolerance to delay of gratification was reported in a tool-using task for this species (Evans & Westergaard, 2006). Therefore, chimpanzees were able to postpone a payoff for a duration 24 times longer than that measured in capuchin monkeys. This also contrasts with humans, for whom tolerance for delay of gratification can be measured in months or years (Rachlin, Raineri, & Cross, 1991). However, the delays observed make the chimpanzee results comparable to reports of a maximum tolerance for 5-min delays in children tested using a similar paradigm (Mischel et al., 1989).

Animals do not have at their disposal the conceptual and technological means that humans use to estimate time intervals or to cognitively travel in time (Roberts, 2002; Suddendorf & Corballis, 1997). Not only is their time understanding rather limited compared with that of humans, it is also strongly asymmetrical. Whatever their perception of temporal distance from the present, it is a common finding that animals can remember specific events for months or years. In comparison, their representation of the future appears considerably shorter. In experiments, rats anticipated a future reward at a time scale of about half an hour (Roberts, 2002). Monkeys planned travel routes of hundreds of meters, meaning some minutes in advance, when looking for food sites (*Macaca tonkeana*, Chauvin & Thierry, 2005; *Cebus apella*, Janson, 1998). Chimpanzees spontaneously saved tokens to use them in the near future, indicating that they anticipated a delayed opportunity to exchange them for food (Sousa & Matsuzawa, 2001). However, it was suggested that tokens may have become secondary reinforcers in the task. In the wild, chimpanzees walked hundreds of meters in dense vegetation to pick up and transport tools necessary to crack nuts open (Boesch & Boesch, 1984), and a bonobo (*Pan paniscus*) was reported to travel for 50 min before arriving at a sought location (Menzel, Savage-Rumbaugh, & Menzel, 2002). In these studies, it was suggested that the transport of tools might be bound to the present defined by their current motivational state (Suddendorf & Corballis, 1997). Silverberg, Widholm, Bresler, Fujita, and Anderson (1998) noted that chimpanzees exhibited *temporal myopia*—the inability to anticipate a future need—because they were unable to stock fruits in advance. However, in both common chimpanzees and bonobos species, animals trained to use symbols were able to announce intended action and travel destination plans (Menzel et al., 2002). More recently, orangutans and bonobos were shown to anticipate a night ahead a coming task and to select and transport the adequate tool so as to fulfill their future need (Mulcahy & Call, 2006). Such cases, however, do not prove that animals are aware of the time needed to reach their goals. Indeed, there was no need for them to keep a mental record of the time elapsed between the moment they anticipate some reward and the receipt of this reward, because there was no immediate and durable cost for the animals. In our study, chimpanzees could be said to incur an immediate cost, in that they had to refrain from eating the initial reward at increasing delays in anticipation of a larger, preferred reward.

Two different but nonexclusive types of processes may limit the duration of the maximum waiting periods in chimpanzees: the relative value of delay versus reward, and action inhibition during the test. On the one hand, relative valuation of the expected reward can help in deciding whether to wait or not. On the other hand, if the reward is considered worth the wait, the chimpanzee must still inhibit its consumption for as long as requested by the task.

Concerning the first process, future reward evaluation, at least two mechanisms are known to influence choice in animals: shortsighted rules and temporal discounting. First, many animals appear to favor immediate action (Stephens, 2002; Stevens, Rosati, Ross, & Hauser, 2005), dismissing any solution that requires an estimation of future benefits. The use of such shortsighted rules may explain why many animals prefer immediate small rewards over delayed large rewards. Because we found that chimpanzees matched their waiting time to the expected food amount, we may rule out the occurrence of shortsighted rules as an explanation for their limited waiting time. The second mechanism, temporal discounting, involves the subjective value of benefits reducing with delay (Mazur, 1987; Stevens, Hallinan, & Hauser, 2005). In the present study, chimpanzees sustained longer waiting times for larger returns, supporting a temporal discounting explanation. In choice tasks, pigeons, rats, tamarins, and marmosets also seemed to discount the value of delayed rewards (Baker & Rachlin, 2002; Mazur, 1987; Richards et al., 1997; Stevens, Hallinan, & Hauser, 2005), yet the length of the delay was measured in seconds, not minutes. Therefore, although the mechanism may be similar, the capacity to delay appears to be much more developed in chimpanzees than in the other tested species.

Differences between chimpanzees and other species may be linked to the second process, action inhibition during the test. Our results show that chimpanzees could suppress food consumption for 4 to 8 min. The current test, however, differed in one important aspect from other temporal discounting tests. The chimpanzees were not only requested to suppress their urges at the start of the task but also to inhibit their impulses during the whole trial in order to bridge the time interval between decision to wait and the receipt of the reward (Ramseyer et al., 2005). If they failed late in the trial, they received no more reward than if they failed at the start of the trial. This suggests that the current task was more difficult than choice tasks such as reverse-delayed reward contingency tasks (Mazur, 1987). In the reverse-delayed reward contingency task, the decision to wait for a larger reward or to eat the smallest available reward is made at the beginning of the trial. An animal cannot opt for the alternative option during the delay. In addition, there is no need to keep track of the elapsed time because a decision, once made, is always rewarded accordingly. Chimpanzees tested in a reverse-delayed reward contingency task may therefore tolerate longer delay than in our task.

Action inhibition has been suggested to provide "free" time to discriminate between options and improve decision making (Stephens, 2002). We further investigated the mechanisms behind decision making by examining chimpanzees' giving up times. If chimpanzees assessed the cost of the combined effect of delay and exchange reward size, they might make the decision to consume the initial reward early in the trial. We showed that chimpanzees' failure time occurred earlier than would be expected if chimpanzees exhibited a constant rate of giving up. This suggests that chimpanzees anticipated the duration of the delay in combination with the size of the exchange reward and reversed their preference to the smaller immediate reward. The alternative, lower level explanation only implies associative learning. The delay would have caused a reduction in the association between the initial choice and the exchange reward, resulting in an extinction of the exchange behavior. This interpretation could be supported by the behavior of Tho in Phase 2 because Tho gradually stopped waiting for longer delays. The behavior of the other 4 chimpanzees, however, was not consistent with this interpretation. Although these subjects consumed the small immediate reward in a number of consecutive trials, seemingly indicating the extinction of the waiting behavior, they subsequently waited again for a long delay to obtain the exchange reward (see the Appendix). Therefore, our data suggest that chimpanzees anticipate the duration of the delay to a reward and may be able to decide at the beginning of a trial whether to opt for the small immediate reward or wait for the larger one.

Despite the small number of subjects, the present findings have important implications for the occurrence of delayed reciprocity in animals. Our study indicates that chimpanzees are not exclusively bound to the present because they appeared to anticipate the duration of the delay before exchange. Although our results do not directly support the hypothesis of mental time travel in animals (Suddendorf & Corballis, 1997) because chimpanzees were working for a current goal from the start of the trials, the capacity to accept some cost in the present (waiting and controlling the impulse to eat food) according to future consequences opens the possibility for chimpanzees to make use of calculated reciprocity. Our results are also consistent with the recent conclusions of Mulcahy and Call (2006), who reported planning capacities in bonobos and orangutans.

Despite the fact that a delay of more than 8 min in our experimental setting is quite long in terms of abilities demonstrated by other animals, it still constitutes a rather limited time window. Our results conflict with expectations that chimpanzees exchange food for mating or support in coalitions on a long-term basis by using calculated reciprocity (de Waal, 1989; Mitani & Watts, 2001; Stanford, Wallis, Matama, & Goodall, 1994) or that they can plan social strategies and predict their eventual outcome several weeks or months in advance (de Waal, 1982; Nishida, 1983). It might be that food-related tasks are not an optimal choice for assessing mechanisms of reciprocal altruism. Recent studies on chimpanzees have failed to show altruistic or other-regarding behavior toward conspecifics in food-acquisition situations (Jensen, Hare, Call, & Tomasello, 2006; Silk et al., 2005) but revealed other-regarding behavior in nonfood situations (Warneken & Tomasello, 2006). Similar effects might reduce the delay to reward in food-related tasks. The current results suggest that chimpanzee anticipation of a loss is restricted to a time scale counted in minutes, which would preclude the occurrence of long-term, calculated reciprocal altruism. Future studies should test whether delayed exchanges using variable associated costs or non-food-related items may provide different time windows into the future.

References

Abeyesinghe, S. M., Nicol, C. J., Hartnell, S. J., & Wathes, C. M. (2005). Can domestic fowl, *Gallus gallus domesticus*, show self-control? *Animal Behaviour, 70,* 1–11.

Baker, F., & Rachlin, H. (2002). Self-control by pigeons in the prisoner's dilemma. *Psychonomic Bulletin & Review, 9,* 482–488.

Beran, M. J. (2002). Maintenance of self-imposed delay of gratification by four chimpanzees (*Pan troglodytes*) and an orangutan (*Pongo pygmaeus*). *Journal of General Psychology, 129,* 49–66.

Beran, M. J. (2004). Long-term retention of differential values of Arabic numerals by chimpanzees (*Pan troglodytes*). *Animal Cognition, 7,* 86–92.

Beran, M. J., & Beran, M. M. (2004). Chimpanzees remember the results of one-by-one addition of food items to sets over extended time periods. *Psychological Science, 15,* 94–99.

Beran, M. J., Savage-Rumbaugh, E. S., Pate, J. L., & Rumbaugh, D. M. (1999). Delay of gratification in chimpanzees (*Pan troglodytes*). *Developmental Psychobiology, 34,* 119–127.

Boesch, C., & Boesch, H. (1984). Mental map in wild chimpanzees: An analysis of hammer transports for nut cracking. *Primates, 25,* 160–170.

Brosnan, S. F., & de Waal, F. B. M. (2002). A proximate perspective on reciprocal altruism. *Human Nature, 13,* 129–152.

Brosnan, S. F., & de Waal, F. B. M. (2004). A concept of value during experimental exchange in brown capuchin monkeys, *Cebus apella. Folia Primatologica, 75,* 317–330.

Brosnan, S. F., & de Waal, F. B. M. (2005). Responses to a simple barter task in chimpanzees, *Pan troglodytes. Primates, 46,* 173–182.

Chauvin, C., & Thierry, B. (2005). Tonkean macaques orient their food search from olfactory cues conveyed by group mates. *Ethology, 111,* 1–10.

de Waal, F. B. M. (1982). *Chimpanzee politics.* London: Jonathan Cape.

de Waal, F. B. M. (1989). *Peacemaking among primates.* Cambridge, MA: Harvard University Press.

de Waal, F. B. M. (2000). Attitudinal reciprocity in food sharing among brown capuchin monkeys. *Animal Behaviour, 60,* 253–261.

de Waal, F. B. M., & Luttrell, L. M. (1988). Mechanism of social reciprocity in three primates species: Symmetrical relationship characteristics or cognition? *Ethology and Sociobiology, 9,* 101–118.

Drapier, M., Chauvin, C., Dufour, V., Uhlrich, P., & Thierry, B. (2005). Food exchange with humans in brown capuchin monkeys. *Primates, 46,* 241–248.

Dufour, V., & Sterck, E. H. M. (2007). *Planning for an exchange task in chimpanzees (Pan troglodytes).* Unpublished manuscript.

Evans, T. A., & Westergaard, G. C. (2006). Self-control and tool use in tufted capuchin monkeys (*Cebus apella*). *Journal of Comparative Psychology, 2,* 163–166.

Haccou, P., & Meelis, E. (1992). *Statistical analysis of behavioural data.* Oxford, England: Oxford University Press.

Hemelrijk, C. K. (1996). Reciprocation in apes: From complex cognition to self-structuring. In W. C. McGrew, L. F. Marchand, & T. Nishida (Eds.), *Great ape societies* (pp. 185–195). Cambridge, England: Cambridge University Press.

Hyatt, C. W., & Hopkins, W. D. (1998). Interspecies object exchange: Bartering in apes? *Behavioural Processes, 42,* 177–187.

Janson, C. H. (1998). Experimental evidence for spatial memory in foraging wild capuchin monkeys, *Cebus apella. Animal Behaviour, 55,* 1229–1243.

Jensen, K., Hare, B., Call, J., & Tomasello, M. (2006). What's in it for me? Self-regard precludes altruism and spite in chimpanzees. *Proceedings of the Royal Society of London, B, 273,* 1013–1021.

Lefebvre, L. (1982). Food exchange strategies in an infant chimpanzee. *Journal of Human Evolution, 11,* 195–204.

Mazur, J. E. (1987). An adjusting procedure for studying delayed reinforcement: The effects of delay and intervening events on reinforcement value. In M. L. Commons, J. E. Mazur, J. A. Nevin, & H. Rachlin (Eds.), *Quantitative analyses of behavior* (Vol. 5, pp. 55–73). Hillsdale, NJ: Erlbaum.

Melis, A. P., Hare, B., & Tomasello, M. (2006, March 3). Chimpanzees recruit the best collaborators. *Science, 311,* 1297–1300.

Menzel, C. R. (1999). Unprompted recall and reporting of hidden objects by a chimpanzee (*Pan troglodytes*) after extended delays. *Journal of Comparative Psychology, 113,* 426–434.

Menzel, C. R., Savage-Rumbaugh, S. E., & Menzel, E. W. (2002). Bonobo (*Pan paniscus*) spatial memory and communication in a 20-hectare forest. *International Journal of Primatology, 3,* 601–619.

Milinski, M. (1987, January 29). Tit for tat and the evolution of cooperation in sticklebacks. *Nature, 325,* 433–435.

Mischel, W., Shoda, Y., & Rodriguez, M. L. (1989, May 26). Delay of gratification in children. *Science, 244,* 933–938.

Mitani, J. C., & Watts, D. P. (2001). Why do chimpanzees hunt and share meat? *Animal Behaviour, 61,* 915–924.

Mulcahy, N. J., & Call, J. (2006, May 19). Apes save tools for future use. *Science, 312,* 1038–1040.

Nishida, T. (1983). Alpha status and agonistic alliance in wild chimpanzees (*Pan troglodytes schweinfurthii*). *Primates, 24,* 318–336.

Packer, C. (1977). *Reciprocal altruism in Papio anubis. Nature, 265,* 441–443.

Padoa-Schioppa, C., Jandolo, L., & Visalberghi, E. (2006). Multi-stage mental process for economic choice in capuchins. *Cognition, 99,* B1–B13.

Rachlin, H., Raineri, A., & Cross, D. (1991). Subjective probability and delay. *Journal of Experimental Analysis of Behavior, 55,* 233–244.

Ramseyer, A., Pelé, M., Dufour, V., Chauvin, C., & Thierry, B. (2005). The temporal limits of reciprocity in brown capuchin monkeys. *Proceedings of the Royal Society of London, B, 273,* 179–184.

Richards, J. B., Mitchell, S. H., de Wit, H., & Seiden, L. S. (1997). Determination of discount functions in rats with an adjusting-amount procedure. *Journal of Experimental Analysis of Behavior, 67,* 353–366.

Roberts, W. A. (2002). Are animals stuck in time? *Psychological Bulletin, 128,* 473–489.

Savage-Rumbaugh, E. S., Rumbaugh, D., & Boysen, S. (1978). Linguistically mediated tool use and exchange by chimpanzees (*Pan troglodytes*). *Behavioral and Brain Sciences, 4,* 539–554.

Seyfarth, R. M., & Cheney, D. L. (1984, April 5). Grooming, alliances, and reciprocal altruism in vervet monkeys. *Nature, 308,* 541–543.

Siegel, S., & Castellan, J. N. (1988). *Non parametric statistics for the behavioral sciences.* New York: McGraw-Hill.

Silk, J. B., Brosnan, S. F., Vonk, J., Henrich, J., Povinelli, D. J., Richardson, A. F., et al. (2005). Chimpanzees are indifferent to the welfare of other group members. *Nature, 435,* 1357–1359.

Silverberg, A., Widholm, J. J., Bresler, D., Fujita, K., & Anderson, J. R. (1998). Natural choice in nonhuman primates. *Journal of Experimental Psychology: Animal Behavior Processes, 24,* 215–228.

Sousa, C., & Matsuzawa, T. (2001). The use of tokens as rewards and tools by chimpanzees (*Pan troglodytes*). *Animal Cognition, 4,* 213–221.

Stanford, C. B., Wallis, J., Matama, H., & Goodall, J. (1994). Patterns of predation by chimpanzees on red colobus monkeys in Gombe National Park, 1982–1991. *American Journal of Physical Anthropology, 94,* 213–228.

Stephens, D. W. (2002). Discrimination, discounting and impulsivity: A role for an informational constraint. *Philosophical Transactions of the Royal Society of London, B, 357,* 1527–1537.

Stevens, J. R., Cushman, F. A., & Hauser, M. D. (2005). Evolving the psychological mechanisms for cooperation. *Annual Review of Ecology and Systematics, 36,* 499–518.

Stevens, J. R. Hallinan, E. V., & Hauser, M. D. (2005). The ecology and evolution of patience in two New World monkeys. *Biological Letters, 1,* 223–226.

Stevens, J. R., & Hauser, M. D. (2005). Cooperative brains: Psychological constraints on the evolution of altruism. In S. Dehaene, J. R. Duhamel, G. Rizolatti, & M. D. Hauser (Eds.), *From monkey brain to human brain* (pp. 159–187). Cambridge, MA: MIT Press.

Stevens, J. R., Rosati, A. G., Ross, K. R., & Hauser, M. D. (2005). Will travel for food: Spatial discounting in two New World monkeys. *Current Biology, 15,* 1855–1860.

Suddendorf, T., & Corballis, M. C. (1997). Mental time travel and the evolution of the human mind. *Genetic, Social, and General Psychology Monographs, 123,* 133–167.

Szalda-Petree, A. D., Craft, B. B., Martin, L. M., & Deditius-Island, H. K. (2004). Self-control in rhesus macaques (*Macaca mulatta*): Controlling for differential stimulus exposure. *Perceptual and Motor Skills, 98,* 141–146.

Tobin, H., Logue, A. W., Chelonis, J. J., Ackerman, K. T., & May, J. G. (1996). Self-control in the monkey *Macaca fascicularis. Animal Learning and Behaviour, 24,* 168–174.

Trivers, R. L. (1971). The evolution of reciprocal altruism. *Quarterly Review of Biology, 46,* 35–57.

Warneken, F., & Tomasello, M. (2006, March 3). Altruistic helping in human infants and young chimpanzees. *Science, 311,* 1301–1303.

Westergaard, G. C., Liv, C., Rocca, A. M., Cleveland, A., & Suomi, S. J. (1998). Token-mediated tool-use by a tufted capuchin monkey (*Cebus apella*). *Animal Cognition, 1,* 101–106.

Westergaard, G. C., Liv, C., Rocca, A. M., Cleveland, A., & Suomi, S. J. (2004). Tufted capuchin (*Cebus apella*) attribute value to foods and tools during voluntary exchanges with humans. *Animal Cognition, 7,* 19–24.

Wilkinson, G. S. (1984). Reciprocal food sharing in the vampire bat. *Nature, 308,* 181–184.

Appendix

Waiting Duration per Chimpanzee in the Longest Time Lag in Phase 2

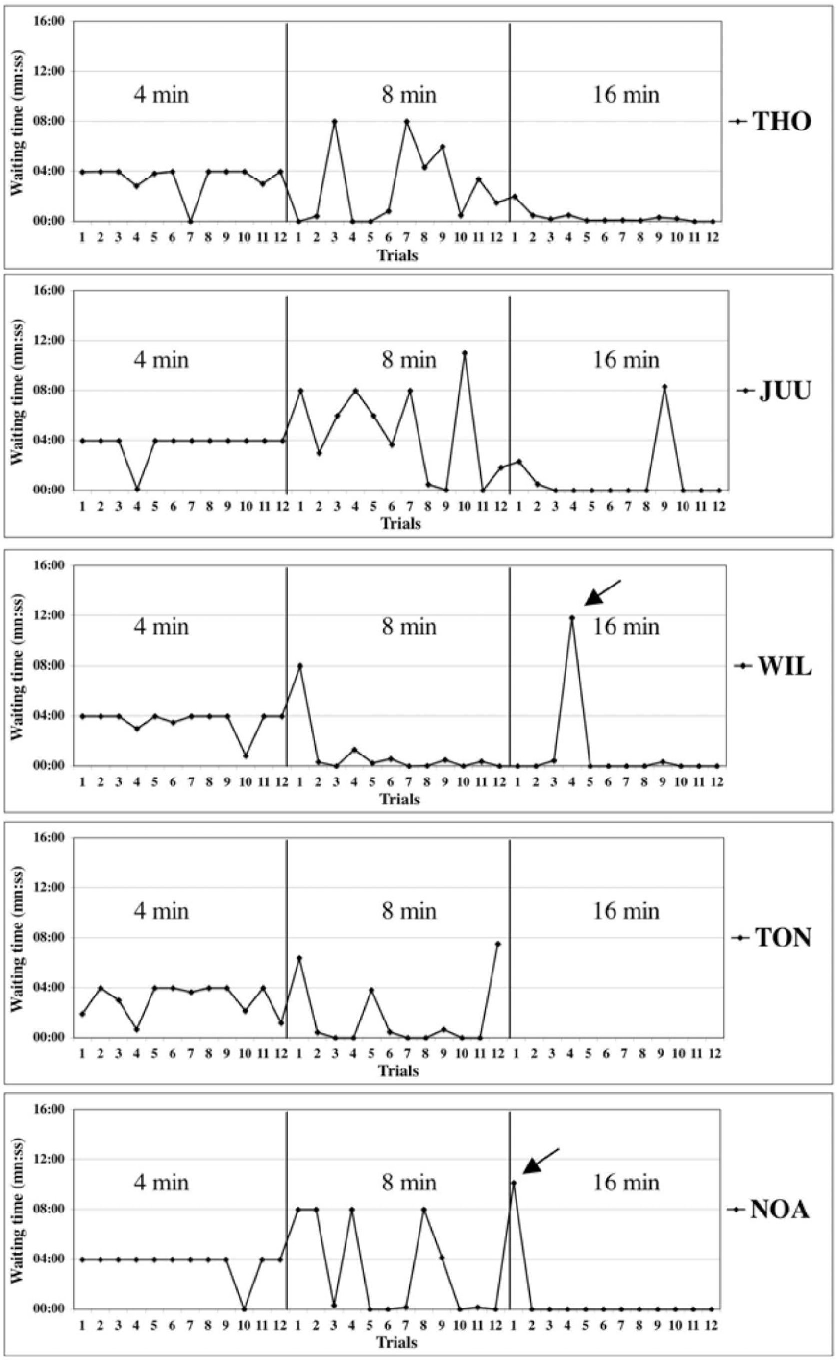


Figure A1. Individual waiting time per trial at 4, 8, and 16 min in chronological order. Of the chimpanzees, 4 of the 5 still attempted to wait for long durations despite previous consecutive failures. Wil (after 14 consecutive failures) and Noa (after 4 consecutive failures) waited for the longest duration observed in the study when tested at the 16-min time lag. They waited, respectively, for 11 min 48 s and 10 min 25 s (see arrows).

Received May 2, 2006
Revision received December 12, 2006
Accepted January 10, 2007 ■

Article 2

L’estimation de la valeur et l’anticipation de l’attente chez les macaques à longue queue

Article publié dans *Animal Cognition*

RESUME DE L’ARTICLE 2

Introduction

L’étude a pour but de mesurer la capacité à attendre de macaques à longue queue au cours d’un échange et de reconnaître certains des facteurs susceptibles de limiter leurs performances en répondant aux questions suivantes. Des singes sont-ils capables de différer le retour d’une récompense au cours d’un échange d’items alimentaires ? Cette capacité est-elle fonction de la quantité de la récompense ? Dans quelle mesure l’inhibition de la consommation et la dépréciation de la récompense avec le temps influencent-elles le comportement d’attente des macaques ?

Méthodes

J’ai testé neuf macaques à longue queue au cours d’une série de quatre expériences. Dans les deux premières expériences, les sujets devaient rendre un morceau de biscuit à un expérimentateur en échange d’un plus gros morceau dont la dimension pouvait être égale à deux, quatre, huit ou quarante fois la dimension du premier. Le délai imposé entre le don du premier morceau et le retour de la récompense allait de 2 s à 5 mn 20 s pour l’expérience 1, et de 10 s à 42 mn 40 s pour l’expérience 2. Lors d’une troisième expérience, j’ai permis aux sujets de rendre le petit morceau de biscuit avant d'attendre un plus gros morceau. Cette condition a permis d’étudier l’influence de l’inhibition de la consommation sur l'aptitude des sujets à tolérer la période d'attente. Au cours d’une quatrième expérience, j’ai testé les sujets dans une tâche d’accumulation de la récompense. L’expérimentateur plaçait toutes les 9 s un petit morceau de biscuit à portée de main du sujet. Dès que celui-ci s’emparait des biscuits accumulés, l’essai était considéré comme terminé. Les sujets devaient donc être capables d’attendre pour maximiser leur récompense. Cette condition a permis de d’étudier l’influence de la dépréciation de la récompense au cours du temps sur l’aptitude des sujets à attendre.

Résultats

Au cours des deux premières expériences d’échange, les sujets ont attendu entre 1 et 10 mn en fonction de la dimension de la récompense et des individus. L'analyse du temps de renoncement a révélé leur aptitude à anticiper la durée d'attente et à prendre leur décision en fonction de celle-ci et de la dimension de la récompense. Dans la troisième expérience, le contrôle du facteur de l’inhibition de la consommation a permis aux individus de doubler leurs performances. Dans la tâche d’accumulation, les sujets ont montré des performances équivalentes à celles mesurées au cours de l’expérience 1.

Conclusion

Des macaques à longue queue peuvent différer de plusieurs minutes l'obtention d'une récompense alimentaire. Ils se montrent capables d’anticiper la durée d'attente et d’ajuster leur décision en fonction de ce délai et de la dimension de la récompense. L’augmentation significative des performances des sujets au cours de l’expérience 3 démontre que l’inhibition de la consommation est un facteur limitant la tolérance au délai. Au cours de l’expérience 4, les délais attendus par les individus sont identiques à ceux mesurés dans l’expérience 1 pour les mêmes quantités de nourriture. L’accumulation de la récompense au cours du temps n’a pas permis de minimiser l’effet de la dépréciation de la récompense avec le temps. Cependant, les résultats obtenus au cours de l’expérience 4 valident ceux obtenus au cours des tâches d’échange. Les macaques à longue queue peuvent attendre plusieurs dizaines de minutes dans certaines conditions. On peut faire l'hypothèse que cette aptitude à tolérer un délai est en rapport avec les stratégies complexes dont font preuve les macaques dans leurs relations sociales.

Anim Cogn
DOI 10.1007/s10071-009-0264-6

ORIGINAL PAPER

Long-tailed macaques display unexpected waiting abilities in exchange tasks

Marie Pelé · Valérie Dufour · Jérôme Micheletta · Bernard Thierry

Received: 10 March 2009 / Revised: 30 June 2009 / Accepted: 2 July 2009
© Springer-Verlag 2009

Abstract The ability of animals to delay gratification is crucial for complex goal-directed action. It may help them in making effective decisions when facing a choice. We tested the ability of nine long-tailed macaques (*Macaca fascicularis*) to delay gratification in several experiments. In exchange tasks, subjects had to keep a small piece of cookie before returning it to an experimenter in order to get a larger food amount. Results showed that animals could wait between 10 s and 10 min depending on individual and sizes of reward. In another experiment, subjects could immediately give back the initial piece of cookie then wait for the return. Their performances more than doubled, demonstrating the role of consumption inhibition in postponing gratification. Such achievements underscore delays of gratification which until now were not thought possible in monkeys. Finally, subjects were presented with an accumulation of food pieces added at short intervals until they seized them. They mostly waited between 30 s and 1 min, which points at the consistency of our data, compared to those of other studies. Our results indicate that long-tailed macaques anticipated the duration of delays. We may account for their remarkable performances by their achievements in the social context.

Keywords Delay of gratification · Exchange · Decision-making · Economics · *Macaca fascicularis*

Introduction

In many circumstances individuals use future interests to guide current decisions. The ability to delay gratification is crucial for complex goal-directed action and planning (Mischel 1974; Kacelnik 2003). Being able to wait or persevere when facing a delay qualifies as patience in humans; it may involve internal components and refers to even-tempered control or tolerance to provocation. Exploring patience in animals is challenging since we have no direct access to the internal dimension of behaviors. We can yet measure their capacity to wait in tasks in which subjects have to sustain a temporal gap between their decision to wait for a gratification and the occurrence of the gratification.

In everyday life, delaying gratification can help animals in making a decision when facing a choice. In being too impulsive, a predator may reveal its presence and fail to catch its prey. In food competition, subordinates often have to wait to get access to resources in order to avoid aggression from higher-ranking conspecifics. The higher the quality of food, the more unlikely a subordinate is to access it immediately. Waiting also has a cost, since food can be depleted by the time access is finally granted. Thus, when waiting for more, an individual needs to evaluate expected outcomes and decide how long it may be worth waiting for. Such ability can be decisive in cooperative situations where the return of a service such as grooming, food sharing or

---

Electronic supplementary material The online version of this article (doi:10.1007/s10071-009-0264-6) contains supplementary material, which is available to authorized users.

M. Pelé (✉) · V. Dufour · J. Micheletta · B. Thierry
Département Ecologie, Physiologie et Ethologie, IPHC,
Centre National de la Recherche Scientifique,
Université de Strasbourg, 23 rue Becquerel,
67087 Strasbourg, France
e-mail: marie.pele@c-strasbourg.fr

V. Dufour
School of Psychology, University of St Andrews, St Andrews, UK

Published online: 14 July 2009

support in conflict is not immediate. In defining reciprocal altruism, Trivers (1971) stated that a donor needs to produce a costly behaviour, beneficial to a recipient, before both individuals alternate their roles, thus displaying delayed reciprocity. When asking whether calculated reciprocity occurs among animals, displaying some capacity or willingness to wait is a primary component (Trivers 1971; Ramseyer et al. 2006; Stevens et al. 2005a).

Delayed-reward contingency tasks are amongst the most frequent techniques used to test the ability of animals to postpone gratification (Mischel 1974). Subjects are given a choice between an immediately available, but less preferred reward, and a delayed, but more preferred one. Once the choice is made, subjects have no further opportunity to modify their response during the entire duration of the trial. Pigeons (*Columbia livia*: Mazur 1987), domestic fowl (*Gallus gallus*: Abeyesinghe et al. 2005) and rats (*Rattus norvegicus*: Richards et al. 1997) opt for the small immediate reward when the delay surpasses a duration of a few seconds. Monkeys like marmosets (*Callithrix jacchus*) and tamarins (*Saguinus oedipus*) can delay gratification between 5 and 20 s (Stevens et al. 2005b). Great apes like bonobos (*Pan paniscus*) and chimpanzees (*Pan troglodytes*) can wait about 1 and 2 min, respectively (Rosati et al. 2007) while long-tailed macaques (*Macaca fascicularis*) and brown capuchin monkeys (*Cebus apella*) rate at about 30 s (Amici et al. 2008; see also Tobin et al. 1996; Szalda-Petree et al. 2004) in the same set up. The capacity of animals to wait has been investigated in further delay-maintenance tasks in which subjects have the possibility to alter their choice at any time during the waiting period (Toner and Smith 1977; Toner et al. 1979). The ability to postpone gratification is then measured as the duration of time a subject refrains from making an impulsive response during a trial. Pigeons (Grosch and Neuringer 1981) and rats (Killeen et al. 1981) can control themselves for several seconds. Rhesus macaques (*M. mulatta*) wait for 2 min to obtain preferred food (Evans and Beran 2007a) and chimpanzees up to 18 min (Evans and Beran 2007b). A further task consists of presenting subjects with food items accumulating at regular time intervals—usually of a few seconds—within reachable distance of the subject. Once the subject reaches for the accumulated pile, no further items are presented. As in previous tasks, the subject must inhibit taking food for as long as possible to maximize its gain. With this procedure, four chimpanzees and one orang-utan (*Pongo pygmaeus*) were able to delay gratification for 3 min (Beran 2002), whereas rhesus macaques tested in a comparable task were not able to bridge a delay longer than 30 s (Evans and Beran 2007a). It should be kept in mind that experimental methods, and the amount of reward in particular, could vary across studies; caution is then required when concluding about interspecific differences.

Compared to humans who may wait weeks or months for larger monetary rewards (Rachlin et al. 1991), animals have been qualified as impulsive (Stephens and Anderson 2001; Stevens et al. 2005b). In the context of feeding, however, humans and chimpanzees display similar performances, limited to waiting periods of few minutes when tested in similar experimental situations (Rosati et al. 2007). This tolerance to delay does not mirror the full extent of human patience, indicating that contextual factors significantly influence the ability or the willingness to wait in delay of gratification tasks (Stevens et al. 2005b; Hayden and Platt 2007; Rosati et al. 2007). The capacity to control impulsivity may not be the only factor liable to affect subjects' responses. Temporal discounting, whereby the subjective value of benefits reduces with time, has also been suggested to affect choices when current and future rewards are in conflict (Mazur 1987; Stevens et al. 2005a).

We recently enrolled chimpanzees (Dufour et al. 2007) and capuchin monkeys (Ramseyer et al. 2006) in an exchange task designed to measure their ability to face a waiting period. Subjects had to return a small piece of cookie after a given time lag to obtain a larger one from a human experimenter. As in delay-of-gratification tasks, they had to evaluate the value of the reward relative to the delay they had to wait for and inhibit their impulse to consume the initial piece of cookie. Capuchin monkeys did not wait for over 40 s before returning food (Ramseyer et al. 2006). Chimpanzees could postpone returns for up to 8 min (Dufour et al. 2007). Moreover, an analysis of giving-up time revealed that chimpanzees considered the duration of expected delays when deciding whether to give up or to wait for the reward.

In a recent study, Amici et al. (2008) concluded that action is motivated more by immediate goals and interests in species living in cohesive groups (capuchin monkeys and macaques) than in species undergoing frequent splitting and merging of subgroups (chimpanzees, bonobos, orang-utans, and spider monkeys, *Ateles geoffroyi*). By favouring behavioural flexibility, social dynamics based on fission and fusion would enhance inhibitory skills in the latter species. On the other hand, macaques are known to use sophisticated social tactics like coalitions and reconciliations. There is evidence that they can reciprocate support, take revenge and affiliate with third parties outside the context of aggression (e.g., de Waal and Luttrell 1988; Aureli et al. 1992; Silk 1992; Petit and Thierry 1994; Das 2000; Gumert 2007). Such behaviours involve time distance from the present. It was even proposed that macaques are able to calculate reciprocity (de Waal and Luttrell 1988; Aureli et al. 1992; Silk 1992) although there is no experimental evidence for this assumption.

If the social tactics achieved by macaques require a significant capacity to postpone gratification, they should be able to sustain delays longer than those measured so far in delay-of-gratification tasks. To know whether the waiting periods achieved by long-tailed macaques are closer to those previously measured in capuchin monkeys or chimpanzees, we investigated their ability to maximise pay-off in exchange tasks where time intervals and reward quantities were controlled. To recognize the possible influence of action inhibition and temporal discounting, we additionally tested subjects in two different conditions. In one experiment, we relaxed the food-keeping condition to minimize the need for control of impulsivity. In another experiment, we fractioned the delay in several time intervals using a cumulative task (Beran 2002); if subjects consider one interval at a time, they should wait longer than in comparable exchange tasks, thus minimizing the effects of temporal discounting.

General methods

Subjects and conditions

We tested nine male long-tailed macaques kept at the Primatology Centre of the University of Strasbourg, France. Two subjects (Zeb, 4 year-old; Zor, 4) belonged to a social group of five individuals and were housed in an indoor-outdoor enclosure of 30 m^2. Three subjects (Lou, 10; Ram, 15; Sad, 11) were housed together in an indoor enclosure of 10 m^2. Other subjects (Cas, 11; Don, 15; Jac, 15; Joe, 10) were individually housed in cages of 125 × 80 × 80 cm. Subjects were trained to exchange for the purpose of the study. They had never been tested in cognitive tasks. For testing, group-living subjects were temporarily separated from their conspecifics into individual compartments. Commercial monkey diet pellets and water were provided ad libitum. Subjects were never deprived of food.

Exchange procedure

Experiments 1–3 were conducted using food exchange tasks. Prior to these experiments subjects had been trained to exchange food items with humans (see ESM S1). During testing, the experimenter stood in front of the subject's compartment, showing the subject two different sized pieces of cookie in each hand for 3 s. The experimenter then gave the smaller piece to the subject. The larger piece (the reward) remained visible in the experimenter's second hand for the whole duration of the waiting period at that trial (see relevant method section for each experiment). After the waiting period had elapsed, the experimenter held out their empty hand while still presenting the reward on the other hand. If the subject gave back the small piece of cookie, he received the larger one. If the subject did not give back the initial piece, the experimenter did not reward the subject and stepped back, thereby ending the trial. Whenever the individuals had dropped or eaten the cookie before the end of the waiting period, the experimenter ended the trial by stepping back. Depending on the size of the rewards, the experimenter waited for 30 s (Experiment 1) and 20 min (Experiments 2 and 3) after the end of food consumption before beginning another trial.

Statistics

We used the Friedman test to compare the percentages of returns for the different sizes of cookies at each time lag in Experiment 1 and the Wilcoxon matched-pairs test to compare the percentages of return in the different experiments (Siegel and Castellan 1988). Given the small number of individuals, we applied the exact test procedure of the statistical software SPSS 16©.

We ran an analysis on the timing of giving-up—the time at which long-tailed macaques gave up waiting before the end of the trial. We compared the distribution of observed giving-up times with the distribution of times to be expected under the null hypothesis of a constant giving-up chance during the trial. If the long-tailed macaques anticipate the duration of the delay remaining, they should decide early on whether to wait or not. To test this hypothesis, we calculated the estimated (observed) probability of continuing to wait at each point of time that the subject gave up waiting by using the Kaplan Meier survival analysis. This analysis includes both the failure times and the times of successful return at the end of the trial (as censored data). In this analysis, the survival probability is expressed as the percentage of chance to wait longer than the time already elapsed in the trial. Against this observed survival function, we calculated the expected (exponential) distribution of giving-up times under the null hypothesis of a constant giving-up chance. The two distributions, the expected and the observed one, were then compared using an adjusted Kolmogorov–Smirnov test (Haccou and Meelis 1992). A statistically significant difference between both distributions leads to the rejection of the null hypothesis that a subject has a constant chance to give up, independently of the time elapsed in the trial. We ran the analysis on Experiment 1 by combining all cookie sizes: 2, 4, and 8 times the original size ($N = 48$). In Experiment 2, only one size of reward was tested; therefore, the analysis was run on a smaller number of events ($N = 12$).

Significance level was set at 0.05 for all analyses. Average values are given in the text and figures as mean and SEM.

Experiment 1: testing the effect of quantity on waiting periods

We designed Experiment 1 to test whether the duration of the waiting period sustained by long-tailed macaques would vary according to the relative value of the items being exchanged.

For each trial, the experimenter first offered a small piece of cookie (1 × 2 × 0.5 cm), then presented to the subject a piece of cookie of a larger size: 2 × 2 × 0.5 cm (twofold the size of the initial item), 2 × 4 × 0.5 cm (fourfold) or 4 × 4 × 0.5 cm (eightfold). Subjects were run in a succession of stages comprising of four sessions in total for each stage. Each stage differed by the time-lag tested: 2, 5, 10, 20, 40, 80, 160, 320 s. To avoid satiation, we limited the number of trials in a session to 12 in which each of the three possible cookies sizes was presented four times in random order. Time-lags were successively tested until the individual performance dropped to 0% of return. Subjects received one session per day. Failure to return the initial piece of cookie was recorded, as well as the timing of the error (time elapsed after the beginning of the trial in seconds as measured with a stopwatch).

The results showed that most individuals succeeded in exchanging until the delay exceeded (or reached) 1 min 20 s. Only two macaques (Zeb, Zor) stopped returning the initial item at 20 s. Two individuals (Ram, Jac) still returned the small item at 2 min 40 s and stopped at a time-lag of 5 min 20 s (see ESM S2). We compared the subjects' performances for each time-lag for the three different cookie sizes using Friedman tests. This showed that the waiting periods of subjects significantly increased with the size of the reward at the 2-, 5-, 20-, 40- and 80-s time lags (Fig. 1).

The amount of food and the duration of delay affected the waiting time of subjects. It may be that long-tailed macaques considered that a rather small food item was not worth waiting for. If they anticipated the time duration before they could exchange and receive the second cookie, they may have decided early on whether to wait or to give up. When comparing the distribution of observed giving-up times with the distribution of times to be expected under the null hypothesis of a constant giving-up chance during the trial, all but one subject (Zeb) gave up earlier than predicted by the model from a time lag of 20 s for Joe, Lou, Ram, Sad, Zor; 40 s for Don; 80 s for Cas and 2 min 40 s for Jac (Table 1).

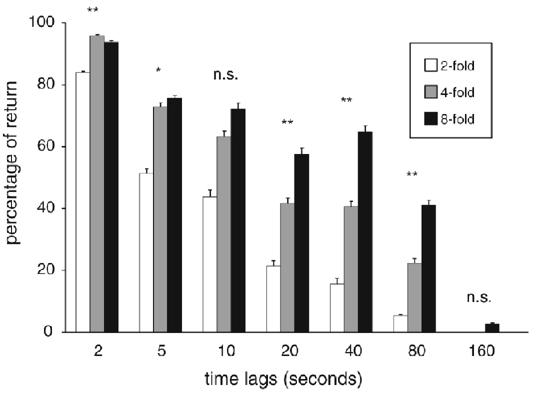


Fig. 1 Percentages of return for each size of cookie (2, 4, and 8 times) at each time lag in Experiment 1 (Friedman tests, $N = 9$, $*P < 0.05$, $**P < 0.01$)

In Experiment 1, long-tailed macaques adjusted their waiting duration to the amount of reward. In addition, giving-up time suggested that they estimated early whether the reward was worth waiting for and decided accordingly to wait or to give up.

Experiment 2: assessing maximum waiting periods

In Experiment 2, we considerably increased the final payoff to assess whether individuals could sustain longer waiting periods.

Subjects were offered a reward 40-fold the size of the initial food item: five pieces of cookie, each sizing 4 × 4 × 0.5 cm. Each subject was run in 12 trials for each time lag: 10, 20, 40, 80, 160, 320, 640, 1,280, 2,560 s. Considering the larger size of the reward, sessions were reduced to two trials per day, separated by a minimal 20-min interval. If a subject succeeded at least once in a session, he was tested at the next time lag. As in Experiment 1, timing of failures was also recorded.

Three individuals (Zeb, Zor, Sad) gave up exchanging at time lags of 40, 80 s and 2 min 40 s, respectively. The other six subjects still returned the initial item at 2 min 40 s. The performances of three of these subjects (Joe, Ram, Lou) dropped to 0 at 5 min 20 s. One subject (Cas) gave up exchanging at 10 min 40 s. The last two individuals (Jac, Don) still exchanged at 10 min 40 s and 21 min 20 s, respectively, though they then gave up at longer time lags (see ESM S2).

Considering rates of giving-up, four individuals (Joe, Lou, Zeb, Zor) never gave up earlier than predicted by the model (Table 1). The other five individuals gave up significantly earlier than predicted, Ram and Sad at the 80-s time-lag, Cas at the 5 min 20 s time-lag, and Jac and Don at the 10 min 40 s time lag.

We calculated the extinction of exchanges for each individual by examining their waiting time per trial for the three longest time lags that they sustained (see ESM S3). Six subjects (Jac, Joe, Lou, Sad, Zeb, Zor) gradually stopped exchanging as delays were extended. The other three individuals (Cas, Don, Ram) displayed different patterns. They were able to resume exchanges after failure in several consecutive trials.

In Experiment 2, long-tailed macaques sustained long-lasting periods when offered rewards 40 times the size of

Table 1 Maximum values obtained from the Kolmogorov–Smirnov statistical test used to compare the expected and observed distribution of giving-up times

Subjects	Cas	Don	Jac	Joe	Lou	Ram	Sad	Zeb	Zor
Experiment 1									
2 s	0.07	0.55	0.68	0.28	0.07	0.35	0.55	0.21	S
5 s	0.66	0.24	0.27	0.17	0.67	0.25	0.34	0.88	0.73
10 s	0.9	0.11	0.08	0.96	1.06	0.44	0.17	0.57	0.77
20 s	1.04	0.29	0.31	2.11***	1.23*	2.11***	2.41***	0.67	1.55***
40 s	0.93	1.83***	0.13	3.14***	2.79***	3.79***	3.06***	NT	2.59***
80 s	2.23***	2.53***	0.7	4.29***	3.81***	4.88***	3.85***	NT	NT
160 s	2.63***	3.86***	2.92***	2.97***	3.60***	5.07***	2.31***	NT	NT
320 s	NT	NT	2.30***	NT	NT	2.54***	NT	NT	NT
Experiment 2									
10 s	S	S	S	S	S	S	S	0.22	0.11
20 s	S	0.18	0.5	S	0.11	0.84	S	0.38	S
40 s	S	S	S	0.08	S	0.47	0.54	0.43	0.48
80 s	S	0.78	0.2	0.24	S	1.17**	1.65***	NT	0.6
160 s	0.7	0.1	0.22	0.92	0.41	1.67***	0.55	NT	NT
320 s	1.84***	0.28	0.37	0.62	0.72	0.89	NT	NT	NT
640 s	1.73***	1.26**	1.19**	NT	NT	NT	NT	NT	NT
1,280 s	NT	2.33***	2.07***	NT	NT	NT	NT	NT	NT
2,560 s	NT	0.33	NT	NT	NT	NT	NT	NT	NT

A statistically significant effect was observed when maximum values surpassed the critical values as follows. Experiment 1, $N = 48$: critical value = 1.07 for $P < 0.05$, critical value = 1.26 for $P < 0.01$, critical value = 1.45 for $P < 0.001$. Experiment 2, $N = 12$: critical value = 1.03 for $P < 0.05$, critical value = 1.22 for $P < 0.01$, critical value = 1.43 for $P < 0.001$

NT Non tested, *S* 100% of success

$^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$

the initial item. As in Experiment 1, the early giving-up time suggested that they estimated early whether the reward was worth waiting for.

Experiment 3: testing the effect of action inhibition on waiting

In Experiments 1 and 2, long-tailed macaques had not only to accept the exchange and keep the small piece of cookie intact throughout the duration of the test; they also had to inhibit the consumption of the initial item. In the following experiment we attempted to reduce the need to control for food consumption, to detect how continuously refraining from consumption may have affected their performances in former experiments. We relaxed the food-keeping condition by requesting subjects to give back the initial food item 3 s after they received it. Only then was the waiting period applied. Once it ended, the experimenter gave the larger reward to the subjects.

We applied the same procedure as in Experiment 2: for each subject, 12 trials for each time-lag: 10, 20, 40, 80, 160, 320, 640, 1,280, 2,560 s were run, and if the subject succeeded at least once in a session he was tested at the next time lag. Subjects were tested in two daily trials separated by a 20-min interval. Once subjects had given the initial piece of cookie back, it was placed beside the larger reward (40-fold the initial piece), in front but out of reach of the subjects. Then, the waiting period started: 10, 20, 40, 80, 160, 320, 640, 1,280, 2,560 s. If subjects failed to return the initial item, the trial ended. If they succeeded, they obtained the larger reward at the end of the time lag. For reasons irrelevant to the study, one of the subjects (Zor) could not be tested in this experiment or in Experiment 4.

All subjects accepted to exchange when the reward was delayed for at least 10 min 40 s. Three individuals (Don, Sad, Zeb) stopped exchanging for delays of 21 min 20 s and four individuals (Ram, Cas, Jac, Lou) for delays of 42 min 40 s. One subject (Joe) still exchanged for this delay with a percentage of return of 58.3%; we did not test him further (see ESM S2).

The suppression of the food-keeping condition in Experiment 3 significantly increased the duration of waiting periods sustained by all individuals compared to their performances in Experiment 2 (Fig. 2). This indicates that the need to control for impulsivity by refraining from eating

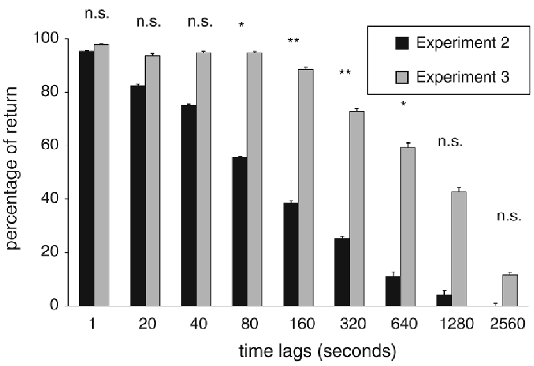


Fig. 2 Percentages of return at each time lag in Experiments 2 and 3 (Wilcoxon tests, $N = 8$; $^{*}P < 0.05$, $^{**}P < 0.01$)

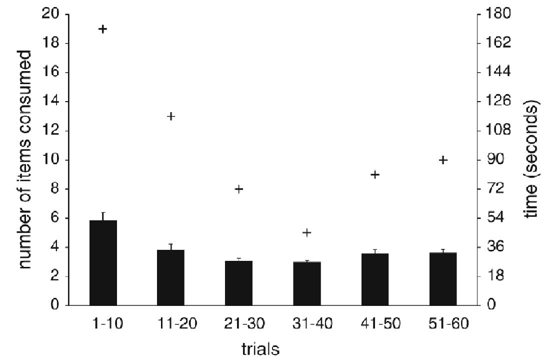


Fig. 3 Mean number of food items consumed by all subjects by series of ten trials in Experiment 4. Maxima are indicated by *black crosses*

the initial cookie acted as a limiting factor in delay of gratification.

Experiment 4: testing the ability to wait in an accumulation task

To test for the possible influence of temporal discounting in the performances of long-tailed macaques, we presented the subjects with an accumulation of food pieces added at fractioned time intervals, following the procedure devised by Beran (2002). There are hints that subjects could treat such sequences of food items not as a whole but as a collection of independent items (see Brunner and Gibbon 1995). If the subjects consider one interval at a time, they should wait for longer periods than for non-fractioned periods.

The apparatus consisted of one PVC panel comprised of two tablets 1 and 2, separated by 5 cm, and small pieces of cookie sizing 1 × 2 × 0.5 cm. During the test, we placed the panel in front of the subject, with tablet 2 remaining within reach of the subject and tablet 1 being loaded with 81 pieces of cookie out of reach. Every 9 s, the experimenter transferred a piece of cookie from tablet 1 to tablet 2. Subjects were allowed to take the items on tablet 2 at any time. If they did, the trial ended and the experimenter threw the food items remaining on tablet 1 in a bucket. We ran daily sessions of two trials per day separated by a 20-min interval. Each subject was submitted to a total of 60 trials.

Six individuals successfully passed the training criteria (see ESM S1). The number of food items taken by the subjects decreased over sessions (Fig. 3). On average, subjects could wait between 27 and 54 s before seizing the rewards. The maximum waiting period recorded was 2 min 11 s (Fig. 3).

Fractioning time periods led to waiting durations that were comparable to those measured in Experiment 1 using similar reward amounts. This result does not support the hypothesis that fractioning minimized the influence of temporal discounting on subjects' responses.

Discussion

Our results reveal waiting durations in long-tailed macaques that had not been previously reported for monkeys. In the exchange task of Experiment 1, subjects were able to adjust their waiting durations to the size of rewards. They sustained longer time-lags for larger food items, as previously reported for brown capuchin monkeys (Ramseyer et al. 2006) and chimpanzees (Dufour et al. 2007). Most long-tailed macaques waited until 40–80 s for rewards eight times the size of the initial food item. When offered rewards 40 times the size of the initial item in Experiment 2, subjects significantly increased their waiting duration, some tolerating delays longer than 5, 10 or even 21 min. Such waiting durations are much longer than those reported in most species tested in different experimental situations. They are outstanding relative to those of brown capuchins who did not postpone payoff beyond 40 s in the same task (Ramseyer et al. 2006). They also compare favourably with those of chimpanzees who reached 8 min in an exchange task (Dufour et al. 2007), or up to 18 min in a cumulative delay-of-gratification task (Evans and Beran 2007b). Such performances do not support the idea of an evolutionary gap between presumably patient hominids and impulsive animals like monkeys (see Rosati et al. 2007).

Monkeys anticipate the location, distance and value of food sites (Chauvin and Thierry 2005; Janmaat et al. 2006; Janson 2007), but so far we have no strong evidence that they are able to plan future needs, whereas we do have such evidence in the great apes (Mulcahy and Call 2006; Dufour and Sterck 2008; Osvath and Osvath 2008). In the exchange task, there was no need for long-tailed macaques to keep a mental record of the time elapsed between the moment they anticipate a reward and the receipt of the reward. Given their ability to delay action for long periods, however, it should be asked whether they were aware of the time needed to reach their goals. We investigated the mechanisms behind decision-making by examining subjects giving-up times. In both Experiments 1 and 2, a majority of individuals gave up earlier than predicted. Similar results were found in chimpanzees (Dufour et al. 2007). We propose that macaques anticipated the duration of the delay in combination with the size of the exchange reward and reversed their preference to the smaller immediate reward early in the trial. An alternative explanation would be that delays led to a reduction in the association between the initial choice and the exchange reward, resulting in an extinction of the exchange behaviour. In Experiment 2, three individuals succeeded in waiting for long delays after consecutive failures, however, which does not support the hypothesis of associative learning. Therefore, our data indicate that long-tailed macaques anticipated the duration they would have to wait for and decided accordingly whether to wait or to give up.

In Experiments 1 and 2, subjects had to suppress food consumption and keep the initial piece of food intact in their hand in order to bridge the interval between their decision to wait and the return of the reward. In Experiment 3, we tested the hypothesis that action inhibition constrained their ability to postpone gratification by asking subjects to give back the initial item before waiting. As in a delayed-reward contingency task, individuals faced a single decision: to accept or not accept the exchange. They could not modify their choice within a given trial, but they could re-evaluate it in the next one. Results showed that long-tailed macaques dramatically improved their maximum waiting time compared to Experiment 2, albeit amounts of rewards were identical. Several subjects accepted a time-lag of 21 min 20 s and one went as far as to tolerate 42 min 40 s. This demonstrates the role of action inhibition as a limiting factor in the ability to postpone gratification. It should be stressed that most instances of reciprocation in monkeys deal with services like grooming, mating or support in conflict (Seyfarth and Cheney 1984; de Waal and Luttrell 1988; Silk 1992) that do not require consumption inhibition. In comparison, active food sharing regularly occurs in chimpanzees (de Waal 1989; Mitani and Watts 2001), and trading goods is typical of economical transactions in humans, which are likely to be more demanding in terms of self-control.

The results of Experiment 3 stand in sharp contrast with those recorded in more conventional reverse delayed-reward contingency tasks. This is surprising, since experimental procedures were rather similar in both types of studies, with animals having to decide at the beginning of a trial whether to wait for a reward or not. A major variation between previous studies and the present one is the difference in quantity between immediate and delayed rewards. The first reward sized as one-third of the second reward in previous studies (Szalda-Petree et al. 2004; Stevens et al. 2005b; Rosati et al. 2007; Amici et al. 2008), whereas the ratio here was 1/40. The same can be said regarding the performances of non-primate species (Mazur 1987; Richards et al. 1997; Grosch and Neuringer 1981; Killeen et al. 1981). On the other hand, the durations measured in Experiment 3 are comparable with those reported in a recent study demonstrating that great apes can decline to take an immediate food reward in favour of a tool that they will use 70 min later to get a larger food reward (Osvath and Osvath 2008).

In Experiment 4, we made the assumption that the temporal discounting effect would be minimized by fractioning waiting durations. Subjects could at any time seize the rewards accumulating every 9 s. They mostly waited between 1/2 and 1 min. Such results in long-tailed macaques appear intermediate between those reported for rhesus macaques (Evans and Beran 2007a) and chimpanzees (Beran 2002). Unexpectedly, waiting periods were comparable to those measured in Experiment 1; subjects appeared to be content with a low number of food items, which was equivalent to the eightfold reward received in Experiment 1. It could be that subjects considered the total amount of reward or the whole duration of trials, instead of each time interval separately. Contrary to our initial prediction, temporal discounting may have influenced the decision of subjects to wait for larger reward or not.

At the group level, it appears that subjects sustained consistent delays in Experiments 1 and 4 for equivalent quantities of food. This points at the robustness of our measures of gratification delays in the exchange and accumulation tasks. Besides, the temporal bridging capacities of long-tailed macaques in Experiments 2 and 3 outperform those described in capuchin monkeys and are not far from those reported in chimpanzees. Such results do not support the flexibility hypothesis, which predicts that animals living in cohesive groups should display a lesser ability to wait than those living in fission–fusion communities (Amici et al. 2008). To be fair, more comparative data are needed before drawing firm conclusions about the relevance of the hypothesis. So far, delays of gratification have been assessed in a limited number of primate species, and all studies including the present one rest upon a small number of subjects. Different populations of the same species may differ according to the environment and conditions of socialization. Furthermore, different methods and factors such as age or sex may bring different results regarding the propensity of individuals to cope with delay. Caution is thus required when comparing studies (Stevens et al. 2005b; Hayden and Platt 2007; Rosati et al. 2007).

In humans, the ability to delay gratification is considered to be a personality trait critical to life success (Shoda et al. 1990). In animals, the ability to postpone gratification may be a pre-requisite for making decisions that are future oriented. Temporal bridging capacities would contribute to fitness for individuals involved in complex interactions. We note that primates like macaques display elaborate social strategies where they have to implement multiple tactics to reach their goals. The social intelligence hypothesis posits that complex social life promotes the development of higher cognitive capacities (Humphrey 1976; Byrne and Whiten 1988). Future research should look for evidence about the links between delay of gratification and various dimensions of the social realm.

Acknowledgments The authors are grateful to A. Beauvy and C. Gaertner for animal care and to L. Bahans, S. Bauer, M. Bordaberry, N. Bourbia, M. Demontfaucon, V. Grondin, C. Morin, A. Navarre, A. Racca, F. Vogelweith and C. Wagner for valuable assistance in experiments. The research was supported by a grant from the Agence Nationale de la Recherche (ANR-08-BLAN-0042-01).

References

Abeyesinghe SM, Nicol CJ, Hartnell SJ, Wathes CM (2005) Can domestic fowl, *Gallus gallus domesticus*, show self-control? Anim Behav 70:1–11

Amici F, Aureli F, Call J (2008) Fission-fusion dynamics, behavioral flexibility and inhibitory control in primates. Curr Biol 18:1415–1419

Aureli F, Cozzolino R, Cordschi C, Scucchi S (1992) Kin-oriented redirection among Japanese macaques: an expression of a revenge system? Anim Behav 44:283–291

Beran MJ (2002) Maintenance of self-imposed delay of gratification by four chimpanzees (*Pan troglodytes*) and an orangutan (*Pongo pygmaeus*). J Gen Psychol 129:49–66

Brunner D, Gibbon J (1995) Value of food aggregates: parallel versus serial discounting. Anim Behav 50:1627–1634

Byrne RW, Whiten A (1988) Machiavellian intelligence: social expertise and the evolution of intellect in monkeys, apes and humans. Clarendon Press, Oxford

Chauvin C, Thierry B (2005) Tonkean macaques orient their food search from olfactory cues conveyed by group mates. Ethology 111:1–10

Das M (2000) Conflict management via third parties: post-conflict affiliation of the aggressor. In: Aureli F, de Waal FBM (eds) Natural conflict resolution. University of California Press, Berkeley, pp 263–280

de Waal FBM (1989) Food sharing and reciprocal obligations among chimpanzees. J Hum Evol 18:433–459

de Waal FBM, Luttrell LM (1988) Mechanisms of social reciprocity in three primate species: symmetrical relationships characteristics or cognition? Ethol Sociobiol 9:101–118

Dufour V, Sterck EHM (2008) Chimpanzees (*Pan troglodytes*) fail to plan in an exchange task, but succeed in a tool using procedure. Behav Proc 79:19–27

Dufour V, Pelé M, Sterck EHM, Thierry B (2007) Chimpanzee (*Pan troglodytes*) anticipation of food return: coping with waiting time in an exchange task. J Comp Psychol 121:145–155

Evans TA, Beran MJ (2007a) Delay of gratification and delay maintenance by rhesus macaques (*Macaca mulatta*). J Gen Psychol 134:199–216

Evans TA, Beran MJ (2007b) Chimpanzees use self-distraction to cope with impulsivity. Biol Lett 3:599–602

Grosch J, Neuringer A (1981) Self-control in pigeons under the Mischel paradigm. J Exp Anal Behav 35:3–21

Gumert MD (2007) Payment for sex in a macaque mating market. Anim Behav 74:1655–1667

Haccou P, Meelis E (1992) Statistical analysis of behavioural data. Oxford University Press, Oxford

Hayden BY, Platt ML (2007) Temporal discounting predicts risk sensitivity in rhesus macaques. Curr Biol 17:49–53

Humphrey N (1976) The social function of intellect. In: Bateson PPG, Hinde RA (eds) Growing points in ethology. Cambridge University Press, Cambridge, pp 303–317

Janmaat KRL, Byrne RW, Zuberbühler K (2006) Evidence for a spatial memory of fruiting states of rainforest trees in wild mangabeys. Anim Behav 72:797–807

Janson CH (2007) Experimental evidence for route integration and strategic planning in wild capuchin monkeys. Anim Cogn 10:341–356

Kacelnik A (2003) The evolution of patience. In: Loewenstein G, Read D, Baumeister R (eds) Time and decision: economic and psychological perspectives on intertemporal choice. Russell Sage Foundation, New York, pp 115–138

Killeen PR, Smith JP, Hanson SJ (1981) Central place foraging in *Rattus norvegicus*. Anim Behav 29:64–70

Mazur JE (1987) An adjusting procedure for studying delayed reinforcement: the effects of delay and intervening events on reinforcement value. In: Commons ML, Mazur JE, Nevin JA, Rachlin H (eds) Quantitative analyses of behavior, vol 5. Erlbaum, Hillsdale, pp 55–73

Mischel W (1974) Processes in delay of gratification. In: Berkowitz L (ed) Advances in experimental social psychology. Academic Press, New York, pp 249–292

Mitani JC, Watts DP (2001) Why do chimpanzees hunt and share meat? Anim Behav 61:915–924

Mulcahy NJ, Call J (2006) Apes save tools for future use. Science 312:1038–1040

Osvath M, Osvath H (2008) Chimpanzee (*Pan troglodytes*) and orangutan (*Pongo abelii*) forethought: self-control and pre-experience in the face of future tool use. Anim Cogn 11:661–674

Petit O, Thierry B (1994) Aggressive and peaceful interventions in conflicts in Tonkean macaques. Anim Behav 48:1427–1436

Rachlin H, Raineri A, Cross D (1991) Subjective probability and delay. J Exp Anal Behav 55:233–244

Ramseyer A, Pelé M, Dufour V, Chauvin C, Thierry B (2006) Accepting loss: the temporal limits of reciprocity in brown capuchin monkeys. Proc R Soc B 273:179–184

Richards JB, Mitchell SH, de Wit H, Seiden LS (1997) Determination of discount functions in rats with an adjusting-amount procedure. J Exp Anal Behav 67:353–366

Rosati AG, Stevens JR, Hare B, Hauser MD (2007) The evolutionary origins of human patience: temporal preferences in chimpanzees, bonobos, and human adults. Curr Biol 17:1663–1668

Seyfarth RM, Cheney DL (1984) Grooming, alliances, and reciprocal altruism in vervet monkeys. Nature 308:541–543

Shoda Y, Mischel W, Peake PK (1990) Predicting adolescent cognitive and self-regulatory competencies from preschool delay of gratification: identifying diagnostic conditions. Dev Psychol 26:978–986

Siegel S, Castellan NJ (1988) Nonparametric statistics for the behavioral sciences. McGraw-Hill, Singapore

Silk JB (1992) The patterning of intervention among male bonnet macaques: reciprocity, revenge, and loyalty. Curr Anthropol 33:318–325

Stephens DW, Anderson D (2001) The adaptive value of preference for immediacy: when shortsighted rules have farsighted consequences. Behav Ecol 12:330–339

Stevens JR, Cushman FA, Hauser MD (2005a) Evolving the psychological mechanisms for cooperation. Ann Rev Ecol Syst 36:499–518

Stevens JR, Hallinan EV, Hauser MD (2005b) The ecology and evolution of patience in two New World monkeys. Biol Lett 1:223–226

Szalda-Petree AD, Craft BB, Martin LM, Deditius-Island JK (2004) Self-control in rhesus macaques (*Macaca mulatta*): controlling for differential stimulus exposure. Percept Mot Skills 98:141–146

Tobin H, Logue W, Chelonis JJ, Ackermann KT, May JG (1996) Self-control in the monkey *Macaca fascicularis*. Anim Learn Behav 24:168–174

Toner IJ, Smith RA (1977) Age and overt verbalization in delay-maintenance behavior in children. J Exp Child Psychol 24:123–128

Toner IJ, Lewis BC, Gribble CM (1979) Evaluative verbalization and delay maintenance behavior in children. J Exp Child Psychol 28:205–210

Trivers RL (1971) The evolution of reciprocal altruism. Q Rev Biol 46:35–57

Electronic Supplementary Material S1: Training Methods.

Experiment 1

We trained subjects to exchange one piece of cookie for a larger one with humans with the following successive steps. Subjects had first to return a token, for a food reward (raisin). They first received the reward when they dropped the token or threw it. In a second step, we rewarded subjects only when they dropped or threw the token outside the fence of their compartment. In a third step, we rewarded subjects when they dropped the token toward the experimenter's hand. Finally, subjects received the reward only when they placed the token in the experimenter's hand. Subjects required between 27 and 37 training days of 20-30 trials per day in order to reach this final step.

In the second training stage, we trained subjects to give back an edible item. Subjects first had to exchange a less desirable item, i.e. monkey diet pellet, against a more desirable one, i.e. raisin. In the next step, we trained subject to return a small piece of cookie of 1 x 2 x 0.5 cm for a larger one sizing 4 x 2 x 0.5 cm. We tested subjects in sessions of 12 trials, run with a maximum of one training session per half-day. We required the subjects to succeed in 80% of trials during two consecutive sessions in order to be ready for experiments. They required between 3 and 13 sessions to reach this criterion.

Experiment 2

Testing maximal delays eventually led to an extinction of exchanges in Experiment 1. Before starting Experiment 2, subjects' exchange behaviour had to be refreshed. We ran subjects in three successive steps. They first had to give back a diet pellet with a 2-s time lag to get a small piece of cookie (2 x 2 x 0.5 cm). In a second step they had to exchange a small piece of cookie against a 4-fold larger one with the same time lag. In a last step, time lag was extended to 5 s. Subjects were required to exchange in 80% of trials during two consecutive sessions to proceed in the next step and be ready for testing.

Experiment 3

Exchange behaviour had to be refreshed prior to this experiment, applying the same steps and criteria as in Experiment 2.

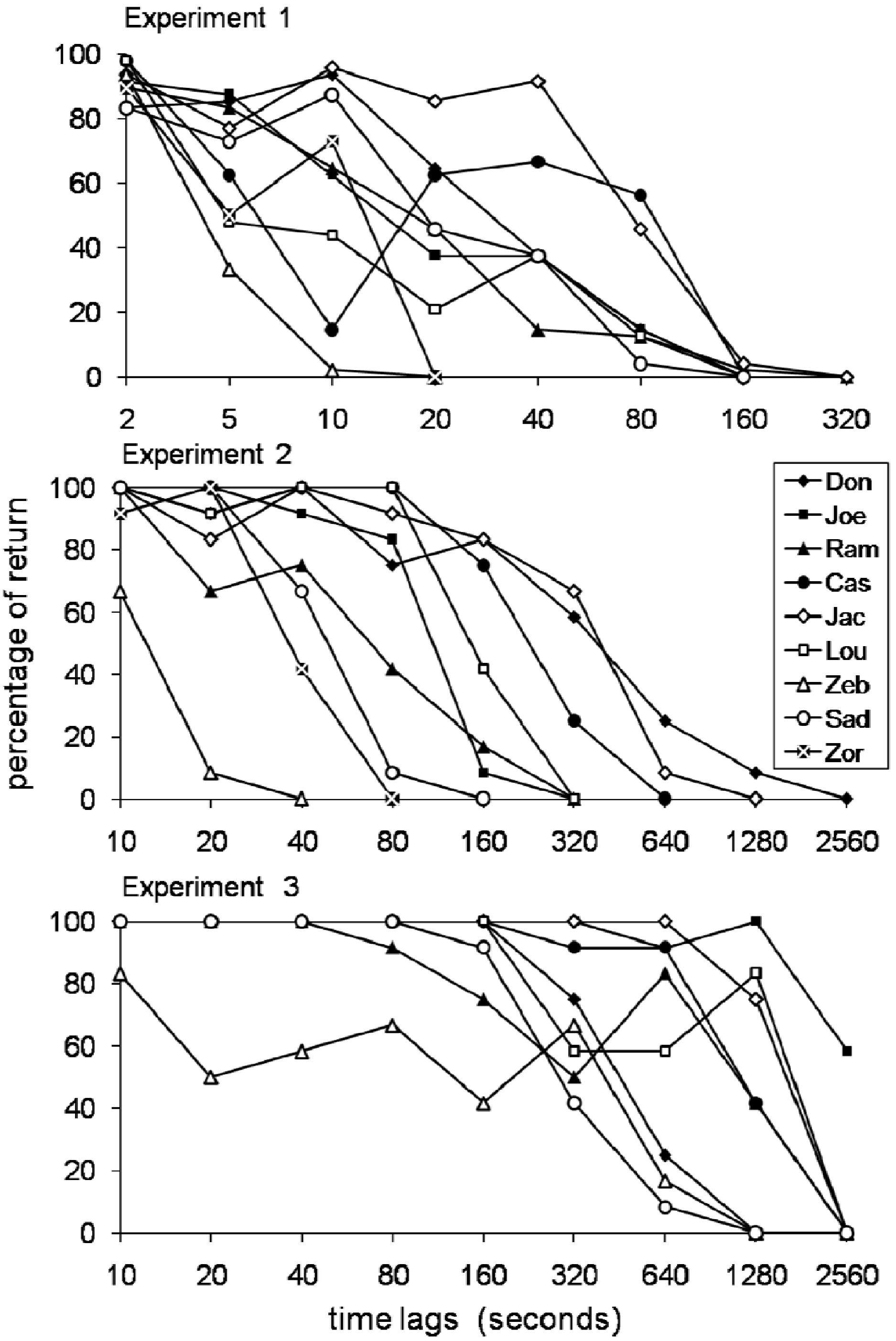
Experiment 4

The first training stage consisted of a demonstration of the transfer of five pieces of cookie, one at a time, at a rate of 1 every 3 s, from tablet 1 to tablet 2 (both tablets being out of reach of subjects). Once the five pieces of cookie were on tablet 2, the experimenter moved the panel closer to subjects and allowed them to take the food items. A session was composed of six demonstrations separated by two minutes after the end of food consumption by the subject. We ran four sessions at this stage with no more than two daily sessions separated by an interval at least 20-min long. In the second training stage, we alternated six demonstration trials with six training trials; in the latter, subjects had access to tablet 2, i.e. they might take items at any time, which ended the trial. As previously four sessions with no more than two daily sessions separated by an interval at least 20-min long were run. In the third stage, demonstrations ceased and sessions consisted of six training tests with items being transferred from one tablet to another every 3 s. The experimenter waited for 30 s after the end of subject food consumption before starting another trial. A minimum of three pieces of cookie per trial and 20 pieces of cookie per session during two consecutive sessions was required to proceed to the next training stage. In the final stage, subjects were run as in stage 3 and using the same criterion of success, except that items were transferred every 6 s.

If individuals had not reached success criteria after 20 training sessions, we stopped training them. Two subjects, Don and Zeb, did not reach the success criterion at 3 s. At such time lag, they waited at maximum for 4 and 5 pieces of cookie, respectively.

Electronic Supplementary Material S2: Individual performances.

Individual percentages of return as a function of time lag in Experiments 1, 2 and 3.
Experiment 1 (9 subjects): all sizes of cookies combined.
Experiment 2 (9 subjects): rewards 40 times the size of the initial food item.
Experiment 3 (8 subjects): return before waiting; rewards 40 times the size of the initial food item.

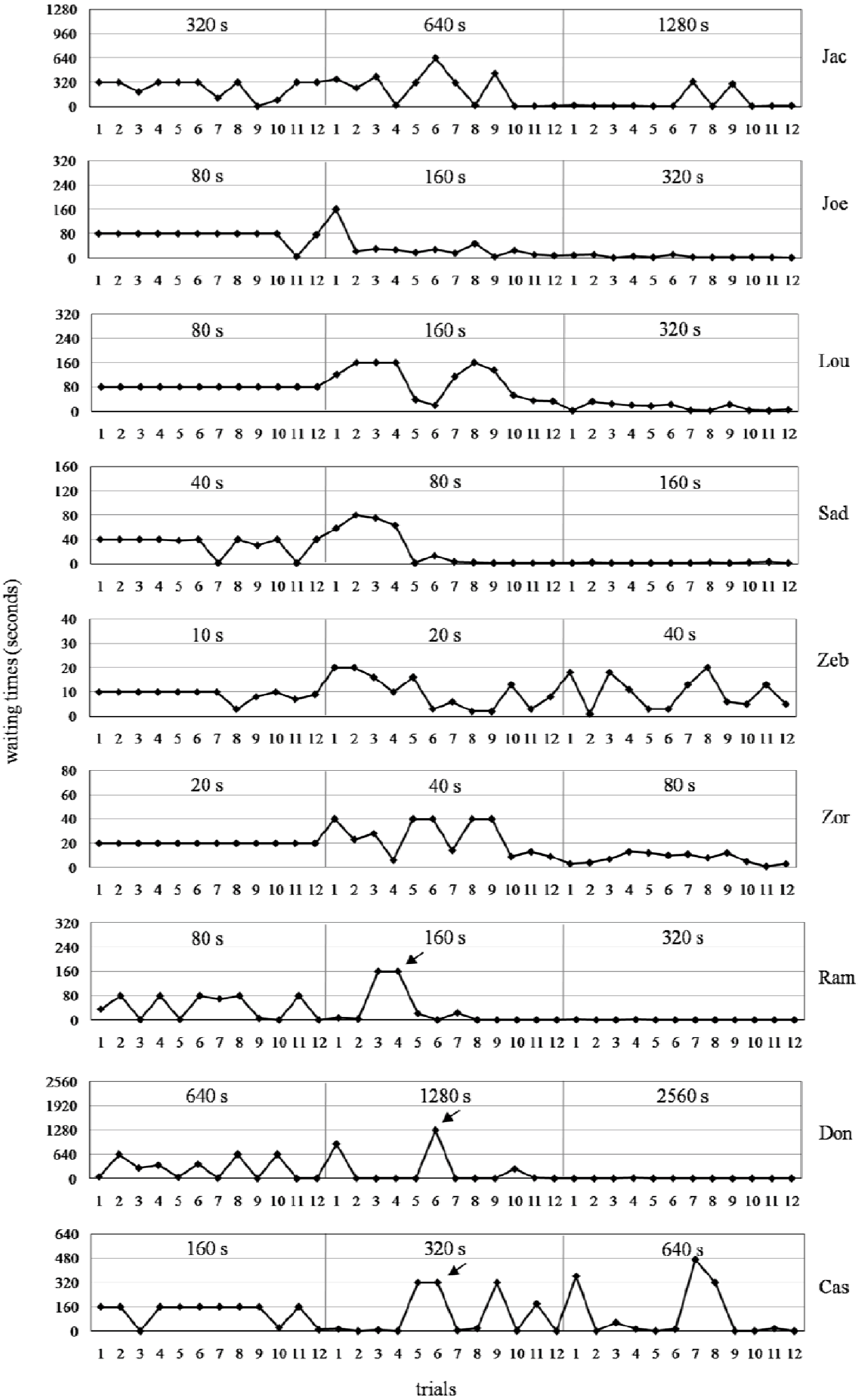

Experiment 1

Experiment 2

Experiment 3

Electronic Supplementary Material S3: Extinction of exchanges.

Waiting duration per trial for the three longest time lags sustained by subjects.
Six subjects (Jac, Joe, Lou, Sad, Zeb, Zor) gradually stopped to exchange when delays were extended. Three subjects (Ram, Don, Cas) succeeded in waiting for long durations despite previous consecutive failures (see arrows).



Article 3

L’estimation de la valeur et l’anticipation de l’attente chez les macaques de Tonkean et les capucins bruns

Manuscrit soumis

RESUME DE L’ARTICLE 3

Introduction

L’étude a pour but de mesurer la capacité à attendre de macaques de Tonkean et de singes capucins au cours d’un échange et de reconnaître certains des facteurs susceptibles de limiter leurs performances en répondant aux questions suivantes. Des singes sont-ils capables de différer le retour d’une récompense au cours d’un échange d’items alimentaires ? Cette capacité est-elle fonction de la quantité de la récompense ? Dans quelle mesure l’inhibition de la consommation et la dépréciation temporelle de la récompense influencent-elles le comportement d’attente des singes ?

Méthodes

J’ai testé dix macaques de Tonkean et sept capucins au cours d’une série de quatre expériences. Dans les deux premières expériences, les sujets devaient rendre un morceau de biscuit à un expérimentateur en échange d’un plus gros morceau dont la dimension pouvait être égale à deux, quatre, huit ou quarante fois la dimension du premier. Pour l’expérience 1, le délai imposé entre le don du premier morceau et le retour de la récompense allait de 2 à 320 s pour les macaques et de 2 s à 160 s pour les capucins. Pour l’expérience 2, il allait de 10 à 320 s pour les macaques et de 10 à 320 s pour les capucins. Lors d’une troisième expérience, j’ai permis aux sujets de rendre le petit morceau de biscuit avant d'attendre un plus gros morceau. Cette condition a permis d’étudier l’influence de l’inhibition de la consommation sur l'aptitude des sujets à tolérer la période d'attente. Au cours d’une quatrième expérience, j’ai testé les sujets dans une tâche d’accumulation de la récompense. L’expérimentateur plaçait toutes les 9 s un petit morceau de biscuit à portée de main du sujet. Dès que celui-ci s’emparait des biscuits accumulés, l’essai était considéré comme terminé. Les sujets devaient donc être capables d’attendre pour maximiser leur récompense. Cette condition a permis de d’étudier l’influence de la dépréciation de la récompense au cours du temps sur l’aptitude des sujets à attendre.

Résultats

Au cours des deux premières expériences d’échange, les macaques de Tonkean ont attendu entre 20 et 80 s et les capucins entre 10 et 40 s en fonction de la dimension de la récompense et des individus. L'analyse des temps de renoncement a révélé l’aptitude des macaques et des capucins à anticiper la durée d'attente et à prendre leur décision en fonction de celle-ci et de la dimension de la récompense. L’étude de la dépréciation temporelle de la récompense par les individus a révélé une différence entre les macaques et les capucins. Contrairement aux macaques, la dépréciation temporelle des capucins n’est pas proportionnelle à la dimension de la récompense. Dans la troisième expérience, le contrôle du facteur de l’inhibition de la consommation a permis à plusieurs macaques d’attendre jusqu’à 42 mn. La majorité des capucins a attendu jusqu’à 10 mn et certains ont réussi à attendre un délai de 21 mn. Dans la tâche d’accumulation, les sujets ont montré des performances équivalentes à celles mesurées au cours de l’expérience 1.

Conclusion

Des macaques de Tonkean et des singes capucins peuvent différer de plusieurs minutes l'obtention d'une récompense alimentaire. Ils se montrent capables d’anticiper la durée d'attente et d’ajuster leur décision en fonction de ce délai et de la dimension de la récompense. L’augmentation significative des performances des sujets au cours de l’expérience 3 démontre que l’inhibition de la consommation est un facteur limitant la tolérance au délai. Au cours de l’expérience 4, les délais attendus par les individus sont identiques à ceux mesurés dans l’expérience 1. L’accumulation de la récompense au cours du temps n’a pas permis de minimiser l’effet de la dépréciation de la récompense avec le temps. Dans certaines conditions, les macaques de Tonkean et les capucins peuvent attendre plusieurs minutes, voire dizaines de minutes. On peut faire l'hypothèse que cette aptitude à tolérer un délai est en rapport avec les compétences cognitives dont peuvent faire preuve les singes dans leurs environnements physique et social.

Delay maintenance in Tonkean macaques and brown capuchin monkeys

Marie Pelé[1], Jérôme Micheletta[1], Bernard Thierry[1], Pierre Uhlrich[1] & Valérie Dufour[1,2]

[1]Département Ecologie, Physiologie & Ethologie, IPHC, Centre National de la Recherche Scientifique, Université de Strasbourg, Strasbourg, France

[2]Scottish Primate Research Group and Centre for Social Learning and Cognitive Evolution, University of St Andrews, St Andrews, United Kingdom

Abstract

Animals commonly face choices requiring them to wait and postpone action. The ability to delay gratification is a pre-requisite for making future-oriented decisions. We investigated the ability of brown capuchins (*Cebus apella*) and Tonkean macaques (*Macaca tonkeana*) to delay benefits in several experiments. In exchange tasks, subjects had to return a piece of cookie after a given time lag to obtain a larger one from an experimenter. The results showed that capuchins could wait 10-40 s and macaques 20-80 s depending on subjects and the size of rewards. Both groups were able to anticipate delay durations, but unlike macaques, capuchins discounted all sizes of reward at the same speed, meaning that delay maintenance in them was not affected by the reward size. When the subjects could immediately give back the initial piece of cookie then wait for the return, their performances increased to 10-21 min for capuchins and 21-42 min for macaques, demonstrating the role of consumption inhibition in postponing gratification. In a further task, subjects were presented with an accumulation of food pieces added at short intervals until they seized them. Our results confirmed that brown capuchins were more impulsive than Tonkean macaques. We did not find significant differences between the waiting performances of the Tonkean macaques and those previously reported in long-tailed macaques. The ability to delay gratification should be related to the skills of animals in the physical and social domains.

Keywords delay of gratification . exchange . decision-making . economics . primates

INTRODUCTION

Individuals commonly face decisions requiring them to delay action and wait. The ability to delay gratification is crucial for complex goal-directed action and planning (Kacelnik 2003; Mischel 1974). In humans, Mischel (1974) measured the ability of children to forgo an immediate, less preferred reward for a future, more preferred one. He offered them a choice between one marshmallow available immediately and two marshmallows available only after some waiting. To obtain the larger reward, subjects had first to choose waiting (*delay-choice*) and then to bridge the delay interval by maintaining their decision (*delay-maintenance*). Depending on their age and the type of instruction received, children could either demonstrate patience for more than 15 min, or be impulsive and eat the marshmallow without waiting (Mischel 1974).

In animals, delay of gratification has been studied using similar procedures. In delay-choice tasks, subjects are given a choice between an immediate reward and a delayed but more valued one. When subjects opt for the delayed option, however, they have no further opportunity to modify their response during the entire duration of the trial. In such task, domestic fowl (*Gallus gallus*), pigeons (*Columbia livia*) and rats (*Rattus norvegicus)* opted for the small immediate reward when the delay exceeded a few seconds (Abeyesinghe *et al.* 2005; Mazur 1987; Richards *et al.* 1997). Marmosets (*Callithrix jacchus*) and tamarins (*Saguinus oedipus*) postponed gratification between 5 and 20 s (Stevens *et al.* 2005a), whereas long-tailed macaques (*Macaca fascicularis*) and brown capuchin monkeys (*Cebus apella*) waited about 30 s (Amici *et al.* 2008), and spider monkeys (*Ateles geoffroyi*), bonobos (*Pan paniscus*) and chimpanzees (*Pan troglodytes*) between 1 and 2 min (Amici *et al.* 2008; Rosati *et al.* 2007).

In tasks where subjects can alter their choice at any time during the waiting period, pigeons (Grosh and Neuringer 1981) and rats (Killeen *et al.* 1981) waited for several seconds. In non-human primates, rhesus macaques (*Macaca mulatta*) waited for 2 min to obtain preferred food (Evans and Beran 2007a) and chimpanzees up to 18 min (Evans and Beran 2007b). Another test consists of presenting subjects with food items accumulating at regular time intervals – usually of some seconds – within reachable distance of the subject. Once the subject reaches for the accumulated pile, no further items are presented. As in previous tasks the subject must inhibit taking food for as long as possible to maximize its gain. In this food-accumulation task, on average macaques did not delay gratification beyond 15-60 s (Evans and Beran 2007a; Pelé *et al.* 2009) and chimpanzees and orang-utans for 2-3 min (Beran 2002).

Non-human primates can readily engage in exchanges of valuable goods with humans, which creates situations in which we can examine their skills in comparing costs and benefits (Addessi *et al.* 2007, 2008; Brosnan and de Waal 2004, 2005; Chalmeau and Peignot 1998; Drapier *et al.* 2005; Hyatt and Hopkins 1998; Lefebvre 1982; Westergaard *et al.* 2004). The ability to delay benefits is a basic capacity needed for economic transactions. We directly investigated this ability in an exchange task where subjects had to return a piece of cookie after a given time lag to obtain a larger one from an experimenter. When offered food rewards 40 times the size of the initial piece, brown capuchin monkeys (*Cebus apella*) did not wait for more than 20-40 s before returning food (Ramseyer *et al.* 2006), whereas chimpanzees postponed returns for up to 4-8 min (Dufour *et al.* 2007). Tested in the same conditions, most long-tailed macaques tolerated time lags about 2-5 min long but a few of them were able to postpone returns up to 10-21 min in several trials (Pelé *et al.* 2009).

In the food-exchange task, subjects have to assess the value of rewards in relation to incurred delays. The analysis of the timing of failure to return food in chimpanzees and long-tailed macaques showed that individuals anticipated the duration they would have to wait for and decided accordingly whether waiting or giving up (Dufour *et al.* 2007; Pelé *et al.* 2009). Moreover, temporal discounting – whereby the subjective value of benefits reduces with time – could also affect choices when current and future rewards are in conflict (Mazur 1987; Stevens *et al.* 2005b). This decrease in value may occur because of the increased risk involved in waiting for rewards, or because of the decreased rate of reward associated with increased waiting time (Green and Myerson 1996). Another feature of the food-exchange task is that subjects have to restrain their impulse to consume an available food. When the food-keeping condition was relaxed by asking the subjects to give back the initial item before applying the time lag, long-tailed macaques doubled their waiting performances up to 40 min (Pelé *et al.* 2009).

According to Amici and colleagues (2008), action would be motivated more by immediate goals and interests in species living in cohesive groups (e.g., macaques and capuchin monkeys) than in species undergoing frequent splitting and merging of subgroups (e.g., chimpanzees, and orang-utans). By favouring behavioural flexibility, social dynamics based on fission and fusion would enhance inhibitory skills in the latter species. We yet found comparable waiting performances in chimpanzees and long-tailed macaques in the food-exchange task, whereas capuchin monkeys sustained significantly lower time lags than the previous two species. We assumed that the sophisticated social tactics observed in the former two species could be related to higher abilities in reciprocating and postponing gratification (Pelé *et al.* 2009).

In the present investigation, we submitted brown capuchin monkeys and Tonkean macaques (*Macaca tonkeana*) to different conditions of delay maintenance in the food-exchange task and the food-accumulation task in order to test the robustness of our previous findings and extend them to another macaque species. Tonkean macaques display higher levels of social tolerance than long-tailed macaques and they are featured by more relaxed dominance relationships (Thierry 2007). We asked whether their ability to delay gratification would significantly differ from those measured in long-tailed macaques.

GENERAL METHODS

Subjects

We tested ten Tonkean macaques and nine brown capuchin monkeys maintained at the Primatology Centre of the University of Strasbourg, France. The Tonkean macaques belonged to three different social groups. Four subjects (Rim, She, Sim, Syb) were housed together in an indoor-outdoor enclosure of 15 m^2. Two subjects (Jan, Mil) were housed together in an indoor-outdoor enclosure of 15 m^2. Four subjects (Gae, Lad, Olg, Sha) belonged to a social group of 12 individuals living in a 0.5-ha park. The capuchins belonged to a social group of 18 individuals and were housed in an indoor-outdoor enclosure of 70 m^2. Commercial monkey diet pellets and water were provided *ad libitum*. Subjects were never deprived of food. For testing, subjects were temporarily separated from their conspecifics. The age and sex of subjects are provided in Table 1.

Table 1. Name, age and sex of subjects.

Tonkean macaques			Brown capuchins		
Name	Age (years)	Sex	Name	Age (years)	Sex
Gae	12	male	Acc	12	male
Jan	12	male	Arn	10	male
Lad	11	female	Aso	19	female
Mil	12	male	Bib	9	male
Olg	8	female	Clo	12	male
Rim	6	male	Pet	7	female
Sha	5	male	Pis	7	male
She	5	male	Pop	7	male
Sim	5	male	Rav	7	male
Syb	5	female			

Regarding capuchins, note that some data come from Ramseyer et colleagues (2006) for Experiments 1 and 2 (subjects Acc, Arn, Aso, Bib, Clo, Pis). For reasons irrelevant to the study, one capuchin (Bib) was tested in Experiment 1 only, and another (Clo) in Experiments 1 and 2 only. Three additional capuchins (Pet, Pop, Rav) were tested in the present study, allowing to analyse the time of giving up in Experiments 1 and 2.

Exchange Procedure

During testing, the experimenter stood in front of the subject's compartment, showing the subject two different sized pieces of cookie in each hand for 3 s. The experimenter then gave the smaller piece to the subject. The larger piece – i.e. the reward – remained visible in the experimenter's second hand for the whole duration of the waiting period. After the waiting period had elapsed, the experimenter held out her empty hand while still presenting the reward on her other hand. If the subject gave back the small piece of cookie, he received the larger one. If the subject did not give back the initial piece, the experimenter did not reward the subject and stepped back, thereby ending the trial. Whenever the individual had dropped or eaten the cookie before the end of the waiting period, the experimenter ended the trial by stepping back. The experimenter waited for 30 s after the end of food consumption before beginning another trial.

Statistics

We used the Friedman test to compare the percentages of return for the different sizes of cookies at each time lag in Experiment 1 and the Wilcoxon matched-pairs test to compare percentages of return in Experiments 2 and 3 (Siegel and Castellan 1988). Given the small number of individuals, we applied the exact test procedure of the statistical software SPSS 16©.

We ran an analysis on the timing of giving up – the time at which capuchins and macaques gave up waiting before the end of the trial. We compared the distribution of observed giving-up times with the distribution of times to be expected under the null hypothesis of a constant giving-up chance during the trial. If the long-tailed macaques anticipate the duration of the delay that remained to be waited for, they should decide early on whether to wait or not. To test this hypothesis, we calculated the estimated (observed) probability of continuing to wait at each point of time that the subject gave up waiting by using the Kaplan Meier survival analysis. This analysis included both the failure times and the times of successful return at the end of the trial (as censored data). In this analysis, the survival probability was expressed as percentage of chance to wait longer than the time already elapsed in the trial. Against this observed survival function, we calculated the expected (exponential) distribution of giving up times under the null hypothesis of a constant chance of giving up. The two distributions, the expected and the observed one, were compared using an adjusted Kolmogorov–Smirnov test (Haccou and Meelis 1992). A statistically significant difference between both distributions leads to the rejection of the null hypothesis that a subject has a constant chance to give up independent of the time elapsed in the trial. We ran the analysis on Experiment 1 by combining all cookie sizes: 2, 4, and 8 times the original size (N = 48). In Experiment 2, only one size of reward was tested; therefore, the analysis was run on a smaller number of events (N = 12).

We used linear regression analyses to assess relationships between the percentage of return and time. To study the influence of temporal discounting on the subjects' ability to wait, we contrasted the decreasing rates of returns as a function of time for each reward size in Experiments 1 and 2 using comparison tests of regression slopes.

Data were processed using SPSS 16.0 (SPSS Inc., Chicago, IL, USA) and R (The R Foundation for Statistical Computing, Vienna, Austria). The significance level was set at 0.05. Average values are given in text and figures as means and SEM.

EXPERIMENT 1: TESTING THE EFFECT OF QUANTITY ON WAITING PERIODS

We tested whether the duration of the waiting period sustained by Tonkean macaques and brown capuchins would vary according to the relative value of the items being exchanged.

Methods

For each trial, the experimenter first offered a small piece of cookie (1 x 2 x 0.5 cm), then presented the subject with a larger piece of cookie: 2 x 2 x 0.5 cm (2-fold the size of the initial item), 2 x 4 x 0.5 cm (4-fold) or 4 x 4 x 0.5 cm (8-fold). Trials were run on subjects in a succession of stages comprising of four sessions in total. Each stage differed by the time lag tested: 2, 5, 10, 20, 40 s *etc*. Each session comprised of twelve trials in which each of the three possible cookies sizes was presented four times in random order. Time lags were successively tested until the individual performance dropped to 0% of return. Subjects received one session per half-day. Failure to return the initial cookie was recorded as well as its timing.

Results

Percentage of return

In Experiment 1, most of the macaques succeeded in exchanging until 40 s of delay. Only four subjects (Gae, Olg, Sha, She) stopped exchanging at lesser time lags. Two macaques (Lad, Sim) stopped returning the initial item at 80 s and two others (Mil, Syb) at 160 s of delay. The last two subjects (Jan, Rim) still returned the small item at 2 min 40 s and stopped at 5 min 20 s (ESM). Capuchins succeeded until 10 s of delay. Five subjects (Arn, Aso, Clo, Pis, Pop) stopped exchanging at 20 s. Two others (Acc, Bib) stopped returning the initial item at 40 and one (Rav) at 80 s, respectively. A last subject (Pet) still returned the small item at a time lag equal to 80 s and stopped at 160 s (ESM).

For the two species, we compared the subjects' performances in each time lag for the three different cookie sizes exchanged against the initial item using Friedman tests. The waiting periods of macaques significantly increased with the size of the reward at time lags equal to 2, 5, 10, 20, 40 and 80 s (Fig. 1). The waiting periods of capuchins significantly increased with size at 5, 10 and 20 s (Fig. 1).

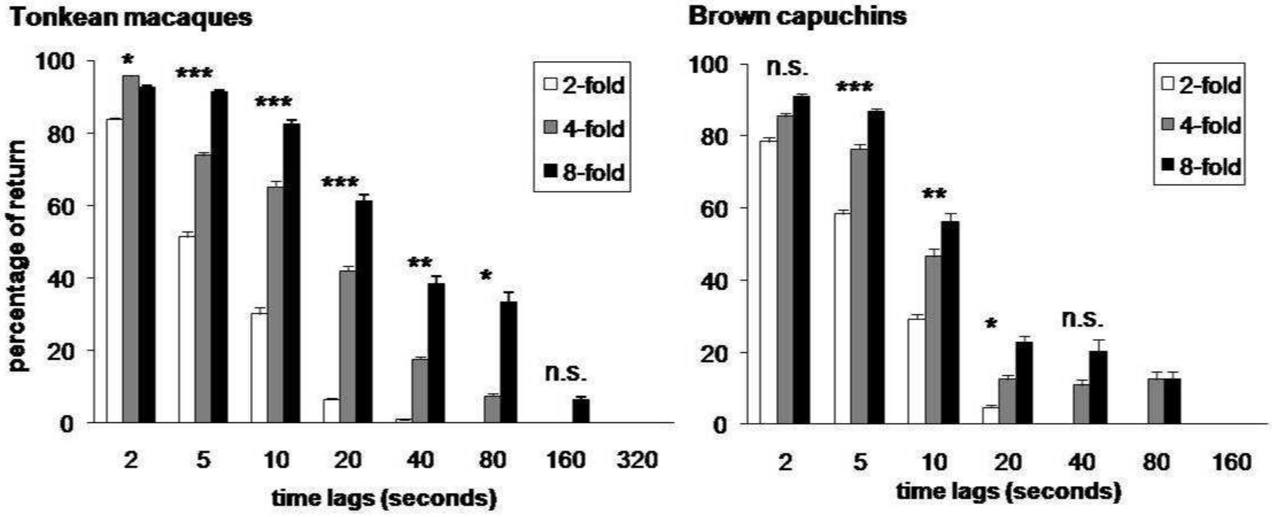


Figure 1. Percentages of return for each size of cookie (2, 4 and 8 times) at each time lag in

Experiment 1 for macaques (Friedman tests, $N = 10$, $*p < 0.05$, $**p < 0.01$, $***p < 0.001$) and capuchins ($N = 9$, $*p < 0.05$, $**p < 0.01$, $***p < 0.001$).

Time of giving-up

The size of the reward affected the waiting time of subjects. It may be that subjects considered that a rather small food item was not worth waiting for. If they anticipated the time duration before they could exchange and receive the second cookie, they may have decided early on whether to wait or to give up. We compared the distribution of observed giving-up times of macaques with the distribution of times to be expected under the null hypothesis of a constant giving-up chance during the trial; all but one subject (She) gave up earlier than predicted by the model; from a time lag of 5 s for Rim, Sha; 10 s for Gae, Jan; 20 s for Lad, Mil, Olg, Sim; and 40 s for Syb (Table 2). The same analysis in capuchins showed that the three subjects gave up significantly earlier than predicted; from a time lag of 5 s for Pop; 10 s for Pet; and 40 s for Rav (Table 2).

Table 2. Results of Kolmogorov-Smirnov tests comparing the subjects' expected and observed distributions of giving-up for each time lag in Experiment 1 (48 trials). Only maximal values are reported.

Time-lag	Brown capuchins		
	Pet	Pop	Rav
2 s	S	0.14	0.14
5 s	0.34	1.33**	0.76
10 s	1.11*	1.29**	0.68
20 s	1.32**	2.46***	0.83
40 s	2.23***	NT	1.37**
80 s	4.83***		0.79
160 s	2.46***		NT
320 s	NT		

Time-lag	Tonkean macaques									
	Gae	Jan	Lad	Mil	Olg	Rim	Sha	She	Sim	Syb
2 s	0.14	S	0.28	6.30***	0.07	0.47	0.35	0.21	0.14	0.87
5 s	0.54	1	0.37	0.36	0.70	1.80***	1.16*	0.68	S	1.10*
10 s	1.70***	2.36***	0.79	0.55	0.69	1.36***	2.01***	0.41	0.18	0.08
20 s	2.63***	2.31***	1.18*	1.99***	2.32***	2.18***	2.97***	0.70	1.30**	0.22
40 s	1.95***	3.61***	2.72***	4.00***	NT	2.72***	3.72***	1.06	1.58***	1.77***
80 s	NT	4.50***	2.92***	4.00***		3.77***	NT	NT	1.25*	2.45***
160 s		4.96***	NT	2.55***		5.38***			NT	5.15***
320 s		2.46***		NT		4.23***				NT

NT = non tested; S = 100% of success.
A statistical significant effect was observed when the maximum value was higher than the following critical values: 1.07 for $p < 0.05$*, 1.26 for $p < 0.01$**, 1.45 for $p < 0.001$***.

EXPERIMENT 2: ASSESSING MAXIMAL WAITING PERIODS

In this experiment, we considerably increased the final pay-off to assess whether macaques and capuchins could sustain longer waiting periods than those measured in the previous experiment.

Methods

Subjects were offered a reward 40-fold the size of the initial food item: 5 pieces of cookie, each sizing 4 x 4 x 0.5 cm. Each subject was run in 12 trials for each time lag: 10, 20, 40, 80 s *etc*. Considering the larger size of the reward, sessions were reduced to two trials per day, separated by a minimal 20-min interval. If a subject succeeded at least once in a session, he was tested at the next time lag. The timing of failures was recorded as in Experiment 1.

Results

Percentage of return

Compared with Experiment 1, subjects of both species increased their performances. All macaques still returned the initial item until a time lag of 40 s. The percentage of return of four individuals (Gae, Olg, Sha, She) dropped to 0% for a time lag of 80 s. Five other individuals (Jan, Mil, Rim, Sim, Syb) stopped exchanging at 160 s of delay. A last individual (Lad) continued to return the initial item until 160 s and stopped at 320 s (ESM). In capuchins, two subjects (Pis, Pop) stopped exchanging the initial item at 20 s of delay. Three subjects (Arn, Aso, Clo) stopped returning the small piece of cookie at 40 s and two others (Acc, Rav) at 80 s. A last individual (Pet) continued to exchange the initial item until 160 s and stopped for a time lag of 320 s (ESM).

Time of giving-up

Considering giving-up rates of the macaques, four individuals (Gae, She, Sim, Syb) never gave up earlier than predicted by the model (Table 3). The other six individuals gave up significantly earlier than predicted by the model; Olg and Sha at the 80-s time lag; Jan, Mil and Rim at 160-s, and Lad at 5 min 20 s (Table 3). In capuchins, all subjects (Pet, Pop, Rav) gave up significantly earlier than predicted; from a time lag of 20 s for Pop; 40 s for Rav; and 80 s for Pet (Table 3).

We calculated the extinction of exchanges for each individual by examining their waiting time per trial for the three longest time lags that they sustained (ESM). Ten subjects (macaques: Jan, Lad, Olg, Rim, Sha, She, Sim, Syb; capuchins: Pop, Rav) gradually stopped exchanging as delays were extended. The other three subjects (macaques: Gae, Mil; capuchin: Pet) displayed different patterns; they resumed exchanges after some failures in several consecutive trials. In this experiment, both macaques and capuchins sustained especially long periods when offered reward 40 times the size of the initial item. As in Experiment 1, the early giving-up time suggested that they quickly estimated whether the reward was worth waiting for.

Table 3. Results of Kolmogorov-Smirnov tests comparing the subjects' expected and observed distributions of giving-up for each time lag in Experiment 2 (12 trials). Only maximal values are reported.

Time-lag	Brown capuchins		
	Pet	Pop	Rav
2 s	S	S	S
5 s	S	S	0.17
10 s	0.26	0.60	S
20 s	0.70	1.27**	0.50
40 s	0.55	NT	1.29**
80 s	1.40**		1.47***
160 s	2.46***		NT
320 s	2.76***		
640 s	NT		

Time-lag	Tonkean macaques									
	Gae	Jan	Lad	Mil	Olg	Rim	Sha	She	Sim	Syb
2 s	NT	NT	NT	NT	NT	NT	NT	NT	NT	NT
5 s	NT	NT	NT	NT	NT	NT	NT	NT	NT	NT
10 s	S	S	S	0.26	0.27	S	S	S	S	0.20
20 s	0.11	0.14	S	S	0.26	S	S	0.42	S	S
40 s	0.35	S	0.11	0.23	0.26	0.12	1.00	0.59	0.26	0.20
80 s	1.00	0.19	0.53	0.69	1.73***	0.15	1.11*	0.52	0.80	0.13
160 s	NT	1.33**	1.02	1.27**	NT	1.15*	NT	NT	0.33	0.41
320 s		NT	1.23**	NT		NT			NT	NT
640 s			NT							

NT = non tested; S = 100% of success.

A statistical significant effect was observed when the maximal value was higher than the following critical values: 1.03 for $p < 0.05$*, 1.22 for $p < 0.01$**, 1.43 for $p < 0.001$***.

Temporal discounting

Engaging with a partner in a delayed exchange incurs the risk that the partner will not return the gift. As the delay to the outcome increases, the subjects' return expectations may decrease. Temporal discounting appears as a possible response to the risk associated with waiting for delayed rewards (Kagel *et al.* 1986). To check for the possible influence of temporal discounting on the subjects' ability to wait, we contrasted the decreasing rates of return as a function of time for each reward size in Experiments 1 and 2 using comparison tests of regression slopes (Fig. 2). In macaques, subjects neither devalued rewards 2-fold the size of the initial item more rapidly than 4-fold rewards (t = - 1.88, df = 5, p = n.s.) despite a weak trend, nor did they devalued 8-fold rewards more rapidly than 40-fold rewards (t = - 0.15, df = 8, p = n.s.). However, they devalued significantly more rapidly 4-fold rewards compared with 8-fold (t = - 2.91, df = 8, p < 0.05) and 40-fold rewards (t = -3.11, df = 6, p < 0.05). In capuchins, subjects devalued 2-fold rewards at the same speed as 4-fold (t = 0.25, df = 4, n.s.) and 8-fold rewards (t = - 0.42, df = 4, n.s.). They also devalued 4-fold rewards at the same speed as 8-fold rewards (t = - 0.42, df = 4, n.s.). Capuchins’ devaluation of 40-fold rewards was slower compared to 2-fold (t = - 5.17, df = 3, p < 0.05), 4-fold (t = - 8.21, df = 3, p < 0.01) and 8-fold rewards (t = - 5.13, df = 3, p < 0.05).

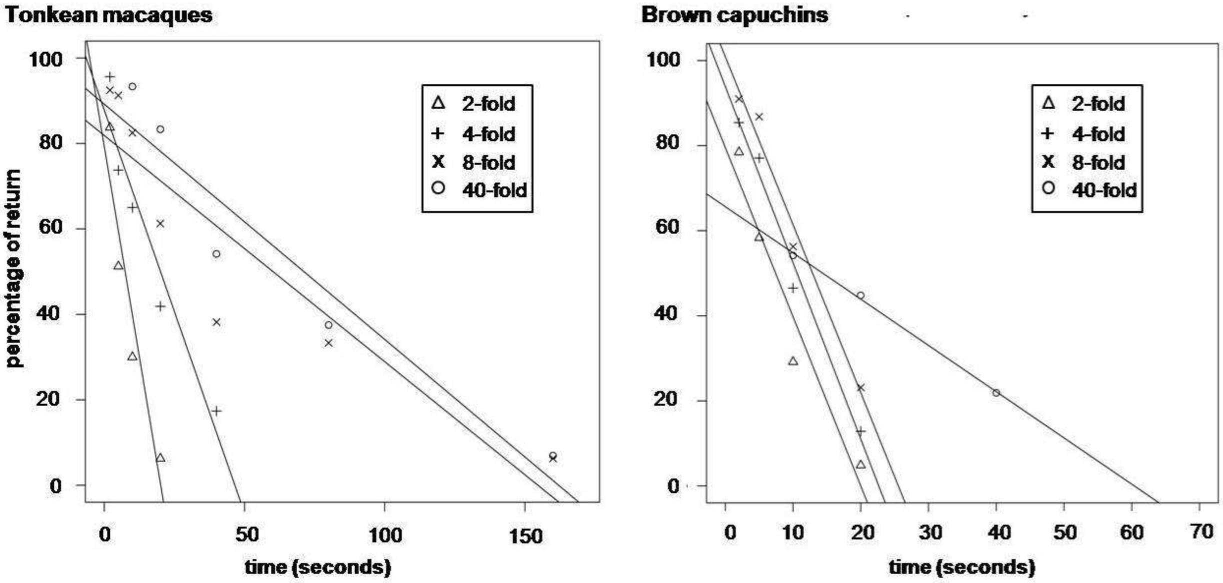


Figure 2. Linear regressions of the percentage of return with time for each reward size in Experiments 1 and 2 for each species.

EXPERIMENT 3: TESTING THE EFFECT OF ACTION INHIBITION ON WAITING

In Experiments 1 and 2, macaques and capuchins had to decide whether to exchange or not. They also had to keep the small piece of cookie intact throughout the waiting period, thus inhibiting the consumption of the initial item. To test how action refraining may have affected their performances, we relaxed the food-keeping condition and requested that subjects give back the initial food item 3 s after having received it. Only then was the waiting period applied. Once it ended, the experimenter gave the larger reward.

Methods

We applied the same procedure as in Experiment 2. Subjects were tested in two daily trials separated by a 20-min interval. Once subjects had given the initial piece of cookie back, it was placed beside the larger reward (40-fold the initial piece), in front but out of reach of the subjects. Then, the waiting period was started: 10, 20, 40, 80 s *etc*. If subjects failed to return the initial item, the trial ended. If they succeeded, they obtained the larger reward at the end of the time lag.

Results

Percentage of return

In Experiment 3, all macaques but one (She) waited until a time lag of 640 s. Three of them (Sha, Sim, Syb) stopped waiting at 21 min 20 s. Lad stopped exchanging at 42 min 40 s, whereas the last four subjects (Gae, Mil, Olg, Rim) continued to wait at this time lag (ESM). In capuchins, all subjects were able to wait for at least 40 s. Two of them (Aso, Pop) stopped exchanging at 80 s and 320 s, respectively. The other five subjects waited until 640 s; two (Pet, Rav) stopped waiting at a time lag of 21 min 20 s, and the other three (Acc, Arn, Pis) at 42 min 40 s (ESM). The comparison of subjects' performances in Experiments 2 and 3 showed that the suppression of the food-keeping condition in the latter experiment significantly increased waiting durations for both species (Fig. 3).

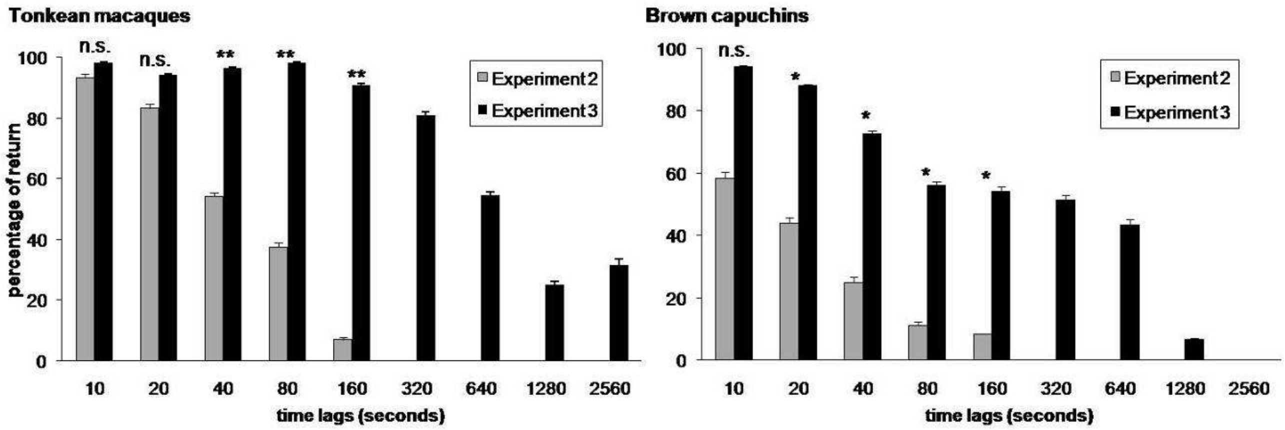


Figure 3. Percentage of return at each time lag in Experiments 2 and 3 for macaques (Wilcoxon test, $N = 10$, ** $p < 0.05$) and capuchins ($N = 7$, *$p < 0.01$).

Temporal discounting

Figure 4 presents the decreasing rates of return as a function of time in Experiments 2 and 3. In macaques, comparing the slope of the curve obtained for Experiment 3 to a null slope did not yield a statistically significant difference (t = - 1.6, n.s.), which indicates that once the constraint of consumption inhibition is removed, macaques still valued the reward regardless of the delay period. We found no effect of temporal discounting on waiting performances of macaques. By contrast, the comparison of the slope of the curve obtained for Experiment 3 with a null slope in capuchins, produced a significant difference (t = - 16.3, $p < 0.05$), which indicates that the subjects declined to exchange depending on the waiting duration despite the fact that consumption inhibition was unnecessary. To test whether capuchins differently devalued the rewards expected in Experiments 2 and 3, we compared the slopes of two linear regressions. A statistically significant difference appeared in devaluation rates between both experiments (t = 6.2, df = 2, $p < 0.05$).

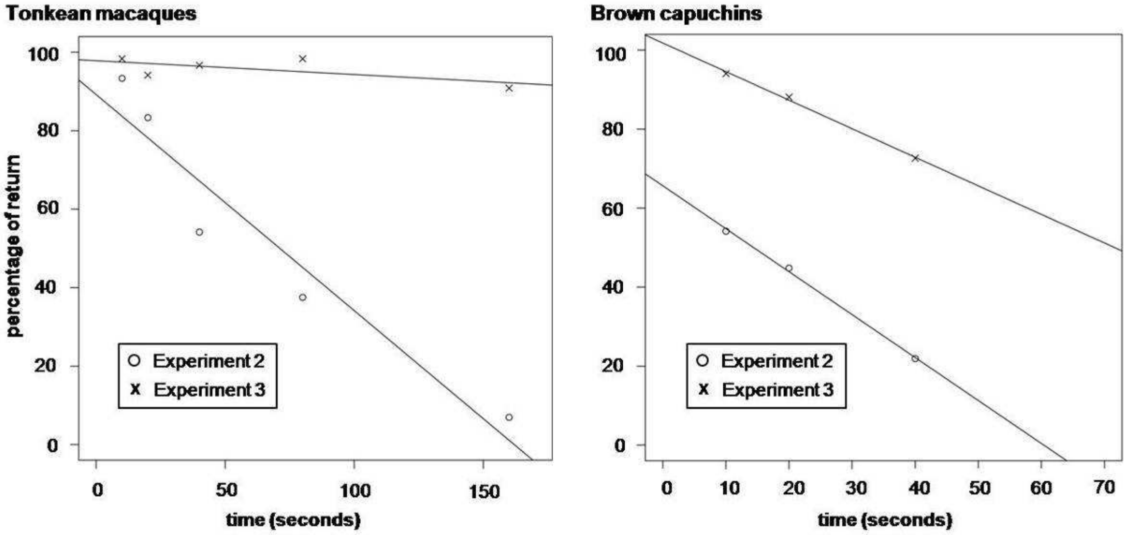


Figure 4. Linear regressions of the return percentage with time in Experiments 2 and 3 for each species.

EXPERIMENT 4: TESTING THE ABILITY TO WAIT IN AN ACCUMULATION TASK

We found different waiting periods in Tonkean macaques and brown capuchins in several conditions of the food-exchange task. To assess their performances in a different delay-maintenance test, we studied subjects in an accumulation task where food pieces were added at fractioned time intervals (Beran 2002). Brunner and Gibbon (1995) suggested that subjects could treat such sequences of food items not a whole but as a collection of independent items. If subjects consider one interval at a time they should wait for longer periods than for non-fractioned periods.

Methods

Training

The apparatus consisted of one PVC panel comprised of two tablets 1 and 2, separated by 5 cm, and small pieces of cookie sizing 1 x 2 x 0.5 cm. The first training stage consisted of a demonstration of the transfer of five pieces of cookie, one at a time, at a rate of 1 every 3 s, from tablet 1 to tablet 2 – both tablets being out of reach for subjects. Once the five pieces of cookie were on tablet 2, the experimenter moved the panel closer to subjects and allowed them to take the food items. A session was composed of six demonstrations separated by two minutes after the end of food consumption by the subject. We ran four sessions at this stage with no more than two daily sessions separated by an interval at least 20-min long. In the second training stage, we alternated six demonstration trials with six training trials; in the latter, subjects had access to tablet 2, i.e. they might take items at any time, which ended the trial. As previously, four sessions with no more than two daily sessions separated by an interval at least 20-min long were run. In the third stage, demonstrations ceased and sessions consisted of six training tests with items being transferred from one tablet to another every 3 s. The experimenter waited for 30 s after the end of subject food consumption before starting another trial. A minimum of three pieces of cookie per trial and 20 pieces of cookie per session, during two consecutive sessions was required to proceed to the next training stage. In the final stage, subjects were run as in stage 3 and using the same criterion of success, except that items were transferred every 6 s. If individuals had not reached success criteria after 20 training sessions, we stopped training them.

Three capuchin monkeys (Pet, Pis, Rav) and six Tonkean macaques (Jan, Lad, Mil, Rim, Sha, Syb) successfully passed the training criteria. In Tonkean macaques, four subjects (Gae, Olg, She, Sim) did not reach the 3 s success criterion. At such time lag, they waited for a maximum of 5, 4, 4 and 4 pieces of cookie, respectively. In brown capuchins, three subjects (Acc, Aso, Pop) did not reach the 3-s success criterion at 3 s, and one (Arn) the 6 s criterion; for 3 s, Acc waited for a maximum of 2 pieces of cookie, Arn 10, Aso 1 and Pop 1, respectively.

Testing

During the test, we placed the panel in front of the subject, with tablet 2 remaining within reach of the subject and tablet 1 being loaded with 81 pieces of cookie out of reach. Every 9 s, the experimenter transferred a piece of cookie from tablet 1 to tablet 2. Subjects were allowed to take the items on tablet 2 at any time. If they did, the trial ended. We ran daily sessions of two trials per day separated by a 20-min interval. Each subject was submitted to a total of 60 trials.

Results

On average, Tonkean macaques could wait between 38 and 72 s and brown capuchins between 33 and 42 s before seizing the rewards. The maximal waiting periods recorded were 5 min 51 s for macaques and 2 min 06 s for capuchins (Fig. 5). In macaques fractioning time periods led to performances that were comparable to those measured in Experiment 1 using similar reward amounts. In capuchins the waiting periods of tested subjects were two or four times longer than those measured in Experiment 1 for similar reward amounts.

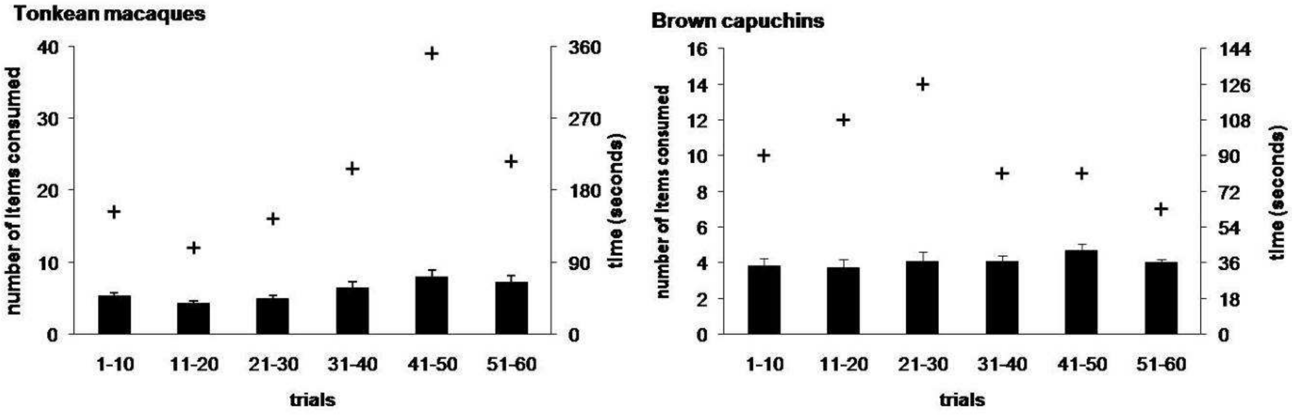


Figure 5. Mean number of food items consumed by subjects of both species by series of 10 trials in Experiment 4. Maxima are indicated by black crosses.

DISCUSSION

When exchanging with an experimenter, capuchin monkeys and Tonkean macaques sustained longer waiting periods for larger food quantities. This is consistent with the results of previous studies in long-tailed macaques, capuchin monkeys and chimpanzees (Dufour *et al.* 2007; Pelé *et al.* 2009; Ramseyer *et al.* 2006). Such a magnitude effect was not found in rats, pigeons, or in marmosets and tamarins, when tested in a delay-choice task (Green *et al.* 2004; Richards *et al.* 1997; Stevens *et al.* 2005a).

In Experiment 1 most Tonkean macaques waited for up to 20-80 s for rewards eight times the size of the initial food item, which compares well with performances of long-tailed macaques under the same conditions (Pelé *et al.* 2009). In brown capuchin monkeys, although one subject waited sometimes for 40 s, the addition of three subjects to our initial sample did not alter our conclusion that the waiting duration of most subjects did not exceed 10-20 s for the same reward size (Ramseyer *et al.* 2006). In Experiment 2, an increase in reward quantity to forty times the size of the initial food item led both capuchins and macaques to double their waiting periods to 20-40 and 40-80 s, respectively. These performances were again consistent with previous measurements brown capuchins (Ramseyer *et al.* 2006). In contrast, most long-tailed macaques were able to postpone returns for 2-5 min (Pelé *et al.* 2009).

A majority of Tonkean macaques and brown capuchins gave up earlier than predicted under a model of constant rate of giving-up in Experiments 1 and 2. It is likely that they anticipated waiting durations in relation to the size of final rewards; they reversed their choice, preferring to consume the smaller reward early in trials. An alternative explanation would only involve associative learning; longer delays would heighten the difficulty to associate the initial exchange acceptance and the final reward, resulting in an extinction of returns. In Experiment 2, however, two macaques and one capuchin succeeded in waiting for long delays after consecutive failures, which does not support the hypothesis of associative learning. Tonkean macaques and brown capuchins could thus anticipate the duration they had to wait for, and decided accordingly whether to wait or give up, as in long-tailed macaques (Pelé *et al.* 2009) and chimpanzees (Dufour *et al.* 2007).

In Experiment 3, we tested the hypothesis that action inhibition constrained the subjects' ability to postpone gratification by asking subjects to give back the initial item before waiting. As in a delayed-reward contingency task, individuals faced a single decision: to accept the exchange or not. They could not modify their choice within a given trial, but they could re-evaluate it in the next one. Results showed that both Tonkean macaques and capuchin monkeys dramatically improved their maximum waiting time compared to Experiment 2 for identical reward amounts, demonstrating that the inhibition of food consumption is a limiting factor for the subjects' ability to postpone gratification (see Pelé *et al.* 2009). Several brown capuchins accepted a time lag of 10 min 40 s and some tolerated some trials at 21 min 20 s. Most Tonkean macaques could sustain the latter durations and half of them were even able to regularly sustain a waiting period of 42 min 40 s. By contrast, most long-tailed macaques did not accept time lags longer that 21 min 20 s (Pelé *et al.* 2009).

The study of temporal discounting pointed at differences between Tonkean macaques and brown capuchins in the maintenance of their decision to wait. The former discounted small rewards faster than bigger ones, indicating that their subjective devaluation of future rewards was proportionally affected by the size of rewards. By contrast, capuchins discounted all rewards at the same speed in Experiment 1, which showed that the maintenance of the decision to wait was not affected by the size of rewards. Moreover, there was no more temporal discounting in Tonkean macaques when relaxing the need to inhibit food consumption in Experiment 3. By contrast, capuchin monkeys still devalued the reward even though they did not have to inhibit eating. They consistently behaved more immediately than macaques.

In the food-accumulation task in Experiment 4, Tonkean macaques tended to wait longer than brown capuchins, with the caveat that several individuals from both species did not reach the criterion needed to be tested. The performances reported in rhesus and long-tailed macaques were also lower than those measured in Tonkean macaques (Evans and Beran 2007a; Pelé *et al.* 2009). We assumed that fractioning the whole waiting period in a series of short intervals could minimize temporal discounting. When comparing the behaviour of subjects for similar reward quantities, it actually appeared that in Experiment 4 subjects had enough with a number of food items which was equivalent in Experiment 1 to the eightfold reward in macaques and the fourfold reward in capuchins. It was as if the subjects assessed the entire waiting duration together with the final reward rather than each time lag separately, meaning that their decision was affected by temporal discounting.

Capuchin monkeys appeared more impulsive than macaques in all respects. We know of no obvious socio-ecological variations liable to explain such differences between species. On the other hand, it is generally held that macaques are more oriented to the social domain compared with brown capuchins which are more physically oriented (Fragaszy *et al.* 2004); it could be that delaying gratification is needed in complex social interactions where elaborate skills of anticipation and social inhibition are necessary to face uncertainties (Amici *et al.* 2009; Pelé *et al.* 2009). Future research should look for possible links between the delay of gratification and the cognitive abilities respectively used in the physical and social domains.

Whereas intra-specific variation appeared weaker than interspecific variation when contrasting capuchins and macaques, we found the converse when comparing the performances of Tonkean macaques with those previously measured in long-tailed macaques. The individuals studied in each species differed by several factors – e.g., age, sex, breeding conditions – and no consistent differences emerged between groups; long-tailed macaques outperformed Tonkean macaques in Experiment 2 but the converse was true in Experiments 3 and 4, and the results from both groups were similar in Experiment 1. Further investigation should deepen our knowledge of interspecific variations in temperament and cognitive abilities among macaques. At present, however, we may conclude that although long-tailed and Tonkean macaques widely differ in their social relationships and levels of social tolerance (Thierry 2007), we did not find significant differences in their willingness to delay gratification. This is what we would expect under the hypothesis that all macaques are gifted with similar abilities to cope with complex social situations.

Acknowledgments

The authors are grateful to N. Poulin and C. Sueur for statistical advices and to A. Delabouglise, C. Dilger, P. Gayet, A. Jacquemin, C. Morin, A. Navarre, F. Vogelweith for valuable assistance in experiments. The research was supported by a grant from the *Agence Nationale de la Recherche* (ANR-08-BLAN-0042-01).

References

Abeyesinghe, S. M., Nicol, C. J., Hartnell, S. J., & Wathes, C. M. (2005). Can domestic fowl, *Gallus gallus domesticus*, show self-control? *Animal Behaviour, 70,* 1–11.

Addessi, E., Crescimbene, L., & Visalberghi, E. (2007). Do capuchin monkeys (*Cebus apella*) use tokens as symbols? *Proceedings of the Royal Society of London B: Biological Series, 274,* 2579–2585.

Addessi, E., Crescimbene, L., & Visalberghi, E. (2008). Food and token quantity discrimination in capuchin monkeys (*Cebus apella*). *Animal Cognition, 11,* 275–282.

Amici, F., Aureli, F., & Call, J. (2008). Fission-fusion dynamics, behavioral flexibility and inhibitory control in primates. *Current Biology, 18,* 1415–1419.

Amici, F., Call, J., & Aureli, F. (2009). Variation in withholding of information in three monkey species. *Proceedings of the Royal Society of London B: Biological Series, 276,* 3311–3318.

Beran, M. J. (2002). Maintenance of self-imposed delay of gratification by four chimpanzees

(*Pan troglodytes*) and an orangutan (*Pongo pygmaeus*). *Journal of General Psychology, 129,* 49–66.

Brosnan, S. F., & de Waal, F. B. M. (2005). Responses to a simple barter task in chimpanzees, *Pan troglodytes*. *Primates, 46,* 173–182.

Brosnan, S. F., & de Waal, F. B. M. (2004). A concept of value during experimental exchange in brown capuchin monkeys, *Cebus apella*. *Folia Primatologica, 75,* 317–330.

Brunner, D., & Gibbon, J. (1995). Value of food aggregates: parallel versus serial discounting. *Animal Behaviour, 50,* 1627–1634.

Chalmeau, R., & Peignot, P. (1998). Exchange of objects between human and captive western lowland gorillas. *Primates, 39,* 389–398.

Drapier, M., Chauvin, C., Dufour, V., Uhlrich, P., & Thierry, B. (2005). Food-exchange with humans in brown capuchin monkeys. *Primates, 46,* 241–248.

Dufour, V., Pelé, M., Sterck, E. H. M., & Thierry, B. (2007). Chimpanzee (*Pan troglodytes*) anticipation of food return: coping with waiting time in an exchange task. *Journal of Comparative Psychology, 121,* 145–155.

Evans, T. A., & Beran, M. J. (2007a). Delay of gratification and delay maintenance by rhesus macaques (*Macaca mulatta*). *Journal of General Psychology, 134,* 199–216.

Evans, T. A., & Beran, M. J. (2007b). Chimpanzees use self-distraction to cope with impulsivity. *Biology Letters, 3,* 599–602.

Fragaszy, D. M., Visalberghi, E., & Fedigan, L. M. (2004). *The complete capuchin: the biology of the genus Cebus.* Cambridge: Cambridge University Press.

Green, L., Myerson, J., Holt, D. D., Slevin, J. R., & Estle, S. J. (2004). Discounting of delayed food rewards in pigeons and rats: Is there a magnitude effect? *Journal of the Experimental Analysis of Behavior, 81,* 39–50.

Green, L., & Myerson, J. (1996). Exponential versus hyperbolic discounting of delayed outcomes: risk and waiting time. *American Zoologist, 36,* 496–505.

Grosch, J., & Neuringer, A. (1981). Self-control in pigeons under the Mischel paradigm. *Journal of Experimental Analysis of Behavior, 35,* 3–21.

Haccou, P., & Meelis, E. (1992). *Statistical analysis of behavioural data.* Oxford: Oxford University Press.

Hyatt, C. W., Hopkins, W. D. (1998). Interspecies object exchange: bartering in apes? *Behavioural Processes, 42,* 177–187.

Kacelnik, A. (2003). The evolution of patience. In G. Loewenstein, D. Read, R. Baumeister (Eds.), Time and decision: economic and psychological perspectives on intertemporal choice (pp. 115–138). New York : Russell Sage Foundation.

Kagel, J. H., Green, L., & Caraco, T. (1986). When foragers discount the future: constraint or adaptation? *Animal Behaviour, 34,* 271–283.

Killeen, P. R., Smith, J. P., & Hanson, S. J. (1981). Central place foraging in *Rattus norvegicus*. *Animal Behaviour, 29,* 64–70.

Lefebvre, L. (1982). Food exchange strategies in an infant chimpanzee. *Journal of Human Evolution, 11,* 195–204.

Mazur, J. E. (1987). An adjusting procedure for studying delayed reinforcement: the effects of delay and intervening events on reinforcement value. In M. L. Commons, J. E. Mazur, J. A. Nevin, H. Rachlin (Eds.), *Quantitative analyses of behavior* vol. 5. (pp. 55–73). Hillsdale: Erlbaum.

Mischel, W. (1974). Processes in delay of gratification. In L. Berkowitz (Ed.), *Advances in experimental social psychology* (pp. 249–292). New York: Academic Press.

Pelé, M., Dufour, V., Micheletta, J., & Thierry, B. (2009). Long-tailed macaques display unexpected waiting abilities in exchange tasks. *Animal Cognition, in press*.

Ramseyer, A., Pelé, M., Dufour, V., Chauvin, C., & Thierry, B. (2006). Accepting loss: the temporal limits of reciprocity in brown capuchin monkeys. *Proceedings of the Royal Society of London B: Biological Series, 273,* 179–184.

Richards, J. B., Mitchell, S. H., de Wit, H., Seiden, L. S. (1997). Determination of discount functions in rats with an adjusting-amount procedure. *Journal of Experimental Analysis of Behavior, 67,* 353–366.

Rosati, A. G., Stevens, J. R., Hare, B., & Hauser, M. D. (2007). The evolutionary origins of human patience: temporal preferences in chimpanzees, bonobos, and human adults. *Current Biology, 17,* 1663–1668.

Siegel, S., & Castellan, N. J. (1988). *Nonparametric statistics for the behavioral sciences.* Singapore: McGraw-Hill.

Stevens, J. R., Hallinan, E. V., & Hauser, M. D. (2005a). The ecology and evolution of patience in two New World monkeys. *Biology Letters, 1,* 223–226.

Stevens, J. R., Cushman, F. A., & Hauser, M. D. (2005b). Evolving the psychological mechanisms for cooperation. *Annual Review of* Ecology *and Systematics, 36,* 499–518.

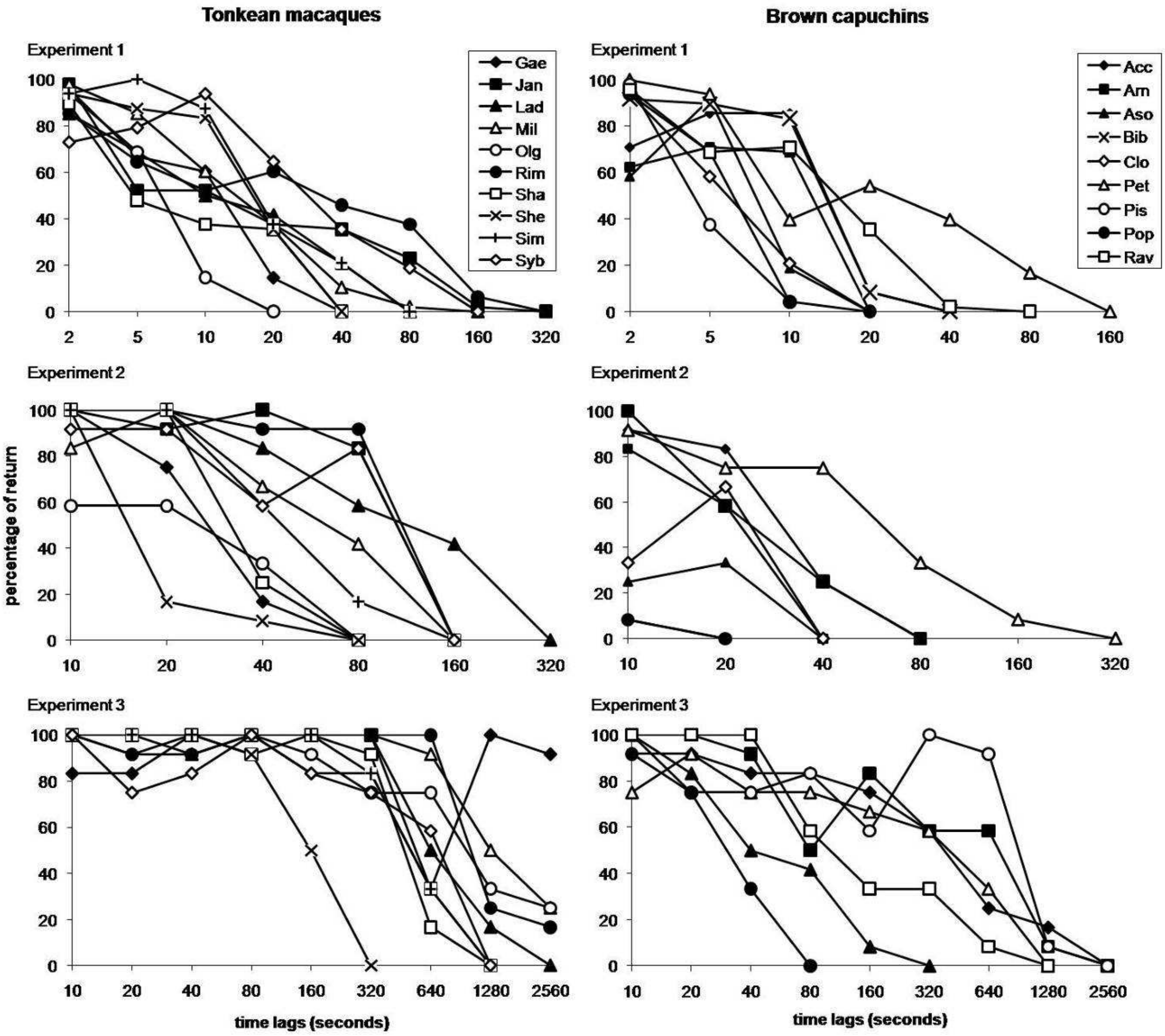
Thierry, B. (2007). Unity in diversity: lessons from macaque societies. *Evolutionary Anthropology, 16,* 224–238.

Westergaard, G. C., Liv, C., Rocca, A. M., Cleveland, A., Suomi, S. J. (2004). Tufted capuchins (*Cebus apella*) attribute value to foods and tools during voluntary exchanges with humans. *Animal Cognition, 7,* 19–24.

Electronic supplementary material

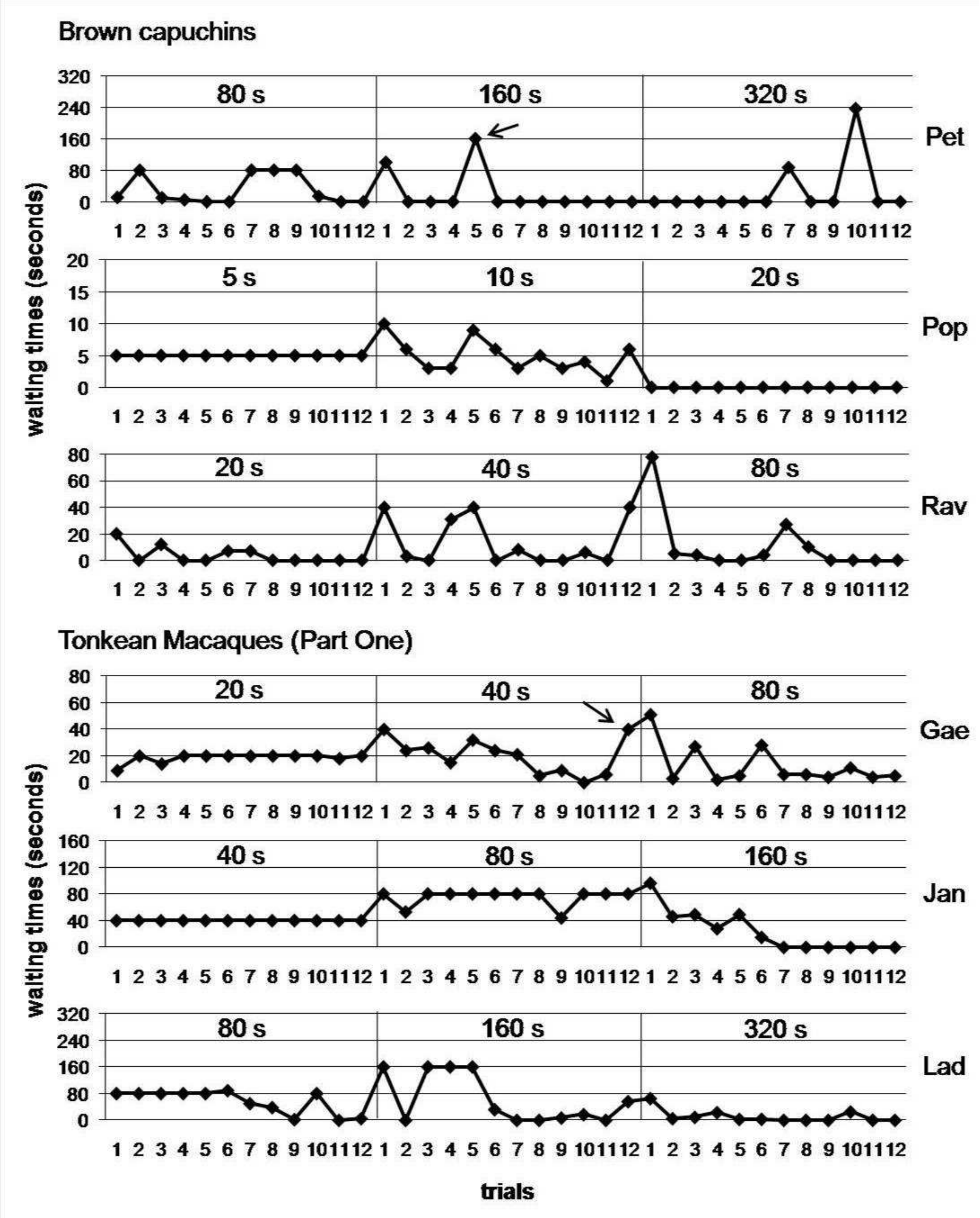
Individual percentages of return as a function of time lag in Experiments 1, 2, 3.

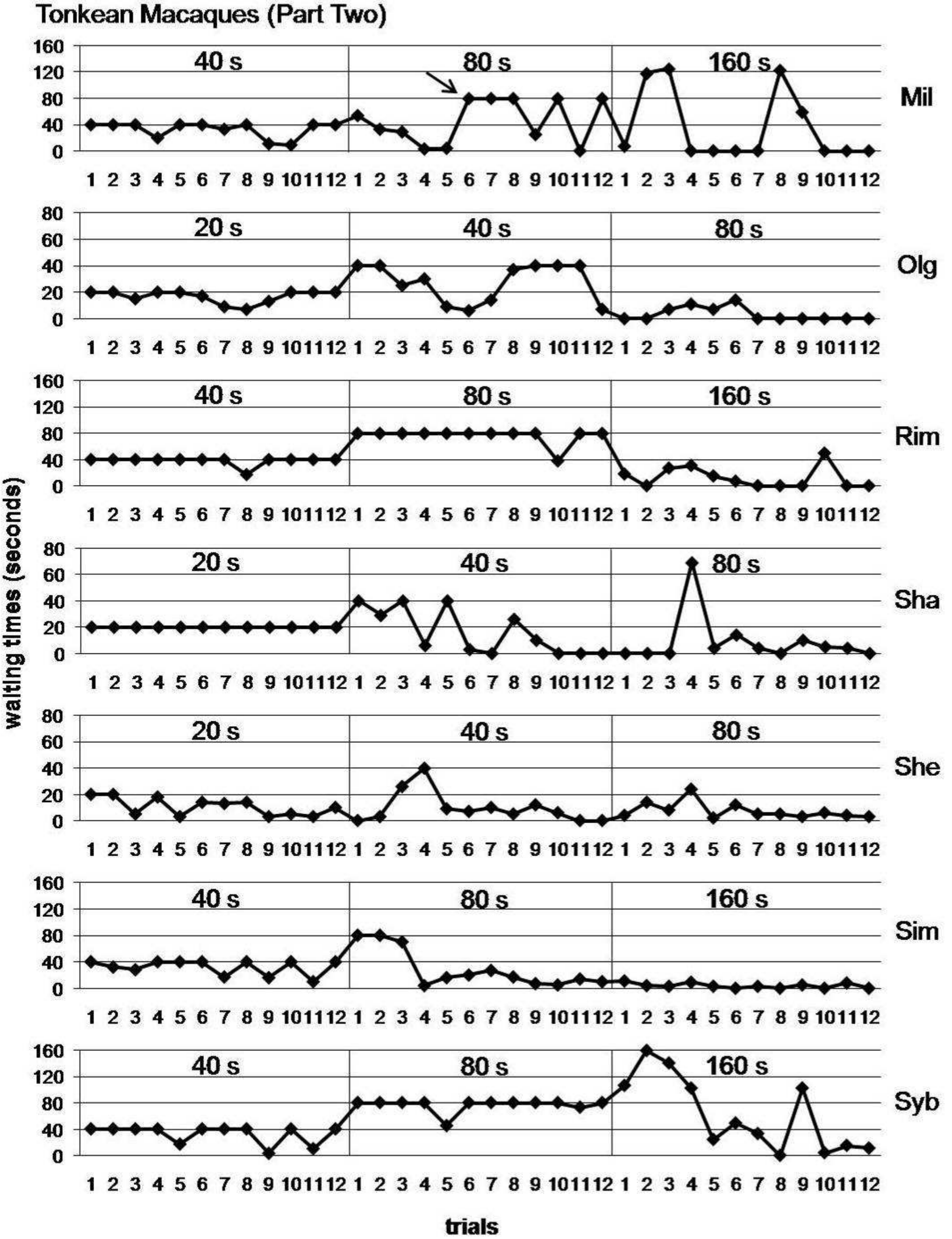
Experiment 1: all sizes of cookies combined
Experiment 2: rewards 40 times the size of the initial food item
Experiment 3: return before waiting; rewards 40 times the size of the initial food item



Extinction of exchanges

Waiting duration per trial for the three longest time lags sustained by subjects. Ten subjects (macaques: Jan, Lad, Olg, Rim, Sha, She, Sim, Syb; capuchins: Pop, Rav) gradually stopped to exchange when delays were extended. Three subjects (macaques: Mil, Gae; capuchin: Pet) succeeded in waiting for long durations despite previous consecutive failures (see arrows).




Tonkean Macaques (Part Two)
waiting times (seconds)
trials
Mil
40 s
80 s
160 s
Olg
20 s
40 s
80 s
Rim
40 s
80 s
160 s
Sha
20 s
40 s
80 s
She
20 s
40 s
80 s
Sim
40 s
80 s
160 s
Syb
40 s
80 s
160 s
0
40
80
120
160
20
60
1 2 3 4 5 6 7 8 9 10 11 12 1 2 3 4 5 6 7 8 9 10 11 12 1 2 3 4 5 6 7 8 9 10 11 12

CHAPITRE IV

LA PRISE DE RISQUE DANS L'ECHANGE

Article 4

La prise de risque chez trois espèces de primates

Manuscrit soumis

RESUME DE L’ARTICLE 4

Introduction

L’étude a pour but de déterminer si des primates non humains sont capables de s’engager dans un échange où un risque de perdre existe. Dans quelle mesure les probabilités de gain et de perte influencent-elles la prise de décision des primates à s’engager dans l’échange ? Les stratégies face au risque sont-elles identiques chez tous les individus ?

Méthodes

J’ai testé quatre orangs-outangs, cinq macaques à longue queue et huit capucins bruns. L’expérimentateur donnait un biscuit de moyenne dimension au sujet et lui présentait six récompenses possibles de différentes dimensions. Celles-ci pouvaient représenter un gain, une perte ou une équivalence par rapport au premier biscuit donné. Si le sujet acceptait de rendre le biscuit en sa possession, il recevait de manière aléatoire une des six récompenses. Plusieurs combinaisons de récompenses ont été proposées aux individus au cours de la phase de test. J'ai testé différents modèles de décision de manière à identifier les stratégie suivies par les individus face au risque : (1) échanger aussi longtemps que les chances de gain sont supérieures aux chances de perte, (2) échanger aussi longtemps qu'il y a des chances de gain et cela quelles que soient les pertes potentielles, (3) cesser d’échanger dès qu'une perte survient et cela quels que soient les gains potentiels.

Résultats

Les orangs-outangs et les singes capucins suivent majoritairement une stratégie rationnelle qui vise à n’échanger que lorsque la probabilité de gain est supérieure à la probabilité de perdre. Les macaques à longue queue quant à eux suivent majoritairement une stratégie riscophile où l'individu échange même si la probabilité de perdre est supérieure à la probabilité de gain. L’analyse des résultats montre que les individus des trois espèces prennent d’abord en compte la probabilité de perdre avant d’échanger. Chez les macaques à longue queue et les capucins, la décision est également influencée par la récompense obtenue lors de l’essai précédent.

Conclusion

Les orangs-outangs, les macaques à longue queue et les capucins sont capables de s’engager avec un expérimentateur dans un échange de nourriture qui comporte un risque de perte. La probabilité de perdre influence d’abord la prise de décision des individus à s’engager dans l’échange. Les primates non humains sont capables de s’engager dans une situation risquée et d’accepter les éventuelles pertes inhérentes à l’échange. Ces résultats contrastent avec ceux de précédentes études qui avaient conclu à une faible tolérance au risque chez les animaux.

Non-human primates take their chance in a food-gambling game

M. Pelé[1], B. Thierry[1], J. Call[2] & V. Dufour[3]

1. Département Ecologie, Physiologie & Ethologie, IPHC, Centre National pour la Recherche Scientifique, Université de Strasbourg, France

2. Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany

3. School of Psychology, University of St Andrews, St Andrews, United Kingdom

Abstract

Animals commonly deal with predictable and unpredictable events in their everyday life. We are aware that risk-sensitivity affects their strategies, but our knowledge about the cognitive processes involved in decision-making remains limited. To find out whether individuals calculate the probabilities of different outcomes, we involved capuchin monkeys (*Cebus apella*), long-tailed macaques (*Macaca fascicularis*) and orang-utans (*Pongo pygmaeus*) in a food-gambling game. We gave to subjects the opportunity to gamble a piece of cookie with a human experimenter, for pieces of larger, equal or smaller sizes. Results highlighted an unexpected capacity of most individuals, in all three species, to engage in gambling. All appeared to be risk prone rather than risk averse, which contrasts with previous findings. While actual losses did not overly affect risk-taking behaviours, most subjects did use probabilistic outcomes, and notably the loss probability to reach for a decision. We conclude that cognitive biases shape the risk-proneness of non-human primates at the time of gambling.

Keywords risk-sensitivity . gambling . exchange . cognition . monkey . great ape

INTRODUCTION

Optimal foraging theory states that organisms should find, capture and consume food containing the most calories in the least possible amount of time (MacArthur & Pianka 1966; Emlen 1966). However, animals deal with some degree of uncertainty when taking decisions. Travelling towards distant resources is potentially associated with predation or depletion, and pondering the probability for risky outcomes is a prominent feature of social life. In the context of cooperation, in particular, animals expect the help of conspecifics when taking a decision, but this help may not arise. On the other hand, in many primates an individual attacking a weaker mate exposes itself to the risk of retaliation by a stronger ally of its victim. Hence, it is to the individuals' interest to consider both the possible advantages and drawbacks of their actions.

The response of animals when facing a choice between predictable and unpredictable outcomes has been mostly investigated in the foraging context (Kacelnik & Bateson 1996). Risk-sensitive foraging theory predicts that individuals should prefer options maximizing their fitness, and that the energy budget consequently drives foraging preferences (Caraco 1980, 1981; Real 1980). Two main variables are thought to affect animals' decisions: the quantity of food to be obtained and the time needed to access it. To test the predictive value of the models, subjects are typically offered a choice between two options: one option where food quantity or delay is held constant from one trial to another and another option where the same variable is manipulated to induce some variance from one trial to the next. However, in both variable and constant options, the overall amount of food or delay is equivalent. Some studies support the model in species where individuals shift strategies depending on their energetic budget (Kacelnik & Bateson 1996). In species that cannot shift preferences, subjects are generally risk averse and occasionally risk prone, a response considered as the best "by-default" strategy for survival (McNamara 1996). Interestingly, a different pattern of response is observed when variability is induced by manipulating the delay in the variable option. In such cases, animals generally exhibit risk-proneness whatever their energetic budget (Kacelnik & Bateson 1996). Choosing the variable option sometimes leads to obtaining the reward faster than in the constant option; temporal discounting of food value – whereby the subjective value of benefits reduces with time – may account for subjects' preference (Green & Myerson 1996); a cognitive ability such as time perception can affect choices in addition to risk sensitivity.

Among the studies that have explored risk-sensitive behaviours in non-humans, few have addressed the cognitive processes involved in decision-making. In the studies cited above, the reward to be obtained was not predictable at a given trial in the variable option, but because both options were equivalent, subjects could learn the general pattern of reward delivery. Starlings (*Sturnus vulgaris*) learned to anticipate the timing of food delivery despite its variable mode (Bateson & Kacelnik 1997). Macaques and apes appeared to predict general outcomes instead of choosing on a trial-by-trial basis (Hayden & Platt 2007; Heilbronner *et al*. 2008). However, in both studies, decision-making may have not been driven by risk-sensitivity since the amount to be gained was known, therefore certain. Introducing variability is not always enough to experimentally assess risk-sensitivity in certain species. As stated by

Cartar and Smallwood (1996), most models on risk-sensitivity imply some knowledge of the probabilistic consequences of a given decision. In a study where macaques played against a computer in a simplified version of a rock paper scissor game, subjects were found to mostly behave according to the outcomes of their previous choices (Lee *et al.* 2005). When the computer's response fitted the subjects' choice, however, subjects took into account the choices made by the computer in addition to their own (Lee *et al*. 2005). This result suggests that rhesus macaques made decision based on a learning strategy rather than on a probabilistic one. Perhaps subjects could not evaluate hypothetical outcomes, or decision-making was biased by other cognitive constraints. To assess the propensity of non-humans to engage in risky situations and the cognitive processes underlying decision-making, we have to study their behaviour under probabilistic payoff with no absolute certainty about the outcome. This will allow determining the extent to which individuals anticipate and calculate the outcomes of their choices.

In this study, we hypothesize that the potential for loss affects primate subjects in a exchange of goods with a human partner. The intentional transfer of food is rarely reported among adults in non-human primates (de Waal 1997; Dufour *et al.* 2009; Pelé *et al.* 2009). Species like brown capuchin monkeys (*Cebus apella*), macaques (*Macaca* sp.) and chimpanzees (*Pan troglodytes*), however, possess some cognitive pre-requisites necessary to engage in calculated transfers of goods. In particular, they are capable of delaying gratification (Amici *et al.* 2008; Dufour *et al.* 2007; Rosati *et al.* 2007; Pelé *et al.* in press), estimating quantity and quality (Ramseyer *et al.* 2006; Hanus & Call 2007; Hauser *et al.* 2000), individual recognition and remembering past interactions (Dasser 1987; Menzel 1991).

We tested brown capuchin monkeys, long-tailed macaques (*Macaca fascicularis*) and orang-utans (*Pongo pygmaeus*) in an exchange task where each decision to trade was a gamble. We gave the individuals an opportunity to gamble a piece of cookie with a human experimenter for pieces of larger, equal or smaller sizes. Subjects could predict the odds of gaining by seeing the content of several cups, but they did not know with certainty which cup they would receive, thus they could lose by obtaining less than the item they bet.

METHODS

Subjects

We tested 8 brown capuchin monkeys and 5 long-tailed macaques maintained at the Primatology Centre of the University of Strasbourg, France, and four orang-utans maintained at the Wolfgang Köhler Research Primate Centre, Leipzig Zoo, Germany. Table 1 presents the age and sex of subjects. Capuchin monkeys and orang-utans were socially housed in enclosures with access to indoor and outdoor areas. Long-tailed macaques were housed in individual cages allowing visual and physical contacts with others. Water was available *ad libitum* and subjects were not food deprived at any time. Prior to the study, all individuals have been involved in exchange tasks: involving food items for monkeys (Drapier *et al*. 2005;

Ramseyer *et al*. 2006; Pelé *et al*. in press) and involving tokens for apes (Pelé *et al*. 2009; Dufour *et al*. 2009). Nonetheless, all individuals were re-trained to exchange different sized food items with a human experimenter for this study (see SEM for details).

Table 1. Age and sex of subjects.

Subjects	Species	Age (years)	Sex
Acc	brown capuchin	10	male
Ali	brown capuchin	8	female
Arn	brown capuchin	8	male
Pao	brown capuchin	6	female
Pet	brown capuchin	6	female
Pis	brown capuchin	5	male
Pop	brown capuchin	6	male
Rav	brown capuchin	5	male
Cas	long-tailed macaque	12	male
Don	long-tailed macaque	16	male
Jac	long-tailed macaque	16	male
Joe	long-tailed macaque	11	male
Ram	long-tailed macaque	16	male
Dok	orang-utan	19	female
Kil	orang-utan	8	female
Pad	orang-utan	11	female
Pin	orang-utan	20	female

Experimental procedure

During a trial, the experimenter typically stood in front of the subject's compartment presenting in one hand an initial piece of cookie measuring 2 x 2 x 0.5 cm, in the other a tray of six aligned plastic cups containing pieces of cookie of various dimensions: 1 x 1 x 0.5 cm, 2 x 2 x 0.5 cm, and 4 x 4 x 0.5 cm (figure 1). The experimenter gave the initial piece of cookie to the subject while still presenting the tray. After 3 s, the experimenter held out her empty hand offering the subject the chance to give the initial item back. If the subject returned it, s/he received the content of one cup chosen randomly. If the subject chose to keep the initial item, the experimenter ended the trial, allowing the subject to consume the initial item. The experimenter then waited 30 s after the end of food consumption before beginning another trial. The probabilities of losing or gaining were manipulated via different combinations of rewards presented in the cups offering the subjects a means to assess the probabilities of losing or gaining compared to the initial item already in hand. The 18 combinations tested for each species are shown in Table 2. The study was conducted by offering a step-by-step decrease in the chances of winning from one combination to another. At the end, however, subjects were tested with two control combinations (17 and 18) where the chances of winning increased again. For each combination, four series of 12 trials each were administered to capuchin monkeys and macaques. Due to experimental availability, only two series of 12 trials per combination were administered to the orang-utans. Individuals were tested at the maximal rate of two series per day, with a minimum of two hours between series.

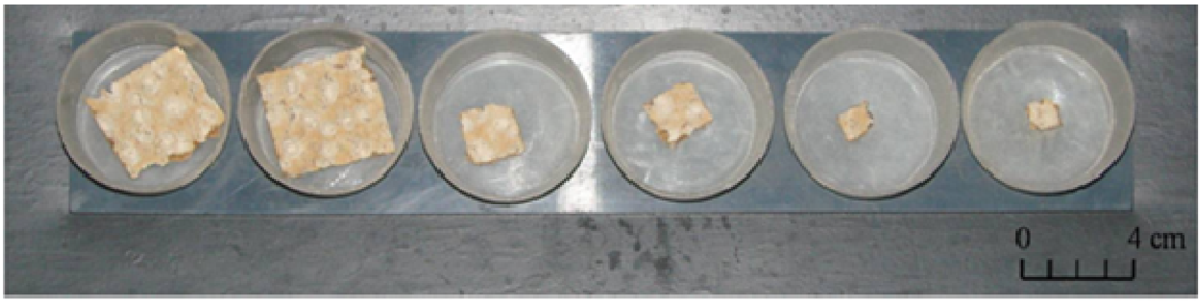


Figure 1. A tray of six plastic cups; two cups containing one piece of cookie of 4 x 4 x 0.5 cm (left position), two cups containing one piece of cookie of 2 x 2 x 0.5 cm (middle position) and two cups containing one piece of cookie of 1 x 1 x 0.5 cm (right position) corresponding to the combination of rewards # 7.

Table 2. Number (#) and content of cups for each combination of rewards.

Combinations of rewards			
#	Content of cups	#	Content of cups
1	1⬛ 2⬛ 3⬛ 4⬛ 5■ 6■	10	1⬛ 2■ 3■ 4■ 5■ 6■
2	1⬛ 2⬛ 3⬛ 4⬛ 5▪ 6▪	11	1⬛ 2■ 3■ 4■ 5■ 6▪
3	1⬛ 2⬛ 3⬛ 4■ 5■ 6■	12	1⬛ 2■ 3■ 4■ 5▪ 6▪
4	1⬛ 2⬛ 3⬛ 4■ 5▪ 6▪	13	1⬛ 2■ 3■ 4▪ 5▪ 6▪
5	1⬛ 2⬛ 3■ 4■ 5■ 6■	14	1⬛ 2■ 3▪ 4▪ 5▪ 6▪
6	1⬛ 2⬛ 3■ 4■ 5■ 6▪	15	1⬛ 2▪ 3▪ 4▪ 5▪ 6▪
7	1⬛ 2⬛ 3■ 4■ 5▪ 6▪	16	1▪ 2▪ 3▪ 4▪ 5▪ 6▪
8	1⬛ 2⬛ 3■ 4▪ 5▪ 6▪	17	1⬛ 2⬛ 3⬛ 4■ 5▪ 6▪
9	1⬛ 2⬛ 3▪ 4▪ 5▪ 6▪	18	1⬛ 2⬛ 3⬛ 4⬛ 5⬛ 6⬛

Small black squares (▪) represent pieces of cookie of dimension 1 x 1 x 0.5 cm, medium black squares (■) represent pieces of cookie of 2 x 2 x 0.5 cm and large black squares (⬛) represent pieces of cookie of 4 x 4 x 0.5 cm.

Statistical Analysis

Results were analyzed through three steps. First, we reported the percentage of return (i.e. the percentage of initial items returned) of each species depending on the reward combinations proposed throughout the study and used the non-parametric Kruskal-Wallis test for analyzing differences between individuals and species, followed by a Dunn's post-hoc test for each mean comparison. Then, we carried out an analysis to determine which variables could influence decision-making in subjects. During each trial, behaviours were coded as: 1 when the subject accepted to bet; 0 when he refused. These logistic data were the dependent variable. We used as independent variables the expected probability of gaining P_G and the expected probability of losing P_L, depending on the combination presented to the subjects. We considered previous outcomes as further independent variables. We distinguished the quantitative outcome O_P received during the immediately preceding trial from the cumulated quantitative outcomes O_{CUM} previously received during the session – O_P being excluded. For instance, when regarding the 5th trial of a session, O_P represented the quantitative outcome received at the 4th trial, and O_{CUM} the sum of quantitative outcomes received from the 1rst to the 3rd trials of the session. To assess the extent to which these variables affected the risk tolerance of individuals, we used a generalized linear model (GLM) in each species. Finally, we ran curve estimation tests to compare individual exchange profiles to three models corresponding to rational, risk-averse and risk-prone strategies.

Data were processed using SPSS 16.0 (SPSS Inc., Chicago, IL, U.S.A) and R (The R Foundation for Statistical Computing, Vienna, Austria). The significance level was set at 0.05. Average values are given as means and standard error of the mean.

RESULTS

Percentage of return over reward combinations

For each species, the mean percentage of return progressively decreased throughout the study from the combination 1 to the combination 16 (figure 2). There were significant differences across species in the percentage of return (Kruskal-Wallis test: $\chi^2 = 13.48$, df = 2, $p < 0.01$). Long-tailed macaques returned significantly more food than capuchin monkeys (Dunn's post-hoc, $p < 0.05$) and orang-utans (Dunn's post-hoc, $p < 0.05$). No significant difference was found between percentages of return of capuchin monkeys and orang-utans (Dunn's post-hoc, $p > 0.05$). Within each group, there were significant differences across individuals in the percentage of return (Kruskal-Wallis test; capuchin monkeys: $\chi^2 = 31.12$, df = 7, $p < 0.001$, long-tailed macaques: $\chi^2 = 13.38$, df = 4, $p < 0.01$, orang-utans: $\chi^2 = 11.13$, df = 3, $p < 0.05$).

When considering combination 16, each species presented a small percentage of return despite its null probability to gain (2.25 % for capuchin monkeys, 16.4 % for long-tailed macaques, 1.0 % for orang-utans). Subjects were tested at the end of sessions with the control combination 17 where the probability of gain was high; the percentage of exchange increased again of the three species (capuchin monkeys: 34.1%; long-tailed macaques: 76.2%; orang-utans: 50.8%). Four capuchins (Acc, Ali, Pao, Pet), two orang-utans (Kil, Pin) and one long-tailed macaque (Joe) did not resume exchanging at combination 17. These seven individuals were then tested with the second control combination, combination 18, where a null probability of losing was proposed; three individuals (Ali, Pet, Joe) resumed exchanging.

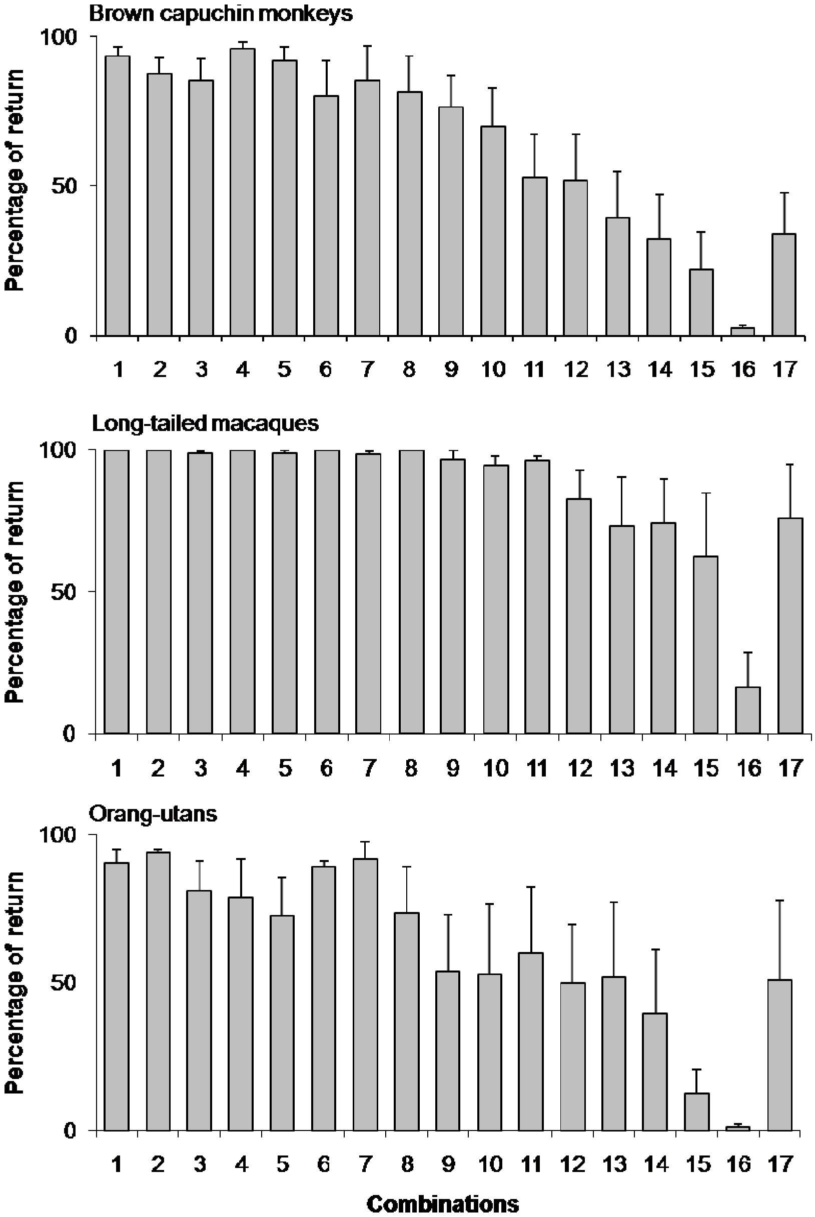


Figure 2. Mean percentage of initial item exchanged (% of return) for each combination of rewards proposed to subjects for each species.

Variables underlying risk tolerance

To investigate the mechanisms underlying decision-making, we applied a generalized linear model (GLM) testing the effect of the expected variables: P_G and P_L, and the variables resulting from previous outcomes: O_P and O_{CUM} (see Methods). In capuchin monkeys, the probability of losing P_L mostly influenced subjects' exchange behaviour ($z = -16.69$, $p < 0.001$), followed by the probability of gaining P_G ($z = 8.64$, $p < 0.001$), O_{CUM} ($z = -4.94$, $p < 0.001$) and O_P ($z = -2.93$, $p < 0.01$). In long-tailed macaques, the probability of losing P_L also mostly influenced exchange ($z = -13.53$, $p < 0.001$), followed by O_P ($z = -5.04$, $p < 0.001$), O_{CUM} ($z = -4.79$, $p < 0.001$) and the probability of gaining P_G ($z = 4.6$, $p < 0.01$). In orang-utans, exchange was influenced by the probability of losing P_L ($z = -8.17$, $p < 0.01$), the probability of gaining P_G ($z = 2.83$, $p < 0.01$) and O_{CUM} ($z = 2.42$, $p < 0.05$); the quantitative outcome received just before O_P did not influence significantly their decisions.

Individual profiles

Figure 3 presents the percentages of return of all individuals and their cumulative quantitative outcomes for each combination of rewards. By the end of the study, one capuchin (Acc) and one macaque (Jac) had a negative outcome (- 7 and - 23 units of cookie of 1 x 1 x 0.5 cm each, respectively).

We compared the individual profiles of exchange to three models corresponding to theoretical strategies: (1) rational strategy: the individual exchanges only when the probability of gaining P_G is higher than the probability of losing P_L; (2) risk-prone strategy: the individual exchanges as long as a probability of gaining exists; (3) risk-averse strategy: the individual stops exchanging each time there is a probability of losing (Table 3). Five capuchin monkeys (Arn, Ali, Pao, Pop, Rav) and two orang-utans (Dok, Kil) significantly followed the rational strategy. One capuchin monkeys (Pis), three long-tailed macaques (Cas, Jac, Ram) and one orang-utan (Pad) significantly followed the risk-prone strategy. Two capuchin monkeys (Acc, Pet), two long-tailed macaques (Don, Joe) and one orang-utan (Pin) significantly followed both rational and risk-prone strategies. None of the individual profiles significantly fitted with the risk-averse strategy.

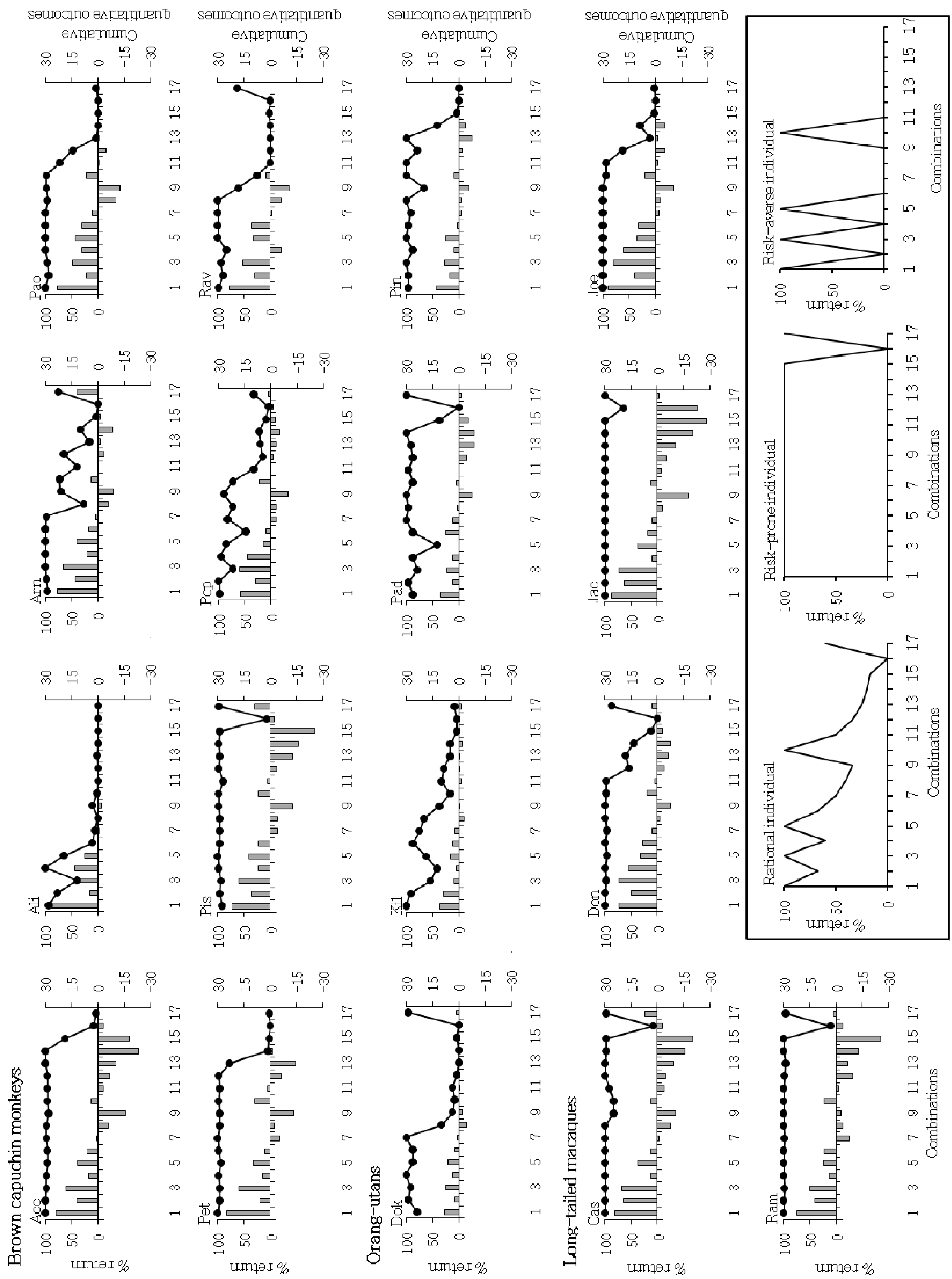


Figure 3. Individual profiles towards risk: For each combination of rewards, black lines represent the percentage of initial item exchanged (% of return) and grey bars the cumulative quantitative outcomes of the individual. Models: Percentage of return at each combination of rewards following risk-prone, risk averse or rational strategies are indicated in a black box.

Table 3. Comparison between individual profiles and theoretical models: rational, risk-prone and risk-averse strategies using curve estimation test.* $p < .05$, ** $p < .01$, *** $p < .001$.

	Rational profile			Risk-prone profile			Risk-averse profile		
Subjects	R^2	$F_{1,14}$	p	R^2	$F_{1,14}$	p	R^2	$F_{1,14}$	p
Capuchins									
Acc	0.27	5.18	*	0.85	81.51	***	0.04	0.55	ns
Arn	0.62	22.95	***	0.20	3.51	ns	0.20	3.52	ns
Ali	0.34	7.21	*	0.03	0.48	ns	0.16	2.58	ns
Pao	0.59	19.87	***	0.18	3.17	ns	0.17	2.81	ns
Pet	0.44	11.07	**	0.30	5.96	*	0.09	1.35	ns
Pis	0.18	3.08	ns	0.99	1040.15	***	0.02	0.32	ns
Pop	0.49	13.61	**	0.17	2.83	ns	0.17	2.93	ns
Rav	0.40	9.23	**	0.09	1.45	ns	0.11	1.73	ns
Macaques									
Cas	0.18	2.99	ns	0.93	199.91	***	0.01	0.20	ns
Don	0.54	16.12	***	0.38	8.74	**	0.11	1.79	ns
Jac	0.19	3.27	ns	1.00	3E+308	***	0.02	0.32	ns
Joe	0.55	16.90	***	0.25	4.62	*	0.13	2.07	ns
Ram	0.20	3.46	ns	0.99	2674.29	***	0.02	0.34	ns
Orang-utans									
Dok	0.41	9.79	**	0.07	1.12	ns	0.09	1.36	ns
Kil	0.35	7.38	*	0.12	1.98	ns	0.05	0.80	ns
Pad	0.05	0.75	ns	0.56	17.68	***	0.01	0.21	ns
Pin	0.49	13.64	**	0.38	8.68	*	0.13	2.10	ns

DISCUSSION

Brown capuchin monkeys, long-tailed macaques and orang-utans were capable of betting with food items in a gambling game. Throughout the study, gambling remained frequent despite an increasing probability of losing from one combination to the next. Some individuals kept on betting despite an accumulation of negative outcomes. By the end of the study, two individuals had given back more cookies than they actually received. Here, continuing to bet cannot be explained by reward contingency since in the latter combinations, subjects all lost more than they gained. These results highlight an unexpected capacity of most subjects, in all three species, to engage in risky situations and to tolerate acute loss when exchanging food items. Those results draw a rather different picture from what would have been expected from current knowledge (Kacelnik & Bateson 1996; McNamara 1996; Real & Caraco 1986) since in foraging choice tasks, animals are typically described as risk-averse, based on the observation that they prefer a constant delivery of food amount over a variable one (Kacelnik & Bateson 1996). Whereas actual losses did not overly affect risk-taking behaviour, the probability of losing did, in the three species. It does make sense for an individual to keep on betting with favourable chances despite earlier unlucky results. But the reverse is also true; continuing to bet when chances of losing are high is not the most rational response.

Another major result was the contrasts observed in the responses of subjects in the gambling game. It is worth noting that large individual differences also stand as a robust finding from economic experiments in humans; e.g. ultimatum and dictator games (Scheres & Sanfey 2006). Individual contrasts may be underpinned by two behavioural traits, risk proneness, with no or little consideration for the potential benefits at stake, and rational evaluation of gain probability. With regard to risk proneness, some individuals might not have recognized the probability to gain. Firstly, they gambled for highly risky combinations and only gave up betting after consequent losses. Second, they did not come back into the game at combination 17, when better chances were offered. However, consequent losses might also have drawn down their interest for the game in a “once bitten, twice shy”- way. By contrast, other individuals resumed the game when offered better chances. Examining profiles amongst these individuals showed that one capuchin, one orang-utan and three long-tailed macaques followed pure risk-prone strategies, betting for as long as there was one large cookie to win. It could be that individual traits – e.g. bold temperament – have overcome a more rational assessment of loss probability by the subjects. With regard to rational evaluation of probabilities, there is further evidence that some individuals took into account the reward combinations presented in the cups before betting; three capuchin monkeys, one orang-utan and one long-tailed macaque showed a pure rational strategy or a combination of both: their behaviour could be explained both by the risk-prone and the rational models. Thus, in our gambling game, most subjects did use probabilistic outcomes to reach for a decision, a capacity that is generally not assessed in more classical tasks.

All three species tested appeared to be risk-prone rather than risk-averse in our experimental situation. In a recent study, bonobos (*Pan paniscus*) were found to prefer a constant option in a foraging choice task, whereas chimpanzees favoured a variable one (Heilbronner *et al*. 2008). Such results may appear as an empirical illustration of risk-sensitivity. Heilbronner and colleagues proposed that divergences in risk sensitivity were driven by the distribution of food resources which acted like selective pressures from the environment. We cannot directly compare our results with this study, however, since contrary to it we tested risk-sensitivity by implementing probabilistic outcomes. We found differences between individuals in the three species tested; given the limited number of subjects being studied, one should avoid to draw conclusions at the species level.

There is risk when a probability is attached to an event (Knight 1921). Our definition of risk sensitivity was closer to those applied in economics than to the one used in behavioural ecology (Kacelnik & Bateson 1996). We also added the potential for negative outcomes, which is a characteristic of human gambling. Humans do not always chose the most rational option (Tversky & Kahneman 1974, 1981; Kahneman & Tversky 1979; Ebert & Willinger 2005), they can keep on betting despite unfavourable odds and repeated losses. As in other gaming activities, gambling may be rewarding in itself by providing amusement. The possibility that our gambling game was sufficiently arousing for the animals to keep on betting cannot be discarded. Besides, irrational risk proneness is sometimes explained by cognitive biases in humans (Kahneman & Tversky 1979). We propose that similar biases shaped the risk-proneness of non-human primates in the gambling game.

For most animals, being able to accept losses and calculate probability of gaining represent valuable skills in everyday foraging because they open the way for flexible responses, favouring adaptation to an ever-changing environment. This holds especially for primates, which live in social environments made up of complex relationships with other group members (Cheney *et al*. 1987). In the context of cooperation, for example, such abilities may help in choosing the best partner or discarding a less trustworthy one, i.e. the one the less likely to help in return (Melis *et al*. 2006). While an individual can be flexible enough to tolerate an occasional lack of return, s/he still needs some assurance that there is at least some chance of gaining when investing in a potential partner. Certainty may not be common, especially between non kin, in primates. We know of a single experimental demonstration of calculated reciprocity where transfers were based on expected returns in non-human primates (Dufour *et al*. 2009); it was found in one pair of orang-utans and was not observed in other great apes (Pelé *et al.* 2009). Low odds of a favour being returned can explain why most primates avoid engaging in immediate reciprocal transfers.

Acknowledgments

We are grateful to C. Arnaud, M. Arnaud, A. Coulon, P.Y. Hell, C. Morin, A. Leroy, A. Ouvrard for their participation in experiments with monkeys, and to M. Lohse, N. Romanowsky and S. Schorr for their assistance with the orang-utans. We are also grateful to C. Sueur and N. Poulin for statistical advice. We thank M. Bowler for proof-reading and helpful comments on the manuscript. The research was supported by a grant from the *Agence Nationale de la Recherche* (ANR-08-BLAN-0042-01).

References

Amici, F., Aureli, F. & Call, J. 2008 Fission-fusion dynamics, behavioral flexibility and inhibitory control in primates. *Curr. Biol.*, **18**, 1415-1419. (doi: 10.016/j.cub.2008.08.020)

Bateson, M. & Kacelnik, A. 1997 Starlings' preferences for predictable and unpredictable delays to food. *Anim. Behav.*, **53**, 1129–1142.

Caraco, T. 1980 On foraging time allocation in a stochastic environment. *Ecology*, 61, 119-128.

Caraco, T. 1981 Energy budgets, risk and foraging preferences in dark-eyed juncos (*Junco hyemalis*). *Behav. Ecol. Sociobiol.,* **8**, 213-217.

Cartar, R. V. & Smallwood, P. D. 1996 Risk-sensitive behavior: where do we go from here? *Am. Zool.*, **36**, 530-531. (doi: doi:10.1093/icb/36.4.530)

Cheney, D. L., Seyfarth, R. M., Smuts, B. B. & Wangrham, R.W. 1987 The study of primates societies. In *Primate Societies* (eds. B. B. Smuts, D. L. Cheney, R. M. Seyfart, R. W. Wangrham & T. T. Struhsaker), pp. 1-8. Chicago: University of Chicago Press.

Dasser, V. 1987 Slides of group members as representations of the real animals (*Macaca fascicularis*). *Ethology*, **76**, 65-73.

de Waal, F. B. M. 1997. Food transfers through mesh in brown capuchins. *J. Comp. Psychol.*, **4**, 370–378. (doi:10.1037/0735-7036.111.4.370)

Drapier, M., Chauvin, C., Dufour, V., Uhlrich, P. & Thierry, B. 2005.Food exchange with humans in brown capuchin monkeys. *Primates*, **46**, 241-248. (doi:10.1007/s10329-005-0132-1)

Dufour, V., Pelé, M., Sterck, E. H. M. & Thierry, B. 2007 Chimpanzee anticipation of food return: coping with waiting time in an exchange task. *J. Comp. Psychol.*, **121**, 145-155. (doi: 10.1037/0735-7036.121.2.145)

Dufour, V., Pelé, M., Neumann, M., Thierry, B., & Call, J. 2009 Calculated reciprocity after all: computation behind token transfers in orang-utans. *Biol. Lett.*, **5**, 172-175. (doi: 10.1098/rsbl.2008.0644)

Ebert, N. & Willinger, M. 2005 L'économie expérimentale. Paris, La Découverte.

Emlen, J. M. 1966 The role of time and energy in food preference. *Am. Nat.*, **100**, 611-617.

Green, L. & Myerson, J. 1996 Exponential versus hyperbolic discounting of delayed outcomes: risk and waiting time. *Am. Zool.*, **36**, 496-505. (doi:10.1093/icb/36.4.496)

Hanus, D. & Call, J. 2007 Discrete quantity judgments in the great apes (*Pan paniscus, Pan troglodytes, Gorilla gorilla, Pongo pygmaeus*): the effect of presenting whole sets versus item-by-item. *J. Comp. Psychol.*, **121**, 241–249. (doi: 10.1037/0735-7036.121.3.241)

Hauser, M. D., Carey, S., & Hauser, L. 2000 Spontaneous number representation in semi-free-ranging rhesus monkeys. *Proc. R. Soc. Lond. B*, **267**, 829–833. (doi: 10.1098/rspb. 2000.1078)

Hayden, B. Y. & Platt, M. L. 2007 Temporal discounting predicts risk sensitivity in rhesus macaques. *Curr. Biol.*, **17**, 49–53. (doi: 10.1016/j.cub.2006.10.055)

Heilbronner, S. R., Rosati, A. G., Stevens, J. R., Hare, B., & Hauser, M. D. 2008 A fruit in the hand or two in the bush? Divergent risk preferences in chimpanzees and bonobos. *Biol. Lett.*, **4**, 246-249.

Kacelnik, A. & Bateson, M. 1996 Risky theories-The effects of variance on foraging decisions. *Am. Zool.*, **36**, 402-434. (doi: 10.1093/icb/36.4.402)

Kahneman, D. & Tversky, A. 1979 Prospect theory: an analysis of decision under risk. *Econometrica*, **47**, 263-291. (doi: 10.2307/1914185)

Knight, F. H. 1921 Risk, uncertainty and profits. Boston, MA: Hart, Schaffner & Marx, Houghton Mifflin.

Lee, D., McGreevy, B. P., Barraclough, D. J. 2005 Learning and decision making in monkeys during a rock-paper-scissors game. *Cognit. Brain Res.*, **25**, 416-430.

MacArthur, R. H. & Pianka, E. R. 1966 On optimal use of a patchy environment. *Am. Nat.*, **100**, 603-609.

McNamara, J. M. 1996 Risk-prone behaviour under rules which have evolved in a changing environment. *Am. Zool.*, **36**, 484-495. (doi: 10.1093/icb/36.4.484)

Melis, A. P., Hare, B. & Tomasello, M. 2006 Chimpanzees recruit best collaborators. *Science,* **311**, 1297-1300. (doi: 10.1126/science.1123007)

Menzel, C. R. 1991. Cognitive aspects of foraging in Japanese monkeys. *Anim. Behav*., **41**, 397-402.

Pelé, M., Dufour, V., Thierry, B. & Call, J. 2009 Token transfers among great apes: species differences, gestural requests and reciprocal exchange. *J. Comp. Psychol*., in press.

Pelé, M., Dufour, V., Micheletta, J. & Thierry, B. 2009 Long-tailed macaques display unexpected waiting abilities in exchange tasks. *Anim. Cogn*. Online

Ramseyer, A., Pelé, M., Dufour, V., Chauvin, C. & Thierry, B. 2006 Accepting the loss: temporal limits in brown capuchin monkeys. *Proc. R. Soc. B*, **273**, 179-184. (doi: 10.1098/rspb.2005.3300)

Real, L. 1980 On uncertainty and the law of diminishing returns in evolution and behavior. In *Limits to action: the allocation of individual behaviour* (eds. J. E. R. Staddon), pp. 37-64. Academic Press, New York.

Real, L. & Caraco, T. 1986 Risk and foraging in stochastic environments. *Ann. Rev. Ecol. Syst*., **17**, 371-390.

Rosati, A. G., Stevens, J. R., Hare, B. & Hauser, M. D. 2007 The evolutionary origins of human patience:temporal preferences in chimpanzees, bonobos, and adult humans. *Curr. Biol*., **17**, 1663-1668.

Scheres, A. & Sanfey, A. G. 2006 Individual differences in decision making: drive and reward responsiveness affect strategic bargaining in economic games. *Behav. Brain Funct*., **2**, 35. (doi:10.1186/1744-9081-2-35)

Tversky, A. & Kahneman, D. 1974 Judgment under uncertainty: heuristics and biases. *Science*, **185**, 1124-1131. (doi: 10.1126/science.185.4157.1124)

Tversky, A. & Kahneman, D. 1981 The framing of decisions and the psychology of choice. *Science*, **211**, 453-458. (doi: 10.1126/science.7455683)

Electronic Supplementary Material : Training Procedure

During a trial, the experimenter typically stood in front of the subject's compartment showing the subject two different food items in each hand for 3 s. Long-tailed macaques and brown capuchin monkeys could exchange the items with the human experimenter through a mesh panel. For safety reason, orang-utans could give and receive the items through three holes (placed on either side and on the middle) of a Plexiglas panel (68 x 48 cm). The experimenter then gave the less preferred item to the subject. After 3 s had elapsed, the experimenter held out their empty hand while still presenting the reward on the other hand. If the subject gave back the initial item, s/he received the reward through a mesh panel placed under the Plexiglas panel. If the subject did not give back the initial item, the experimenter did not reward the subject and stepped back, thereby ending the trial. Whenever the individuals had dropped or eaten the initial item before the end of the waiting period, the experimenter ended the trial by stepping back. The experimenter waited for 30 s after the end of food consumption before beginning another trial. Training was run by sessions of 12 trials.

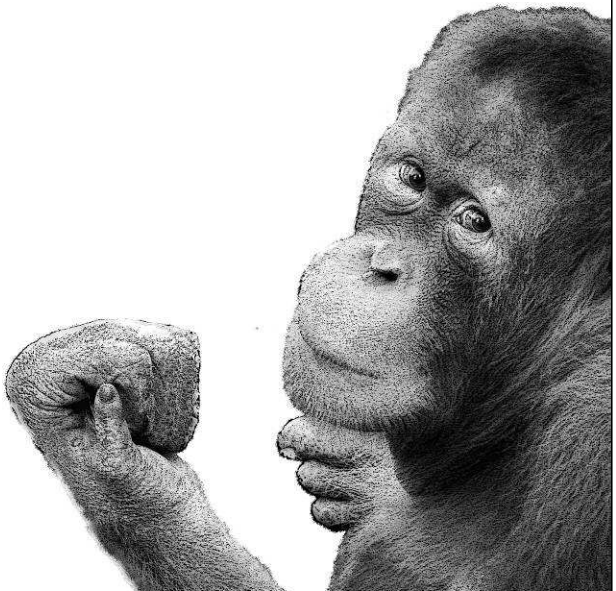
The long-tailed macaques and capuchin monkeys had already been trained to exchange food items of different qualities and quantities with a human experimenter in previous studies (Drapier et al., 2005; Ramseyer et al., 2006; Pelé et al., in press). Concerning the orang-utans, they have been trained to discriminate and exchange tokens with a human experimenter in previous studies (Pelé et al., 2009; Dufour et al., 2008) but never food items. Thus, the orang-utans were trained to exchange food items of different qualities. They were given a small piece of carrot that they had to exchange with the experimenter to obtain a piece of cookie of 2 x 4 x 0.5 cm. This phase was run until orang-utans reached a criterion of 90% of success. This training required a mean of 4.3 ± 0.9 sessions of 12 trials each per subject.

Then, all individuals of the three species were trained as follows: subjects were given a small piece of cookie (1 x 2 x 0.5 cm) that they had to exchange for a larger one (2 x 4 x 0.5 cm). This phase was run until subjects reached a criterion of 100% of success during one session. This training required a mean of 2.5 ± 0.5 sessions for the orang-utans, a mean of 1 session for the macaques and a mean of 1.5 ± 0.3 sessions for the capuchin monkeys.

A last training phase aimed at familiarizing the subjects to the apparatus, which consisted of a tray of six aligned plastic cups. The experimenter presented a piece of cookie of 2 x 2 x 0.5 cm to the subject in one hand and in the other hand a tray of six aligned plastic cups containing each a piece of cookie of 4 x 4 x 0.5 cm. The experimenter gave the small piece of cookie to the subject, and then slowly turned his/her hand upward to present it palm open to the subjects, asking her/him to give the initial item back. If the subject did so, the experimenter rewarded her/him by giving her/him the content of one of the six aligned cups – randomly chosen. In this training phase, reward consisted only of larger pieces of cookie; the subjects therefore always received a reward better than the item they originally gave back. As before, one training session consisted of 12 trials. After reaching a criterion of 90% of return during two consecutive sessions, the subject entered the testing phase. This training required a mean of 2.8 ± 0.3 sessions for the orang-utans, a mean of 2 sessions for the macaques and a mean of 3.5 ± 0.4 sessions for the capuchins.

CHAPITRE V

LES ECHANGES RECIPROQUES ENTRE CONGENERES



Article 5

Les quémandes et les transferts de biens chez les grands singes

Article publié dans *Journal of Comparative Psychology*

RESUME DE L’ARTICLE 5

Introduction

L’étude a pour but de déterminer si des grands singes sont capables de s’engager dans des échanges spontanés et calculés avec un congénère. Sont-ils capables de donner et de rendre des objets à un congénère ? Existe-t-il des comportements de recrutement tels que des gestes ou des vocalisations ?

Méthodes

J’ai entraîné trois gorilles, quatre chimpanzés, cinq orangs-outangs et cinq bonobos à discriminer et à échanger une forme d’objet parmi trois contre une récompense alimentaire. Cet objet était l’objet de valeur pour l’individu car seul il pouvait être échangé contre de la nourriture auprès d’un expérimentateur. Lors de la phase de test, les individus étaient testés par deux dans des compartiments adjacents séparés par une cloison grillagée. Chaque individu possédait le même lot d’objets mais les objets de valeur différaient d’un individu à l’autre. Chaque individu possédait donc 12 objets de valeur (échangeable pour de la nourriture), 12 objets de valeur du partenaire (le partenaire pouvait les échanger pour de la nourriture) et 12 objets sans valeur (aucun individu ne pouvait obtenir de nourriture en échangeant ces objets). Dans la première partie du test, les individus pouvaient échanger la totalité de leurs objets de valeur avec l’expérimentateur. Dans la deuxième partie, les sujets devaient transférer des objets entre eux pour obtenir plus de nourriture de la part de l’expérimentateur.

Résultats

J’ai relevé respectivement 4, 5, 264 et 328 transferts d’objets chez les gorilles, les chimpanzés, les bonobos et les orangs-outangs. Dans les trois premières espèces, la majorité de ces transferts étaient indirects, c'est-à-dire que l’individu plaçait un objet dans le compartiment du partenaire sans qu'un contact physique survienne. Chez les orangs-outangs, la majorité des transferts étaient directs, c'est-à-dire que l’individu donnait de la main à la main un objet à son partenaire. Des comportements de quémande comme tendre la main vers le partenaire ou pointer vers un objet ont été relevés chez les chimpanzés et les bonobos et plus particulièrement chez les orangs-outangs. Une paire d’orangs-outangs a également été capable au cours d’un test de transférer des objets de manière réciproque. L’analyse des données n’a cependant pas permis de mettre en évidence de réciprocité au niveau d’autres transferts ou des interactions sociales.

Conclusion

Les grands singes testés n’ont pas été capables d’échanger des objets de manière réciproque. On ne peut conclure à l'existence d'une réciprocité calculée. Chez les chimpanzés et les bonobos, la compétition sociale pourrait limiter l’émergence des échanges. Chez les orangs-outangs, la fréquence élevée de dons et de quémandes révèle une plus grande aptitude des individus à interagir et à coopérer avec un congénère.

Journal of Comparative Psychology
2009, Vol. 123, No. 4, 375–384

© 2009 American Psychological Association
0735-7036/09/$12.00 DOI: 10.1037/a0017253

Token Transfers Among Great Apes (*Gorilla gorilla*, *Pongo pygmaeus*, *Pan paniscus*, and *Pan troglodytes*): Species Differences, Gestural Requests, and Reciprocal Exchange

Marie Pelé
Université de Strasbourg

Valérie Dufour
University of St. Andrews

Bernard Thierry
Université de Strasbourg

Josep Call
Max Planck Institute for Evolutionary Anthropology

Great apes appear to be the nonhuman primates most capable of recognizing trading opportunities and engaging in transfers of commodities with conspecifics. Spontaneous exchange of goods between them has not yet been reported. We tested gorillas (*Gorilla gorilla*), orangutans (*Pongo pygmaeus*), bonobos (*Pan paniscus*), and chimpanzees (*Pan troglodytes*) in a token-exchange task involving two conspecifics and a human experimenter. Tested in pairs, subjects had to exchange tokens with a partner to obtain food from the experimenter. We observed 4, 5, 264, and 328 transfers of tokens in gorillas, chimpanzees, orangutans, and bonobos, respectively. Most gifts were indirect in gorillas, chimpanzees, and bonobos, whereas most were direct in orangutans. The analysis showed no evidence of calculated reciprocity in interactions. A main finding of the study was the high rate of repeated gifts and begging gestures recorded in orangutans. This raises the question of the meaning of pointing in great apes and their ability to understand the communicative intent of others.

Keywords: reciprocity, exchange, tokens, begging, great apes

Animals engage in reciprocal interactions, but they do not commonly exchange goods or services like humans do. On the basis of mental scorekeeping of given and received favors (de Waal & Lutrell, 1988), calculated reciprocity would approach the economic computations performed by humans. Several authors have assumed that calculated reciprocity accounts for exchanges of commodities in chimpanzees (*Pan troglodytes*); for example, males groom females to increase their chances of mating, or they share meat according to the amount of help provided in hunting (de Waal, 1989; Mitani & Watts, 2001). Finding correlations between given and received actions, however, is not sufficient to demonstrate that chimpanzees take into account the costs and benefits of reciprocated behaviors (Hemelrijk, 1996). Measuring the extent to which apes exchange commodities on the basis of calculation is a tricky issue, and any correspondence between gifts and returns must be considered with caution (Seyfarth & Cheney, 1988). Benefits exchanged by individuals may vary in nature from one individual to another and from one occasion to the next. In addition, the same currency may have a relative value depending on individuals, value that would be based on factors such as age, size, and dominance status.

Although it is difficult to appreciate the expectations of an individual who gives a service to another in the social context, experimental studies allow one to control for the value of goods about to be exchanged. Studies of chimpanzees and brown capuchin monkeys have demonstrated that they readily engage in exchanges with human experimenters, creating situations in which one may examine the cognitive abilities necessary for trading. They give food to receive another food that is quantitatively or qualitatively more desirable (Drapier, Chauvin, Dufour, Uhlrich, & Thierry, 2005; Lefebvre, 1982; Lefebvre & Hewitt, 1986; Padoa-Schioppa, Jandolo, & Visalberghi, 2006). They exchange nonedible tokens for food with an experimenter (Brosnan & de Waal, 2005; Hyatt & Hopkins, 1998; Westergaard, Liv, Chavanne, & Suomi, 1997; Westergaard, Liv, Rocca, Cleveland, & Suomi, 2004). They learn the use of tokens from conspecifics (Brosnan & de Waal, 2004; Sousa, Okamoto, & Matsuzawa, 2003); chimpanzees even stock the tokens needed to obtain rewards (Sousa & Matsuzawa, 2001), and capuchin monkeys use tokens as symbols

---

Marie Pelé and Bernard Thierry, Département Ecologie, Physiologie, and Ethologie, Institut Pluridisciplinaire Hubert Curien, Centre National pour la Recherche Scientifique, Université de Strasbourg, Strasbourg, France; Valérie Dufour, School of Psychology, University of St. Andrews, St. Andrews, Scotland; Josep Call, Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany.

This research was made possible by Grant 2451 from the L. S. B. Leakey Foundation and by Grant (ANR-08-BLAN-0042-01) from the Agence Nationale de la Recherche.

We are grateful to the keepers of the zoo of Leipzig—Evelyn Kanzler, Daniela Rogge, Kerstin Schuldei, Martina Hacker, Nico Schenk, Daniel Gessler, Reinald "Mozart" Herrman, Michael Tischmeyer, Stephan Leideritz, Martina Lohse, Nicole Romanowsky, Frank Maxis and Sebastian Schorr—for assistance with the apes. In addition, we thank Martin Schmelz and Martina Neumann for their help with data collection.

Correspondence concerning this article should be addressed to Marie Pelé, Département Ecologie, Physiologie, and Ethologie, UMR 7178, Institut Pluridisciplinaire Hubert Curien, Centre National pour la Recherche Scientifique, 23 rue Becquerel, 67087 Strasbourg Cedex 2, France. E-mail: marie.pele@c-strasbourg.fr

to represent and combine quantities (Addessi, Crescimbene, & Visalberghi, 2007, 2008). The use of tokens makes it possible for experimenters to normalize exchange parameters and to control differences of currencies or the relative values of the goods to be exchanged.

Although numerous studies have shown that primates may exchange with a human experimenter, observations of active transfers between conspecifics remain scarce (de Waal, 1989, 1997). In de Waal's (1997) study, most food transfers recorded in capuchins were passive; food was collected by an individual through a separating mesh after having been dropped by the initial possessor. Active transfers included both indirect transfers—that is, the possessor dropped the item in the partner's cage—and direct transfers—that is, the possessor transferred an item directly to the partner's mouth or hand (de Waal, 1997; de Waal, Luttrell, & Canfield, 1993). Only active transfers might involve intentionality to give, and they were rarely observed (de Waal, 1997; de Waal et al., 1993). In the Westergaard and Suomi (1997) study, capuchins were able to solve a cooperative task by transferring stones through a mesh in an active and indirect way. A similar instance of indirect transfer of a tool was previously reported in a captive hamadryas baboon (*Papio hamadryas*; Beck, 1973). A single case of direct transfers of a tool from one individual to another was observed in chimpanzees. Two young males trained in a symbol language proved being able to ask one another for an appropriate tool needed to obtain food. Once the reward was obtained, it was shared between the individuals, who were also able to reverse their roles of tool requester and food provider (Savage-Rumbaugh, Rumbaugh, & Boysen, 1978). A recent attempt to replicate this study in capuchin monkeys showed that direct gifts of a tool may occur in subjects trained to exchange, but the donor never received a share of the reward (Westergaard, Evans, & Howell, 2007). Until now, no experimental study has addressed the conditions needed for direct transfer of goods to occur among nonhuman primates.

Given their social and cognitive skills, great apes stand as the nonhuman primates most likely to be capable of recognizing potential trading opportunities and to engage in direct transfers with conspecifics. They may notably collaborate with a conspecific partner (chimpanzees, Melis, Hare, & Tomasello, 2006a, 2006b), and recent findings have suggested that they can plan for the future (bonobos and orangutans, Mulcahy & Call, 2006; chimpanzees, Dufour, & Sterck, 2008). To assess great apes' trading capacities, we tested gorillas, orangutans, bonobos, and chimpanzees in a triadic token-exchange task involving two conspecifics and a human experimenter. Each individual had three types of tokens at her or his disposal: self-valued tokens exchangeable for food with the human experimenter, partner-valued tokens that the partner could exchange for food with the human experimenter, and no-value tokens that could not be exchanged. This meant that subjects could exchange their self-valued tokens with the experimenter for food. Additionally, subjects had the option of exchanging their partner-valued tokens with each other and then exchanging the new self-valued token with the experimenter for food. Given their abilities to cooperate with a conspecific (Melis et al., 2006a, 2006b), we expected that chimpanzees and bonobos would show better results than gorillas and orangutans in such task.

Method

Subjects

Subjects were 3 gorillas (*Gorilla gorilla*), 5 orangutans (*Pongo pygmaeus*), 5 bonobos (*Pan paniscus*), and 4 chimpanzees (*Pan troglodytes*) housed at the Wolfgang Köhler Primate Research Center, Leipzig Zoo (Leipzig, Germany). Table 1 presents their age, sex, and rearing history. All subjects were socially housed in enclosures with access to indoor and outdoor areas and sleeping rooms for the night. Water was available ad libitum, and subjects were not food deprived at any time. Before this study, they had been involved in various cognitive tasks, but none involved exchanging objects.

Table 1
Self-Value Tokens and Age, Sex, and Rearing History of Subjects

					Self-value token	
Name	Species	Age (years)	Sex	Rearing history	Set 1	Set 2
Joe	Bonobo	23	Male	Nursery	Green PVC tube	Gray PVC triangle
Lim	Bonobo	11	Male	Nursery	Green PVC tube	Transparent PVC circle
Kun	Bonobo	10	Male	Nursery	Gray PVC cube	L-shaped metallic
Uli	Bonobo	13	Female	Mother	Green PVC tube	L-shaped metallic
Yas	Bonobo	9	Female	Mother	Gray PVC cube	Transparent PVC circle
Bim	Orangutan	26	Male	Mother	Gray PVC cube	L-shaped metallic
Dun	Orangutan	33	Female	Unknown	Gray PVC cube	Gray PVC triangle
Pin	Orangutan	18	Female	Mother	Green PVC tube	L-shaped metallic
Dok	Orangutan	15	Female	Mother	Green PVC tube	Transparent PVC circle
Pad	Orangutan	9	Female	Mother	Gray PVC cube	Transparent PVC circle
N'Di	Gorilla	29	Female	Unknown	Gray PVC cube	No retraining
Beb	Gorilla	27	Female	Unknown	Green PVC tube	L-shaped metallic
Vir	Gorilla	11	Female	Mother	Green PVC tube	Transparent PVC circle
Uny	Chimpanzee	9	Male	Mother	Gray PVC cube	Transparent PVC circle
Jah	Chimpanzee	13	Female	Mother	Gray PVC cube	L-shaped metallic
Ger	Chimpanzee	13	Female	Mother	Green PVC tube	L-shaped metallic
Fif	Chimpanzee	13	Female	Mother	Green PVC tube	Transparent PVC circle

Note. PVC = polyvinyl chloride.

Tokens

Tokens differed in form and color, and some could be exchanged for food in the experiment. Tokens used were 5-cm-long green polyvinyl chloride (PVC) tubes, a gray PVC cube with 5 cm × 5 cm sides, 5-cm-long metallic chain links, a 5-cm-long L-shaped metallic token, a 5 cm × 5 cm × 5 cm gray PVC triangle, and a 5-cm-diameter transparent PVC circle (see Figure 1).

We gave 2 subjects the same set of 36 tokens, consisting of three types of 12 tokens: (a) *Self-valued tokens* were valuable to the subject and valueless to the partner, (b) *partner-valued tokens* were valuable to the partner and valueless to the subject, and (c) *no-value tokens* were not valuable to any animal. Table 1 gives information about each subject's self-value tokens.

Training Procedure

We trained subjects individually to exchange one of three types of tokens for food in a testing room of 25 m^2. Before each training session, we placed the set of 36 tokens in a compartment of the testing room. The experimenter (Marie Pelé) sat in front of the compartment close to the 36 tokens, and the subject entered in the testing room. Subject and experimenter could give and receive tokens through a mesh panel (68 × 48 cm). The tokens had to fit into a 5-cm × 5-cm square and required some effort to be inserted through the mesh. A session typically started with the experimenter requesting tokens by holding an open hand (palm up) next to the fence. To inform the subject that she or he had to select the token to be given (the self-valued token), only one kind of token (e.g., gray cube) was rewarded with a grape or a piece of banana (depending on species). Any correct token was placed in a bowl, whereas an incorrect token (i.e., one with no value for the subject, i.e., partner-valued or no-value tokens) was thrown into a bucket without being rewarded. Once the subject had returned his or her 12 self-valued tokens, the experimenter left the testing room for 3 min. Then the experimenter came back, stayed for 3 min, and then left the room, which ended the session. If during the 3 min the subject gave the remaining incorrect tokens, the experimenter collected them and dropped them in the bucket without rewarding the subject.

Testing started once subjects succeeded in giving more than 90% of the correct tokens first, during three consecutive sessions. Because the dominant gorilla male showed no interest in the task, he was not trained further. All other subjects reached the criterion.

Testing Procedure

Testing took place in the same testing room divided into two testing compartments by a common mesh wall through which subjects could interact and transfer tokens with each other (see Figure 2). The experimenter sat in a rectangular booth facing both testing compartments. The booth had a front window (98 × 95 cm) and two mesh panels (68 × 48 cm) on either side and allowed the apes to look at each other.

We placed the same set of 36 tokens (12 self-valued tokens for subject, 12 partner-valued tokens, and 12 no-value tokens) in each compartment, near the experimenter exchange area and opposite the common mesh wall (see Figure 2). The experimenter resumed a sitting position in the booth, and subjects were let in.

The testing procedure was the same as the training one except that 2 individuals were present in each of two adjacent compartments. In the first part of a session, partners had the possibility of exchanging their self-valued tokens with the experimenter. Once both individuals had given all their 12 self-valued tokens, the experimenter left the room for 3 min to not influence possible transfers between subjects. In the subjects' compartments, only partner-valued and no-value tokens remained. After 3 min elapsed, the experimenter came back and sat with the subjects for a minimum duration of 3 min. If a transfer of a valuable token had occurred, the experimenter asked the subject for the token and exchanged it for food. If a transfer of tokens occurred after the experimenter came back, she also asked the relevant subject for the token and stayed in the testing room until extinction of transfers of any kind. Four cameras recorded subject behavior during the session, and a second observer collected latencies of exchanges with the experimenter.

Twelve trials were run for each pair of individuals. One exception was a pair of chimpanzees (Uny and Jah) for whom only 10 trials were conducted because of some difficulties in selecting the

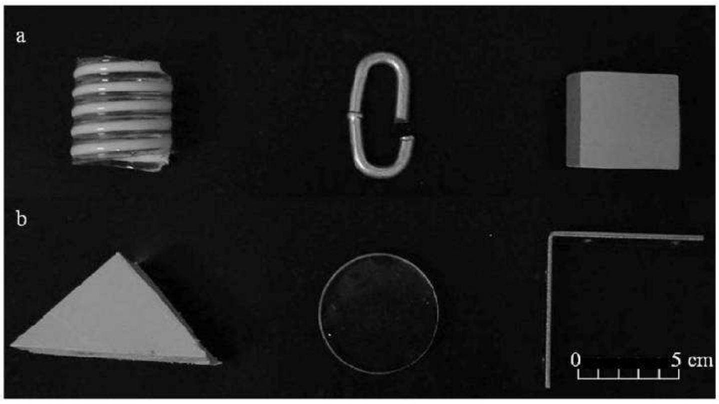


Figure 1. Sets of tokens: (a) Set 1: green polyvinyl chloride (PVC) tube, metallic chain, and gray PVC cube and (b) Set 2: gray PVC triangle, transparent PVC circle, and L-shaped metallic token.

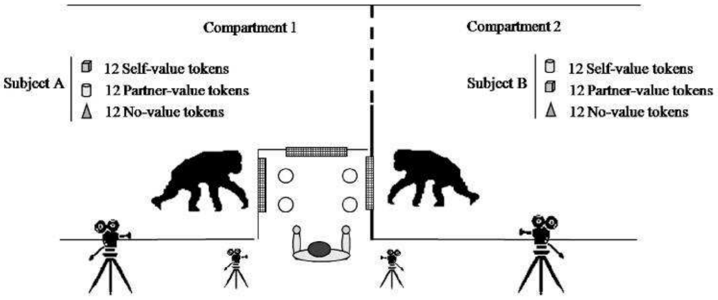


Figure 2. Experimental setting: Two partners, Subjects A and B, receive the same set of tokens: 12 self-valuable tokens, 12 partner-valuable tokens, and 12 no-value tokens. Tokens were placed near the panel mesh of the booth, out of the partner's reach. The common mesh wall (dashed line) is situated at the bottom of the testing room. Tokens could be transferred by passing them through the common mesh or the space existing between the floor and the wall separating the two compartments.

individuals. For each species, we tested all possible pairs of individuals. The number of subjects allowed us to test three pairs of gorillas (24 sessions per individual), 10 pairs of orangutans and bonobos (48 sessions per individual), and six pairs of chimpanzees (36 sessions for Ger and Fif; only 34 sessions for Uny and Jah). Because some individuals shared the same self-valued tokens, they could not be tested together with the original set of tokens. Therefore, training and testing phases were run again with a new set of tokens (see Figure 1).

Video Processing

Test sessions were scored from videotapes using behavioral observation software (The Observer [Noldus Corporation, Leesburg, Virginia] and Interact [Mangold Corporation, Atlanta, Georgia]). The behavioral units recorded during testing sessions were (a) *exchange with experimenter* (a subject passes a token through the mesh to the experimenter); (b) *transfer with partner* (a subject obtains a token that was originally in her or his partner's compartment; (c) *pointing* (a subject puts its fingers through the mesh separating both compartments in the direction of one or more tokens); and (d) *holding out hand* (a subject holds one hand with the palm up in the partner's direction). We recorded the frequency and latency of the first two behaviors as well as the tokens' value. The second two behaviors were the only begging gestures observed during the testing period in all species. We recorded both their frequency and the identities of actor and recipient.

Five different types of transfers were observed during test sessions. In *catch*, the subject places tokens near the common mesh by manipulating or playing with it. The partner takes one token in the subject's compartment. The subject attempts to prevent it or does not see it. In *passive transfer*, a subject brings a token near the common mesh wall and lets the partner take it. In *indirect gift*, a donor places a token in the partner's compartment without physical contact with the partner. In *direct gift*, a subject gives a token to the partner by passing it through the common mesh or under the common wall; transfers occur directly from hand to hand, hand to mouth, mouth to hand, or mouth to mouth. Contrary to indirect gifts, one may safely assume that direct gifts involve an intention to give. For *unknown*, the type of transfer is unknown because it was not clearly visible on the cameras; this might have been the case when the experimenter left the testing room.

Assessment of Social Relationships

Individuals were observed in their social groups to assess the quality of social relationships between subjects. Observational data were collected during the testing period of each group. The observer (Marie Pelé) conducted observations from a platform above the inside enclosures of 264 m^2, 230 m^2, and 175 m^2 for gorillas, orangutans, and chimpanzees, respectively, and the outside enclosure of 2,300 m^2 for bonobos. All members of each species (including juveniles) were observed 1.5 hr per day between 9:00 a.m. and 5:00 p.m., totaling 60 hr for gorillas, 50 hr for orangutans, 34 hr for bonobos, and 60 hr for chimpanzees. Every 5 min, the observer recorded distances between group members (<1 m and physical contact), their locations in the enclosure, and their individual activities—rest, locomotion, feed, play, allogroom, or self-groom—using the scan-sampling method (Altmann, 1974). Seven hundred fifty-three scans per individual were recorded for gorillas, 626 per individual for orangutans, 420 per individual for bonobos, and 760 per individual for chimpanzees.

Statistical Analyses

We used several nonparametric statistics: Kruskal-Wallis test to compare frequencies of transfers and begging gestures between species followed by a Dunn's multiple pairwise comparison for each mean comparison, Wilcoxon's matched-pairs test (one-tailed) to compare the frequencies of the different types of transfers, and Fisher's exact test to compare the percentages of the different types of transfers (Siegel & Castellan, 1988). For each trial, we used data from only 1 subject that we chose by randomization. Thus, for one pair of individuals, we considered data of a subject for six trials and data of his or her partner for the other six trials. In addition, given the small number of individuals of each species, we used an exact test procedure to carry out nonparametric analyses (SPSS 16 [SPSS Inc., Chicago] and GraphPad Prism 5 GraphPad Software, Inc., La Jolla, CA).

To test for reciprocity, frequencies and latencies of behaviors scored were analyzed using matrices. For each behavior, we generated initiator and receiver matrices to compare the amount of behavior given with the amount of behavior received. Matrix correlations were tested using Dietz's test, based on 10,000 permutations (Matman software; de Vries, Netto, & Hanegraaf, 1993).

For all analyses, we fixed the significance level at .05. Average values are given as means ± standard errors of the mean.

Results

Training Phase

To reach the criterion in the discrimination of the self-valued token, apes needed an average of 5.8 ± 0.5 sessions for the first set of tokens and 5.1 ± 0.6 sessions for the second set of tokens (see Figure 3). Speed of learning acquisition for the first set of tokens differed significantly between species, Kruskal-Wallis test: $\chi^2(3) = 8.037$, $p = .027$. Gorillas needed more training sessions than chimpanzees (Dunn's multiple comparison test, $p < .001$; see Figure 3). Speed of acquisition for the second set of tokens did not differ significantly between species, Kruskal-Wallis test: $\chi^2(3) = 1.390$, $p = .736$.

Exchange With the Experimenter

Each testing session started with individuals exchanging their 12 self-value tokens with the human experimenter. The 12 tokens first given by the subject were composed of more than 90% of self-valued tokens for all individuals of all species. The totality of self-valued tokens was exchanged in a mean of 3.83 ± 0.09 min (gorillas, $M = 4.73 \pm 0.31$ min; orangutans, $M = 3.77 \pm 0.14$ min; bonobos, $M = 3.97 \pm 0.18$ min; chimpanzees, $M = 3.23 \pm 0.12$ min).

Transfers of Tokens Between Subjects

The total number of transfers for each species, including catches, passive transfers, and indirect and direct gifts, was 4 for gorillas (0.11 transfer per session), 264 for orangutans (2.20 transfers per session), 328 for bonobos (2.73 transfers per session), and 5 for chimpanzees (0.07 transfers per session; see Figure 4). We discarded those cases in which an individual put a token in the partner's cage and then took it back (61 cases with a female bonobo, Yas; see next section). We also excluded transfers involving infants (gorillas, 12 transfers; orangutans, 37 transfers) from the analysis.

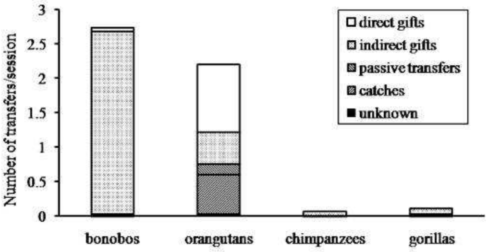


Figure 4. Number of transfers per session for all species.

Orangutans displayed the greatest variety of transfer types, including gifts (67% of the total), catches (26%) and passive transfers (7%). Most of the transfers observed in the other species were represented by gifts (bonobos, 97%; chimpanzees, 80%; and gorillas, 75%). Because gifts accounted for most of the observed transfers in all species, in the following sections we compare the species on frequency of direct and indirect gifts (see Figure 5). Species differed significantly in the frequency of direct gifts, Kruskal-Wallis test: $\chi^2(3) = 9.744$, $p = .011$. In contrast, species did not differ significantly in the frequency of indirect gifts, Kruskal-Wallis test: $\chi^2(3) = 1.772$, $p = .649$.

Value of Tokens Transferred

We analyzed whether the donor preferentially transferred those tokens that were valuable to the partner as opposed to those that were not. Overall, donors did not preferentially transfer tokens that were valuable to the partner in direct gifts (Wilcoxon's test: $z = -1.51$, $p = .125$, $N = 5$, one-tailed, $M_1 = 9.8 \pm 3$, $M_2 = 6 \pm 1.9$) or indirect gifts (Wilcoxon's test: $z = -0.14$, $p = .460$, $N = 8$, one-tailed, $M_1 = 12.2 \pm 10.5$, $M_2 = 5.3 \pm 2.4$). However, there were large individual differences in both the number of tokens transferred and the preference for partner-valued tokens. Table 2 lists those individuals that produced five or more gifts. With regard to direct gifts, 2 orangutans preferentially transferred partner-valued tokens, whereas another orangutan preferentially trans-

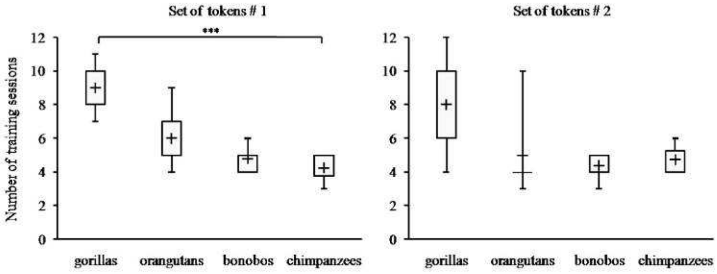


Figure 3. Number of training sessions needed to reach the criterion for all species with the first set of tokens (left panel) and the second set of tokens (right panel). Boxplots represent the interquartile range with minimum and maximum, and black plus signs indicate means. (Dunn's post hoc $p < .001$).

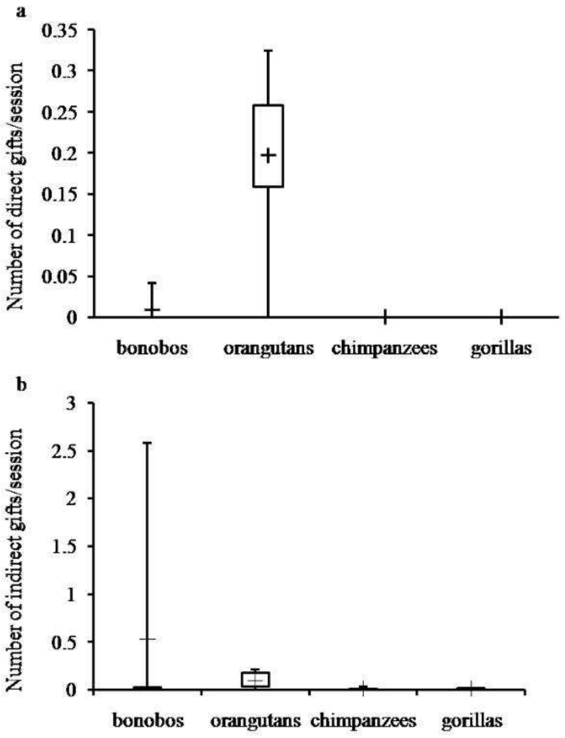


Figure 5. Number of direct gifts per session (a) and number of indirect gifts per session (b) for all species. Boxplots represent the interquartile range with minimum and maximum, and black plus signs indicate means.

ferred no-value tokens. With regard to indirect gifts, 1 bonobo preferentially transferred partner-valued tokens, whereas an orangutan preferentially transferred no-value tokens.

The behavior of this bonobo appeared to be a consequence of her inclination to play with one of the tokens (i.e., green tube) by inserting it through the fence into her partner's cage and attempting to take it back afterward, which she did successfully 61 times. In the remaining cases, the tokens were seized by the partner, who exchanged them for food with the human experimenter. This behavior decreased dramatically (from 7.7 transfers per session to 0.25) with the introduction of the L-shaped metallic token from the second set of tokens.

Gestures: Pointing and Hand Begging

Figure 6 illustrates the occurrence of pointing and hand begging per testing session for all individuals in the four species. Orangutans performed communicative behaviors more often than other species. There were significant differences across species in the frequency of hand begging, Kruskal-Wallis test: $\chi^2(3) = 15.425$, $p < .001$. A Dunn's multiple comparison test showed that orangutans produced significantly more holding-out-hand behavior than each of the three other species ($p < .05$ for each). In contrast, there were no significant differences between species in the frequency of pointing, Kruskal-Wallis test: $\chi^2(3) = 2.400$, $p = 1$. Because the frequency of these behaviors was so low for other species, the next analyses focused exclusively on orangutans. Holding out the hand led to a direct gift from the partner 28.1% of the time and to an indirect gift 7.8% of the time. Pointing led to a direct gift from the partner 17.4% of the times and to an indirect gift 15.2% of the time.

To assess the efficiency of these two behaviors in term of token values, we checked whether an individual received self-valued or no-value tokens after using such gestures. When followed by gifts, 80% (12 cases) of pointing behaviors were followed by gifts of valuable tokens and 20% (three cases) by gifts of no-value tokens. Considering holding-out-hand behavior, we observed that this gesture was followed an equal number of times by gifts of valuable tokens (23 cases) and gifts of no-value tokens (23 cases). We checked whether the number of these two behaviors followed by valuable gifts or by no-value gifts differed significantly from chance. For the subject who produced most begging gestures (Bim for both), we compared the observed probability of self-valuable tokens he received after begging with the chance level calculated for each event in function of the number of valuable tokens and no-value tokens available to the partner. After holding out his hand, Bim did not receive more self-valued tokens than expected by chance (Wilcoxon's test: $z = -0.33$, $p = .372$, $N = 34$, one-tailed, $M_1 = 0.50 \pm 0.01$, $M_2 = 0.44 \pm 0.08$). By contrast, after pointing Bim received more self-valued tokens than expected by chance (Wilcoxon's test: $z = -3.09$, $p < .001$, $N = 14$, one-tailed, $M_1 = 0.45 \pm 0.01$, $M_2 = 0.85 \pm 0.09$).

Reciprocity in Orangutans?

Despite the elevated number of direct gifts observed in orangutans, we did not find a statistically significant correlation between the matrices of the total number of tokens given and received by subjects, nor did we find one for indirect gifts (Dietz's test; $p =$

Table 2
Percentage of Direct and Indirect Gifts in Which the Donor Transferred Tokens That Were Valuable to Her Partner

		Direct			Indirect		
Name	Species	%	*N*	*p*	%	*N*	*p*
Bim	Orangutan	78.9	19	<.0001	50	4	—
Pin	Orangutan	74.4	39	<.0001	83.3	6	<.0001
Dok	Orangutan	62.1	29	.116	60.0	25	.200
Pad	Orangutan	29.0	31	.003	4.8	21	<.0001
Yas	Bonobo	60.0	5	.200	89.6	309	<.0001

Note. Only those subjects with five or more gifts are displayed (Fisher exact test).

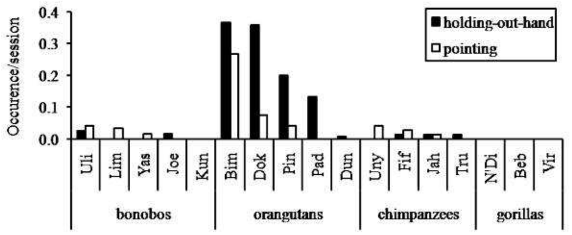


Figure 6. Occurrence per session of holding out the hand and pointing behaviors recorded for all individuals of the four species.

.233, *r*s = .21) or direct gifts (Dietz's test; *p* = .146, *r*s = .56), regardless of the value of tokens transferred. Still, in the 120 sessions conducted for this species, we recorded one likely instance of reciprocal transfers between 2 orangutans in the course of one session. We observed 2 orangutans, 1 male (Bim) and 1 female (Dok), exchanging partner-valued tokens with each other during the seventh session. Transfers occurred in the experimenter's presence. First, the female gave directly to the male a cube that was his valued token. After exchanging this cube with the experimenter for a piece of banana, the male took some tubes and metallic chain links and pushed one tube under the common mesh wall. The female took it and exchanged it with the experimenter for the food reward. Then, the male took a cube that had been placed by the female near the common wall and exchanged it with the experimenter. At this moment, the female grabbed five tubes in the partner's compartment out of his sight. After having exchanged these tubes with the experimenter, the female came back to the common mesh wall and gave a cube directly to the male. The female grabbed again four tubes out of sight of her partner. Later, the male took a branch and gave it to the female, followed by a tube. Finally, once the female had exchanged this tube with the experimenter, she gave two cubes directly to the male, who exchanged them with the experimenter. The whole exchange event took place within 14 min.

Considering the previous likely instance of reciprocal exchange, we checked whether reciprocity might occur within each pair of orangutans tested even if gift reciprocity did not arise at the group level. We did not find any statistically significant correlations between the number of tokens given and received for partner-valued tokens or for no-value tokens among the 12 sessions for any pair of individuals.

Because reciprocity did not appear during other testing sessions, we studied the possibility that gifts could be correlated to social interactions between the subjects when they were back in their social group. Affiliation levels between group members did not explain the gifts observed during testing sessions; number of tokens given were not significantly correlated with the number of scans of allogroom, physical contact, and proximity between apes (Dietz's test; *p* = .685, *r*s = −.13) as the number of tokens received (Dietz's test; *p* = .646, *r*s = −.13).

Discussion

All great ape species learned to exchange the correct tokens with the experimenter. Because transfers in bonobos resulted from a single bonobo's tendency to play, orangutans were the sole species in which transfers occurred consistently. Those transfers, however, were not reciprocal. Only once did we observe an episode involving repeated alternated gifts between a pair of orangutans that might have represented an instance of calculated reciprocity. We found little evidence suggesting that apes took into account the value of the tokens for their partners. Instead, they appeared to transfer tokens spontaneously or in response to gestural requests such as hand begging or pointing toward a particular token. Gifts of tokens were not part of a larger interchange system including social interactions; we found no evidence that the number of gifts was related to the level of affiliation between individuals.

Some abilities required for calculated reciprocity are, however, present in great apes. All four species showed an ability to actively give a token to a conspecific partner. An active gift was the most frequent type of transfer recorded, particularly among orangutans, which sharply contrasts with earlier reports of transfers between conspecifics; in captive capuchin monkeys and chimpanzees, the most commonly reported form of transfer is passive, that is, one individual obtains an item from another without the initial possessor's active help (de Waal, 1989, 1997). In the wild, most transfers between two conspecifics are passive, as in food-sharing and tolerated theft (see Feistner & McGrew, 1989, for review). After chimpanzees' hunting, for example, a possessor of meat tolerates that a previous helper takes some part of the prey (Mitani & Watts, 2001). This tolerance may be interpreted as an interchange system and places the donor as an active partner. As noted by Stevens and Hauser (2005), however, allowing another individual to take appears to be psychologically different from giving. For passive transfers, the calculation between gift and return should not be overestimated, and this result should be considered with caution. Conversely, the occurrence of active gifts in our study indicates that all great apes can intentionally give a good to another when needed.

In earlier studies, active transfers mainly consisted of one individual's laying a good down (Beck, 1973; de Waal, 1997, 1993; Paquette, 1992; Westergaard & Suomi, 1997). Here, we label such transfers *passive*. We observed active transfers, though; they were either indirect gifts when an individual placed a token in the partner's compartment without any physical contact between individuals or direct gifts when one individual delivered a token into the partner's hand or mouth. Indirect gifts were the most frequently observed in three of the four species tested: gorillas, chimpanzees, and bonobos—provided that Yas's unintentional transfers were not taken into account. By contrast, most orangutans' gifts were direct. Such transfers are scarcely observed in nonhuman primates, some have been reported in a few studies involving capuchin monkeys (de Waal, 1997; Westergaard et al., 2007) and symbol language–trained immature chimpanzees (Savage-Rumbaugh et al., 1978). In our study, orangutans appeared to be the only species in which calculation might sustain the gifts observed.

Captive great apes experience physical barriers, so they regularly develop gestures to request desirable but unreachable food and objects from humans (Leavens, Hopkins, & Bard, 2005; see Call & Tomasello, 2007, for a review). Such gestures typically involve the extension of an arm or a hand in a behavior recalling human begging by holding out a hand or pointing gestures. Although most pointing episodes have been observed between nonhuman apes and humans, there are two studies in which pointing occurred between two nonhuman apes. Savage-Rumbaugh (1986) observed a chimpanzee request food from another chimpanzee on repeated occasions during a cooperative task in the laboratory. Veà and Sabater Pi (1998) observed a juvenile bonobo in the wild pointing toward a bush where humans were hiding. In contrast, some form of holding out the hand occurs in food transfers between adults in both captive and wild apes (chimpanzees [Teleki, 1974; van Hooff, 1974], bonobos [de Waal, 1988; Kano, 1992, 1998], and gorillas [Pika, Liebal, & Tomasello, 2003]). Among orangutans, this behavior has mostly been observed among infants begging food from their mother both in the wild and in captivity (Liebal, Pika, & Tomasello, 2006; Rijksen, 1978). In our study, this behavior was not restricted to the mother–infant relationship and occurred between unrelated individuals. Except for gorillas, individuals of each species tested in our study requested tokens by either pointing or holding out the hand, attempting to elicit cooperation from their partner, even though orangutans produced the vast majority of the observed instances. Such occurrences support the view that subjects understood the experimental situation, that is, that they could obtain additional tokens by getting them from their partner. Again, orangutans performed many more begging gestures compared with other apes species, increasing the potential for cooperation from the partner.

The social life of gorillas is characterized by low levels of interactions (Watts, 1996, 2003). Thus, it is understandable that in this study they displayed low rates of gestural communicative signals such as holding out the hand. The lower number of direct gifts and begging gestures recorded in chimpanzees and bonobos than in orangutans is more surprising in view of the mainly solitary life of the latter in the wild, although it has been argued that orangutans are social animals living in an extended social system (Galdikas, 1984; van Schaik & van Hooff, 1996). Nonetheless, bonobos and chimpanzees live in a fusion–fission society (Badrian & Badrian, 1984; Goodall, 1986; White, 1988) in which they face direct competition for mates and food resources (Hare, 2001). They may perceive conspecifics more often as potential competitors than as potential cooperators. The need to out-compete may restrain the emergence of cooperation (Hare, 2001). Recent studies on chimpanzees' cooperation have provided rather contradictory results. Chimpanzees failed to understand the cooperative pointing gesture emitted by a cooperator toward a baited bucket (Herrmann & Tomasello, 2006). Although chimpanzees revealed other-regarding behaviors in nonfood situations (Warneken & Tomasello, 2006) and could solicit partners in a cooperation task (Crawford, 1937), they failed to show altruistic or other-regarding behavior toward conspecifics in food-acquisition situations (Jensen, Hare, Call, & Tomasello, 2006; Silk et al., 2005). Moreover, captive chimpanzees readily solicit help from a human partner, but not from a conspecific (Hirata & Fuwa, 2007).

Compared with other great apes, orangutans face less direct competition on a daily basis (Shumaker, Palkovich, Beck, Guagnano, & Morowitz, 2001). The significant number of gifts recorded in orangutans might underline a greater ability of the individuals to interact with partners, to give, to beg, and to cooperate if not to exchange. Although variations in the social behaviors of the four species tested may partly explain the contrasts found in their rates of gifts, this intriguing result still needs confirmation. It represents a limited number of individuals differing in their developmental history. Further studies with a larger number of individuals and groups will have to confirm that orangutans are more prone to beg and give than other great apes.

The analysis of the gifts performed by orangutans brings insights about their abilities to understand their partner's needs. Economical exchanges are likely to increase when each side knows how partner values the traded item. No doubt the orangutans knew the value of their own tokens because they successfully selected them when exchanging with the experimenter. Knowing whether they understood the value of the token attributed to their conspecific partner is not so clear. We analyzed the gifts after pointing gestures toward tokens and after holding out the hand to the partner. These two behaviors were shown to increase the number of gifts. We found a larger number of valuable tokens were received after pointing, whereas holding-out-hand behavior—that is, directed toward the partner and not toward tokens—was followed by gifts of valuable tokens as often as gifts of nonvaluable ones. From these results, we conclude that donors probably did not understand which tokens were meaningful to their partner.

The occurrence of pointing behavior between orangutans is another intriguing result of our study. Although pointing often occurs in captive apes interacting with humans (Leavens & Hopkins, 1999; Tomasello, 2006), it is generally not reported between two individuals of the same species (but see Savage-Rumbaugh, 1986; Veà & Sabater Pi, 1998). Orangutans had been already trained to point by keepers or human experimenters in previous cognitive tasks, but not in our study. The subjects were not observed pointing at tokens when interacting with the human experimenter, but they did so when interacting with a conspecific. Such instances of pointing appeared to have an imperative motivation ("Give me this"), not a declarative one ("look at this"; Call & Tomasello, 2007; Gómez, Sarrià, & Tamarit, 1993). The recipients of pointing appeared to understand this gesture as a request because they transferred the partner-valued tokens more often than in the absence of pointing. However, these request–comply routines that included the participation of gestures did not develop into full-fledged reciprocal exchanges. Before conventional exchanges, *Hominini* reciprocity may have been partially restrained by social constraints like those found in nonhuman primates. Prosociality and intentional giving likely played an important role in the hominization process (Stoczkowski, 1994), making possible the emergence of complex social rules of exchange based on reciprocity.

References

Addessi, E., Crescimbene, L., & Visalberghi, E. (2007). Do capuchin monkeys (*Cebus apella*) use tokens as symbols? *Proceedings of the Royal Society of London, Series B, 274,* 2709–2715.

Addessi, E., Crescimbene, L., & Visalberghi, E. (2008). Food and token quantity discrimination in capuchin monkeys (*Cebus apella*). *Animal Cognition, 11,* 275–282.

Altmann, J. (1974). Observational study of behavior: Sampling methods. *Behaviour, 49,* 227–267.

Badrian, A., & Badrian, N. (1984). Social organization of *Pan paniscus* in the Lomako forest, Zaire. In R. L. Susman (Eds.), *The pygmy chimpanzee: Evolutionary biology and behavior* (pp. 325–346). New York: Plenum Press.

Beck, B. B. (1973). Cooperative tool use by captive hamadryas baboons. *Science, 182,* 594–597.

Brosnan, S. F., & de Waal, F. B. M. (2004). Socially learned preferences for differentially rewarded tokens in the brown capuchin monkeys (*Cebus apella*). *Journal of Comparative Psychology, 118,* 133–139.

Brosnan, S. F., & de Waal, F. B. M. (2005). Responses to a simple barter task in chimpanzees, *Pan troglodytes. Primates, 46,* 173–182.

Call, J., & Tomasello, M. (2007). The gestural communication of apes and monkeys. Mahwah, NJ: Erlbaum.

Crawford, M. P. (1937). The cooperative solving of problems by young chimpanzees. *Comparative Psychology Monographs, 14,* 1–88.

de Vries, H., Netto, W. J., & Hanegraaf, P. L. H. (1993). Matman: A program for the analysis of sociometric matrices and behavioural transition matrices. *Behaviour, 125,* 157–175.

de Waal, F. B. M. (1988). The communicative repertoire of captive bonobos (*Pan paniscus*) compared to that of chimpanzees. *Behaviour, 106,* 183–251.

de Waal, F. B. M. (1989). Food sharing and reciprocal obligations among chimpanzees. *Journal of Human Evolution, 18,* 433–459.

de Waal, F. B. M. (1997). Food transfers through mesh in brown capuchins. *Journal of Comparative Psychology, 4,* 370–378.

de Waal, F. B. M., & Luttrell, L. M. (1988). Mechanisms of social reciprocity in three primate species: Symmetrical relationship characteristics or cognition? *Ethology and Sociobiology, 9,* 101–118.

de Waal, F. B. M., Luttrell, L. M., & Canfield, M. E. (1993). Preliminary data on voluntary food sharing in brown capuchin monkeys. *American Journal of Primatology, 29,* 73–78.

Drapier, M., Chauvin, C., Dufour, V., Uhlrich, P., & Thierry, B. (2005). Food-exchange with humans in brown capuchin monkeys. *Primates, 46,* 241–248.

Dufour, V., & Sterck, E. H. M. (2008). Chimpanzees (*Pan troglodytes*) fail to plan in an exchange task, but succeed in a tool using procedure. *Behavioural Processes, 79,* 19–27.

Feistner, A. T. C., & McGrew, W. C. (1989). Food-sharing in primates: A critical review. In P. K. Seth & S. Seth (Eds.), *Perspectives in primate biology* (pp. 21–36). New Delhi, India: Today's and Tomorrow's.

Galdikas, B. M. F. (1984). Adult female sociality among wild orangutans at Tanjung Puting Reserve. In M. F. Small (Eds.), *Female primates: Studies by female primatologists* (pp. 217–235). New York: Alan B. Liss.

Gómez, J. C., Sarrià, E., & Tamarit, J. (1993). The comparative study of early communication and theories of mind: Ontogeny, phylogeny and pathology. In S. Baron-Cohen, H. Tager-Flusberg, & D. Cohen (Eds.), *Understanding other minds: Perspectives from autism* (pp. 397–426). Oxford, England: Oxford University Press.

Goodall, J. (1986). *The chimpanzees of Gombe: Patterns of behaviour.* Cambridge, MA: Harvard University Press.

Hare, B. (2001). Can competitive paradigms increase the validity of social cognitive experiments on primates? *Animal Cognition, 4,* 269–280.

Hemelrijk, C. K. (1996). Reciprocation in apes: From complex cognition to self-structuring. In W. C. McGrew, L. F. Marchant, & T. Nishida (Eds.), *Great ape societies* (pp. 185–195). Cambridge, England: Cambridge University Press.

Herrmann, E., & Tomasello, M. (2006). Apes' and children's understanding of cooperative and competitive motives in a communicative situation. *Developmental Science, 9,* 518–529.

Hirata, S., & Fuwa, K. (2007). Chimpanzees (*Pan troglodytes*) learn to act with other individuals in a cooperative task. *Primates, 48,* 13–21.

Hyatt, C. W., & Hopkins, W. D. (1998). Interspecies object exchange: Bartering in apes? *Behavioural Processes, 42,* 177–187.

Jensen, K., Hare, B., Call, J., & Tomasello, M. (2006). What's in it for me? Self-regard precludes altruism and spite in chimpanzees. *Proceedings of the Royal Society of London, Series B, 273,* 1013–1021.

Kano, T. (1992). *The last ape: Pygmy chimpanzee behavior and ecology.* Stanford, CA: Stanford University Press.

Kano, T. (1998). A preliminary glossary of bonobos behaviors at Wamba. In T. Nishida (Eds.), *Comparative study of the behavior of the genus Pan by compiling video ethogram* (pp. 39–81). Kyoto, Japan: Nissho.

Leavens, D. A., & Hopkins, W. D. (1999). The whole hand point: The structure and function of pointing from a comparative perspective. *Journal of Comparative Psychology, 113,* 417–425.

Leavens, D. A., Hopkins, W. D., & Bard, K. A. (2005). Understanding the point of chimpanzee pointing: Epigenesis and ecological validity. *Current Directions in Psychological Science, 14,* 185–189.

Lefebvre, L. (1982). Food exchange strategies in an infant chimpanzee. *Journal of Human Evolution, 11,* 195–204.

Lefebvre, L., & Hewitt, T. A. (1986). Food exchange in captive chimpanzees. In D. M. Taub & F. A. King (Eds.), *Current perspectives in primate social dynamics* (pp. 476–486). New York: Van Nostrand Reinhold.

Liebal, K., Pika, S., & Tomasello, M. (2006). Gestural communication of orangutans (*Pongo pygmaeus*). *Gestures, 6,* 1–38.

Melis, A. P., Hare, B., & Tomasello, M. (2006a). Chimpanzees recruit best collaborators. *Science, 311,* 1297–1300.

Melis, A. P., Hare, B., & Tomasello, M. (2006b). Engineering cooperation in chimpanzees: Tolerance constraints on cooperation. *Animal Behaviour, 72,* 275–286.

Mitani, J. C., & Watts, D. P. (2001). Why do chimpanzees hunt and share meat? *Animal Behaviour, 61,* 915–924.

Mulcahy, N. J., & Call, J. (2006). Apes save tools for future use. *Science, 312,* 1038–1040.

Padoa-Schioppa, C., Jandolo, L., & Visalberghi, E. (2006). Multi-stage mental process for economic choice in capuchins. *Cognition, 99,* B1–B13.

Paquette, D. (1992). Object exchanges between captive chimpanzees: A case report. *Human Evolution, 7,* 11–15.

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.

Rijksen, H. D. (1978). *A field study on Sumatra orang utans (Pongo pygmaeus abelli Lesson 1827): Ecology, behaviour and conservation.* Wageningen, the Netherlands: H. Veenman & Zonen.

Savage-Rumbaugh, E. S. (1986). *Ape language: From conditioned response to symbol.* New York: Columbia University Press.

Savage-Rumbaugh, E. S., Rumbaugh, D., & Boysen, S. (1978). Linguistically mediated tool use and exchange by chimpanzees (*Pan troglodytes*). *Behavioural and Brain Sciences, 4,* 539–554.

Seyfarth, R. M., & Cheney, D. L. (1988). Empirical tests of reciprocity theory: Problems in assessment. *Ethology and Sociobiology, 9,* 181–187.

Shumaker, R. W., Palkovich, A. M., Beck, B. B., Guagnano, G. A., & Morowitz, H. (2001). Spontaneous use of magnitude discrimination and ordination by the orangutan (*Pongo pygmaeus*). *Journal of Comparative Psychology, 115,* 385–391.

Siegel, S., & Castellan, J. (1988). *Nonparametric statistics for the behavioural sciences.* New York: McGraw-Hill.

Silk, J. B., Brosnan, S. F., Vonk, J., Henrich, J., Povinelli, D. J., Richardson, A. F., . . . & Schapiro, S. J. (2005). Chimpanzees are indifferent to the welfare of other group members. *Nature, 435,* 1357–1359.

Sousa, C., & Matsuzawa, T. (2001). The use of tokens as rewards and tools by chimpanzees (*Pan troglodytes*). *Animal Cognition, 4,* 213–221.

Sousa, C., Okamoto, S., & Matsuzawa, T. (2003). Behavioural development in a matching-to sample task and token use by an infant chimpanzee reared by his mother. *Animal Cognition, 6,* 259–267.

Stevens, J. R., & Hauser, M. D. (2005). Cooperative brains: Psychological constraints on the evolution of altruism. In J. R. Dehaene, G. Duhamel, G. Rizolatti, & M. D. Hauser (Eds.), *From monkey brain to human brain* (pp. 159–187). Cambridge, MA: MIT Press.

Stoczkowski, W. (1994). *Anthropologie naïve, anthropologie savante* [*Native anthropology, scholar anthropology*]. Paris: CNRS Editions.

Teleki, G. (1974). *The predatory behavior of wild chimpanzees.* Lewisburg, PA: Bucknell University Press.

Tomasello, M. (2006). Why don't apes point? In N. Enfield & S. Levinson (Eds.), *Roots of human sociality: Culture, cognition and interaction* (pp. 506–524). Oxford, England: Berg.

van Hooff, J. A. R. A. M. (1974). A structural analysis of the social behaviour of a semi-captive group of chimpanzees. In M. von Cranach & I. Vine (Eds.), *Social communication and movement* (pp. 75–162). London: Academic Press.

van Schaik, C. P., & van Hooff, J. A. R. A. M. (1996). Toward an understanding of the orangutan's social system. In W. C. McGrew, L. F. Marchant, & T. Nishida (Eds.), *Great ape societies* (pp. 3–15). New York: Cambridge University Press.

Veà, J., & Sabater Pi, J. (1998). Spontaneous pointing behaviour in the wild pygmy chimpanzees (*Pan paniscus*). *Folia Primatologica, 69,* 289–290.

Warneken, F., & Tomasello, M. (2006). Altruistic helping in human infants and young chimpanzees. *Science, 311,* 1301–1303.

Watts, D. P. (1996). Comparative socio-ecology of gorillas. In W. C. McGrew, L. F. Marchant, & T. Nishida (Eds.), *Great ape societies* (pp. 16–28). Cambridge, England: Cambridge University Press.

Watts, D. P. (2003). Gorilla social relationships: A comparative review. In A. B. Taylor & M. L. Goldsmith (Eds.), *Gorilla biology: A multidisciplinary perspective* (pp. 302–327). Cambridge, England: Cambridge University Press.

Westergaard, G. C., Evans, T. A., & Howell, S. (2007). Token mediated tool exchange between tufted capuchin monkeys (*Cebus apella*). *Animal Cognition, 10,* 407–414.

Westergaard, G. C., Liv, C., Chavanne, T. J., & Suomi, S. J. (1997). Token mediated tool-use by a tufted capuchin monkey (*Cebus apella*). *Animal Cognition, 1,* 101–106.

Westergaard, G. C., Liv, C., Rocca, A. M., Cleveland, A., & Suomi, S. J. (2004). Tufted capuchins (*Cebus apella*) attribute to foods and tools during voluntary exchanges with humans. *Animal Cognition, 7,* 19–24.

Westergaard, G. C., & Suomi, S. J. (1997). Transfer of tools and food between groups of tufted capuchins (*Cebus apella*). *American Journal of Primatology, 43,* 33–41.

White, F. (1988). Party composition and dynamics in *Pan paniscus. International Journal of Primatology, 9,* 179–193.

Received November 19, 2007
Revision received July 31, 2009
Accepted July 31, 2009 ■

Call for Nominations

The Publications and Communications (P&C) Board of the American Psychological Association has opened nominations for the editorships of **Experimental and Clinical Psychopharmacology, Journal of Abnormal Psychology, Journal of Comparative Psychology, Journal of Counseling Psychology, Journal of Experimental Psychology: Human Perception and Performance, Journal of Personality and Social Psychology: Attitudes and Social Cognition, PsycCRITIQUES, and Rehabilitation Psychology** for the years 2012–2017. Nancy K. Mello, PhD, David Watson, PhD, Gordon M. Burghardt, PhD, Brent S. Mallinckrodt, PhD, Glyn W. Humphreys, PhD, Charles M. Judd, PhD, Danny Wedding, PhD, and Timothy R. Elliott, PhD, respectively, are the incumbent editors.

Candidates should be members of APA and should be available to start receiving manuscripts in early 2011 to prepare for issues published in 2012. Please note that the P&C Board encourages participation by members of underrepresented groups in the publication process and would particularly welcome such nominees. Self-nominations are also encouraged.

Search chairs have been appointed as follows:

- **Experimental and Clinical Psychopharmacology,** William Howell, PhD
- **Journal of Abnormal Psychology,** Norman Abeles, PhD
- **Journal of Comparative Psychology,** John Disterhoft, PhD
- **Journal of Counseling Psychology,** Neil Schmitt, PhD
- **Journal of Experimental Psychology: Human Perception and Performance,** Leah Light, PhD
- **Journal of Personality and Social Psychology: Attitudes and Social Cognition,** Jennifer Crocker, PhD
- **PsycCRITIQUES,** Valerie Reyna, PhD
- **Rehabilitation Psychology,** Bob Frank, PhD

Candidates should be nominated by accessing APA's EditorQuest site on the Web. Using your Web browser, go to http://editorquest.apa.org. On the Home menu on the left, find "Guests." Next, click on the link "Submit a Nomination," enter your nominee's information, and click "Submit."

Prepared statements of one page or less in support of a nominee can also be submitted by e-mail to Emnet Tesfaye, P&C Board Search Liaison, at emnet@apa.org.

Deadline for accepting nominations is January 10, 2010, when reviews will begin.

Article 6

La réciprocité calculée chez deux orangs-outangs

Article publié dans *Biology Letters*

RESUME DE L'ARTICLE 6

Introduction

Au cours de l'étude précédente, deux orangs-outangs se sont montrés capables de donner un objet à un congénère pour ensuite l'échanger contre de la nourriture avec un expérimentateur. Quelques dons réciproques ont également été constatés entre ces individus. J'ai simplifié le protocole et soumis ces deux sujets à un plus grand nombre de tests de manière à étudier si une suite d'échanges peut s'instaurer entre ces deux sujets.

Méthodes

Deux orangs-outangs adultes, un mâle et une femelle, avaient été entraînés à échanger un type d'objet parmi trois auprès d'un expérimentateur contre une récompense alimentaire lors d'une précédente étude. Au cours des séances de test, les sujets étaient placés dans deux compartiments adjacents séparés par une cloison grillagée. Lors d'une première phase (une série de 12 tests), les sujets disposaient chacun du même lot d'objets comprenant 12 objets de valeur, 12 objets de valeur du partenaire et 12 objets sans valeur. Lors d'une seconde phase de test (3 séries de 12 tests chacune), les sujets n'avaient plus en leur possession que 12 objets de valeur du partenaire et 12 objets sans valeur. Les sujets devaient obtenir de leur partenaire un objet de valeur afin d'obtenir des récompenses alimentaires auprès de l'expérimentateur.

Résultats

Au cours des 48 tests effectués, 215 transferts d'objets ont été observés entre les deux orangs-outangs. Les sujets ont transféré significativement plus d'objets de valeur du partenaire que d'objets sans valeur. Lors des premiers tests, les objets de valeur étaient majoritairement transférés par la femelle. Au cours des tests, la femelle a de moins en moins transféré d'objets de valeur au mâle alors que celui-ci au contraire en a transféré de plus en plus à la femelle. Les transferts se sont donc équilibrés entre les individus tout au long de l'étude. Au fur et mesure des tests, l'alternance des rôles de donneur et récepteur a également augmenté et elle est passé de deux alternances consécutives dans les premiers tests à cinq alternances consécutives dans les derniers tests.

Conclusion

Une alternance des rôles s'est établie à court terme, pour ensuite se stabiliser sur plusieurs tests, permettant ainsi l'émergence d'un système d'échanges entre les deux orangs-outangs.

Cette étude est la première à apporter la démonstration expérimentale de la faculté des grands singes à faire preuve de réciprocité calculée.

biology
letters
Animal behaviour

Biol. Lett.
doi:10.1098/rsbl.2008.0644

Published online

Calculated reciprocity after all: computation behind token transfers in orang-utans

V. Dufour[1,2,*], **M. Pelé**[2], **M. Neumann**[3], **B. Thierry**[2] **and J. Call**[3]

[1] *School of Psychology, University of St Andrews, St Andrews, Fife KY16 9JP, UK*
[2] *Département of Ecologie, Physiologie & Ethologie, IPHC, CNRS, Université Louis Pasteur de Strasbourg, 67087 Cedex, France*
[3] *Max Planck Institute for Evolutionary Anthropology, 01403 Leipzig, Germany*
**Author for correspondence* (*vmd1@st-andrews.ac.uk*).

Transfers and services are frequent in the animal kingdom. However, there is no clear evidence in animals that such transactions are based on weighing costs and benefits when giving or returning favours and keeping track of them over time (i.e. calculated reciprocity). We tested two orang-utans (*Pongo pygmaeus abelii*) in a token-exchange paradigm, in which each individual could exchange a token for food with the experimenter but only after first obtaining the token from the other orang-utan. Each orang-utan possessed tokens valuable to their partner but useless to themselves. Both orang-utans actively transferred numerous tokens (mostly partner-valuable) to their partner. One of the orang-utans routinely used gestures to request tokens while the other complied with such requests. Although initially the transfers were biased in one direction, they became more balanced towards the end of the study. Indeed, data on the last three series produced evidence of reciprocity both between and within trials. We observed an increase in the number and complexity of exchanges and alternations. This study is the first experimental demonstration of the occurrence of direct transfers of goods based on calculated reciprocity in non-human-primates.

Keywords: reciprocal giving; exchange; bartering; economics; primates

1. INTRODUCTION

Economics in human societies constitute a notable anomaly compared with the animal kingdom. While there are numerous examples of reciprocal transfers of services among animals (Dugatkin 1997), there is little experimental evidence that such transfers rely on calculated reciprocity, i.e. weighing costs and benefits when giving or returning favours and keeping track of those transactions (de Waal & Luttrell 1988). This absence is particularly puzzling because monkeys and apes possess cognitive prerequisites for calculated reciprocity including memory for past interactions, tolerance to delay of gratification and they can readily exchange tokens or food with humans (e.g. de Waal 1989; Westergaard *et al.* 2007).

Although passive food transfers are frequently observed among conspecifics (Mitani & Watts 2001), active transfers are much less frequent (de Waal 1997) and reciprocal food transfers are virtually non-existent in non-human primates. As stressed by Hemelrijk (1996), the correlations observed in the reciprocity of positive behaviours are not sufficient to conclude on the calculation that would sustain this reciprocity. Instead, most transfers may rely on symmetry-based or attitudinal reciprocity (Brosnan & de Waal 2002), two forms of reciprocity where no calculation is involved. Studying active transfers is the best way to assess whether individuals calculate their own losses and gains and keep track of them over time. Capuchin monkeys (*Cebus apella*) were recently shown to exhibit active transfers of tools but the recipient never returned a share of the reward to the donor (Westergaard *et al.* 2007). Savage-Rumbaugh *et al.* (1978) reported cases of direct transfers of tools in young chimpanzees (*Pan troglodytes*), which could be based on computation. Transfers involved subsequent sharing of food and role alternations in both individuals. Subjects in this study were young chimpanzees, symbol-language trained and more likely prone to cooperate than adult wild chimpanzees.

To qualify reciprocal giving as 'calculated giving with return expectancy', it must be shown that (i) giving occurs intentionally from one partner to another, (ii) partners know the value of the traded items for both sides and (iii) partners expect given items to be returned. Directly transferring to the partner's hand or mouth the items, which the donor selected among the available alternatives and which are useful to the partner but useless to the donor, indicates that the donor's actions are intentional and based on knowledge about the value of items for her partner. Return expectancy can only be assessed by the capacity of the donor to adapt to the partner's behaviour. For example, generous donors should give less and less if their transfers are never or infrequently returned, conversely less cooperative individuals should give more and more to secure or maintain their partner's cooperation. Ultimately, a balance should be reached between partners' giving and receiving.

Recently, we have compared the propensity of gorillas (*Gorilla gorilla*), orang-utans (*Pongo pygmaeus abelii*), bonobos (*Pan paniscus*) and chimpanzees to spontaneously exchange tokens of different values with a conspecific (Pelé *et al.* in press). Self-value tokens received from a partner could further be exchanged for food with the experimenter. Orang-utans exhibited the highest number of token transfers. One pair of orang-utans exhibited reciprocal transfers although those transfers were mostly biased in one direction. The present study aimed at exploring whether the propensity to give in orang-utans may depreciate over time and trial repetition owing to a lack of reciprocity or, instead, evolve towards balanced exchanges.

2. MATERIAL AND METHODS

Two orang-utans (*Pongo pygmaeus abelii*), a male (Bim, 26 years old) and a female (Dok, 15 years old) socially housed at the Wolfgang Köhler Primate Research Center, Leipzig Zoo (Germany) were tested. Prior to the present experiments, they had been tested

Electronic supplementary material is available at http://dx.doi.org/10.1098/rsbl.2008.0644 or via http://journals.royalsociety.org.

Received 5 November 2008
Accepted 2 December 2008

This journal is © 2008 The Royal Society

Table 1. Number and direction of active and passive transfers per individual (excluding the offspring) as a function of the token value. (Asterisks indicate that the observed distribution deviated from 50 : 50 (binomial test: $^{*}p<0.01$; $^{**}p<0.001$). Shown in parentheses are the transferred non-token items (valuable: banana peels; valueless: papers, straws and sticks).)

	Dokana→Bimbo			Bimbo→Dokana		
	type of token			type of token		
type of transfer	valuable	valueless	total	valuable	valueless	total
active	59**	25 (2)	86	19 (14)*	6 (8)	47
passive	79**	1	80	2	0	2
total	138**	28	116	35*	14	49

in various cognitive tasks. Dok's offspring, a juvenile male named Pag (also the son of Bimbo), remained with her during testing. Despite being close affiliates, the male and the female were not normally seen sharing food or sitting together.

In a previous study, both subjects had been trained individually to exchange one of three types of tokens for food. A first series of trials conducted one month after the end of the previous study served as a refresher of the exchange procedure and consisted of 12 trials. In this series, both subjects entered their own side of a room divided by a mesh through which they could transfer tokens to each other. Prior to subjects entrance, a set of 36 tokens had been left in each compartment: 12 *self-value tokens*, exchangeable with the experimenter for food, 12 *partner-value tokens* that only their partner could exchange for food and 12 *no-value tokens* for which both subjects received nothing. In the following three 12-trial series, each subject received only 12 partner- and 12 no-value tokens. Thus, each subject first needed to obtain their self-value token from their partner. Subjects were tested at the rate of one trial per day. In the first 3 min, partner could exchange their self-value token with the human experimenter (series 1) or start exchanging tokens with the partner (series 2–4). Then the experimenter left the room for 3 min to avoid influencing possible transfers between subjects and returned afterwards for a minimum duration of 3 min. Whenever transfers of valuable tokens occurred between subjects, the experimenter requested and exchanged them for food. A trial ended when transfers did not occur after 6 min. We recorded active transfers (placing a token into the hand, mouth or cage of the partner) and passive transfers (placing the token in her own cage but near the mesh so that the partner could take it). We also observed transfers of edible (banana peel) and non-edible items (paper, straw). Since edible items were eaten upon receipt and non-edible items were discarded, we treated them as tokens and included them in the analyses.

3. RESULTS

We observed 215 transfers between the two individuals in the course of the four series (48 trials). Table 1 presents the number of active and passive transfers per individual as a function of the token value. The male mostly used active transfers, whereas the female displayed a similar number of active and passive transfers. However, most of the female passive transfers concerned partner-valuable tokens, which she displaced towards the cage fence within the male's reach. In particular, she displaced 63 and 19 partner-valuable and partner-valueless tokens near the fence, respectively. Both subjects transferred more partner-valuable tokens to their partner than non-valuable ones (binomial test, $p<0.001$; see the electronic supplementary material). This result remained unchanged after restricting the analysis to the active transfers (binomial test, $p<0.001$).

Figure 1 presents the number of valuable tokens transferred according to series. Although initially transfers were biased in favour of the male (binomial test: $p<0.001$), values converged over time until no significant difference was found in the last series (binomial test, $p=0.1$). Interestingly, the overall number of valuable transfers remained largely unchanged across series ($n=48$, 42, 39 and 44, respectively).

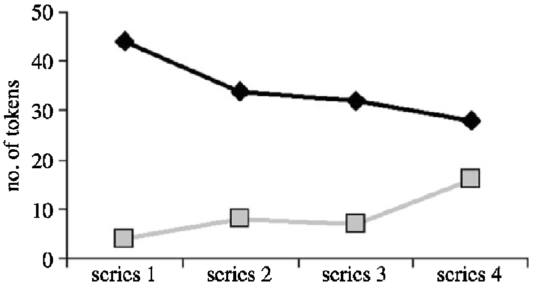


Figure 1. Number of partner-value tokens (including banana peel) transferred by individuals (excluding the offspring) in each of the four series (diamonds, Dok; squares, Bim).

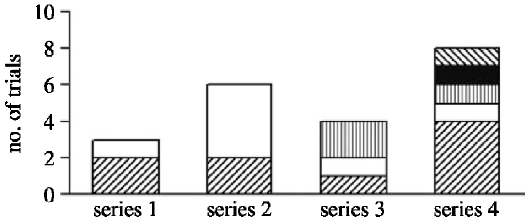


Figure 2. Occurrence of reciprocity and length of consecutive turn-taking per trials between donor and recipient in each of the four test series (excluding the offspring; left-hatched bar, five turn taking; black bar, four turn taking; vertical striped bars, three turn taking; white bars, two turn taking; right-hatched bars, one turn taking).

When considering only the last three series where individuals had to obtain their self-value token from their partner, we found a significant correlation between the number of partner-value tokens received and given (Kendall rank correlation test, $\tau=0.244$, $Z=2.09$, $p=0.036$, $n=36$). From series 2, we also observed an increase in the number of bilateral transfers of valuable tokens involving at least one turn taking compared with series 1 (three transfers in series 1, and 6, 4 and 8 transfers in the following three series, respectively; figure 2). Moreover, the successive turn takings occurring within a trial increased from a maximum of two in series 2 to a maximum of five in series 4. Reciprocation of valuable tokens was not immediate; there was some time delay between receiving and giving back a valuable token (the male: 15–236 s, mean = 84 s; the female: 21–544 s, mean = 149 s). This delay includes the time needed to exchange the token with the experimenter and eat the reward.

The use of gestural communication (pointing and holding-out-hand) differed between the two subjects. The male routinely pointed to tokens (241 times) and held his hand out in the direction of tokens (21 times) to request transfers. His total number of begging gestures increased over time (series 1, 35; series 2, 55; series 3, 82; series 4, 90) yet the percentage of times that begging led to the return of a valuable token sharply decreased over successive series (52.3, 14.3, 16.1 and 12.1%, see the electronic supplementary material). By contrast, the female rarely gestured (one pointing; four holding-out-hands) to request tokens. In addition to the transfers reported earlier, we observed supplementary transfers between the male and the female's offspring. Overall, the female's son transferred a total of 23 tokens (21 of them valuable) to the male whereas the male transferred 8 tokens to the offspring (6 of them valuable). The female took all the valuable tokens from her son upon receipt. The offspring began transferring and receiving tokens from the male in series 2 and 3, respectively. One sequence of transfers between the male and the offspring reached a maximum of four consecutive turn taking within a trial in series 4.

4. DISCUSSION

Both adult orang-utans actively transferred numerous valuable tokens to their partner. This result contrasts with the reports that another ape species, chimpanzees, mainly fail to show prosocial behaviours in an experimental set-up (Melis *et al.* 2008; Vonk *et al.* 2008). However, orang-utans may differ from more prosocial species such as capuchins where giving seems to be self-rewarding (de Waal *et al.* 2008), since they transfer tokens based on computation and return expectancy. Although the transfers were initially biased in one direction, they became more balanced towards the end of the study; data from the last three series produced evidence of reciprocity both between and within trials. We observed an increase in the occurrence and length of consecutive turn taking. This is the first experimental demonstration in non-human primates of the occurrence of calculated reciprocity through the repeated exchanges of goods. It is currently unclear whether simply increasing the number of trials or slightly changing the procedure by compelling orang-utans to exchange with their partner to get valuable tokens was the reason for the appearance of a more sophisticated token transfer system. The intentionality behind giving, the computation based on expected returns, in addition to the shared knowledge of the value of the traded items showed that calculated reciprocity underpinned the transfers of goods.

Orang-utans are known to modify their gestural signals according to the comprehension of their human audience (Cartmill & Byrne 2008). Gesturing to communicate one's needs and complying with requests of their partner show that subjects understood the need of each other and may have used gestural signals to elicit faster responses. Gesturing may have been instrumental in, at least jump starting, the reciprocal transfers. Indeed, communication became less effective over time either because each partner's needs were mutually understood or the female stopped honouring all requests perhaps to press the male into transferring her tokens. An unexpected result was that the juvenile orang-utan spontaneously started transferring and receiving tokens (mostly valuable) from the adult male. The involvement of the juvenile individual may have additionally created some partner-choice opportunities, transforming an initially bilateral situation into a market-like one (Noë 2005). It may have modified the balance of supply and demand. The female often stole the tokens received by her offspring from the male preventing further comparison with a multi-partner trading situation.

Human societies have built complex social networks based on language and cultural norms. Economic trade is another route for complex exchanges between individuals that rests on the mutual comprehension of the value of traded goods and tracking the flow of transactions. Calculated reciprocity may play a similar role in species not relying on language or culture, and provide a further way to extend relationships beyond the affiliative network. Future studies should confirm and extend our results to further individuals and species in more natural contexts. Special attention has to be paid to social tolerance, communication, and request compliance and to the abilities to understand others' needs, which are liable to foster the appearance of mutual exchange.

The work with animals was done according to the principles and guidelines of the German regulations for the treatment of experimental animals.

We are grateful to Marietta Dindo for helpful comments on the manuscript and to the keepers of the zoo of Leipzig for assistance with testing.

Brosnan, S. F. & de Waal, F. B. M. 2002 A proximate perspective on reciprocal altruism. *Hum. Nat.* **13**, 129–152. (doi:10.1007/s12110-002-1017-2)

Cartmill, E. A. & Byrne, R. W. 2008 Orangutans modify their gestural signalling according to their audience's comprehension. *Curr. Biol.* **17**, 1345–1348. (doi:10.1016/j.cub.2007.06.069)

de Waal, F. B. M. 1989 Food sharing and reciprocal obligations among chimpanzees. *J. Hum. Evol.* **18**, 433–459. (doi:10.1016/0047-2484(89)90074-2)

de Waal, F. B. M. 1997 Food transfers through mesh in brown capuchins. *J. Comp. Psychol.* **4**, 370–378.

de Waal, F. B. M. & Luttrell, L. M. 1988 Mechanisms of social reciprocity in three primate species: symmetrical relationship characteristics or cognition? *Ethol. Sociobiol.* **9**, 101–118. (doi:10.1016/0162-3095(88)90016-7)

de Waal, F. B. M., Leimgruber, K. & Greenberg, A. R. 2008 Giving is self rewarding for monkey. *Proc. Natl Acad. Sci. USA* **105**, 13 685–13 689. (doi:10.1073/pnas.0807060105)

Dugatkin, L. A. 1997 *Cooperation among animals: an evolutionary perspective*. Oxford, UK: Oxford University Press.

Hemelrijk, C. K. 1996 Reciprocation in apes: from complex cognition to self-structuring. In *Great ape societies* (eds W. C. McGrew, L. F. Marchand & T. Nishida), pp. 185–195. Cambridge, UK: Cambridge University Press.

Melis, A. P., Hare, B. & Tomasello, M. 2008 Do chimpanzees reciprocate received favours? *Anim. Behav.* **75**, 1557–1770.

Mitani, J. C. & Watts, D. P. 2001 Why do chimpanzees hunt and share meat? *Anim. Behav.* **61**, 915–924. (doi:10.1006/anbe.2000.1681)

Noë, R. 2005 Digging for the roots of trading. In *Cooperation in primates and humans. Mechanisms and evolution* (eds P. M. Kappeler & C. P. van Schaik), pp. 233–261. Heidelberg, Germany: Springer.

Pelé, M., Dufour, V., Thierry, B. & Call, J. In press. Token transfers among great apes: species differences, gestural requests and reciprocal exchange. *J. Comp. Psychol.*

Savage-Rumbaugh, E. S., Rumbaugh, D. & Boysen, S. 1978 Linguistically mediated tool use and exchange by chimpanzees (*Pan troglodytes*). *Behav. Brain Sci.* **4**, 539–554.

Vonk, J., Brosnan, S. F., Silk, J. B., Henrich, J., Richardson, A. S., Lambeth, S. P., Shapiro, S. J. & Povinelli, D. J. 2008 Chimpanzees do not take advantage of very low cost opportunities to deliver food to unrelated group members. *Anim. Behav.* **79**, 1557–1770.

Westergaard, G. C., Evans, T. A. & Howell, S. 2007 Token mediated tool exchange between tufted capuchin monkeys (*Cebus apella*). *Anim. Cogn.* **10**, 407–414. (doi:10.1007/s10071-007-0072-9)

Electronic Supplementary Material

Transfers of valueless tokens

Transfers of valueless tokens were less frequent than transfers of valuable ones (see results). We observed a sharp but short-lived increase of those transfers to the male in series 3 by the female (22 tokens) that did not persist in series 4. Upon receiving valueless tokens, subjects either ignored them or played with them. Subjects never attempted to exchange valueless tokens received from their partner. Giving back valueless tokens initially received from the partner was observed on 5 occasions (4 by the male, 1 by the female).

Giving to the experimenter valueless (8) or partner valuable tokens (25) occurred occasionally but mostly towards the end of the trials. Those exchanges remained rare compared to the total number of transfers to the partner (215). The female handed most of the incorrect tokens to the experimenter (22 for her compared to 4 for the male). Whether she expected to receive a reward for those tokens is difficult to assess. When an incorrect token was handed back to the experimenter, the experimenter discarded it in a “bin-bucket”. This bucket was different from the one where correct tokens were stored after they had been exchanged. Interestingly, on one occasion, the female discarded a partner valuable token in the “bin-bucket”, without first attempting to give it to the experimenter. This observation as well as the fact that giving to the experimenter mostly occurred after the extinction of any other type of transfers, suggests that she knew that no reward could be collected from those tokens.

Previous experience in attempting to exchange valueless tokens cannot have driven the subjects to preferentially select and transfer partner valuable tokens. During their initial training (see Pelé et al., in press), subjects had learned that only their own valuable tokens could be exchanged for a reward. Therefore, both valueless and partner valuable tokens had an equivalent lack of value at the start of this study.

Behavioural responses to expectancy violation?

Exploring the behavioural response performed in case of expectancy violation is a challenging task. Subjects did not show behavioural signs that would reflect frustration, if their expectancies had been violated. The male sometimes “displayed” but not in a way obviously related to the females’ propensity to cooperate. Gestural requests is one behaviour where context of emission can be clearly identified and attributed (or not) to expectancy violation. As shown in the results, the male produced gestural requests on numerous occasions throughout the study. Mostly, he gestured whenever the female or the offspring would be manipulating tokens close from the fence, or after having himself exchanged a self-value token with the experimenter, therefore requesting even more tokens from the female. As the study progressed, the male increased his number of transfers and his gestural requests became more frequent, while at the same time being less successful. Gestural requests could therefore be understood as a response to expectancy violation, whereby it would be produced mostly after a transfer failed to be rewarded by a return. In the male, occurrences of pointing or holding out a hand just before or after a transfer to the female were observed (series 1: 4; series 2: 18, series 3: 25, series 4: 35) but did not represent the majority of the gestural requests (series 1: 35, series 2: 55, series 3: 82, series 4: 90). Those occurrences mainly consisted in sequences with repeated alternations between gestural requests and transfers to the female. For each of those sequences, transferring first and then gesturing occurred in 22 occasions (token transferred: 15 partner valuable, 7 valueless). Gesturing unsuccessfully first and then transferring occurred on 12 occasions (9 partner valuable; 3 valueless). In the first case, expectation-violation may explain the production of gestural request, in the second case, unsuccessful request may be followed by transfers to "secure" the female cooperation. None of those scenarios however predominantly explain the amount of gestural requests observed. As for the female, the decrease of transfers of partner valuable tokens throughout the study (see results) is probably the most obvious response to expectancy violation.

Article 7

L’absence de quémande et de dons chez les macaques de Tonkean et les capucins bruns

Article soumis

RESUME DE L’ARTICLE 7

Introduction

L’étude a pour but de déterminer si des singes sont capables de s’engager dans des échanges spontanés et calculés avec un congénère. Sont-ils capables de donner et de rendre des objets à un congénère ? Existe-t-il des comportements de recrutement tels que des gestes ou des vocalisations ?

Méthodes

Trois macaques de Tonkean et quatre capucins bruns ont été entraînés à discriminer et à échanger une forme d’objet parmi trois contre une récompense alimentaire. Cet objet était l’objet de valeur pour l’individu car seul il pouvait être échangé contre de la nourriture auprès d’un expérimentateur. Lors de la phase de test, les sujets étaient testés deux par deux dans des compartiments adjacents séparés par une cloison grillagée. Chaque individu possédait le même lot d’objets mais les objets de valeur différaient d’un individu à l’autre. Chaque individu possédait donc 12 objets de valeur (échangeable pour de la nourriture), 12 objets de valeur du partenaire (le partenaire pouvait les échanger pour de la nourriture) et 12 objets sans valeur (aucun individu ne pouvait obtenir de nourriture en échangeant ces objets). Dans la première partie du test, les sujets pouvaient échanger la totalité de leurs objets de valeur avec l’expérimentateur. Dans la deuxième partie, les individus devaient transférer des objets entre eux pour obtenir plus de nourriture de la part de l’expérimentateur.

Résultats

J’ai relevé respectivement 10 et 56 transferts d’objets chez les macaques et les capucins. Seuls des transferts passifs au cours desquels un individu prend un objet dans la cage de son partenaire ont été observés. L’analyse des résultats montre que les capucins ont manipulé de préférence les objets de valeur de leur partenaire à proximité de la cloison grillagée. Aucun comportement de quémande n’a été constaté.

Conclusion

Les macaques de Tonkean et les capucins bruns ne se sont pas montrés capables de donner des objets à leur partenaire de manière active et intentionnelle. Chez ces espèces, l’absence de dons et de comportements de quémande pourraient traduire l'incapacité des individus à saisir les besoins de l'autre. Une telle limite cognitive rendrait difficile voire impossible l’émergence de la réciprocité calculée chez ces espèces.

Monkeys fail to reciprocate in an exchange task

Marie Pelé[1], Bernard Thierry[1], Josep Call[2], Valérie Dufour[3]

[1] Département Ecologie, Physiologie & Ethologie, IPHC, Centre National de la Recherche Scientifique, Université de Strasbourg, Strasbourg, France

[2] Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany

[3] Scottish Primate Research Group and Centre for Social Learning and Cognitive Evolution, University of St Andrews, St Andrews, United Kingdom

Abstract

Exchanges form the basis of human economies. Animals too can engage in reciprocal interactions but they do not barter goods like humans, which raises the question of the abilities necessary for trading to occur. Previous studies have shown that non-human primates can exchange food with human partners. Here, we tested the ability of brown capuchin monkeys and Tonkean macaques to reciprocate in a task requiring two conspecifics to exchange tokens in order to obtain rewards from an experimenter. We recorded 56 transfers between subjects in capuchin monkeys and 10 in Tonkean macaques. All transfers were passive in both species. Capuchins preferentially picked up tokens valuable for them in the partner's compartment. They tended to manipulate the partner-valued tokens more often than the no-value ones, leading to more opportunities for these tokens to end up within reach of the partner. Despite optimal conditions where values of goods were defined and known by partners, however, none of the pairs tested engaged in short term reciprocal interactions. These results indicate that calculated reciprocity was difficult if not impossible in the animals tested.

Keywords reciprocity . exchange . tokens . economics . monkeys

INTRODUCTION

Gift and exchange lie at the core of human societies (Mauss 1923/1924); they form the basis of their economies. In traditional societies individuals provide goods for the community; they share the benefits of their skills with others, thus sustaining what has been called natural economics (Sahlins 1972). In Western societies, gift is motivated by expected reciprocity; goods are traded for others, which gives rise to formalist economics. Exchanges of goods or favours are reported in nature too (Dugatkin 1997), but animals do not reciprocate like humans do i.e. based on expected returns, which raises the question of the skills necessary for trading to occur.

Different categories of reciprocation have been reported among unrelated individuals in non-human primates. Partners linked by social bonds interact in a symmetrical way when they react similarly to each other without stipulating equivalent returns (‘symmetry-based reciprocity’: de Waal and Luttrell 1988). Alternatively, when partners behave positively toward each other as a consequence of prior friendly interactions, both mirror the partner attitude, leading to either short-term (‘attitudinal reciprocity’: de Waal 2000) or long-term reciprocal interactions (‘emotional bookkeeping’: Aureli and Schaffner 2002).

A further mode of reciprocation is based on the mental scorekeeping of given and received favours, similar to the calculations involved in the trading of human economics. Such calculated reciprocity could account for the exchange of services like grooming and support in conflict, for instance (Seyfarth and Cheney 1984; de Waal and Luttrell 1988). Correlations drawn from observations in the social context are yet insufficient to demonstrate contingencies between gifts and receipts (Hemelrijk 1996). To assess whether exchanges are based on calculated reciprocity, one needs to show that (1) gifts from one partner to another are intentional, (2) partners know the value of the exchanged items for both sides, and (3) partners expect given items to be returned (Dufour et al. 2009). In an experiment based on the exchange of tokens between conspecifics, we recently showed that a pair of orang-utans (*Pongo pygmaeus*) could achieve reciprocal and balanced transfers based on expected returns (Dufour et al. 2009; Pelé et al. 2009a).

In monkeys, macaques and capuchins possess some of the cognitive pre-requisites required for calculated reciprocity. They form long-lasting bonds and recognize each other (Dasser 1988; Thierry 2007; Pokorny and de Waal 2009). They can delay gratification (Ramseyer et al. 2006; Amici et al. 2008; Pelé et al. 2009b) and estimate the quantity and quality of goods (Hauser et al. 2000; Drapier et al. 2005). In experimental situations, macaques and capuchins are also capable to exchange non-edible items (Westergaard et al. 1998, 2004; Brosnan and de Waal 2004a, b; de Waal et al. 2008) and edible items (Drapier et al. 2005; Ramseyer et al. 2006; Pelé et al. 2009b) with humans. When considering exchanges between conspecifics, individuals of two groups of captive capuchins have been observed transferring tools and food from one group to the other (Westergaard and Suomi 1997). Two capuchins also performed active transfers of tools between each other even though the recipient never returned a share of the reward to the donor (Westergaard et al. 2007).

In this study, we tested the ability of brown capuchin monkeys and Tonkean macaques to reciprocate in a task requiring two subjects to exchange tokens in order to obtain rewards from an experimenter. By monitoring the intentionality of the transfers, the value of goods exchanged and the alternation of roles between individuals, we aimed at assessing the extent to which monkeys may purposefully engage in reciprocal behaviours with conspecifics.

METHODS

Subjects

We tested 4 brown capuchin monkeys (*Cebus apella*) and 3 Tonkean macaques (*Macaca tonkeana*) maintained at the Primatology Centre of the University of Strasbourg, France. Table 1 presents the age and sex of individuals. Subjects lived in social groups housed in enclosures with access to indoor and outdoor areas. Water was available *ad libitum* and subjects were never food deprived. Subjects of both species had been involved in food exchange tasks with humans prior to this study (Drapier et al. 2005; Ramseyer et al. 2006).

Tokens

We used three kinds of tokens differing in shape, material and colour for the exchange task (pink PVC caps, wooden cubes and metallic nuts, see Fig. 1).The tokens used with the capuchins were smaller than those used with the macaques (2cm vs. 4cm in length) to compensate for the hand size of each species.

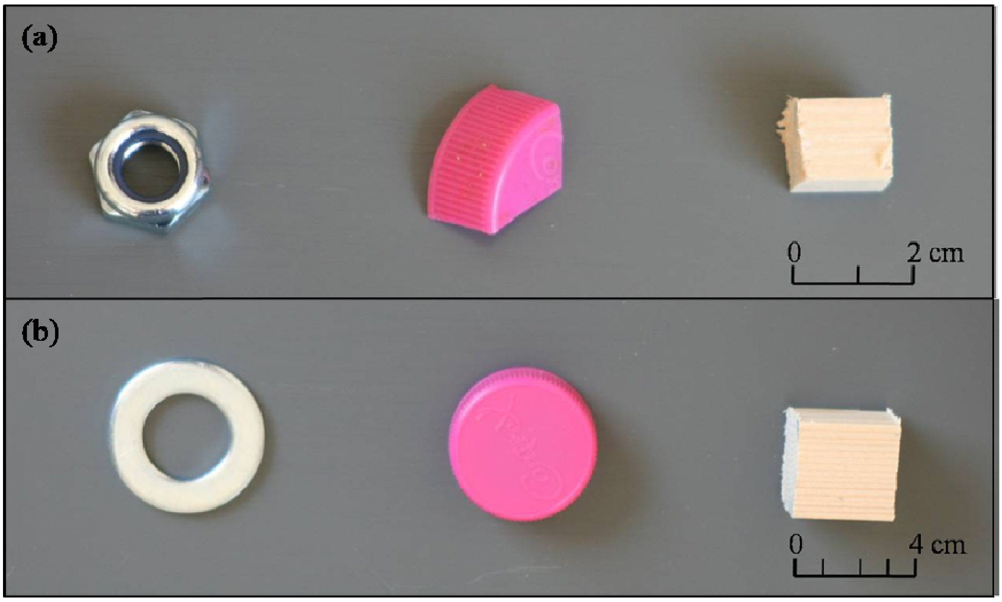


Figure 1. Set of tokens: metallic nut, pink PVC cap and wooden cube. Different sizes were used for capuchin monkeys (a) and Tonkean macaques (b).

For each pair of subjects, we gave to both partners the same set of 36 tokens composed by three types of 12 tokens: (1) *Self-valued tokens* were valuable to the subject and valueless to the partner; (2) *Partner-valued tokens* were valuable to the partner and valueless to the subject; (3) *No-value tokens* were not valuable for any partner. Table 1 gives information about the self-valued tokens of each subject.

Table 1. Age and sex of subjects, and types of self-valued tokens.

Name	Species	Age (years)	Sex	Self-valued tokens
Arn	*Cebus apella*	10	male	metallic nut
Kin	*Cebus apella*	17	female	metallic nut
Pis	*Cebus apella*	7	male	pink PVC cap
Pop	*Cebus apella*	7	male	wooden cube
Rim	*Macaca tonkeana*	6	female	wooden cube
She	*Macaca tonkeana*	5	female	metallic nut
Syb	*Macaca tonkeana*	5	female	pink PVC cap

Training procedure

Subjects were trained individually to exchange one of the three types of tokens for food in one compartment of the testing room. The experimenter (M.P.) sat in front of the subject and placed the 36 tokens in the compartment. Subject and experimenter could give and receive tokens through the cage mesh. A session typically started with the experimenter requesting tokens by holding an open hand (palm up) next to the fence. The experimenter only rewarded (with a piece of banana) the transfer of subject-valued tokens. All other tokens were accepted by the experimenter (and dropped on a bucket) but no reward was given in return. Once the subject had returned his/her 12 self-valued tokens, the experimenter ended the session. Subjects advanced to the testing phase upon giving more than 90% of the correct tokens first during three consecutive sessions.

Testing procedure

Testing took place in the same testing room divided into two compartments by a common mesh wall (Fig. 2). Three pairs were tested in each species (capuchins: Arn/Pis, Pis/Pop, Kin/Pis; macaques: Rim/Syb, Rim/She, She/Syb). Twelve tests were run for each pair of individuals. Only 10 tests could be conducted in one pair of capuchins (Arn/ Pis).

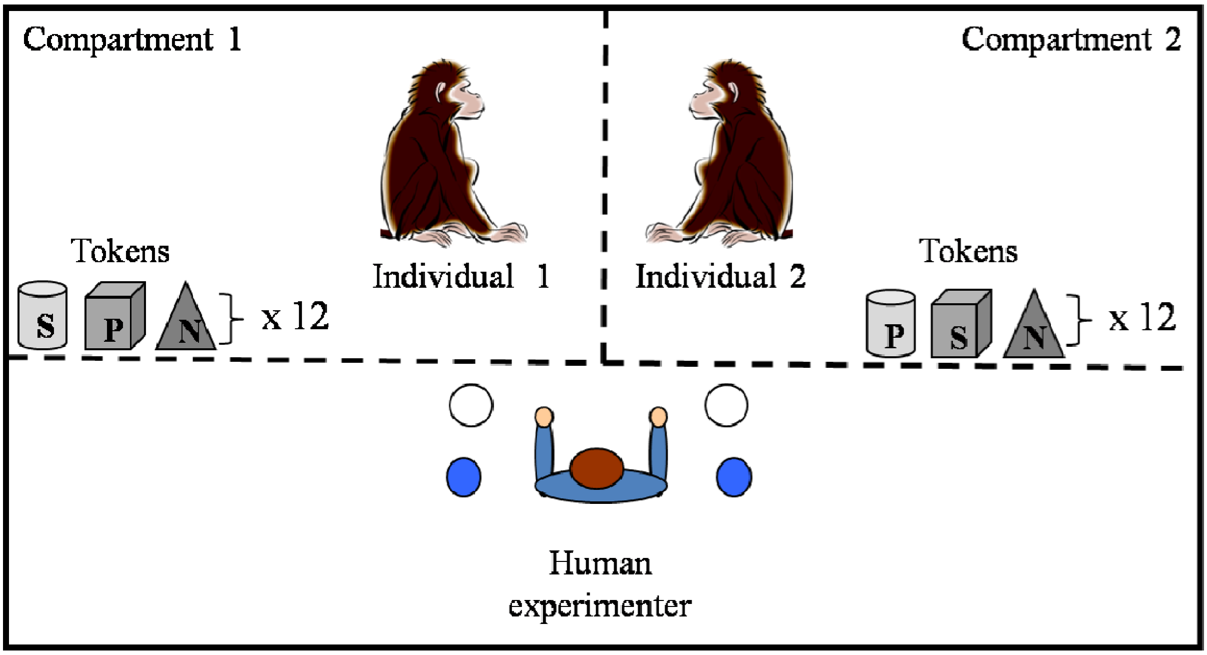


Figure 2. Experimental setting: two subjects are placed in adjacent compartments separated by a common mesh wall (- - -). Both partners receive the same set of tokens: 12 self-valued tokens (S), 12 partner-valued tokens (P) and 12 no-value tokens (N). Tokens are placed 1 m 20 away from the common mesh wall, out of partner's reach. Tokens can be transferred by passing them through the common mesh.

The testing procedure was the same as the training one except that two individuals were present in each of two adjacent compartments. The experimenter placed the same set of 36 tokens (12 self-valued tokens, 12 partner-valued tokens and 12 no-value tokens) in each compartment and resumed a sitting position facing both compartments. In the first part of each test, partners had the opportunity to exchange their self-valued tokens with the experimenter. Once both individuals have given all their 12 self-valued tokens, the experimenter faced the partners for a time period of 10 minutes. At this stage, only partner-valued tokens and no-value tokens remained in each compartment. If transfers of valuable tokens occurred, the experimenter asked for it and exchanged it for food with the subject.

During testing sessions, the experimenter recorded different behavioural units using a handheld recorder: *Exchange with experimenter*: a subject passes a token through the mesh to the experimenter. *Transfer with partner*: a subject obtains a token that was originally in her/his partner compartment. The frequency, latency and token value of these two behaviours were scored. The experimenter also recorded the type of transfer: *Passive transfer*: a subject places a token near the common mesh wall and the partner takes it. *Active transfer*: a subject places a token in the compartment of the partner.

Statistical analyses

We used Wilcoxon matched-pairs tests to compare frequencies of exchanges, transfers and manipulations by each individual using the exact test procedure on SPSS 16© (Siegel and Castellan 1988; Mundry and Fischer 1998) and the Fisher method for combining probabilities from independent tests of significance (Sokal and Rohlf 1969). The significance level was set at 0.05. Average values are given as means and SEM.

RESULTS

Exchanges with the experimenter

In the training phase, capuchin monkeys needed an average of 10.3 ± 1.0 sessions to discriminate (i.e., preferentially exchange) their self-valued tokens from the others whereas Tonkean macaques needed an average of 15.3 ± 3.7 sessions. We checked whether subjects showed a preference for one type of tokens by comparing the 12 first given tokens at the first training session to an equal distribution of the tokens. None subjects from any species appeared to show a preference for one of the three types of tokens (Chi-square Test, n.s. for each subject). During the testing phase, each test started with individuals exchanging their 12 self-valued tokens with the human experimenter. As a mean, the 12 first given tokens were composed of 11.2 ± 0.1 self-valuable tokens in capuchins, and of 11.7 ± 0.1 self-valuable tokens in macaques. The whole set of self-valued tokens was exchanged in a mean of 416 ± 33 seconds for capuchins and in a mean of 268 ± 15 seconds for macaques. Figure 3 presents the mean number of valueless tokens given to the experimenter by each subject. When comparing the value of the tokens given, two capuchins (Arn, Kin) gave significantly more no-value tokens than partner-valued tokens to the experimenter. On the contrary, one capuchin (Pop) and one macaque (Rim) gave significantly more partner-valued tokens than no-value tokens to the experimenter.

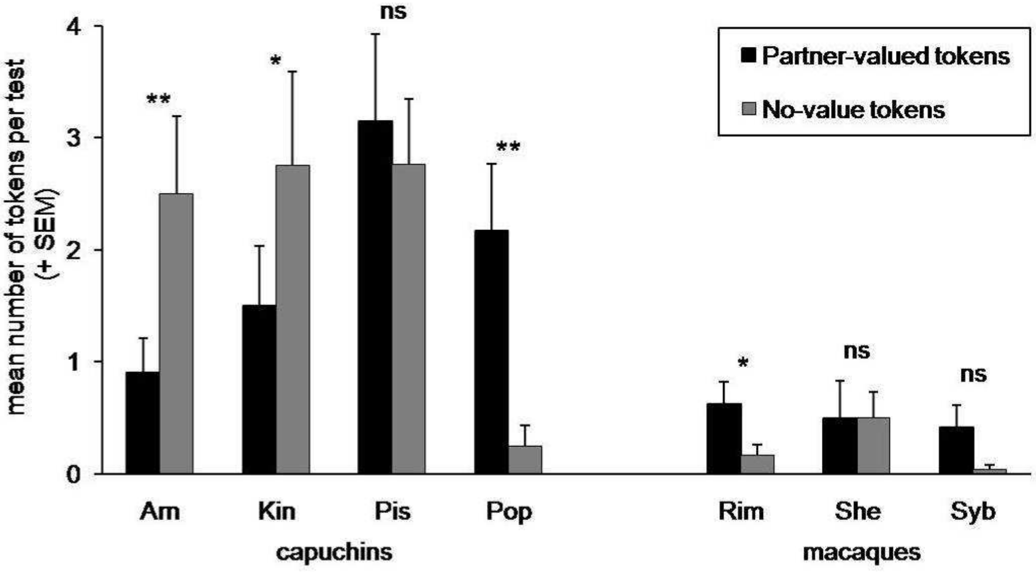


Figure 3. Number of valueless tokens given to the experimenter by each subject (Wilcoxon test, one-tailed, * $p < 0.05$, ** $p < 0.01$).

Transfer with partner

We recorded 56 transfers in capuchins (1.64 transfers per test) and 10 transfers in macaques (0.27 transfers per test). In both species, all transfers recorded were passive, i.e. all tokens transferred were taken by the subject from the compartment of the partner. Consequently, we analyzed whether individuals brought those tokens that were valuable for the partner closer to the common mesh as opposed to those that were not. Figure 4 presents the mean number of tokens brought to and manipulated near the common mesh wall by each individual. Two capuchins (Pis, Pop) manipulated significantly more partner-valued tokens than no-value tokens near the common mesh. Since the other two capuchins tended to show the same pattern, we combined the probabilities from the independent tests of significance; capuchins manipulated significantly more partner-valuable tokens than non-valuable ones near the mesh (Fisher test, $\chi^2 = 23.6$, df = 8, $p < 0.01$).

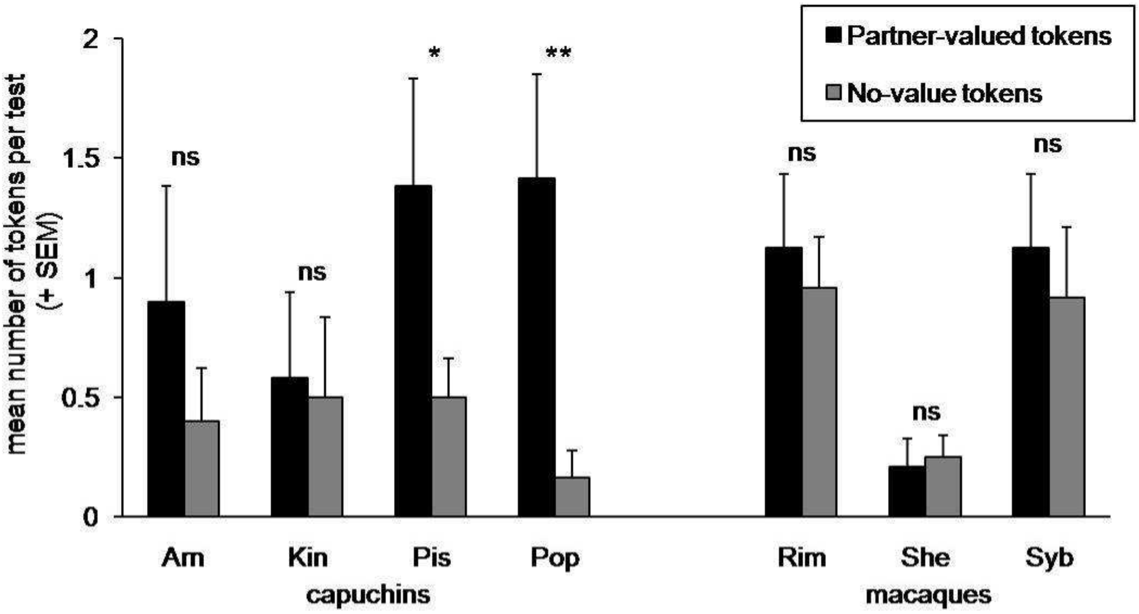


Figure 4. Number of valueless tokens manipulated by subjects near the common mesh wall (Wilcoxon test, one-tailed, * $p < 0.05$, ** $p < 0.01$).

Not surprisingly, valuable tokens represented 86% of the tokens taken by capuchins and 70% of the tokens taken by macaques from their partner's compartment (Figure 5). One capuchin (Pis) took significantly more self-valuable tokens than non-valuable ones from the compartment of his partner. Since the other three capuchins tended to show the same pattern, we combined the probabilities from the independent tests of significance; capuchins took significantly more self-valuable tokens than non-valuable ones in the compartment of their partner (Fisher test, $\chi^2 = 29.1$, df = 8, $p < 0.001$).

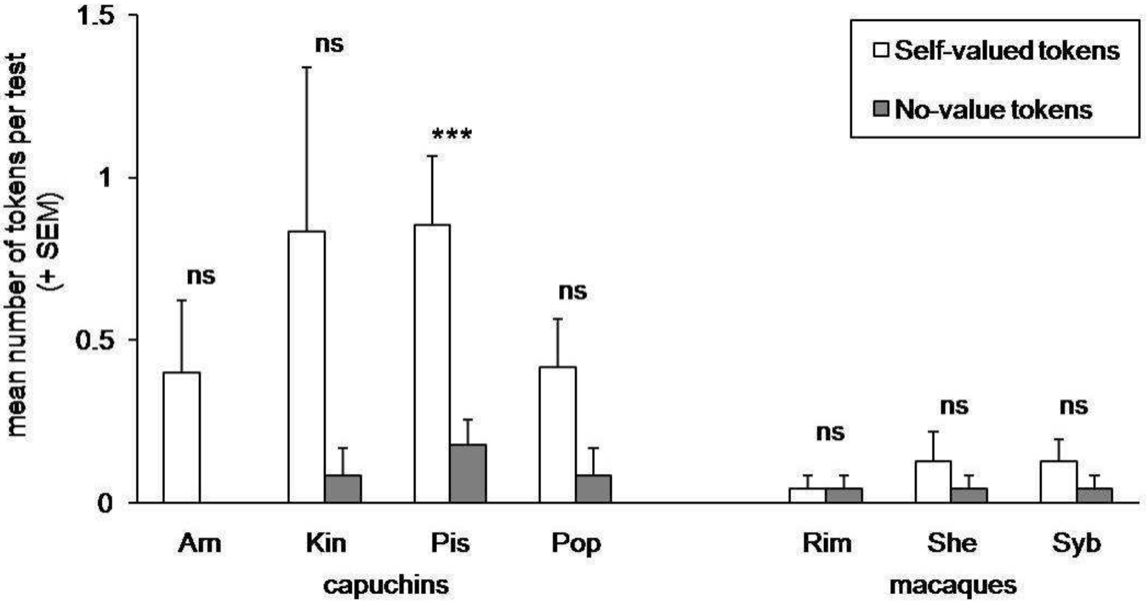


Figure 5. Number of partner- and no-value tokens taken by subjects from their partner's compartment (Wilcoxon test, one-tailed, *** $p < 0.001$).

DISCUSSION

Both Tonkean macaques and brown capuchin monkeys learned to discriminate their own valuable token among three different types, as shown by their preferential choice of those tokens to exchange with the experimenter. This result confirms that monkeys form associations between tokens and food rewards (Westergaard et al. 1998; Brosnan and de Waal 2004a). However, no active transfers of tokens were observed between partners. Instead, we recorded a number of passive transfers, especially in capuchin monkeys, that were enabled by the displacement of tokens towards the common mesh.

Capuchins learned to pick up tokens valuable for them from their partner's compartment. One capuchin (Pis) was even observed frequently walking back and forth along the common wall while monitoring tokens almost within reach. Interestingly, partners displaced a greater proportion of partner-valuable tokens than no-valuable tokens near the common mesh. This differential displacement cannot be attributed to a greater propensity to exchange partner-valued than no-value tokens with the experimenter because they exchanged both types with an equally and low proportion. Although the displacement of one type of token may suggest that this was done purposely, the absence of active transfers makes difficult to evaluate whether partners purposefully placed the tokens valuable to their partners near the common mesh so that they could benefit from them.

The absence of active transfers between subjects differs from some previous observations of active gifts from one individual to another in capuchin monkeys (de Waal et al. 1993; de Waal 1997; Westergaard and Suomi 1997; Westergaard et al. 2007). A parsimonious hypothesis is that the potential roles of receiver and donor in our experiment have not been understood by subjects. As receivers, subjects must understand that their partner is instrumental in providing more tokens. This could be expressed by individuals through solicitation or the use of begging behaviours such as pointing and holding-out-hand gestures as observed in great apes (Pelé et al. 2009a; Yamamoto and Tanaka 2009). In monkeys, brown capuchins have been observed putting cupped hands under the mouth of conspecifics to pick up falling pieces of food which might be interpreted as solicitation gestures (de Waal et al. 1993). In our study, however, neither capuchin monkeys nor Tonkean macaques performed such begging gestures towards their partner.

The lack of solicitations may have further made individual less inclined to act as donors. We never observed our subjects giving a token to their partner. However, capuchins appeared to manipulate the partner-valued tokens more often than the no-value ones, leading to more opportunities for these tokens to end up near the common fence within reach of the partner. While passive, transfers of tokens could be facilitated by the initial possessor as previously reported in a pair of orangutans (Dufour et al. 2009), but we never observed a monkey actually ‘placing’ a token within reach of the partner. Alternatively, by watching their partner successfully exchanging their token for food, subjects may have attributed more value to those tokens than to the no-value ones, and thus manipulated them more. Indeed, capuchin monkeys can learn the value of different tokens by watching others exchanging tokens for food (Brosnan and de Waal 2004b). Nevertheless, we reiterate that they did not attempt to exchange these tokens with the experimenter.

In humans trust is commonly viewed as a ‘lubricant’ of economical transactions (Arrow 1974). It could be as well a critical component of reciprocal interactions in non-human primates. While an individual can be flexible enough to tolerate occasional defection from a partner, he/she still needs some assurance that there is a potential for favours to be returned (Pelé et al. submitted). Such expectations may not be strong enough in monkeys, even preventing individuals to initially invest by giving first to their partners. By comparison, results from a similar experiment run with four great ape species showed that at least one individual in each species actively took the first step (Pelé et al. 2009a). Here, none of the pairs tested engaged in short term reciprocal interactions, despite optimal conditions where values of goods were defined and known by partners. These results indicate that calculated exchange is difficult if not impossible between monkeys. Further studies in a larger number of individuals and species will be necessary to verify the accuracy of this conclusion.

Acknowledgments

We are grateful to E. Suarez and J. Devillechabrolle for valuable assistance with the monkeys. The research was supported by a grant from the *Agence Nationale de la Recherche* (ANR-08-BLAN-0042-01).

References

Amici F, Aureli F, Call J (2008) Fission-fusion dynamics, behavioral flexibility and inhibitory control in primates. Curr Biol 18:1415-1419

Arrow KJ (1974) The limits of organization. Norton, New York

Aureli F, Schaffner CM (2002) Relationship assessment through emotional mediation. Behaviour 139:393-420

Brosnan SF, de Waal FBM (2004a) A concept of value during experimental exchange in brown capuchin monkeys (*Cebus apella*). Folia Primatol 75:317-330

Brosnan SF, de Waal FBM (2004b) Socially learned preferences for differentially rewarded tokens in the brown capuchin monkey, *Cebus apella*. J Comp Psychol 119:133-139

Dasser V (1988) A social concept in Java monkeys. Anim Behav 36:225-230

de Waal FBM (2000) Attitudinal reciprocity in food sharing among brown capuchin monkeys. Anim Behav 60:253-361

de Waal FBM (1997) Food transfers through mesh in brown capuchins. J Comp Psychol 4:370-378

de Waal FBM, Luttrell LM, Canfield ME (1993) Preliminary data on voluntary food sharing in brown capuchin monkeys. Am J Primatol 29:73-78

de Waal FBM, Leimgruber K, Greenberg AR (2008) Giving is self-rewarding for monkeys. Proc Nat Acad Sci USA 105:13685-13689

de Waal FBM, Luttrell LM (1988) Mechanisms of social reciprocity in three primate species: symmetrical relationships characteristics or cognition? Ethol Sociobiol 9:101-118

Drapier M, Chauvin C, Dufour V, Uhlrich P, Thierry B (2005) Food-exchange with humans in brown capuchin monkeys. Primates 46:241-248

Dufour V, Pelé M, Neumann M, Thierry B, Call J (2009) Calculated reciprocity after all: computation behind token transfers in orang-utans. Biol Lett 5:172-175

Dugatkin LA (1997) Cooperation among animals: an evolutionary perspective. Oxford University Press, Oxford

Hauser MD, Carey S, Hauser L (2000) Spontaneous number representation in semi-free-ranging rhesus monkeys. Proc R Soc London B 267: 829-833

Hemelrijk CK (1996) Reciprocation in apes: from complex cognition to self-structuring. In: McGrew WC, Marchant LF & Nishida T (eds) Great apes societies. Cambridge, Cambridge University Press, pp. 185-195

Mauss M (1923/24). Essai sur le don. Ann Sociol 1:30-186

Mundry R, Fischer J (1998) Use of statistical programs for nonparametric tests of small samples often leads to incorrect *P* values: examples from *Animal Behaviour*. Anim Behav 56:256-259

Pelé M, Dufour V, Thierry B, Call J (2009a) Token transfers among great apes: species differences, gestural requests and reciprocal exchange. J Comp Psychol, in press

Pelé M, Dufour V, Micheletta J & Thierry B (2009b) Long-tailed macaques display unexpected waiting abilities in exchange tasks. Anim Cogn, online

Pelé M, Thierry B, Call J, Dufour V. Non-human primates take their chance in a food-gambling game. (submitted)

Pokorny JJ, de Waal FBM (2009) Face recognition in capuchin monkeys (*Cebus apella*). J Comp Psychol 123:151-160

Ramseyer A, Pelé M, Dufour V, Chauvin C, Thierry B (2006) Accepting loss: the temporal limits of reciprocity in brown capuchin monkeys. Proc R Soc London B 273:179-184

Sahlins M (1972) Stone age economics. New York, Hawthorne

Seyfarth RM, Cheney DL (1984) Grooming, alliances and reciprocal altruism in vervet monkeys. Nature 308: 541-543

Siegel S, Castellan NJ (1988) Nonparametric statistics for the behavioral sciences. McGraw-Hill, Singapore

Sokal RR, Rohlf FJ (1969) Biometry: the principles and practice of statistics in biological research. Freeman, San Francisco

Thierry B (2007) The macaques: a double-layered social organization. In: Campbell CJ, Fuentes A, MacKinnon KC, Panger M & Bearder SK (eds) Primates in perspective. Oxford University Press, Oxford, pp 224-239

Westergaard GC, Liv C, Rocca AM, Cleveland A, Suomi SJ (2004) Tufted capuchins (*Cebus apella*) attribute to foods and tools during voluntary exchanges with humans. Anim Cogn 7:19-24

Westergaard GC, Liv C, Chavanne TJ, Suomi SJ (1998) Token-mediated tool-use by a tufted capuchin monkey (*Cebus apella*). Anim Cogn 1:101-106

Westergaard GC, Suomi SJ (1997) Transfer of tools and food between groups of tufted capuchins (*Cebus apella*). Am J Primatol 43:33-41

Westergaard GC, Evans TA, Howell S (2007) Token mediated tool exchange between tufted capuchin monkeys (*Cebus apella*). Anim Cogn 10:407-414

Yamamoto S, Tanaka M (2009) Spontaneously take turns in a reciprocal cooperation task? J Comp Psychol 123:242-249

CHAPITRE VI

DISCUSSION GENERALE

Mon travail de recherche a permis d'apprécier les facultés nécessaires à l'échange chez les primates non humains. J'ai évalué leur capacité à tolérer un temps d’attente et j'ai précisé leurs aptitudes à calculer ou prendre un risque au cours d'un échange. Le modèle expérimental de l’échange m’a permis d’identifier les mécanismes cognitifs sous-jacents aux comportements d’attente et de prise de risque chez les différentes espèces testées. Enfin, j’ai pu déterminer si des primates non humains peuvent s’engager dans des transactions réciproques avec un congénère dans des conditions expérimentales contrôlées.

1. LA DECISION FACE A UNE PERIODE D'ATTENTE

L’écart temporel entre le don et le retour dans un échange différé est un élément crucial de la réciprocité (Trivers, 1971). Il amène les individus à prendre en compte une durée d’attente. Alors que de nombreux travaux ont porté sur l'aptitude des primates non humains à différer une récompense (Amici et al., 2008 ; Beran, 2002 ; Beran et al., 1999 ; Evans & Beran, 2007a,b ; Rosati et al., 2007 ; Stevens et al., 2005b), une seule étude avait été conduite dans le cadre d’un échange de biens avec un expérimentateur humain (Ramseyer et al., 2006).

La première partie de ce travail de thèse avait pour objectif de déterminer la tolérance à un temps d’attente au cours d’un échange chez quatre espèces de primates non humains. L’étude des chimpanzés, des singes capucins et de deux espèces de macaques révèle d'importantes variations entre les groupes. Par exemple, pour une récompense huit fois supérieure à l’item initial, le délai moyen toléré se limite à 10-20 s pour les capucins, 40-80 s pour les macaques, et 1-2 mn pour les chimpanzés. Ces variations dans la capacité à attendre pourraient être attribuées à des différences dans les facultés cognitives des différentes espèces : les espèces présentant les capacités cognitives les plus élaborées auraient plus de facilité à tolérer un long temps d’attente. Le nombre limité de sujets testés dans chaque espèce doit cependant nous inciter à la prudence quant à cette conclusion. L’analyse des résultats obtenus indique des mécanismes similaires de décision chez toutes les espèces étudiées. Les chimpanzés, les macaques et les capucins se montrent capables d’évaluer la valeur de la récompense et d’attendre d'autant plus longtemps qu'elle est élevée (articles 1, 2, 3). L'analyse des temps de renoncement dans l'échange montre que les chimpanzés, les macaques mais également les capucins sont capables d’anticiper la durée d'attente imposée par l’expérimentateur lors de l’échange et de décider d’attendre ou non en fonction de cette durée (articles 1, 2, 3). Au moment de prendre leur décision, il apparaît que dans chaque espèce testée, la majorité des sujets prennent en compte à la fois la valeur de la récompense et la durée d'attente.

Au cours des deux premières expériences, les sujets ont fait preuve de contrôle de soi : ils devaient éviter de consommer le premier biscuit en leur possession et ce durant toute la durée d'attente. Dans une troisième expérience, j’ai levé cette contrainte en proposant aux individus de rendre le premier biscuit avant tout délai. Une majorité des capucins se sont révélés capables d’attendre jusqu’à 10-21 mn et une majorité des macaques jusqu’à 21-42 mn, ce qui démontre le rôle limitant de l’inhibition de la consommation (articles 2 et 3). Dans cette situation les macaques ne déprécient plus la récompense en fonction du temps d'attente. Au contraire, les capucins persistent à déprécier la future récompense en fonction du temps. Les performances des capucins peuvent s'expliquer par une impulsivité plus importante en comparaison avec les autres espèces testées. Quand l'inhibition de la consommation est levée, les macaques sont capables d'attendre plusieurs dizaines de minutes (article 2 et article 3). Il serait nécessaire de tester des chimpanzés dans les mêmes conditions, c'est-à-dire avec levée du facteur d'inhibition de l'action. Cela permettrait de comparer leur tolérance au délai avec celle mesurée chez les macaques.

Certains auteurs proposent que les primates non humains sont capables d'interagir sur la base de la réciprocité calculée, notamment lors d'échanges de services (Mitani & Watts, 2001 ; de Waal, 1982 ; de Waal, 1997a ; de Waal & Luttrell, 1988). Cependant, investir dans un échange de services comme du toilettage pour de la nourriture demanderait probablement aux sujets d'anticiper et planifier leurs actions sur de plus longues durées, par exemple à l'échelle de la journée ou de la semaine. Planifier consiste à produire dans le présent des comportements qui se révèleront utiles dans le futur, et cela sans qu'il y ait entraînement ou que la raison de l'action soit présente (Suddendorf & Corballis, 2007). L'échange de services sur la base de la réciprocité calculée pourrait exiger une planification sur une longue période de temps.

2. L'APTITUDE A ACCEPTER UN RISQUE

Dans un échange, l'écart temporel entre le don et le retour n'engendre pas seulement un temps d'attente pour les individus mais également le risque de perdre. Le partenaire peut détériorer le bien ou ne rien retourner. Le retour peut donc être insuffisant, voire même inexistant. Les individus doivent être capables de juger le risque lié à la situation d'échange différé. L'estimation des probabilités de gain et de perte pourrait être un pré-requis cognitif important dans la décision de s'engager dans une situation risquée. La deuxième partie de ce travail a porté sur l'aptitude de trois espèces de primates à accepter un échange susceptible d'entraîner une perte.

Ce travail a révélé la capacité de la plupart des orangs-outangs, des macaques à longue queue et des singes capucins à s'engager dans un échange risqué. Ceci diffère des résultats obtenus dans les tâches de choix où, face à des options variant en quantité, les animaux favorisent l'option constante (Kacelnik & Bateson, 1996). Cette étude a également révélé la capacité des primates non humains à tolérer une perte dans un échange de nourriture avec un expérimentateur (article 4). Ces résultats contrastent avec ceux obtenus au cours de tâches d'échange chez les capucins bruns (Chen et al., 2006). Les sujets pouvaient choisir d'échanger un jeton avec deux expérimentateurs : le premier leur présentait et leur donnait une récompense, le second leur présentait deux récompenses mais ne leur en donnait qu'une. La préférence des capucins à échanger leurs jetons avec le premier expérimentateur a été interprété par les auteurs comme résultant d'un effet d'aversion pour la perte (Chen et al., 2006). Au vu des résultats obtenus au cours de mon étude, il est plus probable que les résultats obtenus par Chen et collaborateurs (2006) soient liés à un effet de frustration, du fait de ne pas obtenir les deux récompenses présentées, plutôt qu'à une aversion pour la perte.

L'analyse des résultats montre que les sujets des trois espèces prennent d'abord en compte la probabilité de perdre avant d'échanger (article 4). Chez les macaques et les capucins, la prise de décision dépend également de la récompense obtenue à l'essai précédent, ce qui n'est pas le cas chez les orangs-outangs (article 4). Ceux-ci se distinguent des premiers par le fait qu'ils considèrent les essais comme indépendants les uns des autres, ce qui pourrait être le signe d'une meilleure compréhension des probabilités de gain. Les grands singes pourraient se révéler plus enclins à accepter un échange sur la base de leurs intérêts immédiats que sur la base de précédents échanges, ce qui pourrait refléter un meilleur calcul de leur part. Au contraire, les capucins et les macaques apparaissent plus sensibles au résultat obtenu à l'échange précédent. Chez ces derniers, des mécanismes basés sur le comportement du partenaire tels que la réciprocité d'attitude (de Waal, 2000) et la réciprocité d'émotion (Aureli & Schaffner, 2002) pourraient également conditionner la réponse des individus face à une situation d'échange risquée.

Ajoutons que l'étude des profils individuels révèle des comportements face au risque très différents d'un sujet à l'autre, même au sein d'une même espèce (article 4). De fait, les études en économie expérimentale ont montré que de telles différences de réponse entre individus sont également la norme chez l'être humain (Scheres & Sanfey, 2006). Les orangs-outangs et les singes capucins suivent majoritairement une stratégie rationnelle qui vise à n'échanger que lorsque la probabilité de gain est supérieure à la probabilité de perdre. Les macaques à longue queue quant à eux suivent majoritairement une stratégie riscophile où l'individu échange même si la probabilité de perdre est supérieure à la probabilité de gain (article 4). Il est intéressant de noter que dans la première étude, les macaques à longue queue sont parvenus à attendre 21 mn pour une récompense équivalente 40 fois la dimension de l'item initial (article 2) alors que chez les chimpanzés, le délai le plus long attendu pour la même récompense était de 11 mn. Les macaques à longue queue présentent ainsi une importante tolérance au temps d'attente et à la prise de risque sous-jacente à la situation d'échange. On peut cependant se demander s'il est pertinent pour un individu d'attendre très longtemps même pour une récompense « gros lot » et de s'engager dans un échange où la probabilité de gain est faible. L'ensemble des résultats obtenus chez les macaques à longue queue pose la question de l'influence des conditions de vie sur la capacité des individus à calculer un échange. En effet, contrairement aux chimpanzés, macaques de Tonkean et capucins bruns qui étaient maintenus en groupes sociaux, certains macaques à longue queue étaient maintenus isolés. Il est possible que l'isolement, généralement associé à une privation en terme de richesse du milieu, incite les animaux à attribuer plus de valeur à des récompenses rares par nature qu'ils ne l'auraient fait dans des conditions de plus grande diversité.

Au cours de ce travail de thèse, les comportements des individus face à un temps d'attente et une prise de risque ont été étudiés séparément. Plusieurs études ont cependant mis en relation les prises de décision face à un temps d’attente et un risque (Green & Myerson, 1996 ; Hayden & Platt, 2007 ; Kalenscher, 2007). Dans le cas d’un échange, quand le délai entre le don et le retour augmente, la probabilité de recevoir le retour peut diminuer et donc la prise de risque augmenter. On a proposé que la dépréciation de la récompense finale avec le temps puisse représenter une réponse adaptative aux risques de perte liés à l’attente (Kagel et al., 1986). Il serait nécessaire d’étudier la capacité de primates non humains à s’engager dans un échange au cours duquel un temps d’attente mais également un risque de perdre seraient imposés de manière à démontrer la relation entre le risque et la durée d'attente dans la situation d'échange.

3. L’ECHANGE AVEC UN CONGENERE

Les primates non humains sont capables de s’engager dans un échange de nourriture avec un expérimentateur humain sur la base de l’estimation de la valeur des récompenses, de la durée du temps d’attente mais aussi de la probabilité de gain ou de perte. Ceci traduit l'existence de certaines des compétences cognitives nécessaires à l’émergence de la réciprocité calculée. La dernière partie de ce travail a consisté à tester l'aptitude des singes à s’engager dans des échanges de type calculé avec un congénère dans des conditions contrôlées.

Chez les macaques de Tonkean et les capucins bruns, seuls des transferts passifs ont été relevés entre partenaires (article 7). L’absence de transferts actifs, notamment chez les capucins, contraste avec les conclusions d’autres études au cours desquelles des transferts actifs avaient pu être constatés, ces transferts restant toutefois assez rares (de Waal, 1997b ; de Waal et al., 1993 ; Westergaard & Suomi, 1997 ; Westergaard et al., 2007). Bien que les macaques de Tonkean et les capucins bruns soient des espèces caractérisées par une tolérance sociale élevée (Chalmeau et al., 1997 ; Petit et al., 1992), cela n’a pas suffi pour que des comportements coopératifs surviennent entre les partenaires. La nature passive des transferts observés souligne la difficulté des sujets ou même leur incapacité à donner spontanément un bien à un congénère (article 7). En tant que récepteur, les individus devaient comprendre que leur partenaire est un donneur potentiel. Cela aurait pu s’exprimer à travers des signes de communication tels que des gestes de quémande ou des gestes de sollicitation qui auraient incité le partenaire à donner. Aucun comportement de ce type n'a été constaté chez les macaques de Tonkean et les capucins, leur absence pourrait traduire une non-compréhension du rôle du partenaire (article 7). En tant que donneur, un sujet doit comprendre de surcroît le besoin de son partenaire. Récemment, Barnes et collaborateurs (2008) ont testé l’aptitude de singes capucins à aider un expérimentateur à obtenir un objet hors de sa portée. Les résultats montrent que les capucins considèrent peu les gestes de sollicitation de l’expérimentateur et qu’ils sont plus enclins à aider quand une récompense alimentaire leur est proposée (Barnes et al., 2008). Les singes capucins montrent ainsi des difficultés à comprendre les besoins et perspectives d’autrui. Cette incapacité à saisir les besoins du partenaire peuvent expliquer qu’aucun transfert actif n’ait été observé. Pour tester cette hypothèse, il serait nécessaire d'étudier les animaux dans le même contexte expérimental mais avec un partenaire humain et non plus un congénère. Cette procédure intermédiaire permettrait de faire comprendre aux individus leur rôle potentiel de donneur et récepteur ainsi que celui de leur partenaire. En les testant de nouveau avec un congénère par la suite, nous serions en mesure de déterminer si les résultats étaient dus à une réelle incompréhension de la tâche ou au refus des sujets de donner à un congénère. Nous pourrions ainsi établir si les limites qui entravent l'émergence de réciprocité calculée chez ces espèces sont de nature cognitive ou sociale.

Chez les grands singes, les orangs-outangs ont montré plus de facilité que les autres espèces à transférer des objets à un congénère (article 5 et article 6). Le nombre de transferts observés chez les chimpanzés, les bonobos et les gorilles est resté faible comparé au nombre de transferts relevés chez les orangs-outangs – hormis le cas d'une femelle bonobo ayant montré une attirance particulière pour un objet (voir article 5). Par ailleurs, les orangs-outangs sont la seule espèce chez qui des dons directs d'objets ont été constatés entre partenaires (article 5). Seuls des transferts indirects au cours desquels un individu a placé un objet dans la cage de son partenaire ont été relevés chez les trois espèces de grands singes (article 5). Les orangs-outangs se distinguent également des autres espèces par une fréquence élevée de comportements de quémande et de sollicitation de certains sujets tels que le pointage vers un objet ou la main tendue vers le partenaire (article 5). Chez les chimpanzés, on sait que l'existence de gestes de quémande joue un rôle décisif dans la production de comportements d'aide envers un partenaire humain (Warneken & Tomasello, 2006 ; Warneken et al., 2007) mais également envers un congénère (Yamamoto et al., 2009); ils permettent d'attirer l'attention de l'individu sur les besoins du partenaire. Dans mon étude, les gestes de sollicitation et de pointage ont pu faciliter la survenue des transferts d'objets en permettant au partenaire de comprendre que sa participation était nécessaire. Il est intéressant de noter que les deux orangs-outangs qui ont produit le plus de gestes de quémande ont été par la suite les seuls capables d'établir une relation d'échange équilibrée et stable dans le temps (article 6).

On peut tenter d'expliquer les différences observées entre espèces par l'influence du système social propre à chacune. Les comportements de quémande des orangs-outangs ont favorisé les transferts. Par comparaison, on sait que les interactions sociales sont rares chez les gorilles (Watts, 1996, 2003) et, de fait, je n'ai relevé aucun comportement de quémande dans cette espèce, ce qui peut expliquer le faible nombre de transferts enregistrés (article 5). Le faible nombre de transferts et de gestes de quémande constatés chez les bonobos et les chimpanzés est plus surprenant quand on sait que ces deux espèces forment des communautés de type fission-fusion qui peuvent compter plusieurs dizaines d'individus (Badrian & Badrian, 1984 ; Goodall, 1986 ; White, 1988) et qu'elles présentent un important répertoire de comportements de sollicitation (Call & Tomasello, 2007). Récemment, on a même montré que des bonobos montrent plus d'aptitude que des chimpanzés à s'engager dans une tâche de coopération requérant que deux individus tirent chacun un des bouts d'une corde pour attirer un plateau de nourriture (Hare et al., 2007). Le système social des chimpanzés et des bonobos génère cependant une compétition importante pour des ressources telles que la nourriture ou les femelles reproductives. Il est possible que, dans mon étude, les chimpanzés et les bonobos aient d’abord considéré leur partenaire comme un compétiteur plutôt que comme un coopérateur potentiel. De plus, dans l’expérience de Hare et collaborateurs (2007), les individus obtiennent la récompense alimentaire en même temps ce qui n’est pas le cas dans mon étude. Parmi les grands singes, les orangs-outangs ont longtemps été considérés comme une espèce solitaire (Bearder, 1987). De récents travaux démontrent qu’il existe de véritables communautés d'individus qui interagissent régulièrement chez les orangs-outangs bien qu'ils restent dispersés la plus grande partie du temps (Mitra Setia et al., 2009). On a rapporté dans le milieu naturel des transferts de nourriture entre mâles et femelles adultes chez l'orang-outang (van Noordwijk & van Schaik, 2009). En prenant de la nourriture au mâle, une femelle s’informerait sur l’agressivité potentielle de celui-ci (van Noordwijk & van Schaik, 2009). De tels résultats soulignent un niveau de tolérance sociale relativement élevé. Au cours de mon étude, la nature directe des transferts relevés chez les orangs-outangs rend compte également d’un plus grand degré de confiance entre partenaires que chez les chimpanzés ou les bonobos. Avec les comportements de quémande, cela pourrait expliquer la fréquence des transferts relevés chez cette espèce.

Toutefois, seuls deux orangs-outangs ont été capables de mettre en place une véritable relation d’échange (article 6). Ceci n’a été observé qu’après simplification du protocole initial où deux types d’objets étaient disponibles, l’objet de valeur du partenaire et l’objet sans valeur. Pour obtenir de la nourriture de la part de l’expérimentateur, les sujets devaient obligatoirement amener leur partenaire à fournir le bon objet. Alors que le nombre de transferts était initialement biaisé dans une direction, au fur et à mesure des séances de test les transferts se sont équilibrés entre les deux individus (article 6). L’émergence d'une réciprocité calculée entre ces deux orangs-outangs a nécessité la convergence d’un certain nombre de facteurs et ce au sein d’un protocole expérimental déjà très contrôlé. L’existence dans le milieu naturel de conditions aussi favorables apparaît peu probable mais fait partie du domaine du possible.

Les deux orangs-outangs ont compris et répondu aux besoins de leur partenaire. Ils semblent également avoir compris qu’être en possession d’un élément désiré par l’autre leur donnait un certain pouvoir de négociation. Le résultat majeur de cette étude est le fait que, pour la première fois, une alternance des rôles ait pu être mise en évidence à court terme, mais ait pu également se stabiliser sur plusieurs séances, permettant la mise en place d’un système d’échange efficace.

Au cours de ce travail, je me suis focalisée sur l’étude de la réciprocité directe, c’est-à-dire la réciprocité entre les deux mêmes individus (Trivers, 1971). Chez l’être humain, on a proposé que la réciprocité qui est à la base des transactions économiques puisse également se mettre en place de manière indirecte, par l’intervention d’individus tiers (Trivers, 1971). La réciprocité est alors basée sur la réputation des partenaires potentiels (Nowak, 2006). En observant le comportement de l’individu B sur l’individu C, l’individu A s’informe sur le potentiel comportement que B pourrait avoir envers lui. On a déjà montré que des chimpanzés peuvent directement (Melis et al., 2006b) mais aussi indirectement (Subiaul et al., 2008) évaluer l’efficacité de partenaires et les recruter ou non sur cette base. Cependant, rien n’indique à ce jour que des primates non humains soient capables d’agir en tenant compte des possibles conséquences de leurs actes sur leur réputation. Cette question mériterait des investigations approfondies.

4. PERSPECTIVES

Au cours de ce travail de recherche, j’ai tenté de répondre en partie à la question implicitement posée par Adam Smith (1776) concernant les compétences nécessaires à l'émergence de transactions économiques telles qu'on les observe chez l’être humain. J’ai pu mettre en évidence l’existence chez les primates non humains de certains pré-requis cognitifs nécessaires à la réciprocité calculée. Face à un temps d’attente entre le don et le retour, la prise de décision des primates se fait sur la base de mécanismes cognitifs élaborés : l’estimation de la valeur du retour et l’anticipation du délai. Face à un échange risqué, les primates sont capables d’estimer les probabilités de gain et de perte et de prendre en considération ces informations pour décider de s’engager ou non dans l’échange.

Le modèle expérimental de l’échange m’a permis de mettre en évidence chez les primates non humains des facultés d’attente et de prise de risque qui restaient encore insoupçonnées dans les tâches classiques, ce qui souligne l’importance du contexte expérimental dans les performances individuelles. De telles aptitudes semblent favorables à la mise en place de la réciprocité calculée entre deux partenaires. En dépit de ces aptitudes, cependant, seuls deux individus se sont montrés capables de s’engager dans un système d’échange stable et calculé. Chez les capucins et les macaques, la non-compréhension du rôle du partenaire mais également de ses besoins pourrait interdire l’émergence de la réciprocité calculée. Chez les grands singes, même si la réciprocité calculée est possible sur de courtes périodes de temps, elle semble fortement limitée par des facteurs sociaux tels que la confiance envers le partenaire. Chez l’être humain, l’établissement de normes et de conventions au sein des communautés a probablement permis l’apparition d'un système d'échanges économiques. La confiance, la compréhension des besoins de l'autre et l'établissement de normes apparaissent comme autant de mécanismes susceptibles de jouer un rôle important dans la réciprocité calculée et qui devraient faire l'objet de recherches ultérieures.

L’approche comparative utilisée dans ce travail m’a permis de faire apparaître des variations dans le phénomène étudié entre différentes espèces de primates. Afin de déterminer au cours de l’évolution l’apparition des bases biologiques des décisions économiques, il apparaît nécessaire d’élargir le champ de recherche à d’autres espèces animales. Il serait par exemple intéressant d’étudier les facultés d’échange d’espèces non primates présentant des caractéristiques sociales et cognitives proches ou différentes de celles des primates. Par ailleurs, l’étude des facultés d’échange chez des enfants humains de différents âges permettrait également de suivre le développement des transactions de type économique. Les résultats attendus préciseraient les mécanismes à l’origine des décisions et comportements économiques observés chez l’être humain.

REFERENCES

Addessi E, Crescimbene L, Visalberghi E (2007) Do capuchin monkeys (*Cebus apella*) use tokens as symbols? Proceedings of the Royal Society of London B: Biological Series 274: 2579-2585

Addessi E, Mancini A, Crescimbene L, Padoa-Schioppa C, Visalberghi E (2008a) Preference transitivity and symbolic representation in capuchin monkeys (*Cebus apella*). PLOS ONE 3(6): e2414

Addessi E, Crescimbene L, Visalberghi E (2008b) Food and token quantity discrimination in capuchin monkeys (*Cebus apella*). Animal Cognition 11: 275-282

Amici F, Call J, Aureli F (2009) Variation in withholding of information in three monkey species. Proceedings of the Royal Society of London B: Biological Series 276: 3311-3318

Amici F, Aureli F, Call J (2008) Fission-fusion dynamics, behavioral flexibility and inhibitory control in primates. Current Biology 18: 1415-1419

Anderson JR (2007) Primate behaviour : Tolerant primates cooperate best. Current Biology 17: R242-5244

Anderson JR, Awazu S, Fujita K (2000) Can squirrel monkeys (*Saimiri sciureus*) learn self-control? A study using food array selection tests and reverse-reward contingency. Journal of Experimental Psychology: Animal Behavior Processes 26: 87-97

Aureli F, Schaffner CM (2002) Relationship assessment through emotional mediation. Behaviour 139: 393-420

Aureli F, Cozzolino R, Cordschi C, Scucchi S (1992) Kin-oriented redirection among Japanese macaques: an expression of a revenge system? Animal Behaviour 44: 283-291

Austad SN, Fischer KE (1992) Primate longevity: its place in the mammalian scheme. American Journal of Primatology 28: 251-261

Badrian A, Badrian N (1984) Social organization of *Pan paniscus* in the Lomako forest, Zaire. In Susman RL (eds) The pygmy chimpanzee: evolutionary biology and behaviour. New York: Plenum Press, pp. 325-346

Barnes JL, Hill T, Langer M, Martinez, Santos LR (2008) Helping behaviour and regard for others in capuchin monkeys (Cebus apella). Biology Letters 4: 638-640

Bearder SK (1987) Lorises, bushbabies, and tarsiers: diverse societies in solitary foragers. In: Smuts BB, Cheney DL, Seyfarth RW, Wrangham RW, Struhsaker TT (eds) Primates Societies. University of Chicago Press, Chicago, pp. 11-24

Beck BB (1973) Cooperative tool use by captive hamadryas baboons. Science 182: 594-597

Beran MJ (2008) Capuchin monkeys (*Cebus apella*) succeed in a test of quantity conservation. Animal Cognition 11: 109-116

Beran MJ (2004) Chimpanzees (*Pan troglodytes*) respond to nonvisible sets after one-by-one addition and removal of items. Journal of Comparative Psychology 118: 25-36

Beran MJ (2002) Maintenance of self-imposed delay of gratification by four chimpanzees (*Pan troglodytes*) and an orangutan (*Pongo pygmaeus*). Journal of General Psychology 129: 49-66

Beran MJ (2001) Summation and numerousness judgments of sequentially presented sets of items by chimpanzees (*Pan troglodytes*). Journal of Comparative Psychology 115: 181-191

Beran MJ, Evans TA, Leighty KA, Harris EH, Rice D (2008) Summation and quantity judgments of sequentially presented sets by capuchin monkeys (*Cebus apella*). American Journal of Primatology 70: 191-194

Beran MJ, Savage-Rumbaugh ES, Pate JL, Rumbaugh DM (1999) Delay of gratification in chimpanzees (*Pan troglodytes*). Developmental Psychobiology 34: 119-127

Bercovitch FB (1988) Coalitions, cooperation and reproductive tactics among adult male baboons. Animal Behaviour 36: 1198-1209

Bertrand M (1976) Acquistion by a pigtail macaque of behavior patterns beyond the natural repertoire of the species. Zeitschrift fur Tierpsychologie 42: 139-169

Boysen ST, Berntson GG (1989) Numerical competence in a chimpanzee (*Pan troglodytes*). Journal of Comparative Psychology 103: 23-31

Boysen ST, Berntson GG (1995) Responses to quantity: Perceptual versus cognitive mechanisms in chimpanzees (*Pan troglodytes*). Journal of Experimental Psychology: Animal Behavior Processes 21: 82-86

Boysen ST, Berntson GG, Hannan MB, Cacioppco JT (1996) Quantity-based interference and symbolic representation in chimpanzees (*Pan troglodytes*). Journal of Experimental Psychology: Animal Behavior Processes 22: 76-86

Bräuer J, Call J, Tomasello M (2006) Are apes really inequity averse? Proceedings of the Royal Society of London B: Biological Series 273: 3123-3128

Brosnan SF, Beran MJ (2009) Trading behavior between conspecifics in chimpanzees, *Pan troglodytes*. Journal of Comparative Psychology 123: 181-194

Brosnan SF, Jones OD, Lambeth SP, Mareno MC, Richardson AS, Shapiro SJ (2007) Endowment effects in chimpanzees. Current Biology 17: 1704-1707

Brosnan SF, de Waal FBM (2005) Responses to a simple barter task in chimpanzees, *Pan troglodytes*. Primates 46: 173-182

Brosnan SF, Schiff HC, de Waal FBM (2005) Tolerance for inequity may increase with social closeness in chimpanzees. Proceedings of the Royal Society of London B: Biological Series 272: 253-258

Brosnan SF, de Waal FBM (2004a) A concept of value during experimental exchange in brown capuchin monkeys, *Cebus apella*. Folia Primatologica 75: 317-330

Brosnan SF, de Waal FBM (2004b) Socially learned preferences for differentially rewarded tokens in the brown capuchin monkey (*Cebus apella*). Journal of Comparative Psychology 118: 133-139

Brosnan SF, de Waal FBM (2003) Monkeys reject unequal pay. Nature 425: 297-299

Brown GR, Almond REA, van Bergen Y (2004**)** Begging, stealing and offering: food transfer in nonhuman primates. Advances in the Study of Behaviour 34: 265-295

Bshary R, Grutter AS (2002) Experimental evidence that partner choice is a driving force in the payoff distribution among cooperators or mutualists: the cleaner fish case. Ecology Letters 5: 130-136

Bshary R, Schäffer D (2002) Choosy reef fish select cleaner fish that provide high-quality service. Animal Behaviour 63: 557-564

Byrne R, Whiten A (1990) Tactical deception in primates : the 1990 database. Primate Report 27: 1-101

Call J (2000) Estimating and operating on discrete quantities in orangutans (*Pongo pygmaeus*). Journal of Comparative Psychology 114: 136-147

Call J, Tomasello M (2007) The gestural communication of apes and monkeys. New York, LEA

Call J, Rochat P (1997) Perceptual strategies in the estimation of physical quantities by orangutans (*Pongo pygmaeus*). Journal of Comparative Psychology 111: 315-329

Call J, Rochat P (1996) Liquid conservation in orangutans (*Pongo pygmaeus*) and humans (*Homo sapiens*). Individual differences and perceptual strategies. Journal of Comparative Psychology 110: 219-232

Chalmeau R, Peignot P (1998) Exchange of objects between human and captive western lowland gorillas. Primates 39: 389-398

Chalmeau R, Visalberghi E, Gallo A (1997) Capuchin monkeys, *Cebus apella*, fail to understand a cooperative task. Animal Behaviour 54: 1215-1225

Chen MK, Lakshminarayanan V, Santos LR (2006) How basic are behavioral biases? Evidence from capuchin monkeys trading behavior. Journal of Political Economy 114: 517-537

Clayton NS, Bussey TJ, Dickinson A (2003) Can animals recall the past and plan for the future? Nature Reviews Neuroscience 4: 685-691

Clutton-Brock T (2009) Cooperation between non-kin in animal societies. Nature 462: 51-57

Colvin J, Tissier G (1985) Affiliation and reciprocity in sibling and peer relationships among free-ranging immature male rhesus monkeys. Animal Behaviour 33: 959-977

Coussi-Korbel S (1994) Learning to outwit a competitor in Mangabeys. Journal of Comparative Psychology 108: 164-171

Coussi-Korbel S (1993) Influences sociales sur l'acquisition et l'utilisation d'informations relatives à la recherche de nourriture dans un groupe de Cercocèbes (*Cercocebus t. torquatus*). Thèse de doctorat, Université de Rennes I, France

Dasser V (1988) A social concept in Java monkeys. Animal Behaviour 36: 225-230

Dasser V (1987) Slides of group members as representations of the real animals (*Macaca fascicularis*). Ethology 76: 65-73

de Waal FBM (2000) Attitudinal reciprocity in food sharing among brown capuchin monkeys. Animal Behaviour 60: 253-361

de Waal FBM (1998) Chimpanzee politics: Power and sex among apes

de Waal FBM (1997a) The chimpanzee’s service economy: food for grooming. Evolution and Human Behavior 18: 375-386

de Waal FBM (1997b) Food transfers through mesh in brown capuchins. Journal of Comparative Psychology 111: 370-378

de Waal FBM (1989) Food sharing and reciprocal obligations among chimpanzees. Journal of Human Evolution 18: 433-459

de Waal FBM (1982) Chimpanzee Politics. London: Jonathan Cape

de Waal FBM, Leimbruger K, Greenberg AR (2008) Giving is self-rewarding for monkeys. Proceedings of the National Academy of Sciences 36: 13685-13689 de Waal FBM, Berger ML (2000) Payment for labour in monkeys. Nature 404: 563

de Waal FBM, Luttrell LM, Canfield ME (1993) Preliminary data on voluntary food sharing in brown capuchin monkeys. American Journal of Primatology 29: 73-78

de Waal FBM, Luttrell LM (1988) Mechanisms of social reciprocity in three primate species: symmetrical relationship characteristics or cognition? Ethology and Sociobiology 9: 101-118

de Waal FBM, Luttrell LM (1986) The similarity principle underlying-social bonding among female rhesus. Folia Primatoogica 46: 215-234

Drapier M, Chauvin C, Dufour V, Uhlrich P, Thierry B (2005) Food-exchange with humans in brown capuchin monkeys. Primates 46: 241-248

Dubreuil D, Gentile MS, Visalberghi E (2006) Are capuchin monkeys (*Cebus apella*) inequity averse? Proceedings of the Royal Society of London B: Biological Series 273: 1223-1228

Ducoing AM, Thierry B (2003) Withholding information in semi free-ranging Tonkean macaques (*Macaca tonkeana*). Journal of Comparative Psychology 117: 67-75

Dufour V, Sterck EHM (2008) Chimpanzees fail to plan in an exchange task but succeed in a tool-using procedure. Behavioural Processes 79:19-27

Dufour V, Pascalis O, Petit O (2006) Species-specific face recognition in primates, a comparative study in brown capuchin monkeys, Tonkean macaques and humans. Behavioural Processes 73: 107-113

Dugatkin LA (1997) Cooperation among animals: an evolutionary perspective. Oxford, UK: Oxford University Press

Dunbar R (1980) Determinants and evolutionary consequences of dominance among female gelada baboons. Behavioral Ecology and Sociobiology 7: 253-265

Eber N, Willinger M (2005) L’économie expérimentale. Editions La Découverte, Paris

Evans TA, Beran MJ (2007a) Delay of gratification and delay maintenance by rhesus macaques (*Macaca mulatta*). Journal of General Psychology 134: 199-216

Evans TA, Beran MJ (2007b) Chimpanzees use self-distraction to cope with impulsivity. Biology Letters 3: 599-602

Fairbanks LA (1980) Relationships among adult females in captive vervet monkeys : testing a model of rank-related attractiveness. Animal Behaviour 28: 853-859

Fehr E, Schmidt KM (1999) A theory of fairness, competition and cooperation. Quarterly Journal of Economics 114: 817-868

Feistner ATC, McGrew WC (1989) Food-sharing in primates: a critical review. In: PK Seth & S Seth (eds) Perspectives in Primate Biology. New Delhi: Today & Tomorrow, pp. 21-36

Fontenot MB, Watson SL, Roberts KA, Miller RW (2007) Effects of food preference on token exchange and behavioural responses to inequality in tufted capuchin monkeys, *Cebus apella*. Animal Behaviour 74: 487-496

Fragaszy DM, Visalberghi E, Fedigan L (2004) The Complete Capuchin. Cambridge University Press

Fruteau C, Voelkl B, van Damme E, Noë R (2009) Supply and demand determine the market value of food providers in wild vervet monkeys. Proceedings of the National Academy of Sciences 29: 12007-12012

Fujita K, Kuroshima H, Masuda T (2002) Do tufted capuchin monkeys (*Cebus apella*) spontaneously deceive an opponent? A preliminary analysis of an experimental food-competition contest between monkeys. Animal Cognition 5: 19-25

Gilby IC (2006) Meat sharing among the Gombe chimpanzees: harassment and reciprocal exchange. Animal Behaviour 71: 953-963

Gomes CM, Boesch C (2009) Wild chimpanzees exchange meat for sex on a long-term basis. Plos One 4: e5116

Gomes CM, Mundry R, Boesch C (2009) Long-term reciprocation of grooming in wild West African chimpanzees. Proceedings of the Royal Society of London B: Biological Series 276: 699-706

Goodall J (1986) The chimpanzees of Gombe. Cambridge: Belknap Cambridge

Green L, Myerson J (1996) Exponential versus hyperbolic discounting of delayed outcomes: risk and waiting time. American Zoologist 36: 496-505

Gumert MD (2007a) Grooming-infant handling interchange: the relationship between infant supply and grooming payment in *Macaca fascicularis*. International Journal of Primatology 28: 1059-1074

Gumert MD (2007b) Payment for sex in a macaque mating market. Animal Behaviour 74: 1655-1667

Güth W, Schmittberger R, Schwarze B (1982) An experimental analysis of ultimatum bargaining. Journal of Economic Behavior and Organization 3: 367-388

Gygax L (2000) Hiding behaviour of long-tailed macaques (*Macaca fascicularis*): II. Use of hiding places during aggressive interactions. Ethology 106: 441-451

Hamilton WD (1970) Selfish and spiteful behaviour in an evolutionary model. Nature 228: 1218-1220

Hamilton WD (1964) The Genetical Evolution of Social Behavior, I and II. Journal of Theorical Biology 7: 1-52

Hanus D, Call J (2007) Discrete quantity judgments in the great apes (*Pan paniscus*, *Pan troglodytes*, *Gorilla gorilla*, *Pongo pygmaeus*): The effect of presenting whole sets versus item-by-item. Journal of Comparative Psychology 121: 241-249

Harcourt AH, Fossey D, Sabater-Pi J (1981) Demography of *Gorilla gorilla*. Journal of Zoology, London 195: 215-233

Hare BA, Melis AP, Woods V, Hastings S, Wrangham R (2007) Tolerance allows bonobos to outperform chimpanzees on a cooperative task. Current Biology 17 : 619-623

Hare B, Call J, Tomasello M (2001) Do chimpanzees know what conspecifics know? Animal Behaviour 61: 139-151

Hauser MD (1997) Minding the behaviour of deception. In : Whiten A & Byrne RW (eds) Machiavellian intelligence II: Extensions and evaluations, pp. 112-143

Hauser MD (1992) Costs of deception: Cheaters are punished in rhesus monkeys (*Macaca mulatta*). Proceedings of the National Academy of Sciences 89: 12137-12139

Hauser MD, Carey S, Hauser LB (2000) Spontaneous number representation in semi-free-ranging rhesus monkeys. Proceedings of the Royal Society of London B: Biological Series 267: 829-833

Hauser MD, MacNeilage P, Ware M (1996) Numerical representation in primates. Proceedings of the National Academy of Sciences 93: 1514-517

Hauser MD, Teixidor P, Field L, Flaherty R (1993) Food-elicited calls in chimpanzees: effects of food quantity and divisibility. Animal Behaviour 45: 817-819

Hayden BY, Platt ML (2007) Temporal discounting predicts risk sensitivity in rhesus macaques. Current Biology 17: 49-53

Heilbronner SR, Rosati AG, Stevens JR, Hare B, Hauser MD (2008) A fruit in the hand or two in the bush? Divergent risk preferences in chimpanzees and bonobos. Biology Letters 4: 246-249

Hemelrijk CK (1994) Support for being groomed in long-tailed macaques, *Macaca fascicularis*. Animal Behaviour 48: 479-481

Hemelrijk CK (1990) Models of, and tests for, reciprocity, unidirectionality and other social interaction patterns at a group level. Animal Behaviour 39: 1013-1029

Hemelrijk CK, Ek A (1991) Reciprocity and interchange of grooming and “support” in captive chimpanzees. Animal Behaviour 41: 923-935

Henrich J (2004) Inequity aversion in capuchins? Nature 428: 139

Henzi SP, Barrett L (2002) Infants as a commodity in a baboon market. Animal Behaviour 63: 915-921

Henzi SP, Barrett L (1999) The value of grooming to female primates. Primates 40: 47-59

Hirata S, Matsuzawa T (2001) Tactics to obtain a hidden food item in chimpanzee pairs (*Pan troglodytes*). Animal Cognition 4: 285-295

Hutchins M, Barash DP (1976) Grooming in primates: implications for its utilitarian function. Primates 17: 145-150

Hyatt CW, Hopkins WD (1998) Interspecies object exchange: Bartering in apes? Behavioural Processes 42: 177-187

Janson CH (1998) Experimental evidence for spatial memory in foraging wild capuchin monkeys, *Cebus apella*. Animal Behaviour 55: 1229-1243

Jensen K, Call J, Tomasello M (2007) Chimpanzees are rational maximisers in an Ultimatum Game. Science 318: 107-109

Kacelnik A, Bateson M (1996) Risky theories-The effects of variance on foraging decisions. American Zoologist 36: 402-434

Kagel JH, Green L, Caraco T (1986) When foragers discount the future: Constraint or adaptation? Animal Behaviour 34: 271-283

Kahneman D, Knetsch J, Thaler R (1990) Experimental tests of the endowment effect and the Coase theorem. Journal of Political Economy 98: 1325-1348

Kalenscher T (2007) Decision-making: don't risk a delay. Current Biology 17: R58-R61

Kasper C, Voelkl B, Huber L (2008) Tolerated mouth-to-mouth food transfers in common marmosets. Primates 49: 153-156

Keverne EB, Martensz ND, Tuite B (1989) Beta-endorphin concentrations in cerebrospinal fluid of monkeys are influenced by grooming relationships. Psychoneuroendocrinology 14: 155-161

Knetsch J (1992) Preferences and nonreversibility of indifference curves. Journal of Economic Behavior and Organization 17: 131-139

Knetsch J (1989) The endowment effect and evidence of non reversible indifference curves. American Economic Review 79: 1277-1284

Knight FH (1921) Risk, uncertainty and profits. Boston, MA: Hart, Schaffner & Marx, Houghton Mifflin

Koyama NF, Caws C, Aureli F (2006) Interchange of grooming and agonistic support in chimpanzees. International Journal of Primatology 27: 1293-1309

Kummer H (1971) Primate societies: Group techniques of ecological adaptation. Chicago: Aldine

Kummer H, Anzenberger G, Hemelrijk C (1996) Hiding and perspective taking in long-tailed macaques (*Macaca fascicularis*). Journal of Comparative Psychology 110: 97-102

Lakshminaryanan V, Chen MK, Santos LR (2008) Endowment effect in capuchin monkeys. Philosophical Transactions of the Royal Society of London B: Biological Series 363: 3837-3844

Lefebvre L (1982) Food exchange strategies in an infant chimpanzee. Journal of Human Evolution 11: 195-204

Mauss M (1923/24) Essai sur le don. Année Sociologique 1: 30-186

Melis AP, Hare B, Tomasello M (2006a) Engineering cooperation in chimpanzees : tolerance constraints cooperation. Animal Behaviour 72: 275-286

Melis AP, Hare B, Tomasello M (2006b) Chimpanzees recruit the best collaborators. Science 311: 1297-1300

Mischel W (1974) Processes in delay of gratification. In: Berkowitz L. (eds) Advances in experimental social psychology. New York: Academic Press, pp. 249-292

Mitani JC, Watts DP (2001) Why do chimpanzees hunt and share meat? Animal Behaviour 61: 915-924

Mitra Setia TM, Delgado RA, Utami Atmoko SS, Singleton I, van Schaik CP (2009) Social organization and male-female relationships. In : Wich S, Suci Utami Atmoko S, Mitra Setia T & van Schaik CP (eds) Orangutans: Geographic variation, behavioral ecology and conservation. Oxford University Press, pp. 245-253

Moore J (1984) The evolution of reciprocal sharing. Ethology and Sociobiology 5: 5-14

Mulcahy NJ, Call J (2006) Apes save tools for future use. Science 312: 1038-1040

Nishida T (1968) The social group of wild chimpanzees in the Mahali mountains. Primates 9: 167-224

Nishida T, Hasegawa T, Hayaki H, Takahata Y, Uehara S **(**1992) Meat-sharing as a coalition strategy by an alpha male chimpanzee? In: Nishida T, McGrew W, Marler P, Pickford

M, de Waal FBM (eds) Topics in Primatology. Vol. 1. Human Origins. Tokyo: Tokyo University Press, pp. 159-174

Noë R, Hammerstein P (1995) Biological markets. Trends in Ecology and Evolution 10: 336-339

Noë R, Hammerstein P (1994) Biological markets: supply and demand determine the effect of partner choice in cooperation, mutualism and mating. Behavioral Ecology and Sociobiology 35: 1-11

Noë R (1990) A Veto game played by baboons: a challenge to the use of the Prisoner's Dilemna as a paradigm for reciprocity and cooperation. Animal Behaviour 39: 78-90

Nowak MA (1996) Five rules for the evolution of cooperation. Science 314: 1560-1563

Packer C (1977) Reciprocal altruism in *Papio Anubis*. Nature 265: 441-443

Padoa-Schioppa C, Jandolo K, Visalberghi E (2006) Multi-stage mental process for economic choice in capuchins. Cognition 99(1): B1-B13

Parr L, Winslow JT, Hopkins WD (1999) Is the inversion effect in rhesus monkeys face-specific? Animal Cognition 2: 123-129

Parr LA, Dove T, Hopkins WD (1998) Why faces may be special : evidence of the inversion effect in chimpanzees. Journal of Cognitive Neuroscience 10: 615-622

Petit O, Desportes C, Thierry B (1992) Differential probability of « coproduction » in two species of macaque (*Macaca tonkeana*, *M. mulatta*). Ethology 90: 107-120

Ramseyer A, Pelé M, Dufour V, Chauvin C, Thierry B (2006) Accepting loss: the temporal limits of reciprocity in brown capuchin monkeys. Proceedings of the Royal Society of London : Biological Series 273: 179-184

Roberts WA (2002) Are animals stuck in time? Psychological Bulletin 128: 473-489

Roma PG, Silberberg A, Ruggiero AM, Suomi SJ (2006) Capuchin monkeys, inequity aversion and frustration effect. Journal of Comparative Psychology 120 : 67-73

Rosati AG, Stevens JR, Hare B, Hauser MD (2007) The evolutionary origins of human patience: temporal preferences in chimpanzees, bonobos, and human adults. Current Biology 17: 1663-1668

Rumbaugh DM, Savage-Rumbaugh ES, Pate JL (1988) Addendum to "Summation in the chimpanzee (*Pan troglodytes*)." Animal Behavior Processes 14: 118-120

Rumbaugh DM, Savage-Rumbaugh ES, Hegel MT (1987) Summation in the chimpanzee (*Pan troglodytes*). Journal of Experimental Psychology: Animal Behaviour Processes 13: 107-115

Sahlins M (1965) On the sociobiology of primitive exchange. In: Banton M (eds) The relevance of Models for Social Anthropology, London: Tavistock, ASA Monograph 1

Savage-Rumbaugh ES, Rumbaugh D, Boysen S (1978) Linguistically mediated tool use and exchange by chimpanzees (*Pan troglodytes*). The Behavioural and Brain Sciences 4: 539-554

Scheres A, Sanfey AG (2006) Individual differences in decision making: drive and reward responsiveness affect strategic bargaining in economic games. Behavioral and Brain Functions 2: 35

Schino G, Pellegrini B (2009) Grooming in mandrills and the time frame of reciprocal partner choice. American Journal of Primatology 71: 884-888

Schino G, Di Giuseppe F, Visalberghi E (2009) The time frame of partner choice in the grooming reciprocation of *Cebus apella*. Ethology 115: 70-76

Schino G, Aureli F (2008) Grooming reciprocation among female primates: a meta-analysis. Biology Letters 4: 9-11

Schino G, Polizzi di Sorentino E, Tiddi B (2007) Grooming and coalitions in Japanese macaques (*Macaca fuscata*) : partner choice and the time frame of reciprocation. Journal of Comparative Psychology 121: 181-188

Schino G, Scucchi S, Maestripieri D, Turillazzi PG (1988) Allogrooming as a tension reduction mechanism: a behavioral approach. American Journal of Primatology 16: 43-50

Seyfarth RM, Cheney DL (1988) Empirical tests of reciprocity theory: problems in assessment. Ethology and Sociobiology 9: 181-187

Seyfarth RM, Cheney DL (1984) Grooming, alliances and reciprocal altruism in vervet monkeys. Nature 308: 541-543

Silberberg A, Roma PG, Huntsberry ME, Warren-Boulton FR, Sakagami T, Ruggiero AM, Suomi SJ (2008) On loss aversion in capuchin monkeys. Journal of the Experimental Analysis of Behavior 89: 145-155

Silberberg A, Fujita K (1996) Pointing at a smaller food amounts in an analogue of Boysen and Berntson's (1995) procedure. Journal of the Experimental Analysis of Behavior 66: 143-147

Silk (1992) The patterning of intervention among male bonnet macaques: reciprocity, revenge, and loyalty. Current Anthropology 33: 318-325

Silk J (1982) Altruism among female *Macaca radiata*: explanations and analysis of patterns of grooming and coalition formation. Behaviour 79: 162-188

Silk J, Samuels A, Rodman P (1981) The influence of kinship, rank and sex on affiliation and aggression between adult female and immature bonnet macaques (*Macaca radiata*). Behaviour 78: 111-133

Silberberg A, Widholm JJ, Bresler D, Fujita K, Anderson JR (1998) Natural choice in nonhuman primates. Journal of Experimental Psychology : Animal Behavior Processes 24: 215-228

Slater KY, Schaffner CM, Aureli F (2007) Embraces for infant handling in spider monkeys: evidence for a biological market? Animal Behaviour 74: 455-461

Slocombe KE, Newton-Fischer NE (2005) Fruit sharing between wild adult chimpanzees (*Pan troglodytes schweinfurthii*) : a socially significant event ? American Journal of Primatology 65: 385-391

Smith A (1776) An inquiry into the nature and causes of the wealth of nations.

Sousa C, Matsuzawa T (2001) The use of tokens as rewards and tools by chimpanzees (*Pan troglodytes*). Animal Cognition 4: 213-221

Stanford CB, Wallis J, Mpongo E, Goodall J (1994) Hunting decisions in wild chimpanzees. Behaviour 131:1-18

Stevens JR (2004) The selfishness nature of generosity: harassment and food sharing in primates. Proceedings of the Royal Society of London, Series B 271: 451-456

Stevens JR, Cushman FA, Hauser MD (2005a) Evolving the psychological mechanisms for cooperation. Annual Review of Ecology, Evolution, and Systematics 36: 499-518

Stevens JR, Hallinan EV, Hauser MD (2005b) The ecology and evolution of patience in two New World monkeys. Biology Letters 1: 223-226

Subiaul F, Vonk J, Okamoto-Barth S, Barth J (2008) Do chimpanzees learn reputation by observation? Evidence from direct and indirect experience with generous and selfish strangers. Animal Cognition 11: 611-623

Suda C, Call J (2005) Piagetian conservation of discrete quantities in bonobos (*Pan paniscus*), chimpanzees (*Pan troglodytes*), and orangutans (*Pongo pygmaeus*). Animal Cognition 8: 220-235

Suda C, Call J (2004) Piagetian liquid conservation in the great apes (*Pan paniscus*, *Pan troglodytes*, and *Pongo pygmaeus*). Journal of Comparative Psychology 118: 265-279

Suddendorf T, Corballis MC (2007) The evolution of foresight: What is mental time travel, and is it unique to humans? Behavioral and Brain Sciences 30: 299-313

Suddendorf T, Busby J (2003) Mental time travel in animals? Trends in Cognitive Sciences 7: 391-396

Teleki G (1973) The predatory behaviour of wild chimpanzees. Bucknell University Press: Lewisberg

Terry RL (1970) Primate grooming as a tension reduction mechanism. Journal of Psychology 76: 129-136

Thierry B, Singh M, Kaumanns W (2004) Macaques Societies: A Model for the Studies of Social Organization. Cambridge University Press, Cambridge

Tomasello M, Call J (1997) Primate Cognition. Oxford University Press : New-York

Toner IJ, Smith RA (1977) Age and overt verbalization in delay-maintenance behavior in children. Journal of Experimental Child Psychology 24: 123-128

Toner IJ, Lewis BC, Gribble CM (1979) Evaluative verbalization and delay maintenance behavior in children. Journal of Experimental Child Psychology 28: 205-210

Tomonoga M (1994) How Laboratory-raised Japanese monkeys (*Macaca fuscata*) perceive rotated photographs of monkeys : evidence for an inversion effect in face perception. Primates 35: 155-165

Trivers RL (1971) The evolution of reciprocal altruism. The Quaterly Review of Biology 46: 35-57

Tversky A, Kahneman D (1986) Rational choices and the framing of decisions. Journal of business 59: 251-278

Tversky A, Kahneman D (1981) The framing of decisions and the psychology of choice. Science 211: 453-458

van Marle K, Aw J, McCrink K, Santos LR. (2006) How capuchin monkeys (*Cebus apella*) quantify objects and substances. Journal of Comparative Psychology 120: 416-426

van Noordwijk MA, van Schaik CP (2009) Intersexual food transfer among orangutans: do females test males for coercive tendency? Behavioral Ecology and Sociobiology 63: 883-890

Ventura R, Majolo B, Koyama NF, Hardie S, Schino G (2006) Reciprocation and interchange in wild Japanese macaques: Grooming, cofeeding, and agonistic support. American Journal of Primatology 68: 1138-1149

von Neumann J, Morgenstern O (1944) Theory of games and economic behavior. Princeton University Press, Princeton

Warneken F, Hare B, Melis AP, Hanus D, Tomasello M (2007) Spontaneous altruism by chimpanzees and young children. PLoS Biology 5: e184

Warneken F, Tomasello M (2006) Altruistic helping in human infants and young chimpanzees. Science 311: 1301-303

Watts DP (2003) Gorilla social relationships: a comparative review. In: Taylor AB, Goldsmith ML (eds) Gorilla biology: a multidisciplinary perspective. Cambridge: Cambridge University Press, pp. 302-327

Watts DP (2002) Reciprocity and interchange in the social relationships of wild male chimpanzees. Behaviour 139: 343-370

Watts DP (1997) Agonistic interventions in wild Mountain *Gorilla* groups. Behaviour 134: 23-57

Watts DP (1996) Comparative socio-ecology of gorillas. In: McGrew WC, Marchant LF, Nishida T (eds) Great apes societies. Cambridge: Cambridge University Press, pp. 16-28

Werdenich D, Huber L (2002) Social factors determine cooperation in marmosets. Animal Behaviour 64: 771-781

Westergaard GC, Evans TA, Howell S (2007) Token mediated tool exchange between tufted capuchin monkeys (*Cebus apella*). Animal Cognition 10: 407-414

Westergaard GC, Liv C, Rocca AM, Cleveland A, Suomi SJ (2004) Tufted capuchins (*Cebus apella*) attribute value to foods and tools during voluntary exchanges with humans. Animal Cognition **7**: 19-24

Westergaard GC, Liv C, Chavanne TJ, Suomi SJ (1998) Token-mediated tool-use by a tufted capuchin monkey (*Cebus apella*). Animal Cognition 1: 101-106

Westergaard GC, Suomi SJ (1997) Transfer of tools and food between groups of tufted capuchins (*Cebus apella*). American Journal of Primatology 43: 33-41

Wheeler BC (2009) Monkeys crying wolf? Tufted capuchin monkeys use anti-predator calls to usurp resources from conspecifics. Proceedings of the Royal Society of London B: Biological Series 276: 3013-3018

White F. (1988) Party composition and dynamics in *Pan paniscus*. International Journal of Primatology 9: 179-93

Widdig A, Jürgen Streich W, Tembrock G (2000) Coalition formation among male barbary macaques (*Macaca sylvanus*). Americal Journal of Primatology 50: 37-51

Wilkinson GS (1984) Reciprocal food sharing in the vampire bat. Nature 308: 181-184

Wrangham RW (1975) The behavioural ecology of chimpanzees in Gombe National Park, Tanzania. Thèse de doctorat, Université de Cambridge, Grande-Bretagne

Wynn K (1992) Addition and subtraction by human infants. Nature 358: 748-750

Wynne CD (2004) Fair refusal by capuchin monkeys. Nature 428: 140

Yamamoto S, Humle T, Takaka M (2009) Chimpanzees help each other upon request. PLoS ONE 4: e7416

Résumé: Etude comparative des facultés d'échange chez les primates non humains

L'être humain se distingue des autres espèces par le développement des transactions économiques. Des interactions réciproques surviennent chez des animaux comme les primates dans le toilettage social, le soutien dans les conflits ou le partage de nourriture, par exemple. Selon certains auteurs, ces interactions sont basées sur le mécanisme de la réciprocité calculée, c'est-à-dire que les sujets mémorisent les biens ou services donnés et reçus, et en tiennent compte dans leurs échanges futurs. Cependant, la seule observation des interactions ne permet pas de conclure à la contingence des comportements ou à un calcul de la part des individus. Ce travail de thèse a eu pour objectif d'étudier les conditions de la réciprocité calculée (1) en testant si les primates intègrent le coût temporel associé à un échange, (2) en étudiant leur aptitude à prendre en compte le risque inhérent à la situation d'échange, et (3) en recherchant s'ils peuvent s'engager avec un congénère dans des échanges de type calculé dans des conditions contrôlées. J'ai testé sept espèces de primates dans différentes tâches expérimentales basées sur le modèle de l'échange : macaques à longue queue (*Macaca fascicularis*), macaques de Tonkean (*M. tonkeana*), capucins bruns (*Cebus apella*), chimpanzés (*Pan troglodytes*), bonobos (*Pan paniscus*), orangs-outangs (*Pongo pygmaeus*), gorilles (*Gorilla gorilla*). L'étude de la dimension temporelle de l'échange montre que la tolérance au délai varie d'une espèce à l'autre. Pour une récompense huit fois supérieure à l'item initial, le délai moyen toléré est équivalent à 10-20 s pour les capucins, 40-80 s pour les macaques, et 1-2 mn pour les chimpanzés. Chez toutes les espèces, la décision de la majorité des individus se réalise sur la base de mécanismes comme l'estimation de la valeur des biens échangés et l'anticipation du délai d'attente. L'étude de la prise de risque dans l'échange montre que la majorité des orangs-outangs et des capucins n'échangent que lorsque la chance de gagner est supérieure à la chance de perdre. La majorité des macaques à longue queue échange même si la chance de gagner est inférieure à la chance de perdre. Les sujets sont capables d'estimer les probabilités de gain et de perte et de prendre en considération ces informations pour décider de s'engager ou non dans l'échange. L'étude de la réciprocité dans l'échange révèle que seuls deux orangs-outangs ont été capables de s'engager dans un système d'échange stable et calculé. Contrairement aux orangs-outangs, seuls quelques cas de quémandes et de dons ont été relevés chez les chimpanzés, les bonobos et les gorilles ; et les individus n'ont pas été capables d'échanger des biens de manière réciproque. Chez les macaques et les capucins, aucun cas de quémande ou de don n'a été observé. Bien que l'échange spontané de biens s'avère difficile chez les primates non humains, ce travail montre qu'ils possèdent à des degrés divers les facultés nécessaires pour comparer la valeur des biens, accepter un risque de perte ou retarder une gratification, qui sont autant de mécanismes à la base des transactions économiques chez l'être humain.

Mots-clés : primates, économie, réciprocité, décision, cognition, attente, risque, don, échange.

Marie Pelé

Ethologie des Primates, DEPE, IPHC, UMR7178 CNRS-UDS, Strasbourg, France

Abstract: Comparative study of exchange abilities in non-human primates

Trading is a hallmark of human behaviour, and exchanges or even gifts are not commonly seen in other species. Across the animal kingdom, and especially in primates, reciprocal interactions are reported in a diversity of contexts such as social grooming, coalitions and food sharing. Some authors propose that these interactions are based on calculated reciprocity, a mechanism by which individuals keep track of what has been given and returned and consider it for future exchanges. However, the observed interactions do not provide valid support about behaviours contingency and calculation from individuals. This work aimed at studying the conditions necessary for calculated reciprocity to occur (1) by testing whether primates understand the temporal cost associated with an exchange, (2) by studying the capacity of primates to take a risk during an exchange and (3) by searching whether primates are capable to engage with a conspecific in a calculated exchange under controlled conditions. I tested seven species of non human primates in different exchange tasks: long-tailed macaques (*Macaca fascicularis*), Tonkean macaques (*M. Tonkeana*), capuchin monkeys (*Cebus apella*), chimpanzees (*Pan troglodytes*), bonobos (*Pan paniscus*), orang-utans (*Pongo pygmaeus*), gorillas (*Gorilla gorilla*). When considering the temporal dimension of exchange, I observed some variations in the capacity of primates to delay gratification. For a reward equivalent to eight times an initial item, capuchins could wait for 10-20 s, macaques for 40-80 s and chimpanzees for 1-2 min. In all species, both estimation of the value of goods being exchanged and anticipation of the waiting duration underlie the decision of individuals. When considering the capacity of primates to engage in a risky exchange, it appeared that most orang-utans and capuchins exchanged when the chance to gain was higher than the chance to lose. Most long-tailed macaques exchanged even when the chance to gain was lower than the chance to lose. Primates are capable to estimate gain and loss probabilities and to consider it when deciding to engage or not in an exchange. When considering the capacity of primates to reciprocate, two orang-utans were able to engage in a system of exchanges that was both stable and calculated. Contrary to orang-utans, only few begging gestures and gifts were observed in chimpanzees, bonobos and gorillas; and individuals were not capable to reciprocate. In capuchins and macaques, no begging gesture nor gifts has been observed. Although spontaneous exchange is difficult in non-human primates, this work shows that they possess some abilities to evaluate the value of goods, to accept a loss and to delay gratification, which are among the required capacities underlying economics transactions as observed in human beings.

Key words: primates, economics, reciprocity, decision-making, cognition, waiting, risk, gift, exchange.

Marie Pelé

Ethologie des Primates, DEPE, IPHC, UMR7178 CNRS-UDS, Strasbourg, France