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Compétition et coopération chez les psittacidés: Implication des processus cognitifs

Devant le jury composé de

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Pour ceux qui ce demandent pourquoi avoir choisit de travailler avec des perroquets gris du Gabon pour répondre à :

Quels sont les impératifs cognitifs qu'impose la vie en société ?

Je répondrai deux choses

Premièrement

Birds of a feather flock together

Ce qui explique pourquoi ces oiseaux sont sociaux.

Et ensuite

Grey parrot always 'suck seeds'

Et par conséquent il se révélait être le meilleur modèle pour mes travaux.

A mes protégés : Zoé, Léo & Shango

Bon vol !

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INTRODUCTION

Présentation générale du travail réalisé

Ce travail s'intègre en partie dans le cadre d'un projet européen portant sur l'origine des comportements de coopération. Ce projet intitulé INCORE (Integrating Cooperation Across Europe) fait suite au projet RefCom (Referential Communication) et s'inscrit également dans la thématique 'What does it means to be human ? » du sixième PCRD NestPathfinder de la Commission Européenne. Différents laboratoires européens interviennent sur le sujet avec des approches différentes (éthologie, biologie moléculaire, philosophie, etc.) et des modèles animaux variés (perroquets, humains, chiens, etc.). L'objectif principal de ce projet était de mieux comprendre les mécanismes de ce comportement si complexe et pourtant si développé au sein des sociétés humaines. Dans le cadre de ce projet, notre équipe était en charge du pôle 'Intégration des femmes dans la recherche' (projet transversal) et de l'étude des psittacidés pour la partie recherche. Ainsi mes travaux concernent essentiellement les capacités des psittacidés à résoudre des tâches de coopération et leur propension à se comporter de manière prosociale. De plus nous nous sommes intéressés aux interactions Homme-perroquet dans le cadre de l'attribution de perceptions et d'intentions de la part de l'oiseau vis-à-vis de l'humain, ces capacités pouvant également se révéler utiles lors des actions de coopération avec des congénères.

Le manuscrit se présente sous la forme d'une succession d'articles publiés ou soumis.

L'hypothèse du cerveau social

Bien que des insectes, des mamifères ou encore des oiseaux (notamment marins) vivent au sein de colonies pouvant compter plusieurs millions d'individus, aucune autre espèce ne présente cette variété organisationnelle que l'on retrouve au sein des groupes d'*Homo sapiens*. Nous vivons dans des sociétés de tailles variables allant de petites communautés de chasseurs-cueilleurs nomades aux villes où des millions de personnes vivent dans une proximité imposée avec leurs congénères. Nous formons des liens durables avec nos parents mais aussi pour certaines communautés avec notre partenaire sexuel. Notre intelligence pourrait être liée à cette plasticité sociale. En effet, Jolly (1966) puis Humphrey (1976) proposèrent une explication pour l'apparente supériorité cognitive des primates par rapport aux autres espèces. Les contraintes environnementales liées à la recherche et à l'extraction de nourriture ou encore aux stratégies pour échapper aux prédateurs ne sont pas suffisantes pour expliquer les différences observées au niveau des capacités cognitives lors des tests en laboratoire. L'environnement social est sans cesse changeant et non prédictible surtout au sein des groupes où les individus ont des interactions multiples et diverses avec des partenaires différents. Cette proposition –selon laquelle les individus vivant au sein de société et devant gérer des relations multiples et complexes, ont des capacités cognitives supérieures- l'Hypothèse de l'Intelligence Sociale a été reprise par la suite dans une approche focalisée d'une part sur les comportements de manipulation et de tromperie (Hypothèse de l'Intelligence Machiavélique, Byrne & Whiten 1988 ; Whiten & Byrne 1997) et d'autre part sur la relation entre la taille du cerveau et l'organisation sociale d'autre part (Hypothèse du Cerveau Social ; Dunbar 1998). Ces hypothèses ont été proposées pour le cas des primates mais les chercheurs se sont depuis rendus compte que d'autres espèces telles que les dauphins, les hyènes ou encore les éléphants présentaient de nombreuses similarités avec les primates tant au niveau de leur biologie et de leur écologie que de leurs comportements et interactions sociales (McComb 2001 ; de Waal & Tyack 2003 ; Connor 2007 ; Holekamp et al. 2007).

En 1996, Peter Marler (1996) suggère pour la première fois que les oiseaux également présentent des aspects similaires aux primates dans leurs interactions sociales. Par ailleurs, des études concernant la taille de l'encéphale (ou de certains de ses éléments) et l'organisation des structures cérébrales ont permis d'apporter de nouvelles données. Ainsi, les chercheurs ont montré une corrélation entre la taille du groupe social et la taille du néocortex chez les primates (Dunbar 1992), les carnivores, les insectivores (Dunbar & Bever 1998), les chauvessouris (Barton & Dunbar 1997) et les cétacés (Marino 2002; Connor 2007). Chez les ongulés, on retrouve cette corrélation bien que les facteurs écologiques interviennent également (Shultz & Dunbar 2006). Certains oiseaux ont, proportionnellement, un cerveau (partie télencéphalique) aussi gros que celui des chimpanzés (Emery & Clayton 2004). Cependant la possible relation entre la taille du cerveau et le degré de socialité n'a pas pu être démontré chez les oiseaux au cours des différentes études réalisées, qu'il s'agisse de la taille du groupe (Beauchamp & Fernandez-Juricic 2004), de la structure sociale (Emery 2004 ; Emery et al. 2007) ou encore de la présence d'un comportement de coopération au nid (Iwaniuk & Arnold 2004). Seule l'étude réalisée par Burish et al. (2004) a mis en évidence une corrélation entre la taille du télencéphale et la complexité sociale. Cependant, les paramètres considérés étaient une succession de comportement divers et complexes, par toujours liés à des interactions sociales qui plus est (acrobaties aériennes, résolution de problèmes, mémoire, …).

Un des éléments qui, en général, différencie les oiseaux des primates est la monogamie (Lack 1968) et ainsi peut-être qu'il s'agirait plus d'une gestion de la qualité de la relation plutôt que de la quantité. Emery et al. (2007) ont mis en évidence une corrélation entre la taille du néocortex et le système d'accouplement (et la durée de la période monogame). Ainsi la complexité de la relation pourrait expliquer la taille du cerveau chez certaines espèces telles que les corvidés. D'autres auteurs (Scheiber et al. 2008) viennent nuancer ces résultats, notamment en soulignant le nombre limité d'exemples sélectionnés par Emery et al. (2007) pour illustrer leur propos. En effet, il existe d'autres espèces que les corvidés et les psittacidés qui présentent également une organisation monogame de longue durée telles que les oies. Par ailleurs, certaines espèces possèdent un cerveau extrêmement développé bien qu'il s'agisse d'espèces nocturnes et solitaires (i.e. rapaces nocturnes) et chez qui la fonction biologique (vision nocturne) explique la taille du support neuronal (Burish et al. 2004; Iwaniuk & Hurd 2005). Néanmoins la piste de la monogamie (Hypothèse de l'Intelligence Relationnelle) semble encore être la plus adaptée pour expliquer la taille du cerveau chez les oiseaux (Scheiber et al. 2008; Shultz & Dunbar 2010).

Des études ont mis en évidence que les espèces aviaires avec un plus gros cerveau survivaient mieux en nature (Sol et al. 2007), présentaient un niveau d'innovation supérieure (Overington et al. 2009) et une plus grande adaptation aux variations environnementales (Sol et al. 2005 ; Schuck-Paim et al. 2008). Sol (2009) propose une autre hypothèse (Hypothèse de la Cognition Tampon) suggérant que le développement d'un support neuronal plus important permet de répondre aux défis socio-écologiques en facilitant la mise en place ou la modification de réponses comportementales.

Les études réalisées dans le cadre de ma thèse ont pour objectif d'apporter quelques données permettant de confirmer (ou non) ces hypothèses (Hypothèse du Cerveau Social, Hypothèse de l'Intelligence Relationelle).

Le modèle biologique : aspect généraux

Les lignées menant aux mammifères et oiseaux se sont séparées il y a environ 280 millions d'années. Les oiseaux appartiennent à la classe des sauropsides qui inclut aussi les reptiles, le groupe le plus proche étant celui des crocodiles. Au sein des oiseaux, l'ordre des psittaciformes comprend les perroquets et les perruches. Différentes espèces appartenant à la famille des psittacidés ont été testées en fonction des paradigmes investigués mais aussi en fonction des collaborations qu'il était possible d'établir. Les éléments proposés comme pré-requis à l'établissement d'interactions sociales complexes sont la taille du cerveau, la période de développement, la longévité et la constitution de groupes individualisés (stables). Toutes ces caractéristiques se retrouvent chez les psittacidés. Au cours de mes recherches, j'ai été amené à travailler avec cinq espèces différentes.

Les perroquets gris du Gabon (*Psittacus erithacus*) sont originaires d'Afrique (Centrale et de l'Ouest). Ils forment de larges groupes pouvant compter plusieurs centaines d'individus.

Les aras macao (*Ara macao*) peuplent les forêts humides tropicales américaines, de l'est du Mexique à l'Amazonie péruvienne et brésilienne dans les terres basses jusqu'à 500 m d'altitude. Alors qu'elles sont peu fréquentes sur le continent, de grandes colonies d'aras rouges peuvent être observées sur l'ile Coiba sur la côte pacifique du Panama. Les aras canindé (*Ara glaucogularis)* sont endémiques du nord de la Bolivie. Moins grégaires que leurs cousins macao, ils sont le plus souvent observés en couple.

Les conures soleil (*Aratinga solstitialis*) sont originaires du Brésil et de la Guyane. Ils vivent au sein de structures sociales à taille variable allant du couple (structure familiale) à la colonie où les individus participent à l'élevage des jeunes des autres couples.

Les perruches ondulées (*Melopsittacus undulatus*) quant à elles vivent dans les zones semi désertiques d'Australie et se rassemblent en groupes de plusieurs milliers d'individus (Juniper & Parr 1998 ; Luescher 2006). Tous ces oiseaux, en général, ont une dynamique de fission-fusion, ce qui signifie que la structure sociale du groupe varie au cours de la journée en fonction des activités ; ainsi les oiseaux vont fourrager au sol en larges groupes ce qui a pour effet de diminuer le risque de prédation et au contraire fourragent en plus petit nombre dans les arbres diminuant ainsi la compétition entre les animaux compte tenu de la place réduite (et de la quantité de nourriture) que peut offrir les branches nourricières d'un arbre.

Ces oiseaux vivent à l'état sauvage dans des forêts denses au niveau de la canopée (perroquets) ou des zones semi désertiques (perruches) rendant difficile leur observation. La reconnaissance individuelle est difficile compte tenu de la ressemblance phénotypique entre les individus ainsi que du nombre d'individus. De manière générale, il n'y pas de dimorphisme sexuel. Chez les perruches, la couleur de la cire varie en fonction du sexe et de l'état physiologique ; ainsi les mâles arborent une cire de couleur bleue plus ou moins intense et pour les femelles la couleur de la cire varie de la couleur crème au marron foncé lors du pic œstrogénique (Juniper & Parr 1998 ; Luescher 2006). Enfin l'élément majeur justifiant de l'intérêt d'étudier ces espèces en captivité est leur extrême néophobie. Des animaux nés en captivité et manipulés dès leur plus jeune âge sont moins sensibles aux contraintes anthropogéniques. La diversité des espèces permet entre autres de tester des organisations sociales différentes et aussi des capacités cognitives différentes. De même la diversité des relations existantes entre les individus (partenaire sexuel, individu de même couvée, parents-jeunes, individus du même groupe, dominant-subordonné, male-femelle, etc …) permet d'évaluer l'effet de la nature du lien existant entre des partenaires sur la façon dont ils se comportent.

Travaux de recherche

Dans le cadre des interactions sociales telles que l'élevage des jeunes, la gestion des conflits mais aussi afin de pouvoir accéder à certaines ressources les individus sont amenés à communiquer pour signifier leur intentions et à élaborer des solutions pour parvenir à résoudre les défis. Ainsi les occasions de coopérer sont multiples et les avantages d'un tel comportement semblent évidents. Les actions conjointes nécessitent d'avoir les compétences nécessaires pour y parvenir et aussi les conditions (sociales et environnementales) favorables (Huber et al. 2008). On imagine facilement qu'il est d'autant plus facile d'y parvenir si on est capable de se mettre à la place de l'autre, de se rendre compte de ce qui est mieux pour chacun. Ces comportements (attribution de perception, de connaissances, de désirs ou encore sensibilité à l'injustice) nécessitent des compétences cognitives importantes et donc un support neuronal adapté d'où l'existence d'un possible lien entre relation sociale et taille de l'encéphale. Pour certains auteurs, l'importance et la diversité des comportements de coopération présents chez les humains sont tels qu'ils nécessitent une représentation cognitive perspective puissante, d'où un cerveau plus développé (Moll & Tomasello 2007 ; l'Hypothèse de l'Intelligence Vygotskienne).

Etude de la coopération

De nombreux comportements coopératifs sont observés chez des espèces animales autres que l'humain comme par exemple la chasse (fossas ; Lürhs & Dammhahn 2010), le harcèlement (suricates ; Graw & Manser 2007) ou l'élevage des jeunes (pour une revue : Bergmüller et al. 2007). L'on trouve aussi des exemples de coopération entre oisillons d'une même couvée qui coordonnent leur quémande, ce qui aura pour effet d'accroître leurs chances de recevoir de la nourriture de leur parents (Mathevon & Charrier 2004). Cependant, la complexité des mécanismes cognitifs sous-jacents à ces comportements est difficile à évaluer étant donné que la part relative de l'apprentissage par rapport à la prédétermination génétique est difficile à connaitre. Des études en laboratoires et des comparaisons entre espèces employant des paradigmes similaires sont utiles pour étudier les facteurs proximaux qui peuvent être partagés par différentes espèces et pour mettre à jour d'éventuels processus de convergence évolutive. La coopération peut être définie de nombreuses façons, pour nos travaux de recherche nous nous sommes focalisés sur la définition de Noë (2006) où est considérée comme coopération toute interaction (ou série d'interactions) qui apporte(nt) un gain pour chacun des participants.

Une des études en laboratoire concernant la coopération des chimpanzés a été réalisée par Hirata et Fuwa (2007). Ils ont employé le paradigme de la ficelle coulissante, dispositif dans lequel deux individus devaient tirer simultanément une ficelle pour accéder à la récompense. Plusieurs études ont mis en évidence le fait que le degré de tolérance entre les participants influence directement la coopération, aussi bien concernant sa probabilité de se produire que son efficacité. Ainsi, plus les membres d'une dyade sont tolérants l'un envers l'autre, plus ils sont efficaces (capucins ; Mendres & de Waal 2000 ; Chimpanzés : Mélis et al. 2006b ; bonobos : Hare et al. 2007 ; corbeaux freux : Seed et al. 2008). Une étude récente réalisée avec des corbeaux freux a montré que le tempérament des individus jouait aussi sur les performances de la dyade, à savoir que les individus les plus intrépides étaient les plus à même de prendre part à l'action coopérative alors que les plus timides étaient influencés par le comportement de leur partenaire (Scheid & Noë 2010). L'issue de la coopération elle-même peut influencer la probabilité qu'une autre action coopérative se déroule comme l'ont montré Schuster (2002) et Rutte et Taborsky (2008) avec des rats. Au cours de nos expériences, nous avons testé nos perroquets avec différents niveaux de coopération définis en fonction des actions nécessaires pour accéder à la récompense (Boesch & Boesch 1989). Ces différents niveaux reposent sur une classification descriptive de complexité apparente croissante ; ils permettent d'évaluer si les sujets sont capables de résoudre la tâche et si oui, comment ils s'y prennent pour y parvenir. Le **premier niveau** concerne les actions simultanées mais sans considération pour ce que fait le partenaire (**similarité**). Ainsi des études avec les capucins ont montré que les individus testés étaient capables de résoudre le problème mais ne comprenaient pas le rôle de leur partenaire (Chalmeau et al. 1997 ; Visalberghi et al. 2000). Le **second niveau** est atteint quand les individus sont capables de synchroniser leurs actions (**synchronisation**). Des chimpanzés testés dans cette situation ont montré qu'ils étaient capables d'attendre l'arrivée d'un partenaire avant de commencer à tirer sur la ficelle (Melis et al. 2006b). De plus, quand les sujets testés avaient la possibilité de faire entrer un partenaire dans la zone de test, ils le faisaient significativement plus lorsqu'un partenaire était nécessaire pour résoudre le problème. Seed et ses collaborateurs ont conduit la même expérience avec des corbeaux freux mais à l'inverse des chimpanzés, les oiseaux n'ont pas été capables d'attendre. Le **troisième niveau** concerne la **coordination**, c'est-à-dire la synchronisation des actions dans le temps et l'espace. Dans l'expérience de Seed et al. (2008), les sujets testés ont le choix entre deux dispositifs, l'un pouvant être actionné seul (Solo) et le second nécessitant de coopérer (Duo). Les oiseaux étaient testés avec et sans partenaire et pour inciter les oiseaux à coopérer, deux fois plus de nourriture (par individu) était placée dans le dispositif Duo. Ainsi les sujets étaient supposés choisir le dispositif Solo quand aucun partenaire n'était disponible et tenter d'accéder à plus de nourriture en choisissant le Duo dans le cas contraire. Lors de cette expérience avec les corbeaux freux, seuls deux des six oiseaux ont choisi davantage le dispositif Solo quand ils étaient seuls (les autres choisissant au hasard) et aucune coopération n'a été observée. Une expérience récente réalisée avec des hyènes a révélé que les individus étaient capables de coordonner leurs actions (Drea et Carter 2009) tout comme des chimpanzés (Melis et al. 2009). Le **quatrième niveau** (**collaboration**) consiste à réaliser des actions différentes mais complémentaires. L'exemple retrouvé en nature est celui de la chasse collective où les individus qui prennent part à l'action réalisent des actions variées et coordonnées afin de pouvoir rabattre et attraper la proie. Ce comportement a été observé chez plusieurs espèces de mammifères : chimpanzés (Boesch & Boesch 1989), lions (Stander 1992) mais aussi orques (Visser et al. 2008) et plus récemment chez une espèce solitaire, le fossa (Lürhs & Dammhahn 2010).

A l’état naturel, les oiseaux coopèrent mais nous ne connaissons pas le niveau de performance cognitive que cela requiert. En effet, les capacités cognitives sous-jacentes à la coopération ainsi que pour passer d’un niveau à un autre tel que défini par Boesch & Boesch (1989) ne sont pas claires. Néanmoins, le pré-requis majeur concerne la compréhension du rôle du partenaire (Noë 2006) qui permet d’observer la différence entre la similarité et la synchronie. L’écart entre la synchronie et le niveau suivant est plus difficile à évaluer. Pour être capable d’atteindre le dernier niveau (collaboration) sans être simplement conditionnés à le faire, les individus doivent comprendre le rôle de chaque participant et c’est pourquoi, bien que cela ne soit pas précisé dans l’article de Boesch et Boesch (1989), nous avons considéré que les sujets devaient être capable d’échanger leurs rôles.

Les actions de coopération peuvent également être étudiée du point de vue de la situation sociale comme les relations de hiérarchie existant entre les participants ou encore leurs préférences sociales vis-à-vis de potentiels partenaires. En effet, tous ces facteurs peuvent jouer un rôle dans la formation de la dyade et son efficacité. De plus, plusieurs études ont montré que certaines espèces étaient sensibles à l’inéquité (chimpanzés: Brosnan et al. 2010b; capucins: van Wolkenten et al. 2007, Fletcher 2008, Brosnan et al. 2010a; tamarins: Neiworth et al. 2009; chiens: Range et al. 2009) même si les résultats concernant les chimpanzés sont encore controversés (Bräuer et al. 2006, Bräuer et al. 2009). Ainsi l’action coopérative devrait apporter une récompense équivalente à chacun des participants puisque dans le cas contraire on risque de voir un arrêt de la coopération. Une étude a souligné que la tolérance vis-à-vis de l’inéquité pouvait varier en fonction du degré de parenté avec le partenaire (Brosnan et al. 2005) et donc la qualité de la relation (ou sa nature) peut influencer l’issue d’une négociation. D’autres solutions sont envisageables pour résoudre un éventuel conflit d’intérêts pouvant apparaître lorsque la récompense à la suite d’une action conjointe est asymétrique. Ainsi les sujets peuvent alterner leurs rôles pour permettre à chacun d’être récompensé (Trivers 1971 ; Altruisme réciproque) ou encore se partager le butin. Lors d’une expérience sur la résolution d'une tâche de négociation, des chimpanzés avaient le choix entre une situation équitable et une autre injuste, créé par une distribution inéquitable de la récompense (Melis et al. 2009). Les résultats montrent qu'au final, les individus sont parvenus à s'entendre et ont accédé à la récompense en coopérant, bien que les dominants aient essayé de monopoliser la part la plus importante de nourriture. Cependant les subordonnés bien souvent n'ont pas accepté cette solution et sont parvenus à faire changer d'avis leur partenaire de telle sorte que ce dernier vienne coopérer pour accéder à la distribution équitable. Une étude récente réalisée avec des loups montre que dans cette situation, le dominant accède seul à la récompense (Möslinger et al. 2009). Les relations de hiérarchie peuvent expliquer la persistance de ce comportement de coopération (altruiste) de la part du subordonné. Bien que les auteurs n'aient pas observé de comportement de harcèlement comme chez les kéas (perroquet de Nouvelle-Zélande ; Tebbich et al. 1996), il est possible que le subordonné craigne une réaction de son congénère. Les capucins ont montré qu'ils étaient capables d'inverser leurs rôles (Hattori et al. 2005) et de faire preuve d'altruisme réciproque (Brosnan et al. 2006), de même pour les tamarins (Cronin & Snowdon 2008). Chez les chimpanzés, les individus testés n'ont pas échangé spontanément leurs rôles (Yamamoto & Tanaka 2009) et seul un faible effet du comportement du partenaire lors de l'interaction précédente a été mis en évidence (Melis et al. 2008). D'autres expériences réalisées sur le principe d'une paire acteur / bénéficiaire (de la récompense) aboutissent également à une récompense asymétrique et chez les psittacidés testés, différentes stratégies ont été observées : ainsi au sein d'un groupe de kéas, les dominants forcent les subordonnés à actionner le mécanisme (Tebbich et al. 1996) alors que chez les aras chloroptère, les membres d'un couple semblent alterner leurs rôles (Spitzhorn 2009).

Avec nos oiseaux, nous avons repris les quatre niveaux tel que définis précédemment ; dans le dernier niveau (collaboration) où les individus doivent agir de manière différente mais complémentaire, chacun des participants contribue à l'effort (lors de l'interaction avec le dispositif) contrairement à ce qui avait été fait avec les kéas où seul un des participants devait produire un effort (**Article 1**). Nous avons déterminé l'influence de la tolérance sur les performances de chaque dyade mais également essayé de voir si le fait que la proximité soit récompensée lors de la réussite d'une action coopérative influence la tolérance au cours du temps. Ensuite nous avons testé les oiseaux dans une situation où ils avaient ou non le choix du partenaire avec lequel résoudre la tâche. Cette fois-ci encore il s'agit de voir si les animaux peuvent coordonner leurs actions mais également de voir comment les préférences sociales peuvent modifier les stratégies. Enfin, deux de nos oiseaux ont été testés dans une tâche de négociation afin de voir comment les individus allaient résoudre leur conflit d'intérêts et si la nature de leur relation (dominant /subordonné) allait influencer le choix des oiseaux (**Article 2**). Par ailleurs nous avons testé un groupe de perruches avec un dispositif de tir à la ficelle et un autre dispositif pour lequel un individu doit actionner le mécanisme afin qu'un congénère obtienne la récompense. Nous avons cherché à savoir d'une part si les oiseaux allaient être capables de résoudre les tâches et d'autre part comment ils allaient s'y prendre, notamment avec la deuxième expérience où le résultat d'une action aboutit à une asymétrie de récompense. De même nous nous sommes penchés sur les relations sociales et l'existence ou non d'une hiérarchie pour pouvoir mettre en évidence d'éventuelles influences de ces paramètres sur les actions de coopérations (**Article 3**).

Comme nous l'avons dit précédemment, les individus qui actionnent les dispositifs peuvent être amenés à se comporter de manière altruiste pour qu'un congénère puisse atteindre la récompense. Aussi il est pertinent de s'interroger pour savoir si les oiseaux ont des préférences pour ce qui peut être bénéfique à leurs congénères.

Etude de la prosocialité

Les actions altruistes sont hautement valorisées au sein des sociétés humaines est constituent un élément clé de la moralité. Cependant elles sont également observées dans beaucoup de taxons, tout du moins si on les définit de manière fonctionnelle –comme un acte coûteux qui confère un bénéfice aux autres sans retour attendu. Néanmoins comme le souligne de Waal (2008), les discussions concernant les comportements altruistes pâtissent d'un manque de distinction entre fonction et motivation : une action est dite altruiste si elle profite à un autre, que ce soit volontairement ou pas. En effet, quand les animaux sont étudiés en conditions naturelles, il est souvent difficile déterminer leurs intentions sous-jacentes. Si un sujet donne de la nourriture à un congénère, est-ce parce qu'il est sensible au sort de cette individu ou est-ce parce qu'au final cela lui sera profitable et que ce comportement a été génétiquement sélectionné ? Bien que ces explications ne soient pas exclusives (étant donné que le fait de se soucier du bien-être des autres peut être sélectionné comme paramètre permettant d'accroître les chances de survie de l'individu), beaucoup d'animaux peuvent se comporter de manière altruiste parce que leur comportement est génétiquement pré déterminé et nécessite juste certaines conditions sociales pour s'exprimer sans que l'individu ne veuille réellement aider ses congénères. Quand les individus sont testés dans des tâches artificielles, il est possible d'objectiver la motivation d'un sujet à donner de la nourriture à un de ses partenaires. Comme l'acte altruiste vrai (volontaire, avec un coût pour le donneur) n'est pas fréquemment observé, la plupart des études portent sur les comportements prosociaux – c'est-à-dire se comporter d'une manière qui procure un bénéfice à un autre individu à un coût très faible voir nul. Les scientifiques cherchent à déterminer comment ce comportement est apparu, c'est à dire à connaitre les conditions sociales et les éléments comportementaux qui doivent exister pour qu'un tel comportement s'exprime (voir pour revue Kärtner et al. 2010). Par conséquent, la plupart des études se sont focalisées sur la mise en évidence de la présence ou de l'absence de prosocialité chez les enfants et chez plusieurs espèces de primates non-humains et ont cherché à savoir si ce comportement requérait d'avoir le concept de soi et de l'autre.

La prosocialité chez les non-primates a, au contraire, reçu très peu d'intérêt de la part des chercheurs. Cependant, les données concernant les comportements prosociaux chez différentes espèces aviaires pourraient apporter une évidence de la convergence évolutive (ou non) de ce caractère et aideraient donc à déterminer les contraintes écologiques et les supports neurologiques requis pour son existence. D'un point de vue développemental, la plupart des recherches sur la prosocialité ont été conduites chez des humains. Les chercheurs ont initialement pensé que le comportement prosocial nécessitait d'être conscient de soi et des autres comme entité propre et d'avoir de l'empathie (i.e. Barresi & Moore, 1996) ; ainsi les études ont examiné si la capacité d'empathie nécessitait de se reconnaitre dans un miroir (Bischof-Köhler, 1991). Les auteurs n'ont pas observé d'enfants qui aidaient un congénère sans avoir montré en parallèle leur capacité à se reconnaitre, cependant ils ont observé quelques individus qui, bien qu'ils se reconnaissaient dans un miroir, ne venaient pas en aide à un autre individu. Des études développementales transculturelles ont cependant souligné que le contexte socioculturel importait et que le fait que les parents renforçaient les actions sociales positives avait pour conséquence que certains enfants se comportaient de manière prosociale, avant même d'atteindre le stade de reconnaissance dans un miroir (Kärtner et al. 2010). Etant donné que de nombreux primates non humains vivent également en société, de telles données renforcent l'idée d'un processus évolutif qui dépendrait des gènes, de l'environnement ou d'une combinaison des deux (i.e. Bell et al. 2009). Des travaux effectuées sur les grands singes suggèrent cependant une absence de comportement prosociaux, tout du moins quand la récompense alimentaire est directement observable (Jensen et al. 2006 ; Silk et al. 2005 ; Vonk et al. 2008) bien que les comportements existent dans certains cas puisque décrits entre autres dans l'ouvrage de Frans de Waal « Primates and Philosophers » (2006).

Peu d'études se sont intéressés à la façon dont un comportement prosocial pouvait ou non être influencé par le précédent comportement du partenaire (Brosnan et al. 2009, de Waal 1997 ; Melis et al 2008 ; Yamamoto & Tanaka 2009), ce qui semble constituer un élément important lorsque l'on vit en groupe. En effet, la vie de groupe est constituée d'une multitude d'interactions, positives ou non, relatives aux différentes activités et variables en fonctions des congénères. Ainsi un sujet n'est jamais à 'zéro' lors d'une nouvelle interaction et ce qu'il a pu vivre précédemment peut influencer de manière importante ce qui suivra. Seules les études de de Waal (1997) et Melis et al. (2008) ont trouvé un faible effet du comportement précédent du partenaire (dans l'échange de toilettage ou de nourriture). Il est intéressant de noter que les chimpanzés, gorilles et bonobos n'ont pas été capables d'échanger des bouchons entre congénères, même en sachant que le bouchon aurait pu être échangé auprès d'un humain ensuite contre une récompense (Brosnan & Beran 2009 ; Pelé et al. 2009). Les orangs-outangs ont quant à eux réussi lors de cette tâche (Dufour et al. 2009). D'autres travaux (Pelé et al. 2010) ont montré que ni les capucins, ni les macaques de Tonkean n'ont su échanger de manière volontaire avec leur partenaire bien qu'ils aient montré qu'ils savaient échanger avec un humain pour recevoir une récompense (Addessi et al 2007; Brosnan & de Waal 2004). Hattori et al. (2005) et Brosnan et al (2006) ont montré que les comportements altruistes réciproques étaient peu développés chez les capucins dans les expériences où la nourriture était la récompense directe. Les recherches sur les primates non humains se sont également focalisées sur les espèces coopérant lors de l'élevage des jeunes comme les callithricidae, espèces chez lesquelles les interactions sociales sont considérablement développées. Ainsi malgré leur divergence évolutive précoce dans la lignée des primates, ils peuvent représenter un bon modèle pour l'étude des comportements prosociaux (Burkart et al. 2007). Les premières études consistaient à tester un individu avec ou sans partenaire et à observer si il procurait de la nourriture à la cage adjacente mais sans jamais pouvoir recevoir lui-même une récompense et sans pouvoir recevoir en retour du même individu (au contraire des grands singes par exemple Brosnan et al. 2009). Ainsi les marmousets (*Callithrix jacchus*) choisissent préférentiellement de récompenser un partenaire plutôt qu'une cage vide (Burkart et al 2007) au contraire des tamarins (*Saguinus oedipus* ; Cronin et al. 2009 ; Stevens 2010). Néanmoins les tamarins se comportent de manière prosociale quant les sujets testés reçoivent également une récompense (Cronin & Snowdon 2008). Une étude récente sur cette même espèce a révélé que bien que les comportements prosociaux ne soient pas très présents au début ils peuvent apparaitre au cours de l'expérience (Cronin & Snowdon 2010) au fur et à mesure que les animaux se rendent compte que leur partenaire a la possibilité de leur rendre la pareille. Chez les perroquets gris du Gabon, les oiseaux forment de larges groupes (May 2001) et les parents coopèrent lors de la construction du nid ou de l'élevage des jeunes et se comportent de manière altruiste. En effet, on observe les mâles régurgiter à leur partenaire sexuel durant la période de reproduction (Skeate 1984) et pour certains tout au long de l'année (Harrison 1994). Ce comportement d'approvisionnement en nourriture sur plusieurs semaines, de même que la relation exclusive (ou presque) sur le long terme entre les membres d'un couple sont des éléments que l'on ne retrouve pas chez les primates, bien qu'il soit également possible d'observer un partage des ressources alimentaires (capucins: de Waal 2000; ouistitis: Kasper et al. 2008; tamarins: Hauser et al. 2003). En ce qui concerne les chimpanzés, certains auteurs décrivent l'offrande de nourriture en échange de relations sexuelles (Gomes & Boesch 2009) mais les données sont controversées (Gilby et al. 2010). De plus, les perroquets gris du Gabon réalisent des interactions réciproques (toilettage) et sont capables de s'associer pour éloigner des prédateurs (Jones & Tye, 2006). Nous avons donc décidé de tester des perroquets gris du Gabon afin de savoir s'ils allaient immédiatement se comporter de manière prosociale ou alors, comme les tamarins, apprendre à le faire, ou encore ne pas tenir compte du partenaire. Comme indiqué précédemment, le paradigme de l'échange de bouchon est très utilisé dans les études concernant la prosocialité chez les primates (i.e. Dufour et al. 2009, Fontenot et al. 2007 ; Pelé et al. 2009, Pelé et al. 2010). Afin d'accroitre la possibilité de trouver une espèce se comportant de manière prosociale nous avons testé différentes espèces de psittacidés. Nous avons également souhaité comparer l'influence de la nature de la relation entre les individus sur leur propension à être prosocial. En effet, il est possible que les oiseaux prennent davantage en compte le bien-être de congénères avec lesquels ils grandissent (même couvée) ou se reproduisent (partenaire sexuel). Quatre espèces de perroquets (gris du Gabon, ara macao et glaucogularis, conure soleil) ont été testées sur leur propension à récompenser, sans coût supplémentaire, un partenaire. La question est donc de savoir si, toutes choses étant égales par ailleurs (l'effort produit et le contexte social), les oiseaux vont-ils prendre en considération les préférences de l'autre?

On s'attend à ce que la relation entre les individus influence directement leur choix. En fonction de la hiérarchie, de la tolérance et des préférences sociales mais aussi en fonction des évènements précédents, les oiseaux seront plus ou moins prêts à récompenser leur partenaire (i.e., de Waal et al. 2008). Dans une première expérience, deux couples d'aras sont testés avec leur partenaire sexuel et deux mâles conures entre frères de couvée tandis que chez les gris du Gabon sont testés trois individus vivant ensemble mais entretenant différentes relations (**Article 4**). Nous avons également testé deux autres perroquets gris du Gabon avec comme partenaire des humains. En effet, la relation particulière qu'ils développent avec leurs soigneurs du fait qu'ils sont élevés à la main permet de voir si les oiseaux ont des préférences pour l'issue favorable aussi pour les personnes qui quotidiennement leur apportent la nourriture (**Article 5)**. Dans une seconde expérience, on associe le sujet testé avec différents humains dont chacun se comporte toujours de la même manière c'est-à-dire égoïste, altruiste ou imitateur (il agit comme l'a fait le perroquet lors de l'essai précédent). Les oiseaux en question appartiennent au laboratoire d'Irene Pepperberg et ont été entrainés par des humains pendant plusieurs années (i.e., Pepperberg 1999) par conséquent, nous nous attendons à ce que les oiseaux soient capables d'associer une stratégie à un humain en particulier et de réagir de manière appropriée. Nous pensons que les perroquets vont soit imiter le choix de l'humain comme ils ont l'habitude de le faire lors de sessions de modèle/rival (Peppeberg 1999) ou alors tenteront d'agir eux-mêmes comme modèle en choisissant l'item prosocial afin de maximiser les récompenses. (**Article 5**). Dans une autre expérience réalisée avec les perroquets gris du Gabon de Nanterre, nous avons évalué le comportement de l'individu testé au cours d'une situation injuste, à savoir que le partenaire recevait une meilleure récompense que le sujet quand ce dernier choisissait le bouchon prosocial. Ainsi nous pensions que les oiseaux développeraient une préférence pour le bouchon égoïste ou arrêteraient de participer (**Article 4**). Enfin, dans la dernière expérience où seuls deux perroquets participaient, les oiseaux devaient coopérer pour recevoir la récompense. Ainsi le premier individu qui avait le choix parmi les différents bouchons devait en choisir un et le passer à son partenaire qui à son tour pouvait choisir de le donner ou non à l'expérimentateur afin de recevoir la récompense associée. Le sujet qui avait le choix était supposé préférer le bouchon prosocial afin que son partenaire perçoive un intérêt à transmettre le bouchon choisi (**Article 4**).

Etude de l'attribution de perception et d'intentions

La capacité à attribuer des intentions et des préférences à un partenaire peut être très utile pour coopérer, résoudre un conflit d'intérêts ou encore comprendre les actions d'un autre individu. La théorie de l'esprit consiste en un ensemble de capacités cognitives spécifiques permettant de se mettre à la place de l'autre, de lui attribuer des perceptions, des désirs, des intentions ou des croyances (Premack & Woodruff 1978). Jusque dans les années 90, ces capacités étaient largement considérées comme spécifiques à l'homme (Povinelli & Preuss 1995 ; Tomasello & Call 1997) mais bien que cela soit toujours débattu (Povinelli & Vonk 2003 ; 2004), de récentes études chez des primates non humains ont convaincu de plus en plus de chercheurs que certains individus étaient capables d'attribuer des états mentaux à d'autres individus, homo ou hétérospécifiques (Call & Tomasello 2008). Comme le souligne Tomasello et al (2003), il n'y a certainement pas de réponse claire concernant le degré de similitude avec les capacités de l'être humain. Néanmoins il y a des indications que certaines espèces attribuent certains états mentaux (primates non humains: Flombaum & Santos, 2005; Call & Tomasello, 2008; chiens: Call et al. 2003; corvidés: Bugnyar & Heinrich, 2005). La question serait plutôt : lesquels et à quel degré (Call & Tomasello, 2008)? Certaines indices comportementaux sont produits et utilisés plus tôt que d'autres lors du développement. Ainsi des enfants de douze mois comprennent la signification du pointage et du regard (i.e. ils sont capables de suivre ces indices et même de les produire pour indiquer l'objet de leur désir ; Colonnesi et al. 2008). Certaines espèces semblent être performantes dans la compréhension et l'utilisation à bon escient de ces indices lors de tâches de choix par exemple ; tâches dans lesquelles un expérimentateur indique du regard ou du doigt la boîte où se trouve la récompense (Miklosi & Soproni 2006). Certains corvidés sont également capables de répondre à ces indices (von Bayer & Emery 2009). Chez les corvidés, le suivi du regard et le comportement de cache évoluent au cours du développement et la maîtrise du comportement de cache par exemple nécessite une période de maturation, des interactions sociales et des expériences (notamment de pillage) (Schloegl et al. 2007; Bugnyar et al. 2007). Lors d'une expérience récente réalisée avec nos perroquets gris du Gabon, ceux-ci ont été capables, contrairement aux corbeaux (Schloegl et al. 2008), d'utiliser les indices fournis par un humain (Giret et al. 2009a). En effet, les trois oiseaux ont spontanément ou après une courte période d'entrainement utilisé le pointage proximal (à 20 cm) et l'un des perroquets a su suivre le regard (tête et regard orienté vers l'objet qui se trouve à 100 cm). Un de ces oiseaux a également été capable de se servir d'indices visuels ou vocaux fournis par ses congénères pour faire son choix (Giret et al. 2009b). Ainsi nous savons que nos oiseaux sont capables d'utiliser efficacement les indices fournis lors d'une tâche de choix. La capacité à savoir ce qu'un congénère peut percevoir (entendre ou voir par exemple) est un des éléments de la théorie de l'esprit. L'attribution de perception a été mise en évidence chez plusieurs espèces comme les primates non humains (Liebal et al. 2004; Hattori et al. 2010), les chiens (Call et al. 2003; Virányi et al. 2004), les corvidés (von Bayer & Emery 2009) et plus récemment les chevaux (*Equus caballus* ; Proops & McComb, 2010). Un autre élément important de la théorie de l'esprit est l'attribution d'intentions (Call & Tomasello 2008). Quelques chercheurs ont testé cette capacité chez des enfants et des primates non humains en employant des paradigmes tel que de renverser intentionnellement ou accidentellement la récompense sur le sol (Call & Tomasello, 1998; Povinelli et al. 1998). Les trois espèces testées ont su distinguer les intentions des expérimentateurs et se sont dirigés vers celui perçu comme étant de meilleure volonté pour avoir leur récompense, bien que dans l'étude de Povinelli, les résultats ne soient pas aussi marqués. Wood et al (2007) ont également testé des tamarins (*Saguinus oedipus),* des macaques rhésus (*Macaca mulatta)* et des chimpanzés (*Pan troglodytes)* et ceux-ci ont su inférer spontanément les intentions de l'expérimentateur en choisissant la boîte indiquée par l'expérimentateur lorsque que ce dernier indiquait intentionnellement et non accidentellement l'une des deux cibles possibles. D'autres études ont utilisé le paradigme de la personne pas disposée ou pas capable de donner la récompense alimentaire. Les chimpanzés (Call et al. 2004), les enfants (Behne et al. 2005) et même les capucins (*Cebus apella* ; Philipps et al. 2009) testés ont été capables de distinguer les intentions de l'expérimentateur. De manière générale, les individus s'attendent plus à recevoir la récompense alimentaire quand c'est par accident que l'humain ne la leur donne pas plutôt que quand il n'y semble pas disposé. Aussi il semble intéressant de s'interroger sur les capacités d'autres espèces ayant divergé il y plus longtemps au cours de l'évolution comme les oiseaux et plus précisément les corvidés et les psittacidés. En effet, il est possible qu'ils soient amenés à mettre en œuvre de telles capacités lors de leurs interactions au cours de leur vie sociale complexe. Les perroquets en particulier montrent de grandes capacités à s'adapter à des contraintes environnementales parfois très importantes comme c'est le cas lors de la vie en captivité. Très peu d'études ont été réalisées concernant la relation perroquet-humain (Beck & Hatcher, 1989; Barber, 1993; Anderson, 2003), cependant il apparaît que la compagnie de ces oiseaux est perçue comme étant de qualité comparable à celle des carnivores domestiques. De plus, leur capacité vocale d'imitation stimule chez le propriétaire la recherche d'interactions. Comme la majorité des oiseaux détenus en captivité, les perroquets testés ont été élevés à la main et interagissent quotidiennement avec des humains, ce qui pourrait leur faciliter la distinction de comportements humains correspondant à des intentions sous-jacentes différentes. Trois perroquets gris du Gabon appartenant à des particuliers ont été testés sur leur capacité à attribuer des perceptions à l'humain en leur donnant le choix entre des objets soit placés derrière un écran transparent soit derrière un écran opaque. Etant donné qu'en temps normal il leur est interdit de toucher à ces objets sous peine de représailles de la part du propriétaire, les oiseaux sont supposés préférer la situation où ils ne seront pas vus de l'humain pour réaliser leur « méfait » (à savoir détruire ces objets). Une autre expérience en collaboration avec l'équipe de Prague (Laboratoire de communication interspécifique, Dr. Jitka Lindova) est également prévue afin de pouvoir distinguer le cas échéant si les oiseaux choisissent le côté sombre parce que l'expérimentateur ne les voit pas (attribution de perception) ou parce que eux ne le voient pas (perception simple) (**Article 6**). De plus, les trois perroquets de Nanterre ont été testés dans trois conditions inspirées des travaux déjà réalisés concernant l'attribution d'intentions chez les autres espèces mais simplifiées car la diversité des situations présentées dans les autres études n'ont pas abouti à une diversité des réponses de la part des sujets testés (Call et al. 2004, Behne et al. 2005 ; Philipps et al. 2009). En effet, bien souvent les différences entre les situations (l'expérimentateur fait tomber un raisin qui reste visible ou qui disparaît) n'étaient pas suffisamment distinctes (ou pertinentes) pour susciter des réactions comportementales différentes chez les animaux (Call et al. 2004). Les perroquets sont supposés réagir différemment en fonction du fait que l'expérimentateur (toujours le même) ne soit pas disposé (en les narguant) ou pas capable (essaye sans succès) de leur donner une récompense, ou encore soit distrait dans sa tâche (jouant). Ainsi en fonction des indices comportementaux fournis par l'humain dans les diverses situations, les oiseaux, même sans apprentissage, devraient s'attendre à recevoir la récompense lorsque l'humain n'est pas capable plutôt que pas disposé à la leur donner (**Article 7**).

Ainsi mon objectif au cours de cette thèse a été de répondre aux questions suivantes :

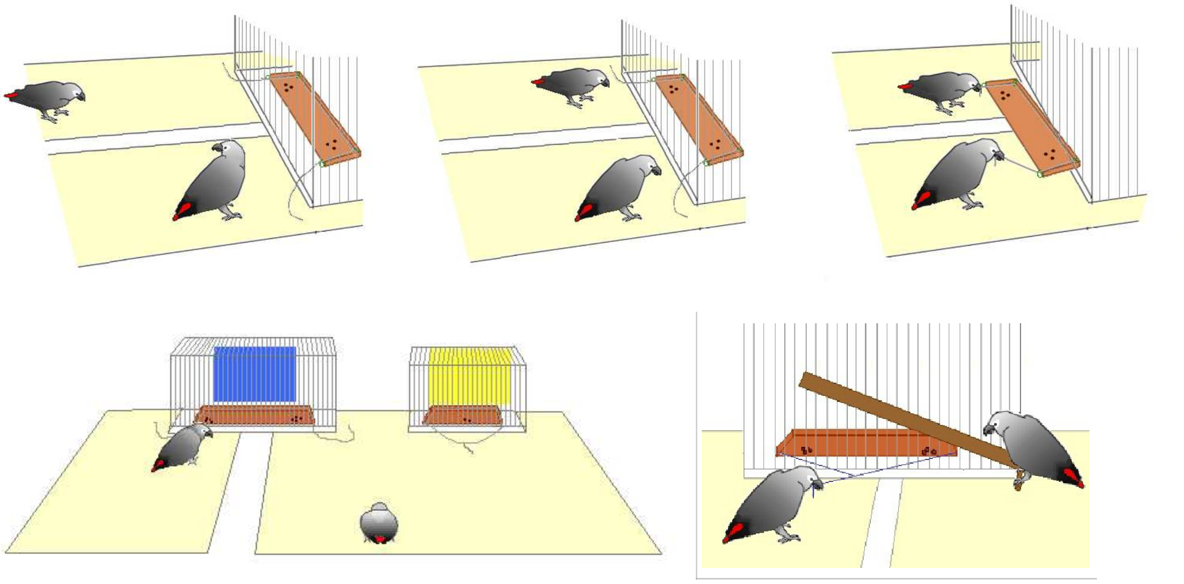
1. **Les perroquets sont-ils capables de coopérer et si oui, quels sont les mécanismes mis en jeu ? (Articles 1, 2 & 3)**
2. **Les perroquets sont-ils sensibles aux préférences de leurs congénères ? Est-ce qu'ils préfèrent une issue favorable à un plus grand nombre plutôt qu'une solution égoïste ? (Articles 4 & 5)**
3. **Les perroquets sont–ils capables d'attribuer des perceptions et des intentions aux humains ? (Article 6 & 7)**

Article 1

Cooperative problem solving in African grey parrots (*Psittacus erithacus*).

Péron F., Rat-Fischer L., Lalot M., Nagle L. & Bovet D

In revision *Animal Cognition*



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Problème biologique

Dans le cadre d'une vie en société, les animaux interagissent fréquemment avec de multiples partenaires, surtout si leur durée de vie est longue. Les individus peuvent être amenés à coopérer afin de pouvoir accéder à une ressource que seuls ils ne pourraient obtenir. Nous nous sommes donc intéressés à leur capacité à résoudre une tâche artificielle et à la manière dont ils y parvenaient.

Hypothèse

Les oiseaux vont parvenir à coopérer mais les relations entre les individus vont influencer les performances des dyades. Les oiseaux vont communiquer pour coordonner leurs actions ou signifier leurs intentions.

Méthodes

Utilisation d'un dispositif où une ficelle coulisse : seules les interventions simultanées permettent de déplacer et d'atteindre la récompense. On teste les individus dans diverses situations : 1) l'un des partenaires est retardé, 2) deux dispositifs sont disponibles et en fonction de l'environnement social et des préférences individuelles les oiseaux doivent décider d'entrer ou non dans une action coopérative, 3) les oiseaux doivent réaliser des tâches différentes mais complémentaires pour pouvoir atteindre la récompense.

Résultats

Les trois perroquets gris du Gabon ont été capables de résoudre les différentes tâches. Ils interagissent plus avec le dispositif quand un partenaire est présent mais ont des difficultés à inhiber leur réponse motrice. Dans la troisième expérience les interactions sociales et la personnalité des oiseaux ont influencé les résultats. Dans l'expérience de collaboration ils ne sont pas parvenus à échanger leurs rôles. Les oiseaux n'ont pas communiqué durant la résolution des tâches.

Conclusion

Nos trois perroquets gris du Gabon sont parvenus à coordonner leurs actions. Ils ont appris à attendre le partenaire. Le tempérament des individus, leurs performances cognitives et leurs préférences sociales ont influencé les résultats observés.

Cooperative problem solving in African grey parrots (*Psittacus erithacus*)

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Abstract

One of the main characteristics of human societies is the extensive degree of cooperation among individuals. Cooperation is an elaborate phenomenon, also found in nonhuman primates during laboratory studies and field observations of animal hunting behaviour, among other things. Some authors suggest that the pressures assumed to have favoured the emergence of social intelligence in primates are similar to those that may have permitted the emergence of complex cognitive abilities in some bird species such as corvids and psittacids. In the wild, parrots show cooperative behaviours such as joint breeding or mobbing. In this study, we tested cooperative problem solving in African grey parrots (*Psittacus erithacus*). Our birds were tested using several experimental setups to explore their behaviours at each level of cooperation as defined by Boesch and Boesch (1989): similarity, synchrony, coordination and collaboration. In our experiments, African grey parrots were able to act simultaneously but mostly failed during the delay task, maybe because of a lack of inhibitory motor response. Tested with the possibility to adapt their behaviour to the presence or absence of a partner, they showed that they were able to coordinate their actions. They also collaborated, acting complementarily in order to solve tasks, but they were not able to switch their roles. This study is the first experiment to our knowledge to test a non-mammal species on the four levels of cooperative behaviour.

Keywords

African grey parrots, cooperation, synchrony, coordination, collaboration, social cognition

Introduction

Many cooperative behaviours have been observed in non-human species, for instance, cooperative hunting (fossas; Lührs, Dammhahn 2010), mobbing (meerkats; Graw, Manser 2007) or cooperative breeding (review; Bergmüller et al. 2007). There are also examples of cooperation among siblings that are able to coordinate their begging in order to increase the probability of receiving food from their parents (Mathevon and Charrier 2004; Blanc et al. in press). However, the complexity of the cognitive mechanisms involved in these cooperation events is often difficult to measure, as it is difficult to know the relative contributions of genetic predetermination vs. learning. Laboratory studies and cross-species comparisons using similar paradigms are useful in studying the proximal mechanisms that can be shared by different species, and to discover convergent evolutionary processes. As many definitions of cooperation can be found, in this paper, we use Noë's (2006) definition, i.e. all interactions or series of interactions that, as a rule (or 'on average'), result in net gain for all participants.

The Social Brain Hypothesis suggests that individuals living in social groups with complex interactions have bigger brains in order to manage social relationships (Joly 1966; Humphrey 1976; Byrne and Whiten 1988; Dunbar 1998). The 'Relationship Intelligence Hypothesis' (Emery et al. 2007) predicts that complex social life and long term monogamous partnership lead to elaborated socio-cognitive abilities, similar to those encountered in primates. Indeed, recent studies conducted in corvids and psittacids have highlighted cognitive abilities as complex as those observed in primates (Emery and Clayton 2004; Pepperberg 2006) and similarities in their neurobiology (e.g. ratio of brain/body size; Iwaniuk et al. 2005) and socio-ecology (e.g. fission-fusion dynamics, long lifetime, long juvenile period, etc.). Thus, these species could represent a good model for social cognition studies. African grey parrots (*Psittacus erithacus*) form stable monogamous couples over breeding seasons and both parents take care of the chicks, although females invest more effort

(Cockburn 2006). Birds reciprocate favours when they preen their partner and males regurgitate food to their females during the reproductive season. Some observations undertaken on Principe Island have reported mobbing events against red kites (*Milvus;* Jones and Tye 2006). Mobbing is a complex behaviour in which birds join forces in order to defend their territory. Reciprocal interactions have been observed in birds during mobbing events (Krams et al. 2008), and the frequency of these events increased when predation risk increased (Krams et al. 2010). Thus, external factors could increase the probability of cooperative actions to occur. All these elements taken together support the hypothesis that African grey parrots could have the cognitive abilities necessary to manage complex social relations and to cooperate.

In our study, we used the ‘loose string paradigm’ proposed by Hirata and Fuwa (2007) with chimpanzees (*Pan troglodytes*) in which two individuals were faced with a tray with food rewards placed out of reach. Both subjects had to pull on a string simultaneously in order to get access to the reward. Several studies have highlighted the fact that tolerance impacts directly on the outcome, as the more tolerant a subject is within the dyad, the better that individual performs (capuchins: Mendres and de Waal 2000; chimpanzees: Melis et al. 2006b; bonobos: Hare et al. 2007; rooks: Seed et al. 2008). A recent study has also highlighted that rooks’ temperament influences the success of the dyad insofar as bolder individuals appeared to be more willing to solve the task, whereas shyer individuals were more influenced by their partner’s behaviour (Scheid and Noë 2010). The outcome of the cooperation itself influences the next successful cooperative attempt as described in rats (Schuster 2002; Rutte and Taborsky 2008).

The aim of this experiment was to test our parrots on different tasks involving different levels of the cooperation as defined by Boesch and Boesch (1989). This definition of cooperation was based on four levels of seemingly growing complexity. Although it was only a descriptive classification, this definition may help us to know more about the underlying mechanisms needed to solve each level of cooperation, and the ability to learn the basic prerequisites of cooperation, like the need to work with a partner.

Firstly, we tested the **first level** of cooperation (**similarity**) in which individuals act simultaneously but do not need to understand their partners role. Studies on capuchin monkeys revealed that they were able to solve the task, but without understanding their partners' role (Chalmeau et al. 1997; Visalberghi et al. 2000). In a second experiment, we tried to see if our birds succeeded in **synchronising**, which represented the **second level** of cooperation as defined by Boesch and Boesch (1989). In a study conducted with brown capuchins, an increase in gazing at a partner was taken as a criterion for highlighting the comprehension that cooperation was required (Mendres and de Waal 2000). Chimpanzees tested on a delay task showed that individuals were able to wait for the partner's arrival before starting to pull (Melis et al. 2006b). Additionally, when the chimpanzee tested could decide to allow a partner to enter, he did it significantly more often when he was facing an apparatus needing cooperation than when facing an experimental setup that he could solve alone. Seed et al. (2008) conducted the same experiment on rooks but, contrary to chimpanzees, corvids were not able to wait for a partner. To test the **third level**, which is the ability to **coordinate** in time and space, we conducted with our parrots the same protocol as Seed et al. (2008) performed on rooks. As emphasised by Noë (2006), coordination is an important proximate mechanism needed to accomplish cooperation. In this experiment, the individual faced two different apparatuses, one that could be solved alone ('Solo') and another baited with twice as much food but which required cooperation to obtain ('Duo'). The subjects were tested in two separate situations: alone or with a partner. We expected that parrots would choose the 'Solo' apparatus in the first situation, while trying the other apparatus when a partner was present in order to get more food. Rooks did not seem to understand the task as only two out of six individuals showed a tendency to prefer the single platform when tested alone and no cooperation was observed at all during the experiment. A recent study conducted in hyenas showed that they were able to coordinate their actions in order to solve a task (Drea and Carter 2009), and chimpanzees have also been shown to coordinate their actions during a negotiation game (Melis et al. 2009). The same ability to synchronise in time and space has been observed with rats during an artificial task (Schuster 2002; Rutte and Taborsky 2008). As the **fourth level**, **collaboration**, involves carrying out different but complementary actions, we designed a more complex apparatus in which one individual had to climb on a perch in order to release the tray that was pulled by the second bird. In this experiment, both birds needed to act on the device, contrary to previous studies conducted with keas in which a seesaw apparatus was used and only one individual had to work (Tebbich et al. 1996; Huber et al. 2008).

Thus, studying cooperative actions could make the link between physical and social cognition. In the wild, animals cooperate but the degree of cognitive processes involved in the achievement of the task is unknown. Indeed, the underlying cognitive abilities necessary to cooperate and to go through each level are not clear. Nevertheless, the primary cognitive aspect involved in a cooperative action is the comprehension of the partner's role (Noë 2006) which can explain the gap between the first two levels as defined by Boesch and Boesch (1989). The difference between synchrony and coordination is more difficult to assess. To be able to reach the last level, collaboration, without being simply conditioned to do so, individuals should understand the role of each participant. That is why, although it was not specifically mentioned by Boesch and Boesch (1989), we considered that individuals should be able to exchange their roles in order to show a real mastery of this level.

Cooperation could be also studied considering the social situation, such as hierarchy, tolerance and social preferences between the potential co-operators, in addition to their individual skills. Indeed, all these factors can play a role in the formation and the performance of the dyad (Noë 2006).

The aim of this study was to assess whether our three grey parrots would be able to solve cooperative tasks and how they would do it. We expected that the relationship would influence the cooperative attempt through avoidance/ affiliation behaviours.

Material and methods

Subjects

We tested three hand-reared African grey parrots, two males (Shango and Léo, four and six years old respectively) and one female (Zoé, six years old). They hatched in captivity and arrived at the laboratory at three months of age. They were housed together in an aviary (340 cm × 330 cm × 300 cm) with three tables (120 × 60 × 75 cm), two large perch structures and many toys, at a constant temperature of 25°C and with a 12/12 h light-dark cycle. The parrots were tested in their aviary. During a test session, subjects that were not tested were placed in a cage in the corridor with water, food and toys available. Parrots were fed daily with fresh fruits and vegetables in the morning and parrot formula (Nutribird A21) in the evening. Water and parrot pellets (Harrison, high potency coarse) were available *ad libitum* and vitamins (Muta-Vit Versele-Laga) were given twice a week. Regarding the hierarchy, we found that Léo was dominant over Shango and Shango over Zoé.

Experimental setup

A flat rectangular cardboard tray (31 × 17 × 4 cm) baited with food (parrot formula and seeds) was placed in a cage (54 × 28 × 36 cm), impeding direct food access. A piece of string was threaded through metal loops placed on the tray so that both ends of the string extended out of the cage by 20 cm. The lower part of the cage had a gap that enabled tray’s movements. Birds could move the tray only by pulling simultaneously both ends of the string (‘loose string paradigm’). The cage was placed on two different tables separated by 15 cm from each other. The string was not attached and each end was on separate tables.

Habituation phase & training

African grey parrots are neophobic birds, so they were previously familiarised individually with each new apparatus or new element of it for one week before each experiment. Birds were trained to pull the string first with both ends of the string attached so that an individual alone could succeed. Then with free ends, and in order to maintain motivation even when one of the two birds was gone, the experimenter pulled the string with the remaining bird. We stopped the training when all birds were able to stay in front of the cage and pulled the string (rarely simultaneously at this point). We completed two sessions (with a variable number of trials) per day lasting about 30 minutes for each session over two weeks.

Test

Experiment 1: Similarity

Each bird was tested with a conspecific for 20 trials in each session, with two sessions per day. This experiment lasted until each dyad reached a rate of 90% of successful cooperation actions among all the trials of a session.

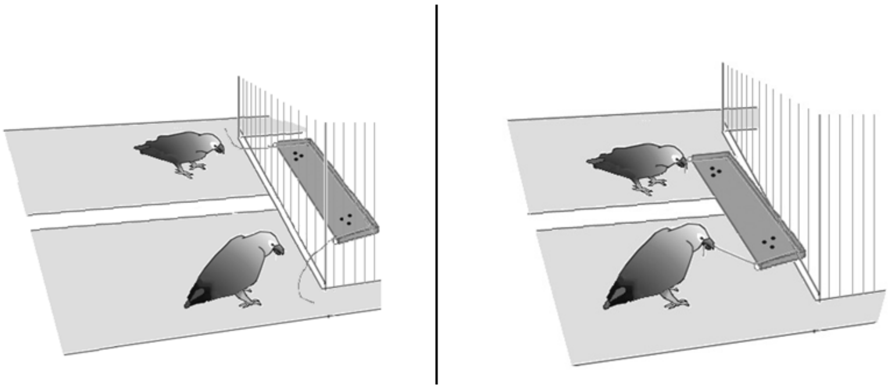

Figure 1: Similarity

Experiment 2: Synchrony

This time, the second bird (partner) was positioned at the end of the table (120 cm from the apparatus) 15 seconds after the first animal was placed in front of the cage. We conducted two sessions a day over ten days. All dyads were tested several times, counterbalancing their roles (tested or partner delayed) so that we obtained 20 cooperative events. Each bird was tested 40 times in each role alternating the partner.

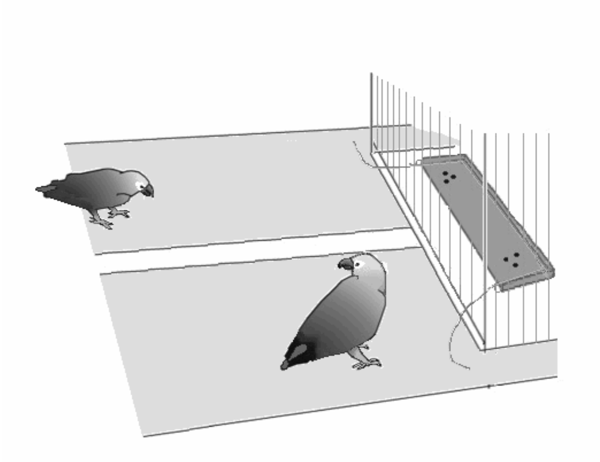

Figure 2: Synchrony

Experiment 3: Coordination

In the third experiment, the birds could choose between two different apparatuses: one that could be solved alone (the two ends of the string were attached) and a second apparatus, similar to the one used in the previous experiment, where the birds had to cooperate to solve the task. We baited the tray differently so that in the second apparatus (‘Duo’) a double amount of food (per individual) was provided in comparison to the other apparatus (‘Solo’), in order to promote cooperation. A study conducted previously at the laboratory highlighted the fact that our birds were able to discriminate between these quantities (Al Aïn et al. 2009). Each experimental setup differed in size (smaller in the case of the ‘Solo’ apparatus) and colour (yellow for the ‘Solo’ apparatus and blue for the ‘Duo’ apparatus) so that the birds could discriminate the two apparatuses easily when placed at the end of the table. Each bird was tested alternatively with and without a partner and placed at the end of the central table whereas the partner (when present) was placed simultaneously in front of the ‘Duo’ apparatus on the other table (Figure 3). Each bird was tested several times so that we obtained 60 trials in which the bird chose one apparatus (20 trials with each partner and 20 trials alone). Two sessions were conducted every day for ten days.

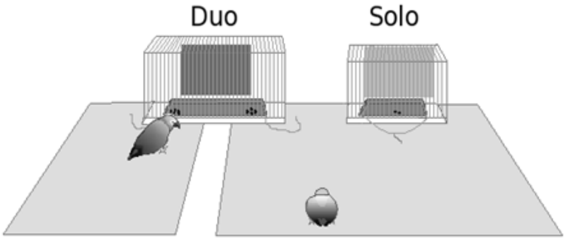

Figure 3: Coordination

Experiment 4: Collaboration

Using only the ‘Solo’ cage, we added a lever (44 cm) connected to a perch (20 cm). One parrot had to climb on the perch, which revolved the lever. This latter action allowed a partner to move the tray baited with food for both birds. However, birds could pull the string but the tray would stay blocked by the lever (see Figure 4). We tested only the more tolerant dyads, Léo-Shango and Léo-Zoé. Birds were trained on both actions but we imposed their place on the table and thus their role at the beginning of the test in order to see if they would be able to switch roles later. Individuals were placed either at the same time (condition 1), or with a delay of 10 seconds (condition 2). In the first phase, we decided arbitrarily to place Léo on the perch side and alternatively the two others on the tray side. We completed 40 trials in condition 1 and 20 in condition 2 for each dyad. In the second step, we exchanged the subjects’ places for 30 trials, with Léo on the tray side and Shango and Zoé alternatively on the perch side (15 trials each). Test sessions took place over two months.

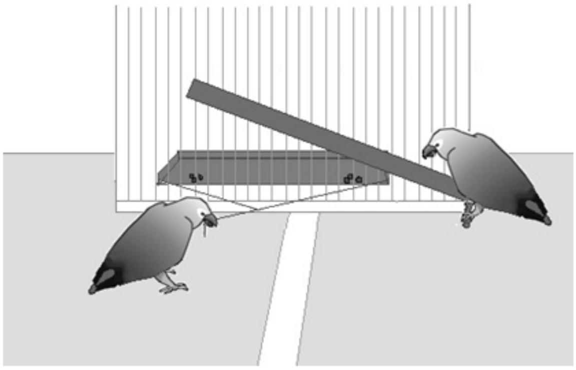

Figure 4: Collaboration

Scoring and data analysis

We reported the number of single pullings before and after the arrival of the partner, simultaneous pullings, the latency times before each parrot pulled the string for the first time, the time spent on the perch (experiment 4) and finally the outcome (access to food or not) for each trial. A trial ended when 1) the individuals reached the reward, 2) the string was out of reach for the partner or 3) the individuals lacked motivation (more than 90 seconds without any behaviour directed towards the apparatus). For the first experiment, we determined the success rate for each session of 20 trials as the number of successful cooperative events over the total number of attempts.

Spearmann correlations were used to assess any changes in behaviour across the testing period. We ran binomial tests in order to evaluate the choices of the birds facing different experimental setups. The significance level was set at $\alpha = 0.05$. When multiple comparisons were made, we used a Bonferroni adjustment ($\alpha' = \alpha/c$ where $\alpha = 0.05$ and c corresponds to the number of comparisons).

Results

Similarity

Birds required between 6 and 9 sessions to solve the task with their partner with a success rate higher than 90%. The number of solitary actions decreased (Spearman rank order correlation; Zoé-Léo: N=9, r_s=-0.702, p=0.0101; Zoé-Shango: N=7, r_s=-0.861, p=0.00609; Léo-Shango: N=6, r_s=-0.853, p=0.0333) and at the same time simultaneous pulling increased. Indeed, each dyad improved the number of successful cooperative actions (Spearman rank order correlation; Zoé-Léo: N=9, r_s=0.685, p=0.0186; Zoé-Shango: N=7, r_s=0.991, p<0.001; Léo-Shango: N=6, r_s=0.853, p=0.0333).

Synchrony

Birds cooperated successfully in 76% of the trials. We noticed that all the subjects pulled more when a partner was available than when they were alone (Wilcoxon: Zoé: W=610.5, N=50 P <0.001; Léo: W=989.5, N=50, P <0.001; Shango: W=367.5, N=50, P <0.001; see figure 3). Two out of three individuals showed no significant change in the number of pullings before the partner's arrival (Spearman: Zoé: r_s = -0.196, N = 50, P = 0.230 and Léo: r_s = 0.292, N = 50, P = 0.104), while Shango showed a significant decrease (r_s = -0.498, N = 50, P <0.05). The latency time (before the first pulling) did not increase significantly across the experiment for Léo and Zoé (Spearman: Léo: r_s = -0.070, N= 50, P = 0.551. Zoé: r_s = -0.201, N=50, P = 0.137) but increased for Shango (r_s = 0.339, N= 50, P = 0.017).

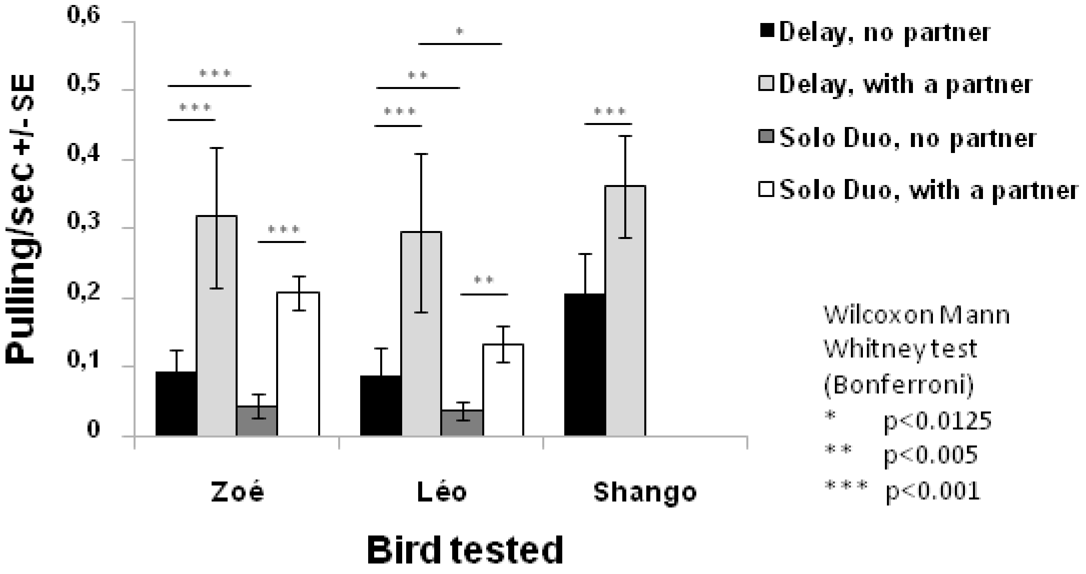

Figure 5: Mean number of pullings before and after the partner's arrival during the 'Delay' (experiment 2) and 'Solo Duo' (experiment 3) tasks. In both experiments, birds pull more when a partner was present and learned to wait across the study as they pulled less in general in the experiment 3.

Coordination

When tested alone, Zoé chose significantly more often the 'Solo' apparatus (Binomial test; P =0.006). Tested with Léo, Zoé always chose the 'Duo' apparatus and on the contrary, when tested with Shango, she went for the 'Solo' cage in all the trials (Binomial test; P<0.001). Shango, tested alone or with a partner opted for the 'Solo' apparatus in all the trials (Binomial test; P<0.001). When alone, Léo did not show any preference for the 'Solo' cage and chose at random (Binomial test; P =0.252). On the contrary, when a partner was present he significantly chose more often the 'Duo' apparatus, cooperating all the time with Zoé (Binomial test; P<0.001) and in 75% of the trials with Shango (Binomial test; P =0.021) (see Figure 6).

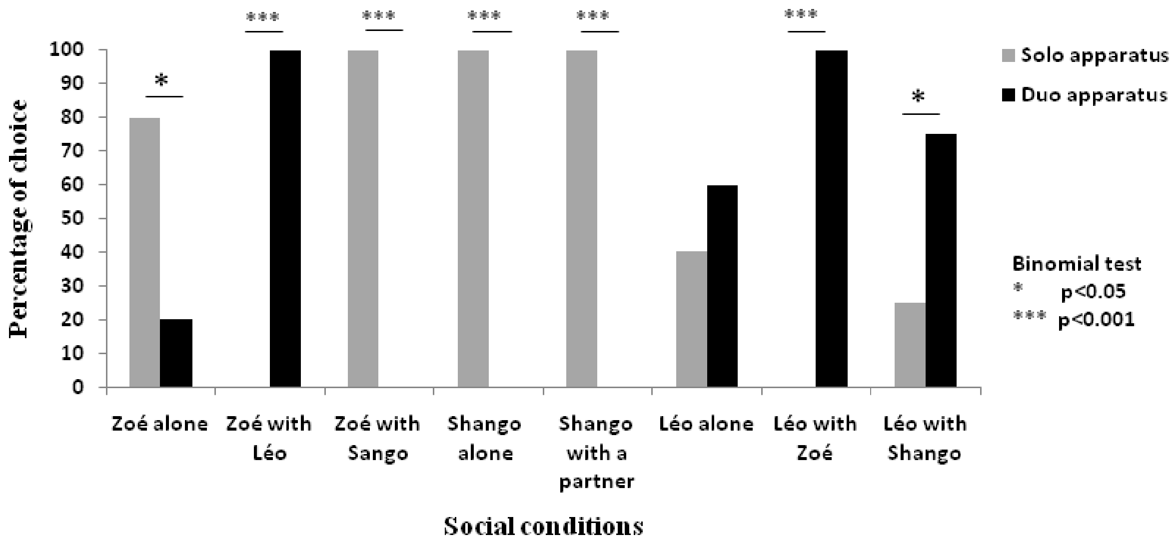

Figure 6: Birds' choices between Solo and Duo apparatuses according the social situation

The three subjects pulled less when they were waiting for a partner (Wilcoxon; Zoé: W = 50, N = 50, P <0.001; Léo: W = 91.5, N=50, P <0.005; Shango: W = 38.5, N = 50, P <0.01). Moreover, the individuals improved these performances between the two experiments.

Indeed, the mean number of pullings in each condition (alone and with a partner) decreased across the study (Comparing ‘Delay’ and ‘Solo Duo’ tasks when alone; Wilcoxon: Zoé: W=848.5, N=, P <0.001; Léo: W = 1016, N=50, P <0.005. Comparing ‘Delay’ and ‘Solo Duo’ tasks when the partner was present; Wilcoxon: Zoé: W = 546.5, N = 50, P =0.34; Léo: W = 985, N = 50, P <0.01; see Figure 5). As Shango always chose the Solo apparatus we were not able to compare his performances.

Collaboration

During condition 1 (no delay), we observed that both dyads (Shango/Léo and Zoé/Léo) performed similarly (75% and 73% success rate, respectively) with a refusal rate that was quite low (5%). However, both birds still had difficulties in waiting as the pulling bird tended to act before Léo was perched. In the delay condition (2), we observed that the success rate of the dyad Shango/Léo dropped mostly when Léo was delayed, since in half of the trials Shango left the testing area and did not wait for Léo’s arrival. We noticed that Zoé kept pulling the string while Léo arrived in 81% of the trials. Once perched, Léo waited for his partners and never went down before the food was accessible but refused several times to participate when Zoé or Shango were delayed (see Table 1). During the second phase in which the positions were exchanged, we observed only three attempts of cooperation across the 30 trials. Léo pulled the string only once, but before Zoé was perched. Zoé and Shango also perched spontaneously once each during the experiment, but Léo did not pull the string.

Nb of trials	Perching bird	Pulling bird	Condition	Success rate	Failure perching bird	Failure pulling bird	No attempt	Pulling before
40	***Léo***	***Shango***	***no delay***	***75%***	***15%***	***10%***	***5%***	***13%***
20	*Léo*	*Shango*	*Shango delayed*	*63%*	*10%*	*15%*	*2%*	
20	*Léo*	*Shango*	*Léo delayed*	*29%*	*4%*	*50%*	*17%*	
40	***Léo***	***Zoé***	***no delay***	***73%***	***18%***	***2%***	***5%***	***15%***
20	*Léo*	*Zoé*	*Zoé delayed*	*80%*	*20%*	*0%*	*0%*	
20	*Léo*	*Zoé*	*Léo delayed*	*88%*	*6%*	*6%*	*0%*	*81%*
15	Shango	Léo	no delay	0%	7%	7%	86%	
15	Zoé	Léo	no delay	0%	0%	7%	93%	

Table 1

Success rate: number of successful cooperative action out of the total number of attempts

Discussion

In experiment 1 (similarity), our three birds had the same goal and solved the task doing the same action (pulling the string). The number of simultaneous pulling occurences increased as their similar actions were completed at the same time. This type of cooperation has also been observed in primates such as cotton-top tamarins (Cronin et al. 2005), ouistitis (Werdenich and Huber 2002), capuchins (Mendres and de Waal 2000), bonobos (Hare et al. 2007) and chimpanzees (Melis et al. 2006a), and more recently in non-primate species such as rooks (Seed et al. 2008), wolves (Möslinger et al. 2009) and hyenas (Drea and Carter 2009). These results showed that the subjects' success rate increased and this was enough to conclude that they could solve the task, but was not enough to conclude on the concept of understanding a partner's role. Indeed, individuals could have been simply attracted by the reward and made a similar action without understanding that cooperation was necessary (Visalberghi et al. 2000).

In experiment 2 (synchrony), one of our subjects (Shango) seemed to adjust his behaviour according to the presence of a partner and pulled less until the partner arrived in front of the cage. On the contrary, Zoé and Léo, like rooks (Seed et al. 2008), seemed unable to wait for the partner but increased their activity when the other individual was present, like capuchins (Mendres and de Waal 2000). Hauser et al. (1999) argue that it could be difficult to inhibit a learned motor pattern such as pulling on a string in order to receive food. Furthermore, experiments conducted in the laboratory on self-control revealed that our three parrots were not able to wait for more than two seconds in a delay of gratification task (Vick et al. 2009). It is possible that the choice of a 15 second delay was too long for our parrots, such that they were unable to refrain from pulling the string despite understanding the need of a partner.

In experiment 3 (coordination), our grey parrots were able to take advantage of the presence of a partner to solve the 'Duo' apparatus and thus to get more reward. In the study by Seed et al. (2008), only two rooks showed a preference in the second half of the trials and this preference was for the single apparatus when they were alone. As well as chimpanzees (Melis et al. 2009) and hyenas (Drea and Carter 2009), African grey parrots were able to coordinate their actions. Nevertheless, we must specify that our birds were placed directly on the table so they were more willing to participate compared to the rooks that were in an adjacent aviary.

Léo and Zoé, when tested with a partner, showed a clear preference for the 'Duo' apparatus, which could support the fact that they understood the advantages of cooperation in order to obtain twice as much food when a conspecific was available. However, Léo behaved at random when alone; this could be because he did not really understand the task and the partner (when present) could represent an attractive stimulus. In previous experiments, our birds showed that they could rely on cues from human (Giret et al. 2009a) and conspecific (Giret et al. 2009b) sources to find hidden food. Thus, it is possible that Léo simply relied on the presence of a conspecific in order to make his decision and showed no difference between partners because he could obtain food with both of them.

Zoé made a clear distinction between conspecifics, and the decision for entering in a cooperation process was a function of the partner himself. While she chose to always cooperate with Léo when he was present, she always went for the ‘Solo’ apparatus when Shango was the partner. She probably understood the advantages of cooperation, but also realised when it was better not to do so. Indeed, Shango was dominant over Zoé and they often had antagonistic interactions. Furthermore, she could have kept in mind that in this experiment he never cooperated (when he was the tested bird). On the contrary, Shango adopted a different behaviour, always choosing the ‘Solo’ apparatus whatever the situation was (tested alone or with a partner, dominant or subordinate). He seemed to prefer to have a smaller reward but to get it by himself without needing a partner who could refuse to participate.

In this experiment, the parrots also seemed to improve their self-control and waited for their partner before pulling the string, contrary to what we noticed in the collaboration task. Indeed, Zoé pulled the string before the arrival of Léo more when partner entry was delayed. Shango did not wait and most of the time preferred to leave the table rather than to wait for his partner. He was also the subject who showed the worst performance in the self-control experiment (Vick et al. 2009).

In experiment 4, all three birds learned to act complementarily in order to reach the tray. However, after we exchanged their positions, they acted appropriately only three times, but it was always unsuccessful. Even if they were trained at the beginning on both tasks, it seems that they specialised in their primary role and then were not able to adapt their behaviour to the new situation. The inability of the parrots to exchange roles was probably due to their inability to understand the general setting and the necessity for the two subjects to engage in complementary actions simultaneously. This is probably different from chimpanzees (Boesch and Boesch 1989) or lions (Stander 1992) who are able to collaborate in the wild, thus without training (some trial and error could probably also be important for them to learn how to collaborate). However, the fact that our parrots tried at least once cooperation attempt could also mean that they had some understanding of the actions needed. An overall laziness and lack of motivation could also explain our results, since the parrots would not even walk a few more steps in order to go to their usual places to solve the task.

Previous experiments conducted with the same birds revealed that they were able to adapt their responses according to the experimenter's intentions (Péron et al. 2010), but in this study, we were not able to make conclusions regarding their mental states. None of our parrots made any recruitment attempt (or even emitted vocalisations), but at the moment, no data from the wild or from captive parrots has shown the presence of this behaviour in African grey species. During our studies, the birds oriented their heads toward their partner most of the time when partner entry was delayed. Nevertheless, regarding the anatomical disposition of their eyes, it is hard to conclude anything based on their gaze direction (Dawkins 2002), so a specific experimental design employing optical equipment such as a laser (Anders et al. 2008) would be needed.

This study was a new step towards a more general comprehension of parrot social cognition. Our three grey parrots were able to solve artificial cooperative tasks and to relate their actions in time and space in order to get access to a resource. Learning clearly accounts for a huge part in their performances. Although our subjects seemed to understand the need of a partner to solve the task, the same effect could probably, as emphasised by Noë (2006), have been achieved by combining the opportunity to gain a reward with a red light or any other cue. However, this ability to learn such contingencies could probably allow parrots in the wild to learn to cooperate more efficiently.

We observed that tolerance impacted on the probability of cooperation to occur and also on a dyad's efficiency. Our observations have been based on three hand-reared African grey parrots, so our conclusions cannot be applied to the species as a whole. However, the vast majority of the data currently available concerning the cognitive and communicative abilities of African grey parrots came from a single individual, Alex (Pepperberg and Brezinsky 1991; Pepperberg 1993; Pepperberg 1994; Pepperberg 1999). There is no doubt that in nature parrots have to face complex social situations during which they must cooperate in order to access a reward or to defend a territory. Our positive results suggest the need to study different groups of grey parrots with different devices in order to evaluate how they deal with their physical and social environment. Indeed, studies conducted in keas (Tebbish et al. 1996; Huber et al. 2008) and macaws (Spitzhorn 2009) revealed that according to the social organisation of the group and the experimental setup, different strategies are used to solve a cooperation task.

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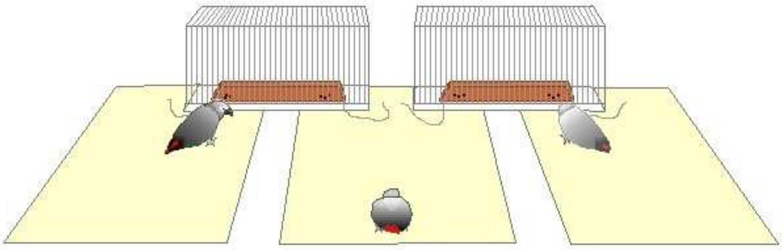
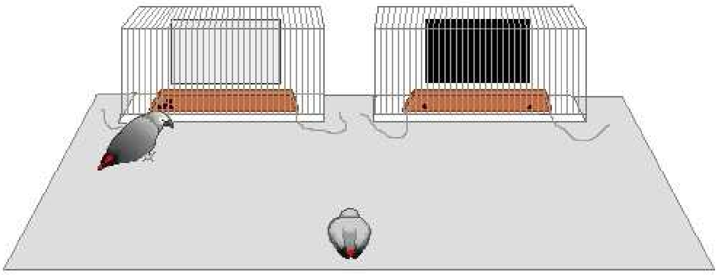
Article 2

Social preferences and negotiations during a cooperative task in African grey parrots (*Psittacus erithacus*).

Péron F., Rat-Fischer L., Lalot M., Nagle L. & Bovet D

Soumis *Journal of Comparative Psychology*





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Problème biologique

Dans le cadre d’une vie en société, les animaux sont amenés à interagir fréquemment avec de multiples partenaires, d’autant plus si leur durée de vie est longue. Les individus peuvent être amenés à coopérer afin de pouvoir accéder à une ressource que seuls ils ne pourraient obtenir. Au sein d’un groupe, les partenaires potentiels peuvent être nombreux et donc il peut être utile de choisir ceux qui ont les mêmes intentions et qui se révèlent être les plus performants.

Hypothèse

Le degré de tolérance entre les individus va conditionner leurs choix et performances dans les tâches de coopération. Dans l’expérience de négociation, les oiseaux vont essayer d’obtenir la plus grande récompense possible et par conséquent il y aura un conflit d’intérêts entre les participants pouvant conduire à l’arrêt de la coopération.

Méthodes

Nous avons évalué la tolérance au sein des dyades et employé un dispositif où une ficelle coulisse pour évaluer leur capacité à travailler ensemble. Seules les interventions simultanées sur le dispositif permettent de déplacer et d’atteindre la récompense. Nous avons aussi testé leurs préférences sociales en leur permettant de choisir leur partenaire. Dans une troisième partie les oiseaux se retrouvent face à deux dispositifs où la répartition de la récompense est soit égale soit inégale.

Résultats

Plus les membres d’une dyade sont tolérants, plus ils participent et meilleurs ils sont. Nous observons que les mâles ne font pas de différence entre les partenaires possibles alors que Zoé ne coopère qu’avec Léo. Dans la dernière expérience, Léo parvient à faire changer le choix de Shango mais ce dernier essaye tout de même d’obtenir la plus grande partie de la récompense. A plusieurs reprise ils partagent la récompense.

Conclusion

On observe que la tolérance influence le choix du partenaire mais également la façon dont les individus choisissent de résoudre un problème. Les relations entre les individus influencent également la manière dont peut être résolu un conflit d’intérêts. Au final les oiseaux partagent la nourriture ce qui permet aux deux individus d’être récompensés pour leurs efforts et donc de poursuivre les tentatives de coopération.

Social preferences and negotiations during a cooperative task in African grey parrots

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Abstract

Cooperative behaviours such as mobbing, hunting and cooperative breeding are encountered among animal kingdom and wildly developed in human societies. Several experiments conducted in non-human primates and few in other mammals and birds reveal that some species are able to coordinate their actions according to physical and social constraints of the environment to solve artificial tasks. In the wild, parrots show cooperative behaviours such as allopreening or mobbing. In this study, we tested African grey parrots (*Psittacus erithacus*) using different artificial tasks, to explore their behaviours when cooperation was needed. First we analysed the efficiency of three dyads according to the relationship between individuals. As expected, the more tolerant dyads obtained better performances. In the second task, three grey parrots could choose between two potential partners in order to solve a cooperative string-pulling task. We observed that birds entered in cooperative actions according to their relationship with the partner, and that hierarchy and tolerance again influenced the performance of the dyad. In the third experiment two birds were presented to a negotiation game in which apparatuses were baited differently: a fair and an unfair food distribution. In this experiment the dominant tried to monopolize the reward whatever the situation was but the subordinated bird was able to influence the behaviour of his partner. In most of the cases the parrots solved the task sharing the food and thus avoiding any conflict or any breakdown of the cooperative behaviour.

Keywords: African grey parrots, tolerance, efficiency, coordination, cooperation, negotiation

Introduction

According to the social brain hypothesis, individuals living in social groups have to manage complex interactions (Jolly 1966; Humphrey 1976; Byrne and Whiten 1988; Dunbar 1998). Monogamous animals have also to avoid conflicts with their mate (valuable relationship hypothesis: Emery et al. 2007). These hypotheses could explain why some species have bigger brains compared to what could be expected when considering their body size. Some birds' families illustrate this phenomenon. Recent studies highlighted that cognitive abilities of corvids and psittacids species were complex and similar to the abilities observed in primates (Emery and Clayton 2004; Pepperberg 2006). African grey parrots (*Psittacus erithacus*) would represent a good model for cooperation studies as they form stable monogamous couples over the breeding seasons; both parents take care of the chicks even if the female invests more (Cockburn 2006). They display reciprocal actions such as allopreening and males regurgitate to females during the breeding season. Moreover, these birds are able to cooperate in order to defend their group: in Principe Island grey parrots have been observed while mobbing against red kites (Jones and Tye 2006). All these elements taken together raise the hypothesis that African grey parrots would have the cognitive abilities necessary to manage complex social relations and to cooperate in an artificial task. They should display flexible behaviours in order to adapt to the situation, thus avoiding potential conflicts that could possibly weaken the relationships (Emery et al. 2007). Many definitions of cooperation can be found; in this paper, we use Noë's (2006) definition: all interactions or series of interactions that, as a rule (or 'on average'), result in net gain for all participants.

In this study we adapted the 'loose string paradigm' proposed by Hirata and Fuwa (2007) with chimpanzees (*Pan troglodytes*): two individuals faced a tray with food rewards placed out of reach. Both subjects had to pull simultaneously a string in order to get access to the reward. Melis et al. testing several dyads of chimpanzees with the same setup showed a positive correlation between tolerance within dyads and success rate (2006b) and that individuals were able to discriminate between two potential partners according to their previous experience with each of them in order to recruit the best collaborators (2006a). Thus, social preferences could develop according to the skills of potential partners. Experiments conducted in rooks (*Corvus frugileus*) showed that individuals solved the task more efficiently if dyads were tolerant (Seed et al. 2008) and bolder individuals appeared more willing to solve the task whereas shyer individuals were more influenced by their partner's behaviour (Scheid and Noë 2009). Social relationships could also influence the performances as individuals could choose their partner according to previous interactions (agonistic or not), their relationship (mate, siblings) and their position within the hierarchy (dominant-subordinate). Several studies revealed that some species were sensitive to inequity (chimpanzees: Brosnan et al. 2010b; capuchins: van Wolkenten et al. 2007, Fletcher 2008, Brosnan et al. 2010a; cotton top tamarins: Neiworth et al. 2009; dogs: Range et al. 2009) even if there are also some controversial findings regarding chimpanzees abilities (Bräuer et al. 2006, Bräuer et al. 2009). Thus cooperative actions should provide equivalent rewards to each participant, as otherwise cooperation could breakdown. A study also revealed that tolerance for inequity could increase with social closeness (Brosnan et al. 2005), thus the quality of the relationship would influence the outcome of the negotiation. Other possibilities to solve a cooperation task with asymmetry in the outcome are to display more flexible behaviours such as tolerated theft (Blurton Jones 1984), reciprocal altruism (Trivers 1971) when individuals take turns so that all participants could access the resource or just sharing the reward. In the negotiation game (Melis et al. 2009) the chimpanzees had the choice between a fair and an unfair reward distribution. The results showed that chimpanzees were successful most of the time as they found a solution and finally cooperated: dominants tried to monopolize the bigger amount of food but subordinates often refused a selfish offer and were able to outwait their dominant partner until finally they obtained equal rewards. Other studies evaluated the reaction of individuals facing unfair situations but they were based on the paradigm of producer/recipient since only one subject provided efforts and another obtained the food. In different psittacids species, individuals solved the task using different strategies such as social harassment for the keas (Tebbich et al. 1996) and reciprocal altruism and tolerated theft for the Green-winged macaws (Spitzhorn 2009). A recent study on wolves showed that they were able to solve the same kind of task but most of the time the dominant accessed the reward (Möslinger 2009). Capuchins were able to reverse their roles (Hattori et al. 2005) and display reciprocal altruism (Brosnan et al. 2006) and cotton top tamarins (Cronin & Snowdon 2008) were also found to be able to reciprocate. In chimpanzees only a weak effect of previous behaviour had been observed (Melis et al. 2008) and they did not spontaneously take turns in a reciprocal cooperation task (Yamamoto & Tanaka 2009). Reciprocal interactions were also observed in birds during mobbing events (Krams et al. 2008) and its frequency increased when the predation risk increased (Krams et al. 2010).

Our birds already participated in several experiments of cooperative string-pulling. We found that they were able to learn to wait for their partner (synchrony task), to adapt to the presence or absence of a conspecific and to coordinate (Péron et al. submitted-a). Indeed, in an experiment (coordination task) in which individuals had the choice between an apparatus that could be solved alone (Solo) and another that required cooperation but where twice more food was provided (Duo), the female (Zoé) chose the Solo apparatus when alone or tested with one of the two males, Shango (who was aggressive toward her) and on the contrary cooperated with the other male, Léo. Shango chose all the time the Solo apparatus whenever he was alone or with a partner and at the opposite Léo cooperated with both individuals when it was possible (Péron et al. submitted-a). But how would they have behaved if more than one partner had been present? The aim of this study was to evaluate the preferences and the performances of birds according to their partner in a cooperative task and then to look at their strategy when facing a negotiation game. First we analysed the efficiency of the dyads according to the relationship between individuals. We hypothesized that if our individuals were able to cooperate, this would increase the tolerance between them. Then our grey parrots could choose between partners and finally, the two males participated in a negotiation game where the trays were baited differently.

Experiment 1: Tolerance and Dyad efficiency

Material & method

Subjects

We tested three hand-reared African grey parrots: two males (Shango and Léo, four and six years old respectively) and one female (Zoé, six years old). They hatched in captivity and arrived at the laboratory at three-months-old. They were housed together in an aviary (340 cm × 330 cm × 300 cm) with three tables (120 × 60 × 75 cm), two large perch structures and many toys, at a constant temperature of 25°C and a 12/12 h light-dark cycle. The parrots were tested in their aviary in pair or all together. During a test session, subjects that were not tested were placed in a cage in the corridor with food, water and toys available. Parrots were fed daily with fresh fruits and vegetables in the morning and parrot formula (Nutribird A21) in the evening. Water and parrot pellets (Harrison, high potency coarse) were available *ad libitum* and vitamins (Muta-Vit Versele-Laga) were given twice a week. As our animals are free flying parrots, all our sessions were based on their motivation to participate. Indeed, they could leave at any time and go to perch elsewhere in the aviary. We used parrot formula and sunflower seeds as reward and birds were not food deprived for the tests but they did not receive these preferred rewards outside of the tests.

Tolerance evaluation

Tolerance was evaluated using a divisible quantity of food placed in a flat rectangular cardboard tray (31 x 17 x 4 cm) large enough for simultaneous access of both animals. The first bird was placed in front of the tray then a second individual was placed near the first one.

Each test lasted one minute and was repeated two to four times for each dyad depending on their motivation for food access. The data recorded were the time during which the birds were eating, all the neutral, affiliative and agonistic (aggression, avoidance) behaviours and also vocalizations.

We defined the degree of tolerance as [the number of affiliative behaviours] minus [the number of antagonistic behaviours] divided by [the numbers of all behaviours] (Coulon 1975). Thus, we created a tolerance index: It = (Me + 1/2 Rc - Pa)/ (Me + 1/2 Rc + Pa) with It: tolerance index ($-1 \leq It \leq 1$); Me: number of time where birds were eating together; Rc: Numbers of occurrences in which individuals stayed under 20 cm of distance to each other; and Pa: Number of occurrences in which one individual moved away when the other approached the food source. Dyads with a score of –1 are considered as intolerant whereas a score of 1 means a high degree of tolerance.

Tolerance rate was evaluated between each dyad before, during and after the testing period (synchrony and coordination experiments; see below).

Dyad efficiency

Birds were tested using the loose string paradigm. A flat rectangular cardboard tray (31 × 17 × 4 cm) baited with food was enclosed in a cage (54 × 28 × 36 cm) to prevent birds from food access. A piece of string was threaded through metal loops placed on the tray so that both ends of the string extended out of the cage for 20 cm. The bottom of this cage had a gap that enabled tray’s movements. Pulling from only one end of the string would be ineffectual because the string would become unthreaded without moving the tray. The parrots could move the tray only by pulling both ends of the string simultaneously. We did not need to familiarize our birds with the device as they have been previously tested on their ability to synchronize and coordinate in order to solve a cooperative string-pulling task (Péron et al. submitted-a). We looked at the average of simultaneous pullings needed for each dyad in order to reach the food for each trial. We used the 40 trials conducted both for the synchrony and coordination task (detailed in the introduction) for each dyad. Thus we obtained variable number of cooperation according the dyad.

Statistical analysis

We ran one way RM ANOVA with all pairwise multiple comparison procedures (Holm-Sidak method) according to the result of the normality test.

Results

Tolerance

Before the experiment, we found a high value for the dyad Léo-Zoé (It (Léo-Zoé) = 1,00) which were highly tolerant toward each other. On the contrary we noted a very low value between Shango and Zoé (It (Shango-Zoé) = -1,00) as Shango was very aggressive toward Zoé so she was afraid of him. Finally, we observed a medium rate for the dyad Léo-Shango (It (Shango-Léo) = -0.33). The results were similar to daily observations made by caretakers and researchers (personal data) and during behavioural studies (Plassais J., unpublished data). These observations could be explained by the fact that Zoé and Léo arrived as chicks at the same time and were bred together, whereas Shango arrived two years later.

We observed variations of the tolerance index during the experiment period: it tended to increase with time. After the experiment the dyad Léo-Zoé stayed at the maximum (=1), the dyad Shango-Léo increased until 1 and finally the dyad Zoé –Shango increased also but until -0.33 only. This could be explained by the influence of the experiment itself: the birds learned to cooperate in order to reach the food and thus proximity was rewarded.

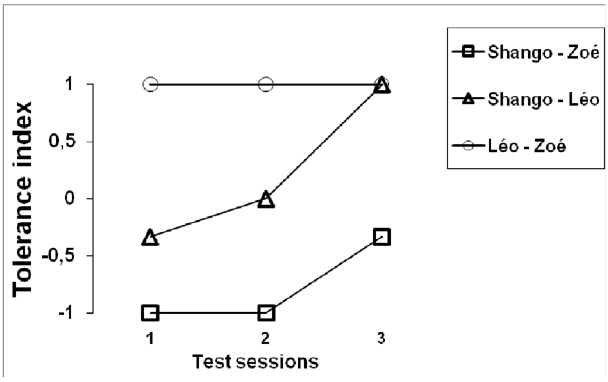

Figure 1: Evolution of the tolerance index across test sessions

Dyad efficiency

The efficiency of each dyad was evaluated during the synchrony and the coordination experiments. First we observed that the results were different for each dyad: Zoé - Léo needed less pulling than the Léo - Shango dyad (Holm-Sidak test; t=2.22, p=0.0301) which was better than the Zoé – Shango dyad (Holm-Sidak test; t=2.53, p=0.0142). When we look at the results in relation with the tolerance index of each dyad (for the tolerance test conducted during the cooperation experiment), we note a strong correlation (r^2=0.999). The more tolerant the dyads are, the more efficient they are: tolerant dyads need less simultaneous pullings in order to reach the baited tray compared with less tolerant ones. The same correlations have been found in other species such as chimpanzees (Chalmeau 1994; Melis et al. 2006), capuchins (Chalmeau et al. 1997), ouistitis (Werdenich & Huber 2002) and rooks (Seed et al. 2008). Moreover more tolerant individuals cooperate more often (see for instance the dyad Zoé-Léo). The number of successful cooperation trials observed for each dyad (Shango- Zoé:13; Shango- Léo: 47 & Zoé-Léo:66) is also strongly correlated with the tolerance (r^2= 0.981)(see figure 3).

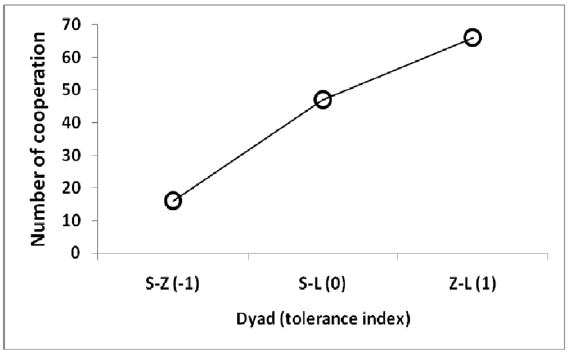

Figure 2: Number of successful cooperation for each dyad across the synchrony and coordination task

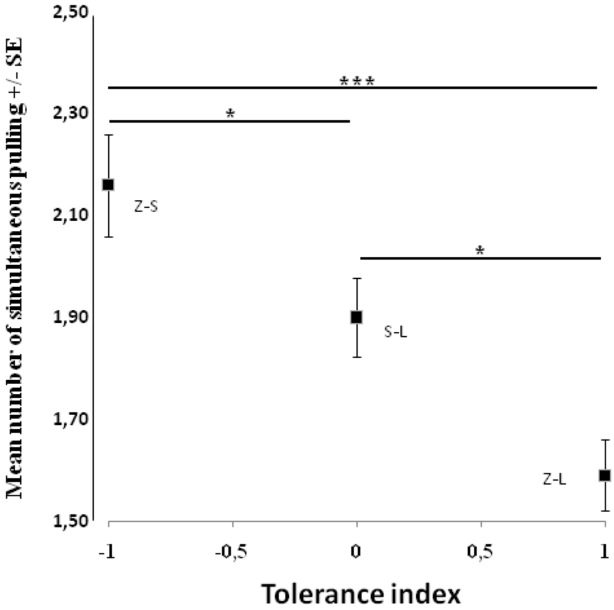

Figure 3: Dyad efficiency; mean number of pulling necessary for each dyad before accessing the baited tray

Experiment 2: Partner choice

Experimental setup

We used the same experimental setup as previously but this time with two similar apparatus placed on the tables (see figure 4).

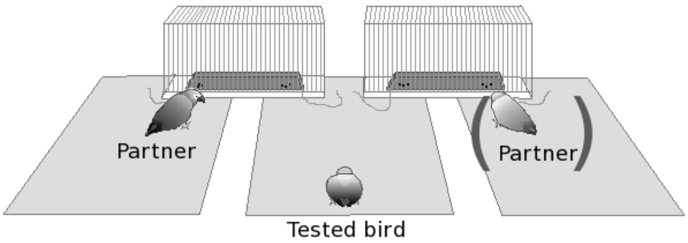

Figure 4: Experimental setup of the partner choice experiment

Cooperation test

The three grey parrots tested in experiment 1 participated also to this experiment. Individuals were tested in pairs or all together with a randomization of the place of each partner. The tested bird was put at the end of the central table whereas one or two partner(s) was (were) placed near the cage(s). We expected the tested parrot to choose his preferred partner when he had the choice and the apparatus with the only partner available in order to reach the food if only one partner was present. For each individual, we made 20 trials in each situation (3 different situations: only one or both partners alternating between left and right side) i.e. 60 trials in total.

Data analysis

Every session was coded directly. We took into account the choice of the tested bird. A trial ended when 1) birds just finished eating the reward, 2) the individuals lacked motivation (more than 90 seconds without any behaviour directed towards the apparatus) or 3) birds failed and did not cooperate or chose the wrong cage where no partner was present.

We ran two-tailed binomial tests to compare the tested bird’s choice between two situations (between the two partners or between one partner and no partner).

Results

In general, our subjects made a correct choice in more than 78% of the trials, going for the apparatus where a partner was waiting in order to solve the task cooperating (as opposed to choosing the apparatus without a partner available).

When tested with one or two partners available, Zoé always chose to cooperate only with Léo ($P<0.001$) and refused to work with Shango even if he was the only partner available. In this situation she stayed away from the apparatus for most of the trials and emitted frustration calls. Léo tested with both partners chose at random (P=0.824) whereas when tested with only one partner he behaved differently. He cooperated significantly when Zoé was the partner (P=0.012) whereas he did not show any significant preference for the apparatus where Shango was (P=0.264). Shango tested with both partners chose at random (Binomial test; P=0.824) and when tested with only one partner he chose significantly to cooperate (with Zoé; P=0.008; with Léo; P=0.002) (see figure 5). During all the trials, the partner accepted to cooperate excepted Léo once (out of 40 trials) with Zoé and Zoé in half of the trials was she was Shang's partner. We observed that most of males incorrect choices were made going on the left side when no partner was present (left position bias).

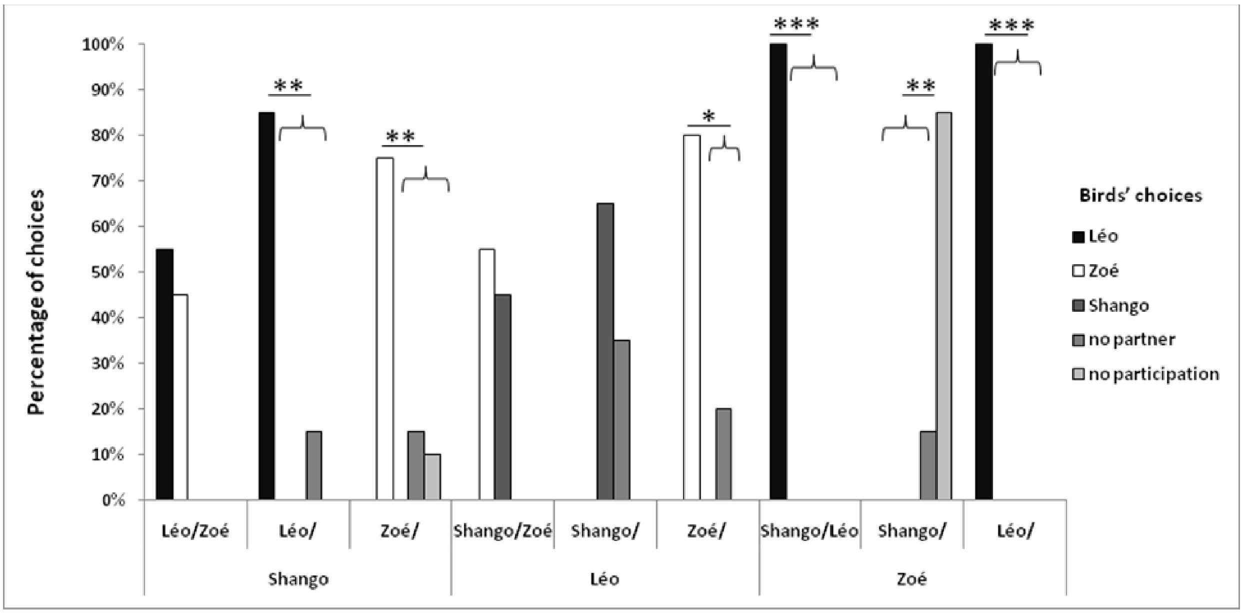

Figure 5 : Choices of the tested bird (in %) during the partner choice experiment

Léo, Zoé or Shango: partner chosen by the tested bird

No partner: the tested bird went for the apparatus where no parrot was present

No participation: the tested bird refuse to choose between the two apparatus

Chi Square analysis; *:p<0.05; **:p<0.005; ***:p<0.001

Discussion

The probability of cooperative actions to occur was linked to the relationship between the participants. Indeed the behaviour of Zoé was consistent with previous experiments as she displayed partner avoidance toward Shango and cooperated mainly with Léo (Péron et al. submitted-a). She was probably so afraid of Shango (who was more aggressive with her during the testing period of the Experiment 2 than during Experiment 1, conducted two months before) that she preferred to give up her reward than to go near Shango in order to be able to cooperate with him. Shango and Léo did not make a difference between the two partners. In the previous study Léo cooperated with both individuals when it was possible and at the opposite Shango chose all the time the Solo apparatus whenever he was alone or with a partner. For Léo it could be explained by the fact that he belonged to tolerant dyads and he could get the food with both partners. Regarding Shango's behaviour, in this experiment, he had no other choice than to cooperate if he wanted to access the reward. Surprisingly, Shango choose at random between the partners even though Zoé left the testing area in half of the cases. According to the biological market theory (Noë & Hammerstein 1994), he should have preferred to cooperate with Léo. Maybe 40 trials with Zoé were not enough for Shango to learn no to choose her, as she cooperated with him during the precedent experiment and in this experiment she accepted to cooperate with him in some trials when she was the partner, maybe because in this situation she was already placed in front of the cage. Our birds did not recruit their collaborators and did not even choose the best one contrary to chimpanzees (Melis et al. 2006a).

Experiment 3: Negotiation game

Material and method

Subjects

Léo and Shango were tested whereas Zoé did not participate in this experiment because of health problems and was brought to another room where food and toys were provided during the sessions. The hierarchy between the birds was observed during the experiment as we coded the agonistic behaviour of the birds.

Experimental setup

We used the experimental design with some modifications. Two apparatus differing from color were placed on the table. We used again parrot formula and sunflower seeds as rewards. One apparatus was baited equally (1:1, Black) and the second unequally (4:0; White) (see figure 6). A study undertaken previously in the laboratory highlighted the fact that our birds were able to discriminate between these quantities (Al Aïn et al. 2009). We chose different color cage backgrounds to help birds to make their choice when placed at the end of the table. Thus the first bird (proposer) placed on the table had the choice and could make three different proposals. He could wait for the partner in front of the equal tray (thus making an equal offer) or in front of the unequal tray. In this latter case two situations were possible: either the bird waited in front of the reward (selfish offer) or in front of in the empty side (altruistic offer). The second bird (partner), placed 30 seconds later could accept the proposal (cooperating with the partner) or refuse it doing another offer (going for the other tray for instance) or just leaving the testing area. During this experiment we observed that Léo was subordinate to Shango.

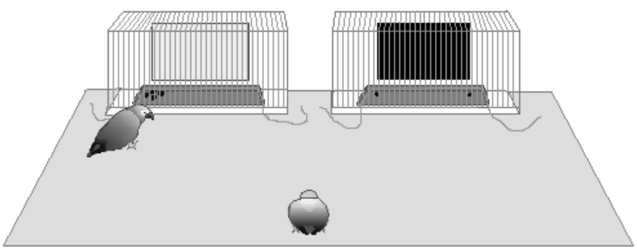

Figure 6: Experimental setup of the negotiation game (selfish offer)

Cooperation test and Data analysis

We conducted 80 trials alternating the place of the cages (and of the reward of the unequal tray) and the proposer (first individual placed). Trials were coded directly and we took into account the first choice of each parrot, the possible switch of birds' choices and finally the outcome of the trial. A trial ended when 1) birds just finished eating the reward, 2) the individuals lacked motivation (more than 90 seconds without any behaviour directed towards the apparatus) or failed to find an agreement on which device to use after 90 seconds.

We ran two-tailed binomial test to compare the birds' choices between the two apparatuses.

Results

We observed 66 cooperative actions. Léo chose at random between the two cages when doing the proposal (Binomial test; P=0.728); he tended to do more selfish proposals when staying in front of the unequal tray but it was not significant (P=0.302). Shango chose more often the unequal cage (P=0.036) and made more often selfish offers (P=0.002) (see figure 6). Shango accepted all the proposals made by Léo whatever the situation was. Léo accepted all the equal and altruistic offers but declined half of the selfish offers. In these cases, he refused to go to the apparatus chosen by Shango and in a third of the selfish offers he made another offer going to the other cage (see figure 7).

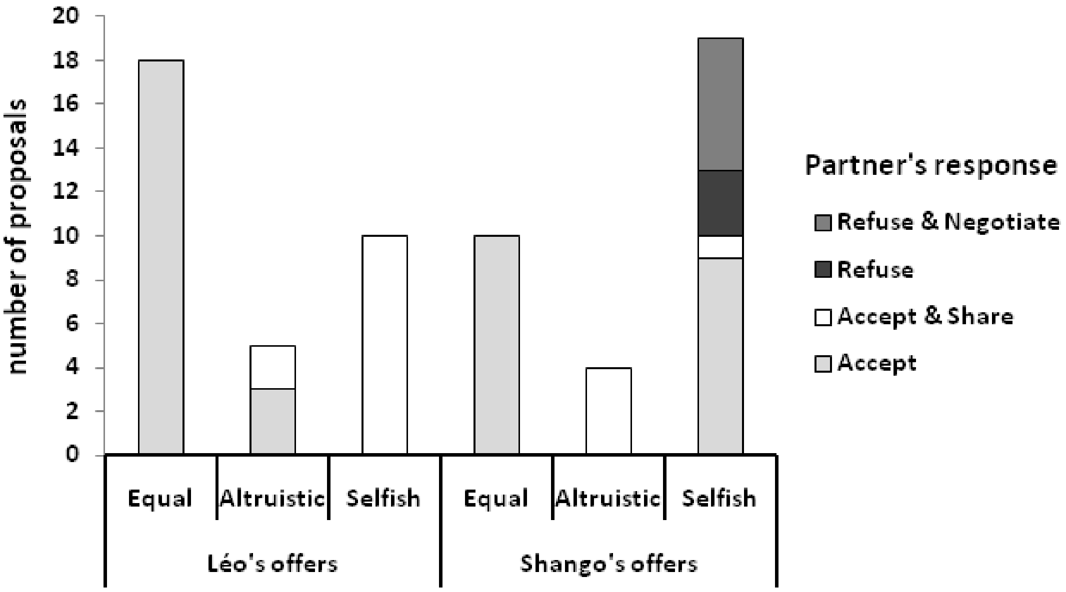

Figure 7: Partner's response according to the proposal during the negotiation task

Accept: birds cooperate. **Accept & Share**: birds cooperate and share the reward. **Refuse**: cooperation breakdown. **Refuse & Negotiate**: the second bird makes another offer finally accepted by the first individual.

Discussion

Birds ended up cooperating, in one way or another, in 95% of the trials in which at least one of the birds made a proposal. We observed that Shango followed Léo in each situation because he always managed to access at least part of the reward threatening sometimes Léo. During one test, while Léo proposed an equal distribution, Shango refused and went for the selfish situation but as Léo did not move he gave up and came back to cooperate for the equal reward. During another trial where the situation was reversed (Léo doing selfish offer), Shango accepted and moved from the equal situation to the other cage. This flexibility could be explained by the fact that Shango always obtained food because Léo who was the subordinate let him do so. When wolves were tested in the same condition (tray only baited in one side) only the dominant accessed the food and in the study conducted in chimpanzees (Melis et al. 2009) individuals did not share either. Nevertheless in the case of the chimpanzees the absence of sharing could be explained by the fact that even the unequal tray was baited on both sides (with different quantities). We observed that Léo, the subordinate bird, did not always accept unequal situations. Like chimpanzees (Melis et al.

2009), our grey parrots (mainly Shango) may have attributed intentions to their partner unwilling to cooperate and understood that he would have preferred to use the other apparatus. In previous studies, our birds showed that they understood that they needed a partner to get the reward (Péron et al. submitted-b) and also behaved differently according to the intentional state of an experimenter, unable or unwilling to give them food (Péron et al. 2010). Therefore, it is possible that the parrots understood the conflicting interests between their partner and themselves, and in order to obtain any food at all they would change their offer. Nevertheless we can also consider a less cognitively demanding explanation such as going where the partner is because success is conditioned by the presence of two individuals. We observed that both birds had a left position bias (64 out of 66 cooperative actions occurred on the cage placed on the left side). Nevertheless due to the fact that cages' positions were counterbalanced and also because birds could switch their choices, we observed that in general birds succeeded. This left position bias could explain why Léo made no difference in his offers choosing at random between the two cages and also why birds made sometimes altruistic offers.

General discussion

We observed that among our three grey parrots, the cooperative dyads where not all equal and some performed better than others. The probability of cooperation to occur, the efficiency of the collaborators and outcome of the interaction was correlated with the tolerance index between the two participants. In rats (Schuster 2002; Rutte and Taborsky 2008), the studies revealed that the outcome of the cooperation itself influences the next successful cooperative attempt, here we observed that tolerance index increased across the testing period, probability because of the fact that proximity was rewarded (during successful cooperation actions). During the experiment in which the parrots had the choice between different partners we found that tolerance also played a role. The hierarchy and previous interactions (agonistic) influenced the probability for the cooperative action to occur. Bird personality may also influence the results as it has been observed in rooks (Scheid & Noë 2010) but our small number of subjects impeded all analysis. In this study, the three grey parrots were able to coordinate according to the spatial disposition of the experimental setup and also to adapt to the social situation. During the experiment we also observed unexpected behaviours suggesting that birds understood the role of the partner. Indeed, each individual had the opportunity to see their nearest neighbour refusing to cooperate or going for the other apparatus. Then during different sessions, each bird jumped once from a table to another in order to go to the right place to solve the task and reach the food (see supplementary data). In this study we bring evidence that psittacids display flexible behaviours according to the physical and social environment. Consistently with previous experiments conducted on cooperation tasks, we did not observe any overt communicative gestures or soliciting behaviours that could have helped to coordinate or solve the negotiation. Chimpanzees also did not communicate in the study in which they had to coordinate their conflicting preferences (Melis et al. 2009). Our two males were able to solve peacefully unfair situations; nevertheless they continued to make selfish offers. Far from being altruistic in these artificial tasks, they managed to maximize the payoff while cooperating and sharing the reward. We observed that our grey parrots were able to adapt to the situation so that finally cooperation did not break down. Thus, studying the abilities of these three birds to solve artificial cooperative tasks bring some answers about the way grey parrots manage their social interactions. Nevertheless it would be necessary to conduct experiments with more individuals and groups in order to explore the wide range of their skills. Indeed, in chimpanzees for instance the number of cooperators acting together vary according to the social group (Boesch 2007). Other studies conducted in different species (keas, macaws, budgerigars) with more individuals suggested also that the quality of the relationship influenced underlying cooperation mechanisms (Tebbich et al. 1996; Huber et al. 2008;

Spitzhorn 2009). Several hypotheses could explain this: because of their life history (reared as siblings, living together) maybe birds tried to avoid conflicts. The valuable relationship hypothesis (Emery et al. 2007) and the tolerated theft hypothesis (Blurton Jones 1984) propose that the cost to defend the resource is bigger than the cost to lose part of it. Furthermore, here we are studying long living animals that would have many opportunities to reciprocate (even not voluntarily), explaining maybe why cooperative actions exist in psittacids. Nevertheless, it could be also possible to explain the behaviours observed in our experiments as mutualism. Indeed, individuals could have acted for their own interest and because of our experimental design this could have led to cooperation. In the same way, mobbing events could be explained by similar individual motivations leading to group actions but without any reciprocal involvement.

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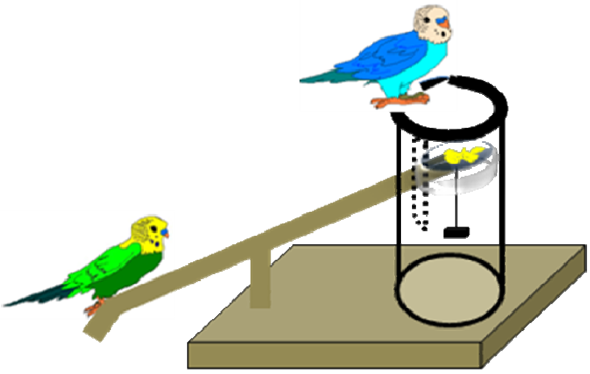
Article 3

Cooperative problem solving in budgerigars (*Melopsittacus undulatus*)

Péron F., Liévin A., Colléony A., Nagle L. & Bovet D.

Soumis *Behavioural Processes*



Article 3: Cooperative problem solving in budgerigars (*Melopsittacus undulatus*)

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Soumis à *Behavioural Processes*

Problème biologique

Dans le cadre d'une vie en société, les animaux sont amenés à interagir fréquemment avec de multiples partenaires, surtout si leur durée de vie est longue. Les individus peuvent être amenés à coopérer afin de pouvoir accéder à une ressource que seuls ils ne pourraient obtenir. Nous nous sommes donc intéressés à leur capacité à résoudre une tâche artificielle et à la manière dont ils y parvenaient.

Hypothèse

Les oiseaux vont réussir à se coordonner pour pouvoir accéder à la nourriture. Les relations entre les individus (partenaire sexuel, relation de dominance) vont conditionner les tentatives d'action conjointes.

Méthodes

Deux catégories de dispositifs ont été employées. Le premier nécessitant l'action d'un individu sur un levier pour qu'un autre puisse accéder à la récompense (dispositif à bascule). Le deuxième dispositif où une ficelle coulisse et pour lequel seules les interventions simultanées permettent de déplacer et d'atteindre la récompense.

Résultats

En majorité les oiseaux ont interagi seuls avec les dispositifs, les actions de coopérations réussies étant peu nombreuses. Avec le dispositif à bascule nous observons que les individus qui se placent au niveau du levier sont en général les subordonnés. Les juvéniles utilisent plus le dispositif que les adultes. Les dyades formées sont multiples et nous n'observons pas de préférence sociale chez les individus prenant part à des actions conjointes. Les oiseaux ne parviennent pas à attendre le partenaire.

Conclusion

Les perruches parviennent à résoudre les tâches cependant nous n'avons pas observé d'éléments permettant de conclure à une réelle compréhension de la tâche ni à une prise en compte du rôle voire de la présence d'un partenaire.

Cooperative problem solving in budgerigars (*Melopsittacus undulatus*)

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Abstract

Cooperation is one of the key elements defining human societies; nevertheless other animals are able to display this complex behaviour. According to some authors, hypothesises considered to have favoured the emergence of social intelligence in primates can be extended to some bird species such as corvids and psittacids. Previous studies conducted in psittacids show that these birds display complex cognitive abilities. Indeed, they are able to act complementarily but also to use social manipulation to achieve their goal. In this study, thirteen budgerigars (*Melopsittacus undulatus*) were involved in two different artificial tasks in order to explore their ability to cooperate and synchronize. In the first experimental setup (seesaw apparatus) one bird has to perch at one extremity so that a partner could reach the food at the other and in the second setup (cooperative string-pulling task) two budgerigars had to pull a string simultaneously in order to reach a baited tray. Budgerigars were able to display flexible cooperative actions but the birds tried to solve the task on their own as much as possible and mostly failed to synchronize. Thus no clear evidence was found of intentional reciprocity or even partner' role understanding.

Keywords: Psittacids, budgerigars, coordination, cooperation, social cognition

Introduction

Cooperation is one of the key elements defining human societies; nevertheless other animals are able to display this complex behaviour. Studying proximal mechanisms that can be shared by species independently to the phylogeny could lead to discover convergent evolution processes. The primary cognitive aspect involved in a cooperative action is the comprehension of the partner' role (Noë, 2006). Other factors such as hierarchy, tolerance and affinities between individuals influence the probability of cooperation to occur and also the performance of the dyad. The Social Brain Hypothesis suggests that individuals living in social groups have to manage complex social interactions (Joly, 1966; Humphrey, 1976; Byrne and Whiten, 1988; Dunbar, 1998). The Relationship Intelligence Hypothesis (Emery et al., 2007) predicts that complex social life and long term monogamous partnership lead to elaborated socio-cognitive abilities. Thus, corvids and psittacids would represent a good model for social cognition studies. Indeed, recent studies highlighted in these birds cognitive abilities as complex as those observed in primates (Emery and Clayton, 2004; Pepperberg, 2006) and also similarities in their neurobiology (e.g. ratio brain/body size; Iwaniuk et al., 2005) and socio-ecology (e.g. fission-fusion dynamics, long lifetime, long juvenile period, etc). Budgerigars (*Melopsittacus undulatus*) form stable monogamous couples over the breeding seasons and both parents take care of the chicks even if the female invests more (Cockburn, 2006). Male regurgitate during the breeding season and mated birds display allopreening. Budgerigars join in groups of more than 1.000 individuals (Juniper, 1998; Luescher, 2006). In budgerigars extra-pair copulations are not rare and one study revealed the fact that birds understand pair-bond relationship and are able to deceive a conspecific, doing more extra pair copulations when the mate is absent (Baltz & Clark, 1997). All these elements taken together raise the hypothesis that budgerigars would have the cognitive abilities necessary to manage complex social relations and to cooperate together.

Experiments conducted in psittacids already revealed that these birds are able to solve artificial cooperative tasks, adapting their behaviour to the social environment: keas use their partners as tools and display social harassment toward subordinate individuals in order to maintain cooperation: dominant birds forced their conspecific to perch so that the reward was accessible (Tebbich et al., 1996). Another study conducted recently in Green-winged macaws, using a seesaw apparatus (one bird perching at an extremity, the producer, so that a partner can reach the reward, the scrounger), revealed that they were flexible in their behaviour and that the quality of the relationship was likely to be responsible for the underlying mechanisms of cooperation (Spitzhorn, 2009). In grey parrots, two individuals faced a tray with food rewards placed out of reach and both have to pull simultaneously the string in order to get access to the reward. Birds were able to coordinate their actions and behaved differently according to their relationships (Péron et al., submitted-a; submitted-b). Several studies revealed that tolerance impact directly on the outcome as more tolerant dyads obtain better performances (Capuchins: Mendres and de Waal, 2000; chimpanzees: Melis et al., 2006b; bonobos: Hare et al., 2007; rooks: Seed et al., 2008; grey parrots: Péron et al., submitted-b). A recent study also highlights that rooks' temperament influences the success of the dyad: bolder individuals appear more willing to solve the task whereas shyer individuals are more influenced by their partner's behaviour (Scheid and Noë, 2010). The outcomes of the cooperation itself influence the next successful cooperative attempts as described in rats (Schuster, 2002; Rutte and Taborsky, 2008). Collaborative solutions of instrumental tasks depend on the cognitive competences and the social conditions (Huber et al., 2008). Nevertheless, in order to maintain this behaviour across the evolution process, joints benefits coming from joint actions are necessary. Recent studies revealed that wolves (Möslinger et al., 2009), hyenas (Drea and Carter, 2009), rooks (Seed et al., 2008), grey parrots (Péron et al., submitted-a) and macaws (Spitzhorn, 2009) were able to relate their action in time. However, studies on capuchin monkeys revealed that they were able to solve the task without any understanding of the partner's role (Chalmeau et al., 1997; Visalberghi et al., 2000). This behavioural response could be defined as similarity (Boesch and Boesch, 1989) or co-production (Petit et al., 1992) when individuals share the same goal but act simultaneously only by chance. In a study conducted with brown capuchins, the increase in gazing at the partner was taken as a criterion for highlighting the comprehension of cooperation necessity (Mendres and de Waal, 2000). However, due to the anatomy of psittacids, gaze direction is difficult to evaluate. Delay tests have been undertaken in chimpanzees: in the study conducted by Melis et al. (2006b), individuals were able to wait for the partner's arrival before starting to pull. Seed et al. (2008) realized the same experiment on rooks but, contrary to chimpanzees, corvids were not able to wait for a partner and in the study with three grey parrots, although all birds pulled more often in the presence than in the absence of a partner, only one bird learned to wait for the partner (Péron et al., submitted-a). In the present study, budgerigars were tested first on cooperative string-pulling task. Thus budgerigars were tested on their ability to synchronize which meant to understand the necessity of a partner and to wait for him in order to succeed in the cooperative task. Secondly we conducted an experiment with a seesaw apparatus similar to the one used by Tebbich et al. (1996) with keas or Spitzhorn (2009) with macaws.

The aim of the study was to assess if these species were able to solve artificial cooperative tasks and if so, how they would maintain cooperation when each action provided asymmetrical outcomes (for the seesaw apparatus). With the seesaw apparatus two birds were expected to coordinate in order to reach the reward, one acting on the device and the other collecting the food. We expected that they would display reciprocal altruism, operating alternatively the device, so that each bird could receive some reward. In the cooperative string pulling, birds were expected to understand the role of their partner and thus to wait for him and then to pull the string together.

Material & methods

Subjects

Thirteen budgerigars, seven adults (two-years-old, three males and four females) and their six juveniles (six-months-old, four males and two females) were tested. They were housed together in a cage (118 x 50 x 300 cm) provided with several perches and toys at a constant temperature (about 22°C) and at a 10h/14 h light-dark cycle. They were fed with seeds (Beyers Deli Nature Budgie), parrot pellets (Harrison, high potency fine) and received every day fresh fruits & vegetables. They were food deprived for two hours before each test. Water was available *ad libitum* and vitamins (Muta-Vit Versele-Laga) were given twice a week. The birds were completely naïve to any kind of problem solving tasks as they had never been tested before. We determined the dominance rank using the CBI (Clutton-Brock Index) as described in Clutton-Brock et al. (1979).

Experimental setups

Loose string paradigm

A flat rectangular cardboard tray (8 ×10 × 2 cm) baited with food (millet) was enclosed in an adjacent part of the cage impeding direct food access. A piece of string was threaded through metal loops placed on the tray so that both ends of the string extended out of the cage for 6 cm through a hole. A transparent plastic sheet was placed in the upper part of the hole allowing birds to see the baited tray. Pulling only one end of the string was ineffectual because the string would become unthreaded without moving the tray. Birds could move the tray only by pulling simultaneously both ends of the string (see figure 1).

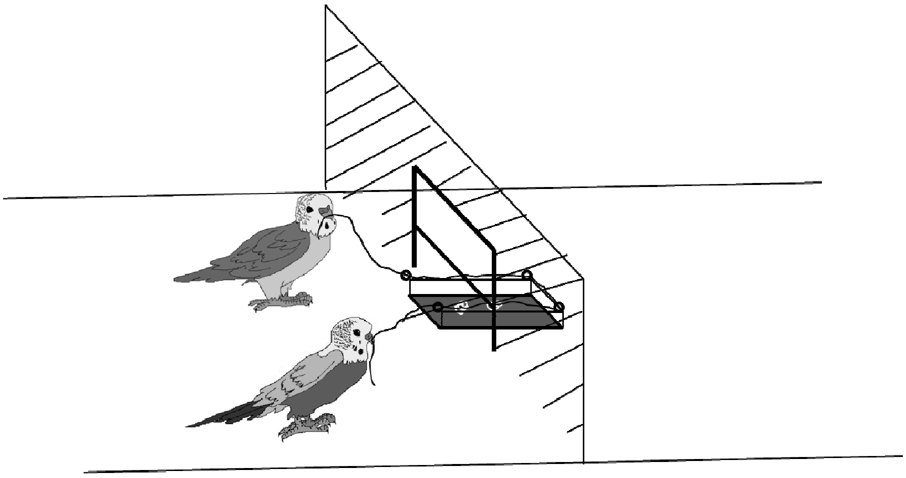


Figure 1

Seesaw apparatus

A transparent plastic tube (diameter: 5 cm, height: 10 cm) was fixed on a wooden platform (15 x 10 cm) and the reward (millet) placed inside could move thanks to a lever (15 cm). Thus a bird (producer) had to perch in order to move up the reward, then a second individual (scrounger) perched on the edge of the transparent tube could easily reach the food (see figure 2).

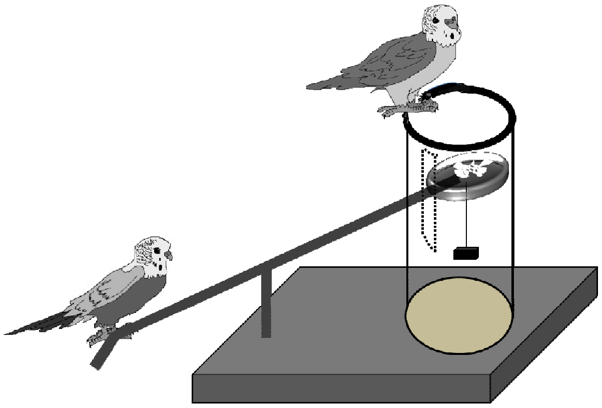


Figure 2

Statistical analysis

We ran Spearman rank order correlation to assess any interaction between the rank and the cooperative actions, Pearson correlation to assess any interaction between the participation in both tasks and Chi Square analysis to evaluate the influence of the sex and the age of the individuals on the formation of the dyads and also the distribution of the roles among the reciprocal dyads.

Procedure

All the individuals were able to access the different apparatus at any time during the testing period. We made 24 training sessions at the beginning and then five training sessions every month in which both ends of the string were attached so that one individual could succeed alone. After the first 24 training sessions, we conducted 60 trial sessions for each device in three months, with sessions of 30 minutes per day. The cooperative string pulling sessions and the seesaw sessions overlapped during two months and during the overlapping period we made one session in the morning and one in the afternoon alternating the devices. For each session all the birds were free to come and interact with the devices. For the cooperative string pulling task we recorded which birds dealt with the device, if their behaviour where simultaneous, if they were able to wait for a partner and finally the result of the action. For the seesaw apparatus we recorded which bird dealt with the devices, which one obtained the food (recipient), which one operated the lever (producer).

Results

The cooperative string-pulling task

Training sessions made with both ends of the string attached revealed that birds were able to pull the string in order to access the baited tray. Nevertheless we observed that not all the individuals tried. Indeed, one bird never pulled the string during training or trial sessions (Deadline) and only eight budgerigars succeeded in the task. During the test sessions we observed in total 250 individual attempts and only 44 cooperative actions made by ten different pairs of birds (between one and fifteen per dyad). Three birds took part in only one dyad, but the five others participated with different partners (until six different for Eugénie). In general budgerigars did not wait for a partner and cooperative actions occurred by chance when at least two individuals were pulling at the same time. Mostly juveniles interacted with the device (61% of the cooperative actions) (see Table 1). We did not notice any effect of age, sex (Chi Square, ddf 4, χ^2=3.125, p=0.537) or status (Spearman, N=13, r_s=0.250, p=0.415) on the performances (see Figure 3 & Table 1).

The seesaw apparatus

We observed 541 solitary actions (415 on the cylinder and 126 on the perch), 344 cooperative actions made by 32 different pairs but only 288 successful cooperations. Indeed, some cooperative actions - meaning that one bird perched so a partner could reach the food- failed when the perching bird left his position too early. We observed that in eight of the dyads, individuals played both roles but not in equal proportion (Chi Square analysis, ddf 7; χ^2=26.15, p<0.001). Budgerigars associated in 42% of the total possible combinations. Three individuals never went on the cylinder (Déclic, Donald & Eliott) and one never perched (Deadline). Only one female never interacted with the apparatus (Dora). Each dyad made between 1 and 87 cooperative actions with an average of 11 actions. Mostly juveniles interacted with the seesaw (70% of the actions). We found a negative correlation between the rank and the frequency of presence on the cylinder: dominant birds occupied more often the cylinder place (Spearman rank order correlation: N=12; r_s= -0.589 p= 0.0416). Nevertheless we did not observe any social manipulation strategy such as harassment as it was the case with keas (Tebbich et al. 1996) (see Table 1). Age and sex did not influence the formation of the dyad (Chi Square, ddf 4, χ^2=3.710, p=0.447). We observed that birds who acted more often on the perch also participated more in cooperative string-pulling task (Pearson correlation: N=13; r_s=0.722, p=0.00536) (see Figure 3 & Table 1).

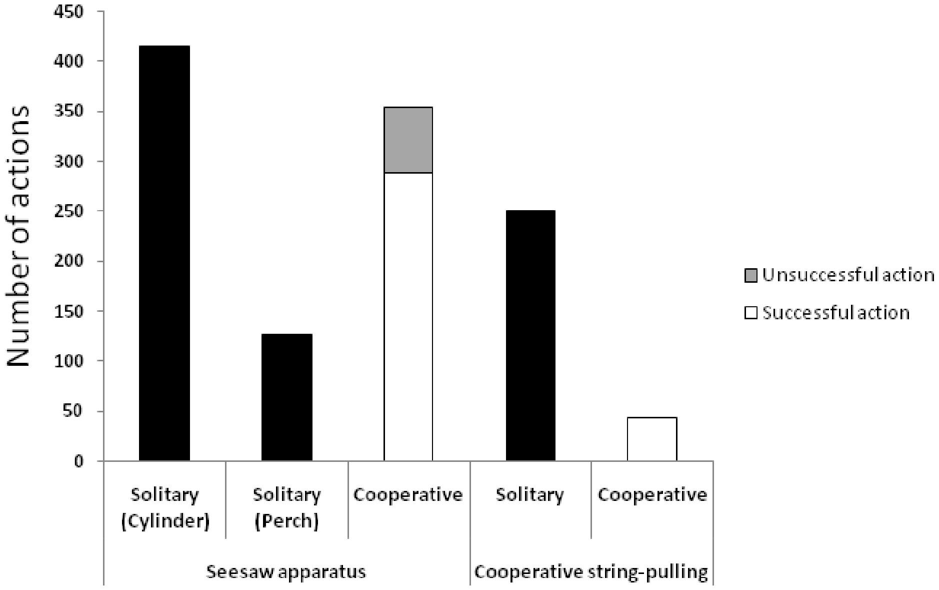
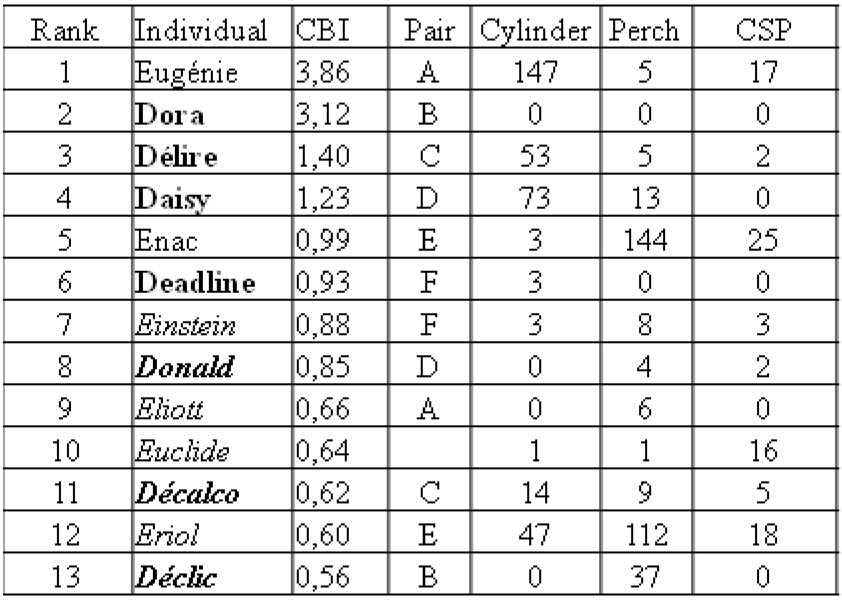


Figure 3: Number of actions on each device



Rank	Individual	CBI	Pair	Cylinder	Perch	CSP
1	Eugénie	3,86	A	147	5	17
2	**Dora**	3,12	B	0	0	0
3	**Délire**	1,40	C	53	5	2
4	**Daisy**	1,23	D	73	13	0
5	Enac	0,99	E	3	144	25
6	**Deadline**	0,93	F	3	0	0
7	*Einstein*	0,88	F	3	8	3
8	***Donald***	0,85	D	0	4	2
9	*Eliott*	0,66	A	0	6	0
10	*Euclide*	0,64		1	1	16
11	***Décalco***	0,62	C	14	9	5
12	*Eriol*	0,60	E	47	112	18
13	***Déclic***	0,56	B	0	37	0

Table 1

in roman: adult, *in italics*: *juvenile*, **in bold: female**

CBI: Clutton-Brock Index

Pair: couple (already bred together) or affiliative behaviours (sexual display, regurgitation)

Cylinder, perch & CSP (cooperative string-pulling): number of successful actions on each device.

Discussion

Budgerigars showed their ability to cooperate in order to obtain food but we obtained few evidence that individuals understood the role of their partner (Chalmeau et al., 1997; Visalberghi et al., 2000) and thus their actions could be considered as co-production (Petit et al., 1992) or similarity (Boesch and Boesch, 1989). These tasks (vertical tube and seesaw apparatus) seemed to be intuitive as individuals could see at any time the reward and the mechanism to reach it. Mendres and de Waal (2000) concluded that capuchins did not succeed in a prior cooperative study (Chalmeau et al., 1997) because the task was not intuitive. Contrary to capuchins (Brosnan et al., 2006) pairs who tended to alternate do not participate in more cooperative actions. This could be explained by the fact that birds did not take turn in a same proportion in each action. We observed that budgerigars were more flexible in the formation of the dyad than the macaws tested with the same paradigm (producer/scrounger) (Spitzhorn, 2009). They were also younger so maybe their activity was correlated with playing behaviour and environmental exploration. In macaws, the authors found that nearly exclusively pair mates acted cooperatively and mostly one pair reversed their roles. If birds reverse their role regularly, thus costs and benefits stay in balance (‘reciprocal altruism’, Trivers, 1971). Individual recognition, stable group and long lifespan are requirements for reciprocal acts. Boyd and Richerson (1988) added that group size has to be small. In our birds, all these requirements were fulfilled and we observed cooperative actions between related and not related individuals, nevertheless we did not observed any reciprocal altruism during our testing period. Reciprocal interactions have been observed in birds during mobbing events (Krams et al., 2008) and their frequency increased when the predation risk increased (Krams et al., 2010). Thus external factors could pressure on the probability of the cooperative actions to occur. Here our birds were food deprived for two hours maximum and this may not have motivated them enough to cooperate. At a simpler level of explanation, we could also propose that cooperation actions were randomly displayed. Budgerigars did not manage to synchronize. They cooperated but there was no evidence of intentional underlying mechanism. Apparent reciprocity could appear when the probability of co action increased. In general, budgerigars are very fast in their actions and their failure in this task could be explained by either difficulties regarding self-control (as found in grey parrots; Vick et al., 2009) or by an absence of comprehension of the partner role. As we found a correlation between the social status and some specifics tasks compared to others (dominant are more likely to monopolize the position where the food will be available), it seems that, like in rooks (Scheid and Noë, 2010) the personality of the individuals impact directly on their performances.

We observed some times that the actor stopped his action when some conspecifics approached the food locations (the same with kea (Huber et al., 2008) and the macaws (Spitzhorn, 2009)). Thus birds could have attributed intentions to their partner: they wanted to take the food. A recent study conducted in grey parrots revealed that they adapt their actions according to the behavioural cues of a human experimenter unable or unwilling to give them food (Péron et al., 2010). Blurton Jones (1984) proposed the tolerated theft hypothesis in which he suggested that sharing may occur when the costs of defending the food is higher than the benefit gained by the food. The sharer benefits by sharing but also he avoids conflicts (and potential injuries) or possible weakening of the partnership and a following loss of social status (Emery et al., 2007). Here, we did not observe voluntary sharing, nevertheless birds were able to receive indirect profit as the scrounger bird (perched at the edge of the seesaw) often dispersed part of the reward while collecting his part. In a study conducted with keas the authors observed that when the researchers switch the form of the reward (from buttered twigs to butter pellets), then birds stopped cooperating as no more indirect profit was possible (Federspiel, 2006). Like in grey parrots (Péron et al., submitted –a, submitted –b) or even chimpanzees (Melis et al., 2009) we did not notice any recruitment attempt (vocalization or gesture). During this short experiment (three months) we observed mainly involuntary cooperation actions as birds tried on their own most of the time. Even though parrots are known to cooperate during mobbing events for instance, there is no ecological relevancy to do so regarding foraging behaviour due to the environmental conditions, contrary to chimpanzees who display hunting behaviour (Boesch and Boesch, 1989). Maybe testing cooperative breeding parrot species could lead to different results as it was the case in callithricidae species (Snowdon and Cronin, 2007). It could be also possible that birds learn across longer period the potential advantage to cooperate. Here we observed that birds' behaviour could be considered as mutualism as they acted for their own interest and sometimes, according to the social situation (birds' motivation, partner proximity) cooperation appear as a by-product of their behavioural flexibility.

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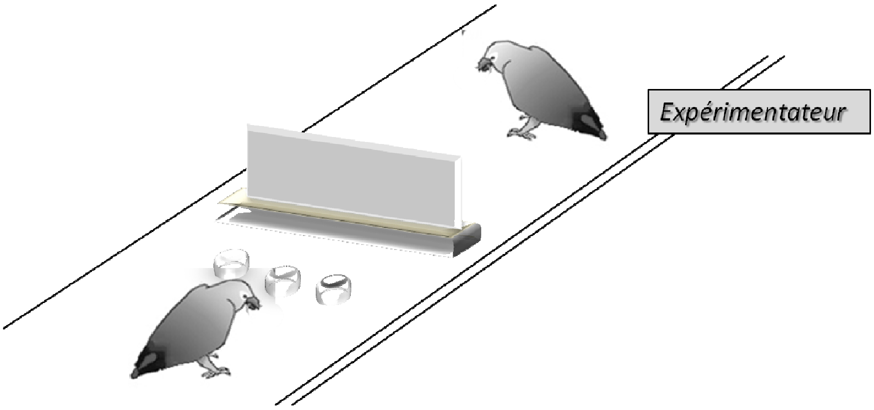
Article 4

Do psittacids take others' welfare into account?

Péron F., Colléony A., Liévin A., Nagle L. & Bovet D.

Soumis *Animal Cognition*



Article 4: Do psittacids take others’ welfare into account?

Péron F., Colléony A., Liévin A., Nagle L. & Bovet D.

Soumis à *Animal Cognition*

Problème biologique

Dans la nature, les perroquets se comportent parfois de manière altruiste ou prosociale. Ainsi les mâles régurgitent de la nourriture aux femelles durant la saison de reproduction. Les oiseaux au sein d’un couple se toilettent mutuellement. Les oiseaux semblent donc sensibles au sort de leurs congénères et plus précisément à celui de leur partenaire.

Hypothèse

Les oiseaux vont profiter de l’occasion pour apporter une récompense sans coût supplémentaire à leur partenaire. Des différences apparaîtront en fonction de la relation entre les participants : les oiseaux en couples étant supposés être plus attentifs au sort de leur partenaire.

Méthodes

En utilisant le principe de l’échange de bouchon, quatre espèces de psittacidés ont la possibilité de récompenser sans coût supplémentaire un partenaire (partenaire sexuel ou individu de la même couvée). Les oiseaux sont testés en dyade et ont le choix entre trois bouchons associé à des récompenses différentes : sans récompense, récompense uniquement pour l’individu testé (égoïste) ou récompense pour les deux oiseaux (prosocial). Dans une seconde expérience, le bouchon prosocial procure soit une récompense égale pour les participants soit une meilleure récompense pour le partenaire. Dans une dernière expérience, un des oiseaux doit transmettre le bouchon à son partenaire qui à son tour doit l’apporter à l’expérimentateur afin de recevoir la récompense.

Résultats

Les oiseaux apprennent rapidement à ne plus prendre le bouchon qui ne les récompense pas mais par contre ils ne semblent pas faire de différence entre celui qui les récompense eux seulement et celui qui permet de les récompenser en même temps que leur partenaire. Les individus testés ne tiennent pas compte du sort de leur partenaire y compris quand ce dernier reçoit une meilleure récompense qu’eux. Les perroquets ont coopéré pour transférer le bouchon mais le premier individu à choisir n’a pas tenu compte du sort du partenaire et par conséquent ce dernier s’est montré réticent à poursuivre la coopération.

Conclusion

Les oiseaux ne se comportent pas de manière prosociale dans une tâche artificielle contrairement à ce qui peut être observé à l’état naturel.

Do psittacids take others' welfare into account?

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Abstract

Prosociality- that is, behaving in a manner that provides benefits to another individual, either at some or no cost to oneself, have been studied in chimpanzees and callithricidae species but other species may also display prosocial behaviour toward their conspecifics. We evaluated the behaviour of three African grey parrots (*Psittacus erithacus*), two blue-throated macaws (*Ara glaucogularis*), two scarlet macaws (*Ara macao*) and two sun parakeets (*Aratinga solstitialis*), tested in dyad, in an experimental situation where they had the possibility to reward a partner at no supplementary cost. The tested bird could choose between 3 different tokens associated to different values: null (no reward), selfish (only the tested bird receives a reward) and prosocial (both the tested bird and his partner receive a reward) tokens. The birds stopped choosing the null token but did not take into consideration their partner welfare as in general they did not make any difference between the selfish and the prosocial tokens. In a second study we tested the three grey parrots by changing the value of the prosocial token in half of the trials, thus creating inequity: the partner received a better treat than the tested bird. We observed that our parrots did not change their preferences and did not react to the unequal situation. In a third study, two African grey parrots had to cooperate in order to receive a reward. One bird had to choose a token and give it to the partner who could decide to bring it back or not to the experimenter in order to receive the associated reward. As the first bird did not develop a preference for the prosocial token, the second bird stopped bringing back the selfish token to the experimenter and finally the frequency of cooperation events decreased.

Keywords: psittacids, value attribution, token exchange paradigm, cooperation, prosocial behaviour, parrots.

Introduction

Altruism is highly valorised in humans and is a key ingredient of human morality. However, it is also found in animals in many taxons, at least in its functional definition – that is, costly act that confers benefits to others regardless of reward prospects. However, as stated by de Waal (2008), discussions of altruistic behaviour tend to suffer from a lack of distinction between function and motivation : an action is called “altruistic” if it benefits a recipient at a cost to the actor regardless of whether or not the actor intended to benefit the other. Indeed, when animals are studied in natural conditions, it is often difficult to know what their intentions are. If a subject gives food to another, is it because it cares for the other’s welfare, or because ultimately it will enhance the subject’s fitness, and hence this behaviour was selected during evolution? Although these explanations are of course not exclusive, since other-regarding preferences can be selected because ultimately they will enhance individual fitness (as it may be the case in primates, including humans, according to de Waal), many animal species may behave altruistically because this behaviour is genetically predetermined and not because they really want to help their conspecifics. When subjects are tested in artificial settings, it is possible to study individual motivation to give food to a conspecific. As real altruism (giving something at a cost) is not frequently found, most experiments study pro-social behaviour, that is, behaving in a manner that provides benefits to another individual, with little or no cost for the subject. Such pro-social preferences are found in humans but also in cooperative breeding species (ouistitis: Burkart et al. 2007, cottontop tamarins: Cronin et al. 2010). Thus researchers thought about a convergent evolution process until recent studies which revealed that non-cooperative breeders such a capuchins (de Waal et al. 2008; Lakshminarayanan et al. 2009), bonobos (Wobber et al. 2010), chimpanzees (Warneken 2007) or even despotic species such as macaques (Massen et al. 2010) display food provisionning. This led to the suggestion that prosociality is an ancestral trait among primates (Lakshminarayanan et al. 2009). Nevertheless other species display prosocial behaviours so that maybe we have to consider an alternative hypothesis that prosociality evolved in several different taxons according to their social and environmental conditions.

Token exchange paradigm has been tested mainly on non-human primates (capuchins and great apes) to test value attribution (Westergaard et al. 1998; Sousa & Matsuzawa 2001; Brosnan & de Waal 2004a), quantity discrimination (Addessi et al. 2008), foraging strategies (Addessi et al. 2010), other regarding preferences (de Waal et al. 2008), inequity aversion (Brosnan & de Waal 2003; Fontenot et al. 2007), social learning (Brosnan & de Waal 2004b), barter (Westergaard et al. 2007) and cooperation (Dufour et al. 2009; Pelé et al. 2009; Pelé et al. 2010). Most of the experiments consisted in exchanges between individuals and human experimenters and only few were conducted studying exchange between conspecifics (Westergaard et al. 2007; Dufour et al. 2009, Pelé et al. 2009; Pelé et al. 2010). Other regarding preferences were also tested using cooperative task (two individuals working) or pull bar task (only one animal working) and prosocial tendencies were found in common ouistitis (Burkart et al. 2007) and capuchins monkeys (Lakshminarayanan & Santos 2008). Contrasted results have been found in cottontop tamarins: according to the experimental setup the individuals displayed or not prosocial behaviour (Cronin et al. 2009; Cronin et al. 2010). Only one recent experiment on chimpanzees showed that they displayed prosocial preferences (Brosnan et al. 2010) while previous studies did not bring evidence of such preferences in chimpanzees (Silk et al. 2005; Vonk et al. 2008). Looking at their ability to maximize the payoff – that is to adapt their behaviours to the partner and to the most profitable situation, researchers found that chimpanzees did not exchange their tokens as efficiently as possible (Brosnan & de Waal 2005) and did not develop contingent reciprocity (Brosnan et al. 2009). They did not spontaneously take turns in a reciprocal cooperation task (Yamamoto & Tanaka 2009) and only the study of Melis et al (2008) found a weak effect of the partner previous behaviour. They have some difficulties to trade with a partner (Brosnan & Beran 2009) and when exchanges were successful it was only indirectly (Pelé et al. 2009). Pelé et al. (2010)

also found that interactions were not reciprocal in Tonkean macaques. Regarding capuchins, controversial findings were made: Brosnan & de Waal (2004a) and Pelé et al. (2010) found that they were not able to display reciprocal interactions, contrary to the results of other studies (Hattori et al. 2005; Brosnan et al. 2006). One experiment conducted on cottontop tamarins revealed that they were able to reciprocate a favour (Cronin & Snowdon 2008).

Non-human primates have been tested due to their proximity with humans in the evolution process. Nevertheless, others species show complex social life, developed cognitive abilities and elaborated behaviour like corvids or psittacids. The 'Relationship Intelligence Hypothesis' (Emery et al. 2007) predicts that complex social life and long term monogamous partnership lead to great socio-cognitive abilities, similar to those encountered in primates. Indeed, recent studies highlighted that cognitive abilities of these bird species were complex and similar to the abilities observed in primates (Pepperberg 1999; Emery & Clayton 2004). In parrots, males regurgitate food to females during the breeding season. This food provisioning during a long period and the long-term and exclusive bond between sexual partners are not found in primates even though these species are able to share food (capuchin: de Waal 2000 attudinal reciprocity in food sharing; common ouistitis: Kasper et al. 2008; cotton-top tamarins: Hauser et al. 2003). Regarding chimpanzees the exchange of meat for sex (Gomes and Boesch 2009) is controversial (Gilby et al. 2010) nevertheless they are able to reciprocate food sharing (Jaeggi et al. 2010) and allogrooming (Schino & Aureli, 2009). Birds display also mutual interactions such as allopreening. African grey parrots are social birds living in large flocks. They join during mobbing events (Jones & Tye 2006). They possess developed cognitive abilities (Pepperberg 1999) and are able to cooperate in artificial tasks (Péron et al. submitted-a; submitted-b) and to adapt their response according to the experimenter' intentions (Péron et al. 2010). In order to increase the probability to find a psittacid species displaying prosocial behaviour, we conducted the experiment on several different species. We also wanted to compare possible influence of the relationship quality on the behaviours studied. Indeed, birds maybe have more consideration for the conspecific they grow with (siblings) or mate with (sexual partner). In capuchins for example, prosocial tendencies increased with social closeness (de Waal et al. 2008).

In the first experiment, four different parrot species were tested on their propensity to reward at no supplementary cost a partner by choosing one token among the three available: a null, a selfish and a prosocial token. Tokens are inherently non-valuable objects that acquire an associative value upon exchange with the experimenter (Addessi et al. 2008). So the question was: do parrots prefer outcomes that benefit a partner over outcomes that do not, everything else being equal? Do they take others' welfare into account?

We expected that the relationship between the birds would influence their behaviour. According to their tolerance and also previous interactions they could be more or less willing to reward their partner. Macaws and parakeets were tested with their mate or their sibling thus we hypothesized that they would show other regarding preferences. Our grey parrots had different relationships within the group. Two individuals (a male and a female) were very tolerant to each other as they were hand-reared together whereas the third one (a male) displayed sometimes aggressive behaviour toward the female. Thus, we thought that the quality of the relationship could impact on other regarding preferences. In the second experiment conducted with African grey parrots only, we evaluated the behaviour of the tested bird in unfair conditions in which the partner received a better treat when the tested bird picked up the prosocial token. Thus, birds were expected to develop a preference for the selfish token or to stop participating. Indeed, in a previous experiment two of them showed that they tended to be selfish when the reward was asymmetrically distributed (Péron et al. submitted-b). Two grey parrots participated in the third experiment in which they had to cooperate. A bird had to pick up one token and give it to the partner who could decide to bring back or not the token to the experimenter in order to receive the associate reward. The grey parrot who had the possibility to choose between the three tokens was expected to adapt his choice to the behaviour of the partner which meant picking the prosocial token so that both animals would be rewarded and the second parrot would continue to cooperate.

Study 1: Other regarding preferences in psittacids

Material & method

Subjects

We tested three hand-reared African grey parrots: two males (Shango and Léo, four and six years old respectively) and one female (Zoé, six years old). They hatched in captivity and arrived at the laboratory (LECC) at three months old. They were housed together in an aviary (340 cm × 330 cm × 300 cm) with three tables (120 × 60 × 75 cm), two large perch structures and many toys, at a constant temperature of 25°C and a 12/12 h light-dark cycle. The parrots were tested in their aviary by pairs and during a test session, the subject that was not tested was placed in a cage in the corridor with food and toys available. Parrots were fed everyday with fresh fruits and vegetables in the morning and parrot formula (Nutribird A21) in the evening. Water and parrot pellets (Harrison, high potency coarse) were available *ad libitum* and vitamins (Muta-Vit Versele-Laga) were given twice a week. We tested other species in the ‘Ferme de Conservation Zoologique’: a two-year-old couple of blue-throated macaws (*Ara glaucogularis*), a ten-year-old couple of scarlet macaws (*Ara macao*) and two one-year-old male siblings sun parakeets (*Aratinga solstitialis*). The sun parakeets were hand-reared together and then shared a cage with six others family members. The *Ara macao* already reproduced together but the *Ara glaucogularis* never bred together before and were in couple just for one year. We observed regurgitation between both couples members and Shango also regurgitated to Léo several time during the testing period. Birds were living in aviaries (indoor: 2 x 2 x 2m & outdoor: 5 x 2 x 2m) and fed with seeds (Verse Laga Premium) and parrot pellets (Verse Laga P15) *ad libitum* and fresh water, fruits and vegetables distributed every day. All birds have been tested in their aviary, outside the breeding season.

As the subjects were free flying parrots, all the test sessions were based on their motivation. Indeed, they could leave at any time and perch elsewhere in the aviary.

Experimental setup

We used the token exchange paradigm in which birds had to choose an object (by touching it or bringing it back to the experimenter) in order to receive the associate reward (see Table 1). Parrots were not food deprived and we used peanuts as reward for the macaws and the parakeets and sunflower seeds for the grey parrots. Birds were tested in dyads and in a session we made ten trials with one bird before switching to the other bird. We made twenty sessions with each dyad and we conducted two repetitions of the experiment using different sets of objects for each individual tested. We controlled for any bias linked to colour or shape (when this latter was also differing): token preferences were tested before training to make sure that certain colors/patterns were not preferred over others. All tokens were presented side by side on a tray, and birds could interact freely with them. Each subject was offered 10 choices, and if any token was chosen eight times or more the token would be replaced. Birds were familiarized with new objects and learned to touch (for the macaws and parakeets) or to bring back the object (grey parrots). We recorded the choice of the tested bird and the behavior of the partner (vocalization and movement). When the tested bird chose the null token the experimenter removed the tokens and stopped interacting during six seconds and when the bird chose one of the two others the experimenter removed the tokens at the same time he gave the reward. The next trial started after the time out or when the parrots stopped eating.

	Reward distribution	
Value attribution	Tested bird	Partner
Null	0	0
Selfish	1	0
Prosocial	1	1

Table 1: Reward distribution according to the value of the token

Statistical analysis

According to the result of the normality test, we ran one way RM ANOVA or Kruskal Wallis analysis with all pairwise multiple comparison procedures (Holm-Sidak method or Tukey Test) in order to compare bird's choices during the last 10 sessions.

Results

The female Macao refused to interact with the objects thus only the male has been tested as his female accepted to come and take the reward. Nevertheless, for this male we obtained some results only during the first experiment as in the two repetitions he kept choosing at random between the tokens, thus it was not possible to conclude if he really understood the task. For the other birds, they rapidly stopped to choose the null and sometimes developed a preference for one of the other tokens (selfish or prosocial, but their choice were not coherent across the repetitions) and sometimes not, choosing at random between both (see Figure 1, 2; see Table 2). Thus as the results vary across the replication for all the birds we can conclude that they did not show other regarding preferences. The grey parrots were tested with two different partners and we found no difference in the behaviour of the tested bird according to the partner (Friedman repeated measures analysis of variance on ranks; $P>0.05$). We observed that some individuals anticipated the outcome as they came closer to the experimenter when the tested bird chose the prosocial token (Comparing the mean number of anticipation of all the individuals according to the token selected; Null: m=0 SE+/- 0; Selfish: m=1.38 SE+/- 0.6; Prosocial: m=45.8 SE+/- 7.1).

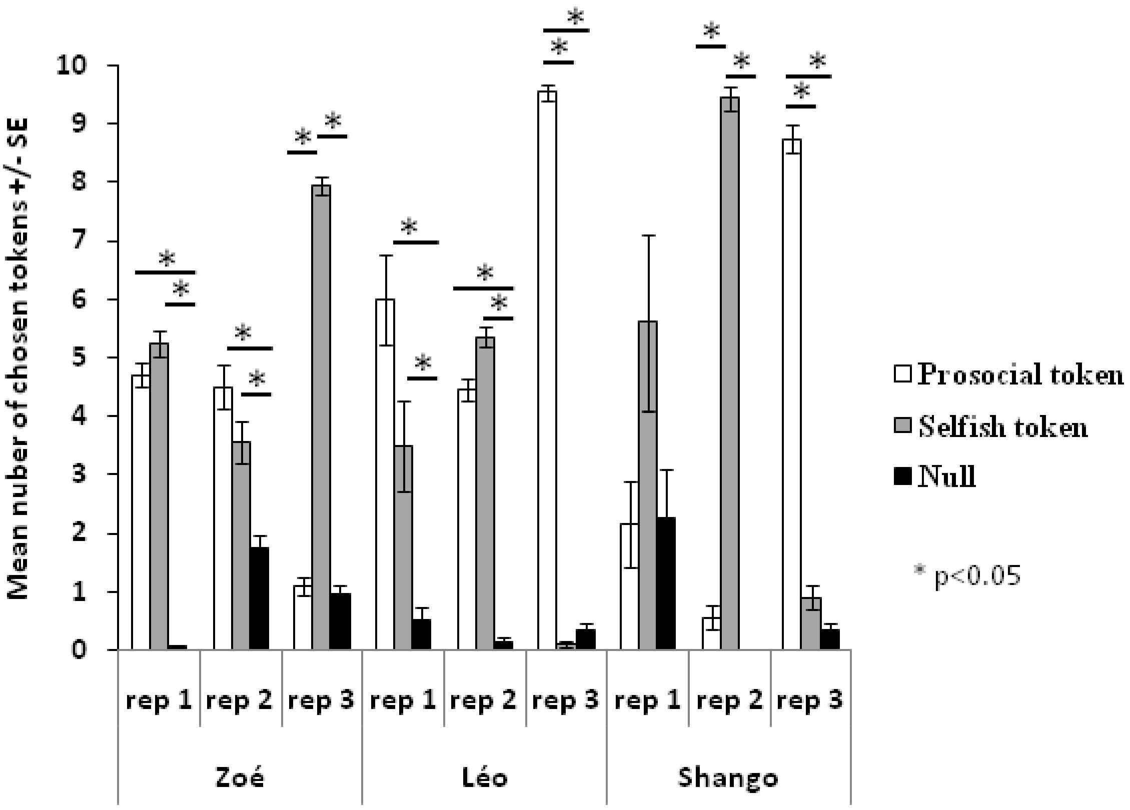


Figure 1: Grey parrots' choices across the three repetitions

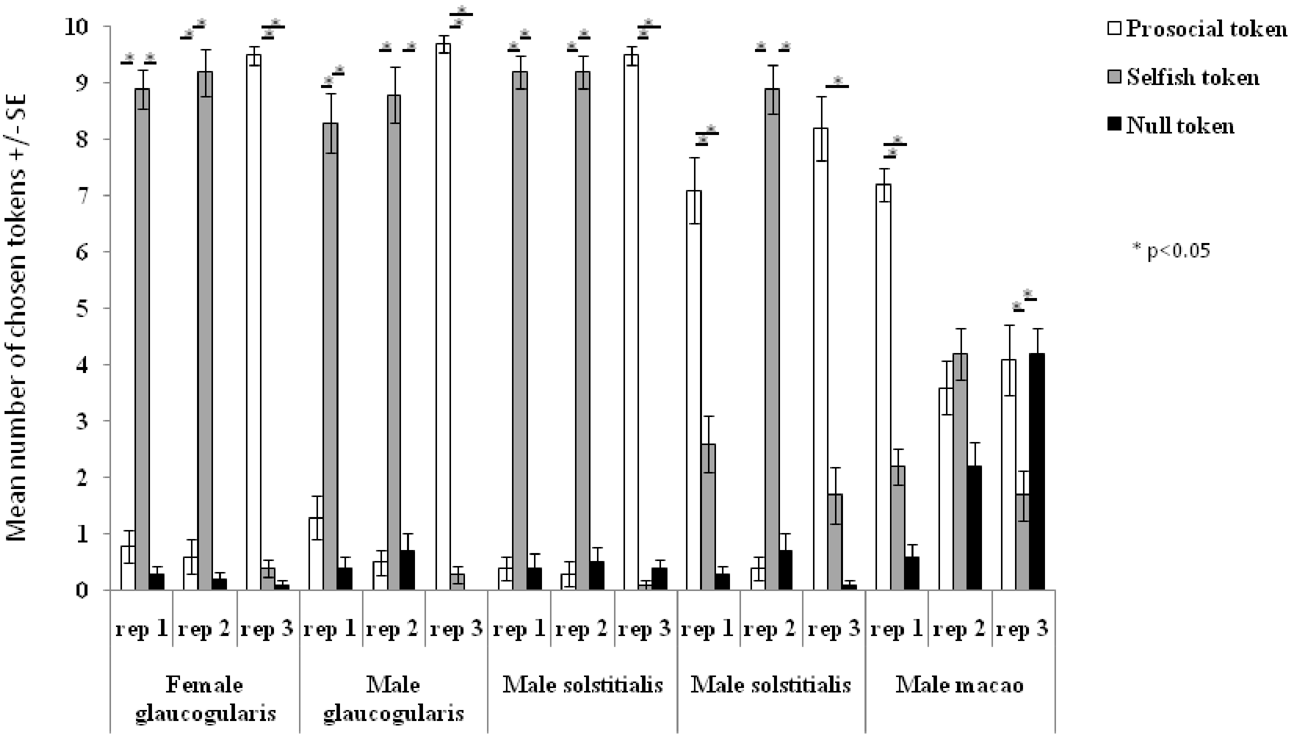
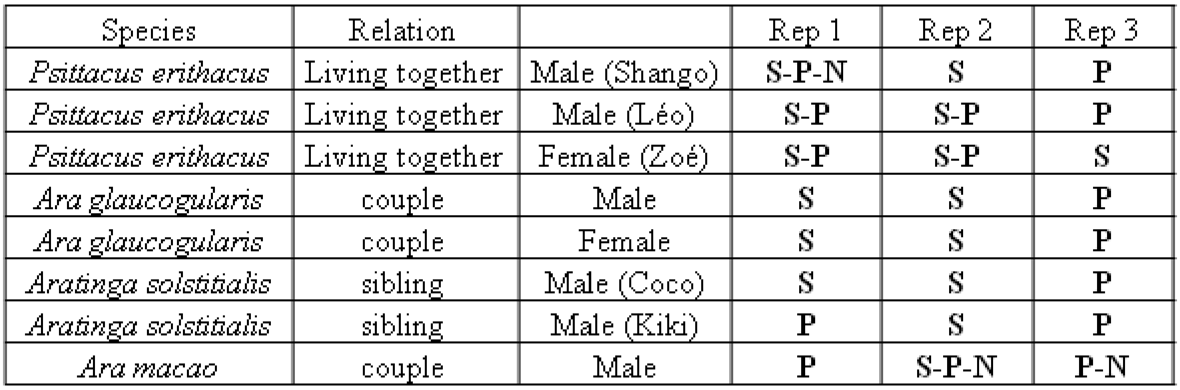


Figure 2: Macaws and parakeets' choices across the three repetitions



Species	Relation		Rep 1	Rep 2	Rep 3
Psittacus erithacus	Living together	Male (Shango)	**S-P-N**	**S**	**P**
Psittacus erithacus	Living together	Male (Léo)	**S-P**	**S-P**	**P**
Psittacus erithacus	Living together	Female (Zoé)	**S-P**	**S-P**	**S**
Ara glaucogularis	couple	Male	**S**	**S**	**P**
Ara glaucogularis	couple	Female	**S**	**S**	**P**
Aratinga solstitialis	sibling	Male (Coco)	**S**	**S**	**P**
Aratinga solstitialis	sibling	Male (Kiki)	**P**	**S**	**P**
Ara macao	couple	Male	**P**	**S-P-N**	**P-N**

Table 2: Results for the three repetitions of the experiment, for each bird.

S: Selfish; **P**: Prosocial; **N**: Null

Study 2: Influence of inequity on other regarding-preferences

Material & method

At the end of the last repetition of the experiment 1 we decided to change the value of the prosocial token. Indeed, at this time, birds had developed preferences for one of the three tokens (selfish for Zoé and prosocial for Léo and Shango). In this new situation the partner received better treats in half of the sessions. We did not test the dyad Shango-Zoé because of agonistic interactions. We conducted eight sessions of 10 trials with each dyad in the control condition (same reward for both individuals) and in the inequity condition (better reward for the partner). We alternated the condition across the sessions.

Statistical analysis

According to the result of the normality test, we ran one way RM ANOVA or Kruskal Wallis analysis with all pairwise multiple comparison procedures (Holm-Sidak method or Tukey Test) in order to compare birds' choices during the sessions.

Results

The parrots did not change their preferences across the sessions. Zoé kept choosing the selfish token whereas the males chose the prosocial token (See figure 3). Thus only the males could have experienced a frustration effect seeing the better treat going to the partner. Nevertheless they did not refuse to participate or change their preferences.

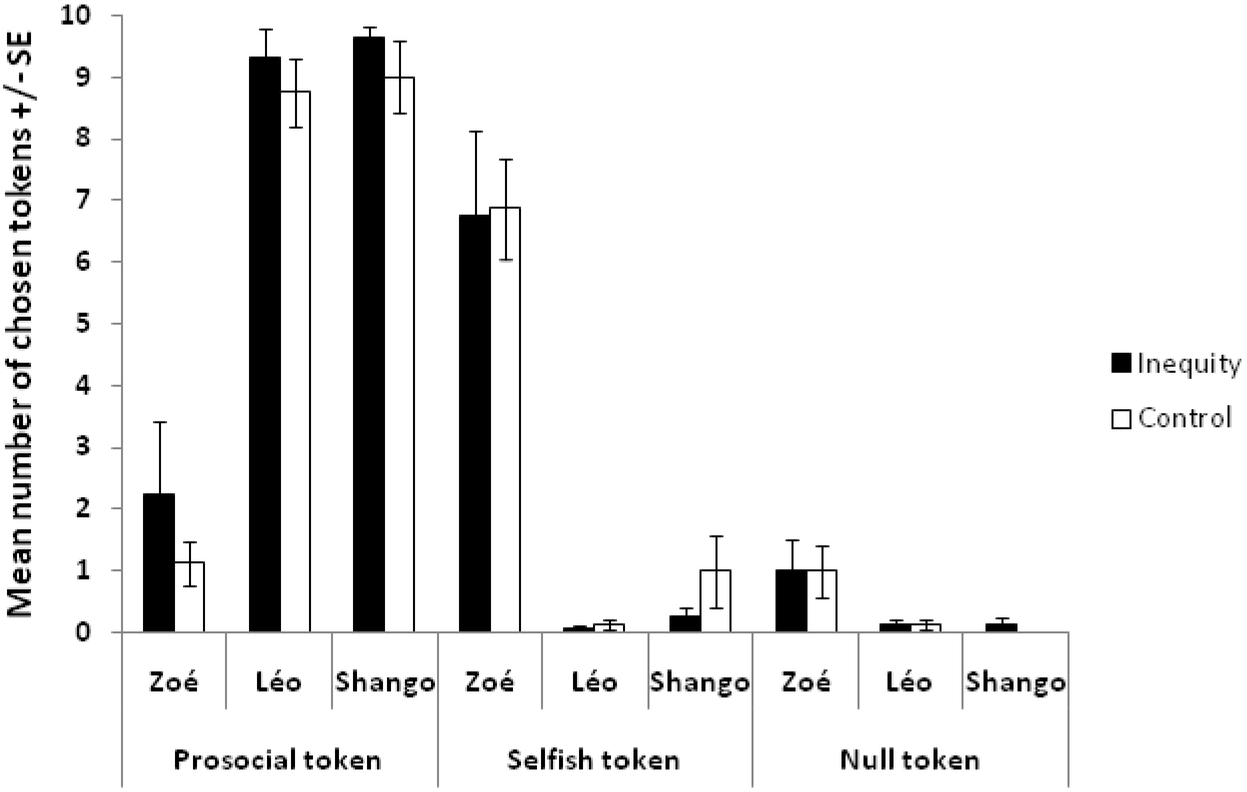


Figure 3: Grey parrots ‘choices in the unequal (prosocial token brings better food to the partner) and control condition (prosocial token brings the same food to both individuals)

Study 3: Influence of other regarding preferences on the maintenance of cooperative behaviour

Material & method

Subjects

One year after the first experiment we tested Shango and Léo. Zoé did not participate in this experiment because of health problems and was brought to another room where food and toys were provided during the sessions. Other species were not tested as it is not possible to interact with them in the same way we do with grey parrots.

Experimental setup

Birds were tested on a table (120 x 60 x 75cm) where two different areas were delimited using a cardboard (65 x 0.6 x 12.5 cm) fixed on a wooden base (55.5 x 6.5x 1.5 cm). Parrots could see each other and have physical contacts over the cardboard. Tokens were placed in the first area so that the bird present had to choose one token and to give it to the partner over the cardboard. Then the second parrot had to bring back the object to the experimenter so that birds could receive the associated reward (see figure 4). Léo was arbitrary placed on the token side because of the results from the first experiment where his preferences widely varied across the repetition. We recorded his choice, the behaviour of the partner and the final outcome. Birds were first familiarized to exchange a token (different from those used during the experiment) over the barrier. We made 22 sessions of 10 trials.

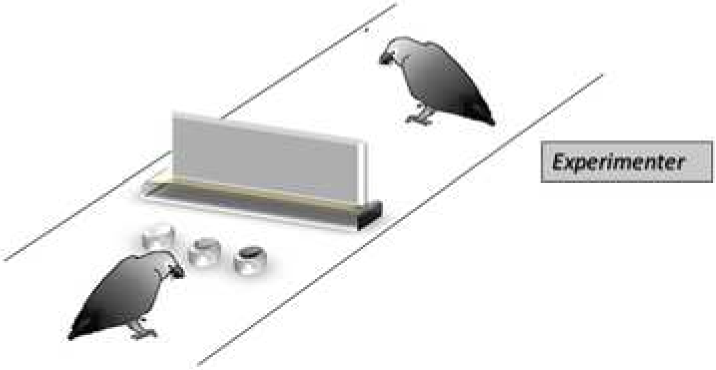


Figure 4: Experimental situation

Coding and statistical analysis

We recorded the choices of Léo (between the three tokens) and Shango (to give or not the token) and their behaviours such as vocalizations and movements. According to the result of the normality test, we ran one way RM ANOVA or Kruskal Wallis analysis with all pairwise multiple comparison procedures (Holm-Sidak method or Tukey Test). To assess the evolution of the choices across the study we ran Spearman rank order correlation.

Results

We observed that Léo chose less often the null token compared to the two others (Tukey test; compared to selfish; q=8.59, P<0.05; compared to prosocial; q=10.32, P<0.05) and did not make any difference between the prosocial and the selfish (Tukey test; q=1.72, P>0.05) across the last ten sessions. Shango transferred more often the prosocial token compared to the selfish (Tukey test; t=5.66, P<0.05) and more the selfish compared to the null token (Tukey test; t=4.25, P<0.05) (see figure 5). Regarding the evolution across the experiment, we observed that the number of selfish tokens transferred by Shango decreased (Spearman, N=22, r_s=-0.701, p<0.001). Regarding the behaviour of Shango, he threw out of the table more often the selfish token compared to the prosocial token (Holm-Sidak test; t=3.30, P<0.001). Shango expressed significantly more frustration (cardboard biting, beak scraping, frustration calls) (Holm-Sidak test; t=5.42, P<0.001 & t=4.08, P<0.001) and flew away more often when Léo failed to transfer a token or chose the selfish one compared to the situation where he chose the prosocial token (Holm-Sidak test; t=4.21, P<0.001 & t=3.13, P=0.002) (see figure 6).

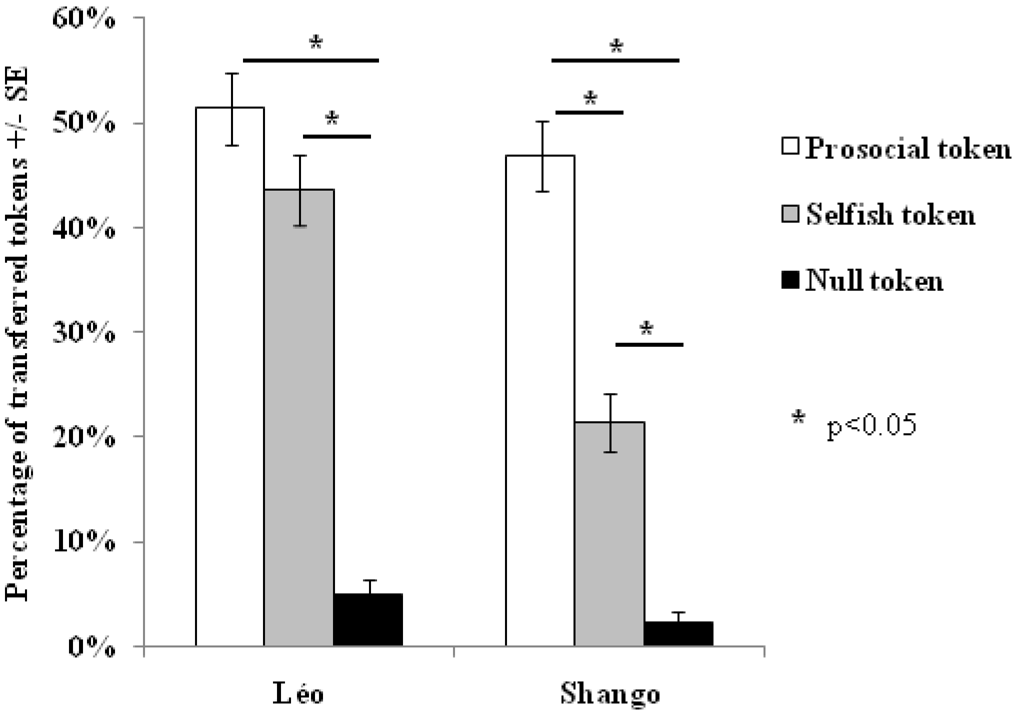


Figure 5: Léo and Shango’s choices during the cooperative token transfer task

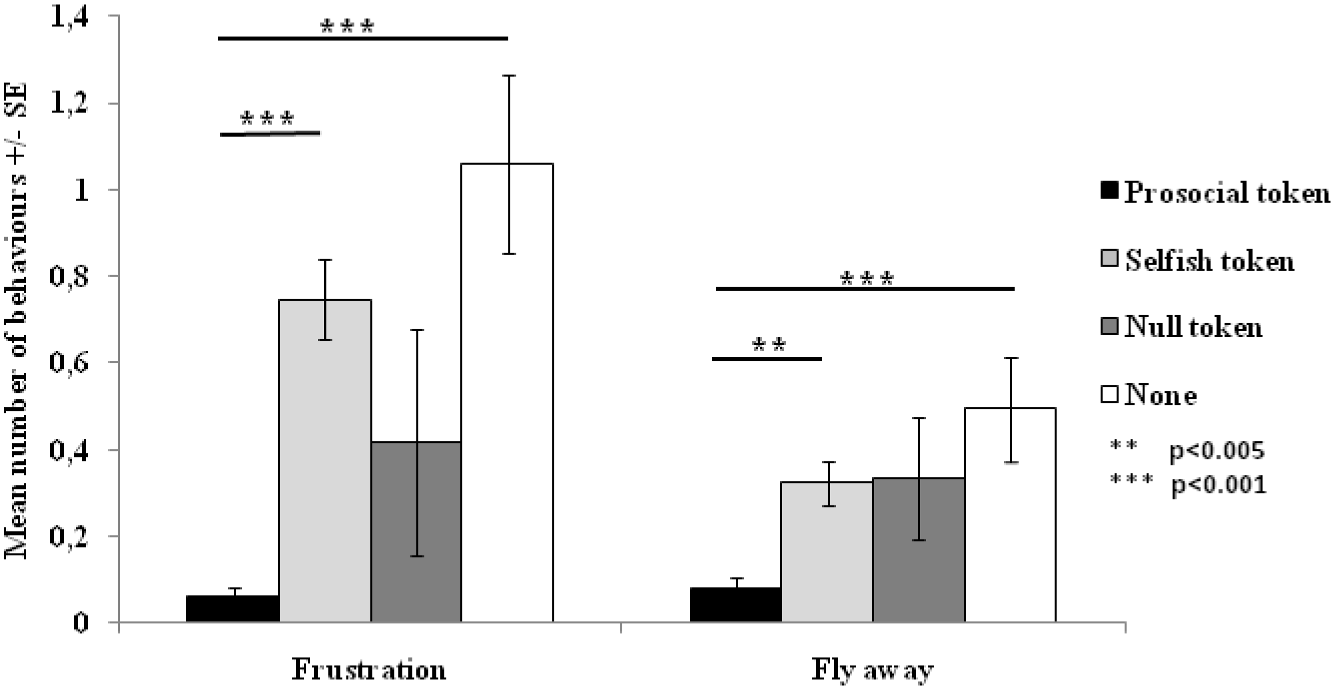


Figure 6: Mean number of Shango’s behaviours of each type, frustration (bites the barrier, scraps his beak on the table, emits frustration calls) or flight (away from the testing zone) according to the token received from Léo.

General Discussion

Testing these nine individuals from four different species we found that in general birds stopped rapidly choosing the null token as they did not receive any reward. Thus they are able to attribute a value to the objects and to discriminate between them according to the outcome. Like chimpanzees (Silk et al. 2005; Vonk et al. 2008) and cottontop tamarins (Cronin et al. 2009) the birds tested did not take advantage to deliver food to a partner at no supplementary cost even if in our study some partners were siblings or mates. Like chimpanzees (Brosnan & de Waal 2005) they did not maximize the pay off as they could have chosen the prosocial token each time and thus both individual would have received a reward in each trial. They did not develop contingent reciprocity like primates (Brosnan & de Waal 2004a; Brosnan et al. 2009; Pelé et al. 2010). We observed that once the Blue-throated macaws male attacked the female after she received the selfish reward. The reaction could be explained by a frustration effect or the food expectation hypothesis as he did not receive any food in this trial. The same bird stole twice the reward from his female during trials in which he picked up the prosocial token. It is possible that the situation in which both birds received a reward and therefore the total amount of food was split in two parts, could have represented a negative association as they have to 'share'. Nevertheless, we did not observe any preferences for the selfish token either. Contrary to our expectations, our tested birds did not develop preference for the prosocial token and grey parrots did not show any different behaviour according to the partner they were tested with. Thus, the partner itself and the nature of the relationship between the parrots (siblings, sexual partner...) did not seem to impact on the choice of the tested bird. Therefore, our tested birds seemed really not to care about the situation of their partner. Even in changing the value of the prosocial token creating inequity birds did not react contrary to capuchins monkeys who stop to be prosocial when the difference between the outcome for the tested individuals and the one for his partner is too high (Brosnan et al. 2010). Like chimpanzees (Bräuer et al. 2006; Bräuer et al. 2009), our grey parrots did not behave differently when facing an unfair situation. In the third experiment, birds learned rapidly to transfer tokens and made many successful voluntary interactions even if direct transfers (beak to beak) were rare. We observed that once again Léo did not develop any preference between the selfish and the prosocial token even though when choosing the selfish one he made Shango reluctant to cooperate. Indeed, we observed that when Léo transferred the Selfish token, Shango stopped cooperating so that none of the bird received a reward and sometimes he even preferred to throw out of the table the selfish token. Cottontop tamarins (Cronin et al. 2009) behaved similarly when one individual had the choice between two unequal baited trays: one providing a reward for the partner and the other empty: monkeys made fewer pulls compared to the situation in which the subject could access the food (rewarding or not the partner). The fact that Léo did not take into account the situation of his partner could be linked to the fact that our birds did not make any difference between the two tokens in the previous experiment. Indeed, they only cared about their own profit. It is also possible that with more trials Léo could have experienced that choosing the prosocial token had a more favourable issue. As we have observed that they were able to neglect the null token, and as Shango transferred mainly the prosocial token, Léo could have learned to differentiate the objects. But the fact that Shango sometimes transferred the selfish token precluded fast learning.

We tested different psittacid species, with pair-bond relationship thinking that the quality of the relationship would influence the results, nevertheless it was not the case. Most individuals of different psittacids species were able to attribute value to objects and grey parrots were able to transfer actively items from a bird to another in order to receive a reward. Because of the small numbers of individuals of each species, it is difficult to generalize our data to the whole species. Nevertheless, our failure to find other regarding preferences in these nine individuals (of four different species) tend to show that prosocial behaviour is not common in psittacids tested with artificial tasks. Maybe testing cooperative breeding species could lead to other issues. Indeed, callithricidae (Common ouistitis: Burkart et al. 2007; cottontop tamarins; Cronin et al. 2010; capuchins: Brosnan et al. 2010) tend to display more prosocial behaviours compared to chimpanzees as only a recent study provide evidence that some individuals were able to have prosocial preferences (Brosnan et al. 2010). We also have to test more individuals and maybe during the breeding season. Because even if we observed regurgitations during our experiments (between the members of macaws couples and also between Shango and Léo) it is possible that individuals would have more consideration regarding their mate during this period. Thus birds in couple (and also isosexual pair) regurgitate to the partner but were not able to take advantage to deliver food to the same partner at no supplementary cost by choosing a token. This difference between genetically predetermined behaviour and responses during an artificial task underline the interest to study prosociality in laboratory.

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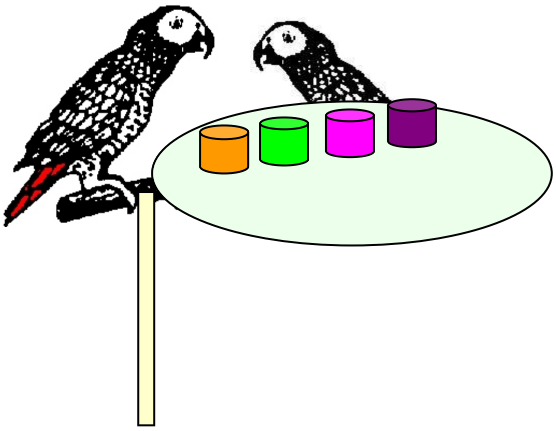
Article 5

Do grey parrots learn prosociality?

Péron F., John, M., Sapowicz, S. Bovet D. & Pepperberg I.M.

Soumis



Article 5: Do grey parrots learn prosociality?

Péron F., John, M., Sapowicz, S., Bovet D. & Pepperberg I.M.

Soumis à *Journal of Comparative Psychology*

Problème biologique

Dans la nature, les perroquets se comportent parfois de manière altruiste ou prosociale. Les mâles régurgitent de la nourriture aux femelles durant la saison de reproduction et les oiseaux au sein d'un couple vont se toiletter mutuellement. Ainsi les oiseaux semblent sensibles au sort de leurs congénères et plus précisément de leur partenaire. Les perroquets élevés à la main considèrent les humains comme faisant partie de leur groupe social et reçoivent de ces derniers la nourriture quotidienne.

Hypothèse

Les oiseaux vont profiter de l'occasion pour apporter une récompense sans coût supplémentaire à leur partenaire. Ils vont adapter leurs comportements à ceux de leur partenaire et la nature de leur relation (dominance) va influencer leurs décisions.

Méthodes

En utilisant le principe de l'échange de bouchon, nous avons mis à la disposition des individus la possibilité de récompenser sans coût supplémentaire un partenaire (conspécifique ou non). Dans une deuxième expérience, les oiseaux ont été testés avec des humains ayant des stratégies différentes (imitateur, égoïste ou altruiste)

Résultats

Les oiseaux apprennent rapidement à ne plus prendre les bouchons qui ne les récompensent pas mais par contre ils ne semblent pas faire de différence entre celui qui les récompense eux seulement et celui qui permet de les récompenser en même temps que leur partenaire. Dans la seconde expérience, les oiseaux tendent à adapter leurs choix à celui de l'humain.

Conclusion

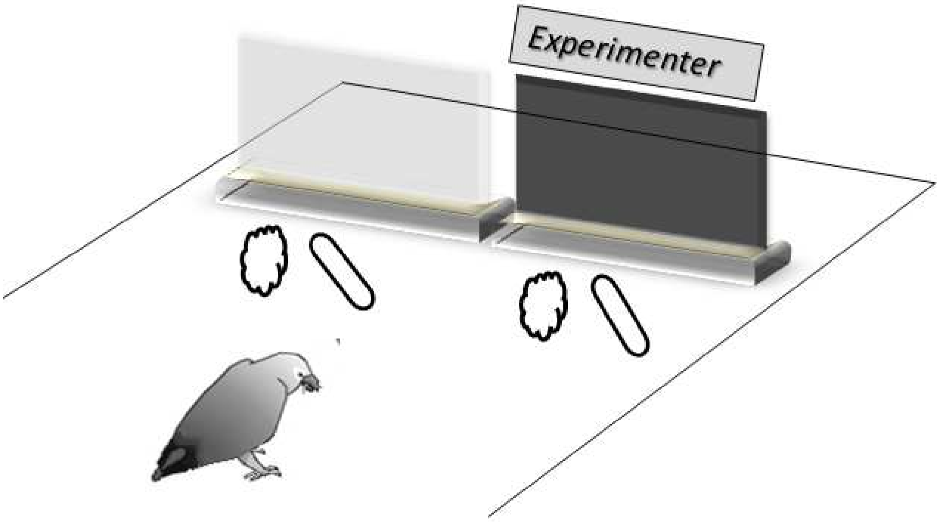
Contrairement aux comportements génétiquement prédéterminés tels que la régurgitation, les oiseaux ne se comportent pas de manière prosociale dans une tâche artificielle. Dans la seconde partie il est difficile de différencier une volonté propre de l'oiseau à récompenser ou non l'humain ou juste une simple imitation.

Article 6

Do African grey parrots (*Psittacus erithacus*) know what an experimenter does and does not see?

Péron F., Chardard C., Nagle L. & Bovet D.

Soumis *Behavioural Processes*



Article 6: Do African grey parrots (*Psittacus erithacus*) know what an experimenter does and does not see?

Péron F., Chardard C., Nagle L. & Bovet D.

Soumis à *Behavioural Processes*

Problème biologique

Dans les situations où les individus sont en compétition pour une ressource ou lorsqu'un prédateur est présent, les individus peuvent adapter leurs comportements notamment en étant capables d'attribuer des capacités de perception à d'autres. Les oiseaux captifs élevés à la main interagissent régulièrement avec leurs soigneurs et intègrent des informations en observant l'humain.

Hypothèse

Les oiseaux vont attribuer des capacités de perception à un humain familier

Méthodes

Nous avons testé les oiseaux dans deux situations différentes où des items étaient placés derrière deux écrans : un opaque et un transparent ; l'expérimentateur se trouvant de l'autre côté. Dans la condition Contrôle de la nourriture (autorisée) est à disposition et donc les oiseaux sont censés choisir au hasard entre les deux écrans alors que dans la condition Test, des objets 'interdits' (que les perroquets n'ont pas le droit de manipuler) sont employés et dans ce cas, afin d'éviter d'être chassés, ils doivent se diriger vers l'écran opaque.

Résultats

Les oiseaux mettent plus de temps pour prendre leur décision dans la condition test comparée à la condition Contrôle. Tous montrent la même tendance à savoir qu'ils préfèrent aller vers l'écran transparent dans la condition Contrôle et vers l'opaque dans la condition Test bien que seul un oiseau se comporte de manière significativement différente entre les situations.

Conclusion

Un individu a montré qu'il était capable d'adapter son comportement en fonction de la situation cependant, compte tenu du protocole, il nous est impossible de différencier entre une réponse perceptive et l'attribution de perception à un autre individu (humain dans notre expérience).

Do African grey parrots (*Psittacus erithacus*) know what a human experimenter does and does not see?

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Abstract

Perspective-taking is a cognitive ability that can be useful to access information during social interactions. This ability is extensively exploited in humans and scientists found some evidence of it in other mammals and also some bird species. In this experiment, three hand-reared grey parrots were tested on their ability to attribute perceptive skills to their caretaker. Two different screens placed on a table separating the human side from the parrot’s side were used: a transparent and an opaque. In the Control condition food was put behind each screens whereas in the Test condition ‘forbidden’ objects (attractive for the bird but normally not accessible) were placed behind each screen. Birds were expected to choose at random between the two screens in the Control condition but to prefer the opaque one in the Test condition in order to avoid be scolded and chased away. All the birds show the same tendency but only the older one chose significantly more the opaque screen in the Test condition. In the Control condition, birds chose at random.

Keywords

African grey parrots, deception, perspective taking, theory of mind

Introduction

Theory of mind is a set of specific cognitive abilities which consists of mental states attribution to others, such as perspective taking, intentions, desires, or beliefs (Premack & Woodruff, 1978). Until the 1990s, this ability was mainly thought to be specific to humans (Povinelli & Preuss, 1995; Tomasello & Call, 1997) but recent studies on non-human primates revealed that there are some indications that some species may attribute some mental states to others (non-human primates: Flombaum & Santos, 2005; Call & Tomasello, 2008; dogs: Call et al., 2003; corvids: Bugnyar & Heinrich, 2005).

Some authors consider that using conspecific or heterospecific cues such as gazing or pointing is related to other abilities that are part of theory of mind. Some species such as dogs (*Canis familiaris*) seem to be efficient in reading and using human given cues in an object-choice task, in which an experimenter points or gaze toward a box (Miklósi and Soproni 2006). One important skill contributing to theory of mind is probably the ability to evaluate whether an individual can see or hear something (perception attribution), thus individuals have to be sensitive to the attentional state of the other. This ability was found in non-human primates (great apes: Liebal et al., 2004; capuchins: Hattori et al. 2007; Hattori et al., 2010), dogs (Call et al., 2003; Virányi et al., 2004) or more recently horses (*Equus caballus)* (Proops & McComb, 2010). In these experiments, subjects beg at (or approach for food) the experimenter who is looking at them, more often than the experimenter who does not see them. In chimpanzees (Hare et al. 2000) and capuchins (Hare et al. 2003), individuals are tested with their conspecifics in a task in which they have to retrieve food in front of a dominant subject. Only chimpanzees show a clear preference for the source of food hidden for the dominant (compared to the visible one). Whereas capuchins are not consistent in their deceptive strategy (Fujita et al. 2002), chimpanzees elaborate tactics to deceive a competitor (Menzel 1971; Hirata & Matsuzawa 2001).

It seems to us interesting to look also at species distantly related to humans, and more precisely to bird species known for their complex cognitive abilities (corvids and psittacids: Emery & Clayton, 2003; Emery, 2004). Indeed, these bird species fit most of the criteria of the social brain hypothesis suggesting that individuals who have to manage complex social interactions need more brain power (Dunbar 1998): social life with complex population dynamics; big relative brain size, long infancy period and lifetime and most of them are monogamous (Emery et al., 2007).

Corvids are able to respond to human given cues such as gazing (von Bayern & Emery, 2009). They prefer to re-cache their food if watched during the caching (Bugnyar & Kotrschal, 2002; de Kort et al., in press). In a recent experiment, three hand-reared African grey parrots were able to use human given cues (Giret et al., 2009a). All the birds used spontaneously or after a short training a proximal pointing cue and one of the three grey parrots learned to use the proximal gazing cue. One of these parrots also used the presence of a conspecific or its vocalisations to find a baited box (Giret et al., 2009b). Thus, these individuals are able to rely on behavioural cues in an object-choice task experiment. The same birds were tested on their ability to attribute intentions to an experimenter and we observed that all the birds adapt their responses according to the intentions of the human, biting the wire mesh when the human is unable to give them food and displaying frustration (frustration calls, beak scraping) and opening their beak when this latter is unwilling to do so (Péron et al., 2010).

Very few studies have been undertaken on the human-bird bond (Beck & Hatcher, 1989; Barber, 1993; Anderson, 2003). Parrots kept in captivity are known for their tendency to destroy many objects. Do parrots rely on any human cues in order to take their decision (when and what to steal and destroy), knowing that if their owner sees them they would be chased? Like most parrots kept as pets, our birds were hand-reared and had daily interactions with us, which could facilitate the distinction between different human attentional states. We tested the birds in two different conditions: 1) a Control condition in which food is provided and 2) a Test condition in which usually ‘forbidden’ objects are accessible. ‘Forbidden’ objects are items of human environment that birds are not allowed to interact with such as rubber, pen, etc. In each condition the items are placed on the table behind two different screens, one opaque and one transparent and the experimenter is standing on the other side, looking in the direction of the bird. Parrots are expected to prefer the opaque screen during the Test condition so that they would avoid scolding.

Material & method

Subjects

Three hand-reared grey parrots were tested: two males (Iris, twelve year old and Doudou, three year old respectively) and one female, Rubis (8 year old), all siblings. They lived with their parents and two others siblings in a room (19m^2) provided with several toys and maintained at about 23°C with 14h/8h light-dark cycle. They were fed with water and seeds *ad libitum* and received every day fresh fruit and vegetables and often came and ate with humans during lunch time.

Procedure

Birds were tested individually in an adjacent room between 10h30 and 12h. The experimental setup consisted in two screens (25 x 40 cm), one opaque and one transparent separated by a cardboard (20 x 40 cm) placed on a table (1 x 1.30 m). Screens were placed separating two different areas: the experimenter’s place and the bird testing area (see figure 1). Birds were not food deprived and not trained but just familiarized with the device: they were free to explore the table (with the screens on it) during one day. We alternated the side of the screens across the sessions. The experimenter was sitting on the other side, looking in the direction of the bird. The parrot is placed at the end of the table and is free to interact (or not) with the items for 90 seconds. We conducted 20 trials in each condition, eight trials during five consecutive days alternating between the conditions (see Figure 1).

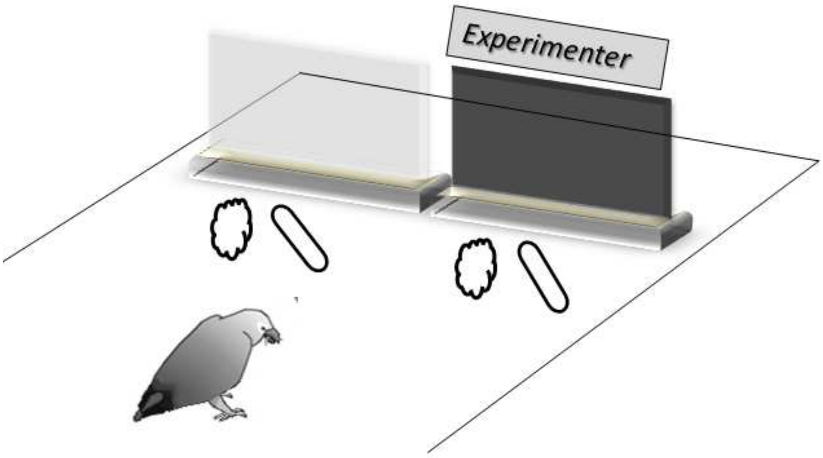

Figure 1

Control situation

Food (grapes and grains) was placed behind each screen and we expected the parrots to choose at random the place where they would eat the food.

Test

Attractive objects (tape, pen, rubber, elastic, empty blister strips, etc.) that parrots were not usually allowed to touch but that they used to steal and destroy when possible, were used for this study and placed behind each screen. For each trial two identical objects were used.

Coding & statistical analysis

We recorded the choice and the latency of each bird. We ran Chi Square analysis in order to compare the choice of the birds according to the condition (control or test), Binomial test in order to compare the choice within a condition and Wilcoxon test to compare the latency time between the conditions.

Results

All the three parrots behaved similarly: they chose more the transparent screen in the Control sessions and more the Opaque screen in the test sessions. Nevertheless, the difference was significant only for Iris (Chi Square analysis; ddf 1; Iris: χ^2= 6.8 & P=0.009; Rubis: χ^2= 1.6 & P=0.206; Doudou: χ^2= 1 & P=0.317). Only in the Test condition (for Iris) we observed that the parrot chose significantly more the opaque screen compared to the transparent (Binomial test; p=0.021). In all the others condition we did not notice any preferences for one specific screen (see Figure 2).

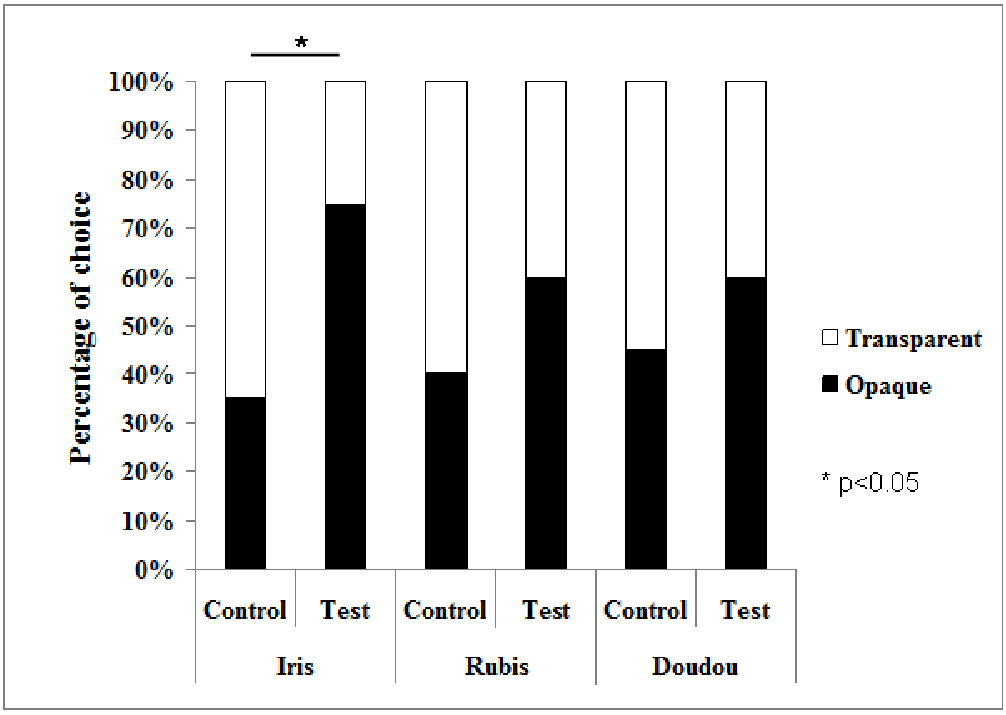

Figure 2

In the Test situation, birds made their choice after a longer latency time compared to the Control condition either with the opaque (Z=-2.377, p=0.017) or the transparent (Z=-3.092, p=0.002) screen. We did not find any difference between the screen within a condition (Control: Z=-1.524, p=0.127; Test: Z=-0.201, p=0.840) (see Figure 3).

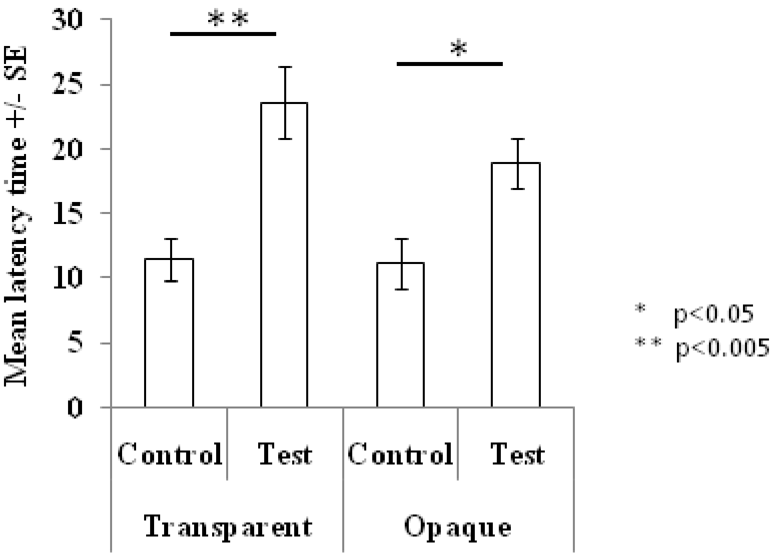

Figure 3

Discussion

We observed that in general birds preferred to go behind the transparent screen when possible (Control condition) maybe because it was brighter or because they could see the experimenter and this sight could be reassuring as the experimenter was the main human they are bond with; seeing the experimenter could also be a way to better control any human actions. Only the older parrot (Iris) chose significantly more often the opaque screen, maybe because he had more opportunities to face this type of situation before, trying to steal any item (food or objects). Nevertheless, birds had a longer latency time in the Test condition compared to the Control one. This could be explained by the nature of the items themselves (food, maybe more attractive, in the control situation versus objects in the test situation) or also because they understood the risk to be chased away. Previous experiments conducted with three other greys revealed that they were able to perform quite well in a cooperative human given cues task (Giret et al., 2009a). In the study conducted with jackdaws (von Bayern & Emery, 2009), the authors showed that birds responses changed according to the experimenter, namely going faster for the reward when this latter was familiar. The same was found for horses that pay more attention to a familiar experimenter and thus tend to go toward him (Krueger et al., 2010). Here only one bird behaved significantly different according to the fact that the experimenter could or could not see him but it is still not possible to say if his decision was lead by simple rule which could be: ‘I go where I am not seeing him’ or to a more complex cognitive attributing perception skills to humans which could be: ‘I go where he could not see me’. This issue is found in many studies even with primates. The second option was found in corvids for instance that preferred to cache in shadowed area (Dally et al., 2004) or in dogs taking the reward when the experimenter had his eyes closed (Call et al., 2003). Researchers found also evidence of perspective-taking in primates species (spiders monkeys (Amici et al., 2009), long-tailed macaques (Goossens et al., 2008), great apes (Braeuer et al., 2005), etc) but for some of them such as capuchins monkeys we observed contrasting results (Hare et al. 2003; Amici et al. 2009) and common ouistitis failed to show context-independent perspective-taking abilities (Burkart and Heschl, 2007). In the wild we can find examples of perspective-taking in budgerigars (*Melopsittacus undulatus*; psittacids species) for instance where extra-pair copulation happen sometimes. A study reveals that individuals copulate when they are not seen by their partner (Baltz and Clark, 1997). Nevertheless, birds were not tested in the condition were they could see the sexual partner but not be seen. Thus we cannot exclude that budgerigars just react at the presence/absence of a conspecific in their visual field. In grey parrots we do not have data regarding extra-pair copulation but perspective-taking ability could be useful in all activities where the presence of several individuals can create competitive conditions such as foraging or mating.

Acknowledgments

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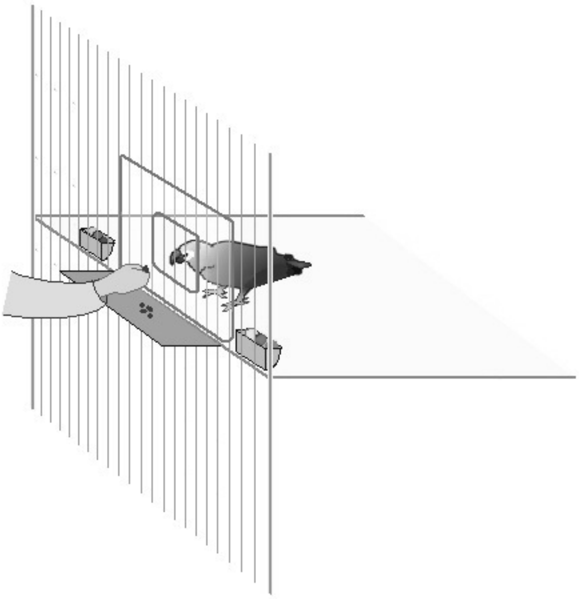
Article 7

Unwilling versus unable: Do grey parrots understand human intentional actions?

Péron F. Rat-Fischer L., Nagle L. & Bovet D.

Interaction Studies 2010, **11**, 3, 428-441



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Problème biologique

Au sein d'un groupe les individus sont amenés à interagir avec leurs congénères. Pour bien des activités, ils doivent adapter leurs comportements à ceux de leurs congénères, qu'il s'agisse de la recherche de la nourriture ou d'un partenaire. Dans le cadre des comportements de coopération, les actions seront d'autant plus performantes si les participants sont capables de prendre en compte les intentions de leurs congénères.

Hypothèse

Les oiseaux testés ont été élevés à la main et par conséquent interagissent régulièrement avec leurs soigneurs. Ils apprennent à discerner les intentions des humains en fonction de leurs comportements.

Méthodes

Un expérimentateur familier ne donne pas la récompense (visible des oiseaux) soit parce qu'il est distrait, soit parce qu'il n'en est pas capable (bloqué) ou soit parce qu'il n'est pas conciliant.

Résultats

Les oiseaux se comportent différemment face à ces situations. Ils mordent plus souvent le grillage quand l'expérimentateur est bloqué alors qu'ils ouvrent significativement plus le bec, émettent des cris de quémande et expriment des comportements de frustration quand l'expérimentateur n'est pas conciliant. Dans la situation où l'expérimentateur est distrait les oiseaux se désintéressent de lui plus rapidement.

Conclusion

Les oiseaux distinguent les variations dans les intentions de l'expérimentateur et se comportent différemment en fonction des indices comportementaux de l'humain.

‘Unwilling' versus 'Unable': Do grey parrots understand human intentional actions?

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Abstract

Intentionality plays a fundamental part in human social interactions and we know that interpretation of behaviours of conspecifics depends on the intentions underlying them. Most of the studies on intention attribution were undertaken with primates. However, very little is known on this topic in animals more distantly related to humans such as birds. Three hand-reared African grey parrots (*Psittacus erithacus*) were tested on their ability to understand human intentional actions. The subjects' attention was not equally distributed across the conditions and their behavioural pattern also changed depending on the condition: the parrots showed more requesting behaviours (opening of the beak and request calls) when the experimenter was unwilling to give them seeds, and bite more the wire mesh that represented the obstacle when the experimenter was trying to give them food. For the first time we showed that a bird species, like primates, may be sensitive to behavioural cues of a human according to his intentions.

Keywords: Grey parrots, intention attribution, theory of mind.

Introduction

The theory of mind is a set of specific cognitive abilities which consists of perspective taking and mental states attribution of intentions, beliefs and desires (Premack & Woodruff, 1978). Until the 1990s, this ability was mainly thought to be specific to humans (Povinelli & Preuss, 1995; Tomasello & Call, 1997) but recent studies on non-human primates revealed that there is some evidence of mental state attribution in these species (Call & Tomasello, 2008), although it is still debated (Povinelli & Vonk, 2003; Povinelli & Vonk, 2004). As stated by Tomasello *et al*. (2003), there is probably no clear-cut answer but to date there is no convincing evidence that any non-human animal possesses a full-blown theory of mind. Nevertheless there are some indications that some species may attribute some mental states to others (non-human primates: Flombaum & Santos, 2005; Call & Tomasello, 2008; dogs: Call et al., 2003; corvids: Bugnyar & Heinrich, 2005).

Some authors consider that using conspecific or heterospecific cues such as gazing or pointing is related to the acquisition of other abilities that are part of theory of mind. Some behavioural cues are displayed and utilised earlier than others in a developmental perspective. Twelve-months-old children understand first pointing and gazing (e.g. they are able to follow or to give such cues to select an object) (Colonnesi et al., 2008). Some species (such as dogs, *Canis familiaris*) seem to be efficient in reading and using these types of cues in an object-choice task, in which an experimenter points or gaze toward a box (Miklósi and Soproni 2006).

Corvids are also able to respond to human given cues such as gazing (von Bayern & Emery, 2009). They prefer to re-cache their food if watched during the caching (Bugnyar & Kotrschal, 2002; de Kort et al., in press). In corvids gaze following and caching change during development. The development of a full and elaborated caching behaviour needs time and maturation (fledging birds), social interactions and experiences (pilfering) (Schloegl et al., 2007; Bugnyar et al., 2007). In a recent experiment, the hand-reared African grey parrots tested in the present study were also able to use human given cues (Giret et al., 2009a). Indeed, all the birds used spontaneously or after a short training a proximal pointing cue (steady pointing with hand at about 20 cm from the baited box) and one of the three grey parrots learned to use the proximal gazing cue (combined head and eye orientation, the distance between the head and the baited box was about 1 m). The same parrots also used the presence of a conspecific or its vocalisations to find a baited box (Giret et al., 2009c). Thus, these individuals are able to rely on behavioural cues in an object-choice task experiment.

On important skill contributing to theory of mind is probably the ability to evaluate whether an individual can see or hear something (perception attribution). This ability was found in non-human primates (Liebal et al., 2004; Hattori et al., 2010), in dogs (Call et al., 2003; Virányi et al., 2004) or more recently in horses (*Equus caballus)* (Proops & McComb, 2010).

An important ability of the set of the ToM, is the attribution of intentions (Call & Tomasello, 2008). Some researchers have tested this ability in children and non-human primates using paradigms such as accidental versus intentional spilling of the food to the floor (Call & Tomasello, 1998; Povinelli et al., 1998). Similar skills were tested by Wood et al., (2007) with cotton-top tamarins (*Saguinus oedipus*), rhesus macaques (*Macaca mulatta*) and chimpanzees (*Pan troglodytes*) that made spontaneous inferences about a human experimenter's goal. Other researchers studied tested different situations in which the experimenter was unable or unwilling to give food to the subjects. Chimpanzees (Call et al., 2004), human children (Behne et al., 2005) and even capuchins (*Cebus apella)* (Phillips et al., 2009) were able to distinguish between the intentional actions of the human experimenter. In general individuals expected more to receive food when the experimenter was unable to give them the reward than when he was unwilling to do so. It seems to us interesting to look also at species distantly related to humans, and more precisely to bird species known for their complex cognitive abilities (corvids and psittacids: Emery & Clayton, 2003; Emery, 2004). Indeed, these bird species fit most of the criteria of the social brain hypothesis (social life with complex population dynamics; big relative brain size, long infancy period and lifetime) and most of them are monogamous (Dunbar, 1998; Emery et al., 2007). Thus, individuals have to deal with complex social interactions and it is not surprising to find in these species social cognitive abilities related to theory of mind.

Parrots show complex and flexible abilities in order to deal with the social complexity of their natural life but also to adapt quickly to a very constrained environment: the 'anthropogenic world'. Very few studies have been undertaken on the human-bird bond (Beck & Hatcher, 1989; Barber, 1993; Anderson, 2003) but nevertheless they reveal that avian companionship is similar qualitatively to the one provided by cats or dogs. However, the vocal ability of parrots stimulates the dialogue-seeking behaviour of the owner. In general, humans tend to attribute intentions to their pets, wittingly or not. But do these parrots attribute some form of intentions to us? Like most parrots kept as pets, our birds were hand-reared and had daily interactions with us, which could facilitate the distinction between different human intentional behaviours.

We decided to test our parrots in three conditions: Unable (the experimenter tries without success to give some food to the birds), Unwilling (the experimenter does not want to give the food to the birds) and Distracted (the experimenter is doing something else). These three conditions were inspired by similar studies conducted in children (Behne et al., 2005), chimpanzees (Call et al., 2004), and capuchins (Philipps et al., 2009). However, we simplified the experimental design by testing only one situation for each condition; as in the experiments of Call et al. (2004) and Behne et al. (2004), the authors had to pool their data because the behaviour of the animals did not reflect the diversity of the situations. Thus we reduced the number of situations as Philipps et al. (2009) did in their experiment 1. For this study, birds were expected to react differently according to the intentions of their caretaker, reading appropriately the behavioural cues available in each situation. Parrots were expected to produce particular vocalisations and behaviours related to frustration and/or food requesting in the ‘Unwilling condition’ compared with the two others. The time spent looking away from the experimenter was expected to be more important in the ‘Unwilling’ and in the ‘Distracted condition’. In the ‘Distracted and Unwilling conditions’, birds were expected to interact with the bottle caps as a behavioural displacement.

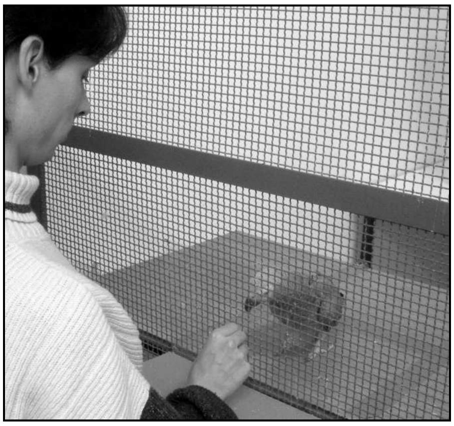
Methods

Subjects

Three hand-reared African grey parrots (*Psittacus erithacus*) were tested: Shango, a four-year-old male, Léo, a six-year-old male and Zoé, a six-year-old female. They were born in captivity and arrived at the laboratory at 3 months old. Since their arrival the animals’ behaviour was observed regularly and they participated in different experiments. They were housed together in an aviary (340 cm x 330 cm x 300 cm) with three tables, two large perch structures and many toys. The ambient temperature remained at about 25°C. The room was lit on a 12:12 h light:dark cycle with two crepuscules of 30 min for both morning and evening. Parrots were fed everyday with fresh fruits and vegetables in the morning and parrot formula (Nutribird A21) in the evening. Water and pellets (Harrisson) were available *ad libitum*. Vitamins (Muta-Vit Versele-Laga) were given twice a week.

Procedure

Birds were tested in their aviary individually with the experimenter seated on the opposite side of the wire mesh with a tray in front of him. During a test session, the two other subjects were carried to another room of 5 m x 2.4 m x 3 m in which food and toys were available. The subject was placed on a table where a testing zone was delimited (30 cm x 30 cm). A transparent plastic sheet (21cm x 29.7cm) was fixed on the wire mesh (experimenter’s side) the day before the beginning of the experiment and remained until the end of the testing period. A hole was made in the centre (6cm x 8.5cm) located at the parrot's head level (see Figure 1). At both sides of the table, bottle caps were placed in containers and were accessible at all times for the parrot. Sunflower seeds were used as a reward during the tests and were not available for the parrots otherwise.



In the testing conditions the experimenter acted either as 'Distracted', 'Unable' or 'Unwilling' to give food to the subjects. Three sessions were conducted on different days. Within the session, each condition (see below) was repeated twice alternatively with motivational trials in which the food was given to the subject. Each test trial lasted for thirty seconds. The order of presentation was pseudo-randomised and different for each bird and between sessions.

Conditions

Distracted: The experimenter played with bottle caps. His hand made back and forth movements near the seeds but did not touch them. The experimenter was looking at the bottle caps and at the bird.

Unable (Blocked): The experimenter tried to give one seed to the bird through the wire mesh but could not do it because of the plastic sheet blocking the way. The experimenter's hand made back and forth movements between the parrot and himself, looking at the seed and at the bird alternatively.

Unwilling (Tease): The experimenter held one seed, his hand making back and forth movements between the bird and himself, and ate the seed while exaggerating swallow sounds and saying once ‘hum it’s good’. The experimenter was looking at the seed and at the bird alternatively.

In all three conditions the seeds were placed visibly at the middle of the tray. The experimenter made the same number of back and forth movements (six) and in the ‘Unwilling condition’ ate the seed after each sequence so that at the end of a test he had eaten six seeds. Hands were also visible at all times and moving close to the wire mesh. During motivational trials, the experimenter gave seeds through the wire mesh. Every session started with two motivational trials in order to attract the bird near the wire mesh, inside the testing area. Then two more motivational trials were randomly conducted within the six test trials. The inter–trial-interval was 15s during which the experimenter left the room. Each trial started when the bird was near the wire mesh and ended after thirty seconds. Unlike in the experiments undertaken with primates, we decided to stop the trial after thirty seconds and not to wait until the parrot left the testing area. This choice was made because our birds are not as active as primates and thus they can stay in the same place for a long time. As the parrot was free to leave the testing area at any time, participation of the bird could be described as voluntary.

Coding

Trials were filmed and acquired digitally (Canon; MVX350i; Adobe Première Pro 2.0) and analysed. We recorded all the behaviours displayed by the subjects, as well as their vocalisations (see Table 1). Because our parrots, unlike the non-human primates (Call et al., 2004; Phillips et al., 2009) were not expected to leave the test area during the test (as explained above), we chose another parameter more adapted to our subjects: we used the time spent looking away as an indicator of disinterest toward the experimenter. This parameter has also been used in experiments with children (Behne et al., 2005). Thus, the amount of time spent looking away from the experimenter was recorded. As parrots usually use both eyes to look at something they are interested at (particularly food), we considered that the bird was looking away when its head was not facing the experimenter. All the behaviours were coded twice (Spearman: r= 0.988) and a second coder, blind to the experimental conditions then recoded the behaviour (Bite: r=0.989; Open: r=0.913; Scrap: r=0.989; Request: r=0.987; Vocalisation: r=0.991) to assess inter-observer reliability. We recorded the number and the category of vocalisations (request call or other), the number of wire mesh biting, table scraping and beak opening. This latter behaviour was coded when the bird moved both the upper and lower part of its beak in the vertical axis without producing sounds and this opening movement did not precede biting or yawning action. Beak opening is displayed when parrots expect to receive food (for instance regurgitation from a conspecific, or hand-feeding). Our parrots are used to display this type of behaviour every day as a request when we give them parrot formula with a syringe.

Statistical analysis

Statistical analysis were made using R Software. Non parametric Kruskal-Wallis rank sum test was run in order to evaluate the effect of the condition on the different parameters. When Kruskal Wallis was significant at α=0.05, a post-hoc test for multiple comparisons was run, using the R function “kruskalmc” from the package “pgirmess”. Therefore, a correction was applied α’= 0.008 (α’=α/[K(K-1)] with K=3; number of samples). Linear regression analyses were made using SigmaStat software in order to assess that birds did not change their behaviour across the sessions.

Results

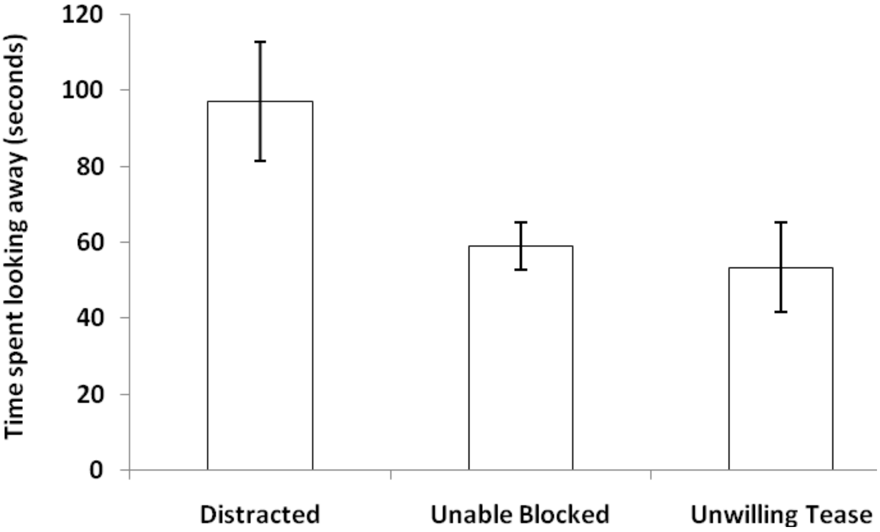
Table 1 shows all behaviours observed during the three sessions and also the total amount of time spent looking away from the experimenter during this period.

	Condition	Time (s)		Wire bite	Beak open	Scrap table	Request call	Other vocalisation
Shango	Unable	56		29	3	0	1	0
	Unwilling	47		0	16	2	4	0
	Distracted	56		0	0	3	0	1
Léo	Unable	46		15	9	0	2	0
	Unwilling	29		0	18	1	3	0
	Distracted	114		0	0	1	0	2
Zoé	Unable	75		22	3	1	6	11
	Unwilling	84		0	15	9	15	4
	Distracted	121		0	0	2	0	2

Table 1. Data from the six trials of each condition (‘Unable’, ‘Unwilling’, ‘Distracted’) for each individual. Time (in seconds): Total duration spent looking away from the experimenter. Total number of behaviours recorded during different experimental conditions.

Time spent looking away

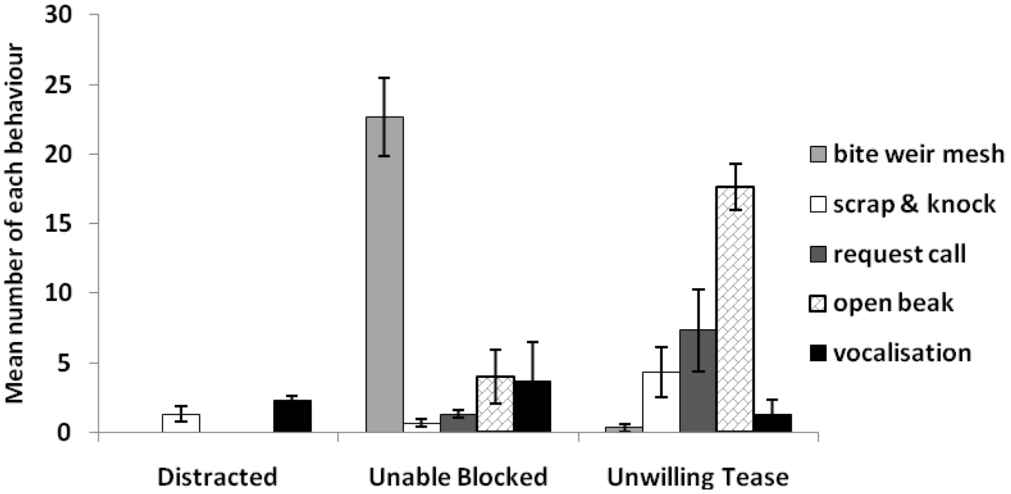
The individuals differ in their attentional state toward the experimenter according to the situation. We observed that they spent more time looking away in the ‘Distracted condition’ compared with the two others (Kruskal-Wallis rank sum test: H=10.89, df=2, p<0.05; post-hoc test, p<0.008). No significant difference has been found between the ‘Unable’ and the ‘Unwilling condition’.



Regarding the change of the behaviour across the sessions we found that Léo and Zoé increased their time spent looking away in the 'Unwilling condition' (Linear regression analysis; Léo *r*= 0.950 & Zoé *r*= 0.881). Zoé looked less away in the 'Unable condition' (*r*=0.835). Nevertheless these changes tend to decrease (or not modify) the difference between the different situations.

Other behaviours

We found that parrots bite more often the wire mesh in the 'Unable condition' compared to the two other conditions (Kruskal-Wallis; H=46.58, df=2, p<0.05; post-hoc test, p<0.008) and opened more often their beak in the 'Unwilling condition' compared with the other conditions (Kruskal-Wallis; H=33.19, df=2, p<0.05; post-hoc test, p<0.008) produced more request calls in the 'Unwilling condition' (Kruskal-Wallis; H=17.6, df=2, p<0.05; post-hoc test, p<0.008) compared with the 'Distracted condition'. There was also a significant difference across all three conditions (but not between two conditions) for scraping and knocking behaviour (Kruskal-Wallis H=10.46, df=2, p<0.05; post-hoc test, p>0.008). No difference between conditions was found for the other vocalisations (Kruskal-Wallis H=0.74, df=2, p=0.69).



None of the birds interacted with the bottle caps placed in the containers during the trials.

Across the sessions, Zoé produced less vocalisations (Linear regression analysis; *r*=0.828) during the 'Unable condition' and scrapped more the table (*r*=0.961) when the experimenter was 'Distracted'. Nevertheless these behaviours, as seen above, are not significantly differently produced across two given conditions.

Discussion

Like primates, grey parrots reacted differently according to the behavioural cues available during the situations. The birds bite more often the wire mesh in the 'Unable condition', opened their beak and produced more request calls in the 'Unwilling condition'. The only contextual cues that changed across conditions were the presence of bottle caps in the tray when the experimenter was 'Distracted'.

It seems that in the 'Unable condition' the parrots tried to solve directly the problem which was how to access the reward through the wire mesh (they mainly bite the wire mesh). The mesh seemed to represent an obstacle for them as they interact physically with it. In the 'Unwilling condition' they tried to attract the experimenter's attention, mainly opening their beak and making noises (request calls) while displaying frustration (scraping & knocking their beak on the table). The beak opening can probably be interpreted as a request, as they do the same thing when they are hand-fed with the parrot formula. The vocalisations produced were categorised into two types: request calls and others. The latter were not specific (they can be emitted in various circumstances), while the first category refers to vocalisations produced when the bird wants something (some food or a toy). The second category, non-specific vocalisations, could have been produced in order to attract the experimenter's attention.

Chimpanzees (Call et al., 2004) and capuchins (Phillips et al., 2009) did not show a significant difference between the 'Unwilling Tease' and the 'Unable Blocked' conditions regarding the latency before leaving the testing area. Using another parameter, time spent looking away from the experimenter we did not find any significant difference either. The fact that our birds spent more time looking away in the 'Distracted condition' could probably be explained also by the fact that the experimenter did not manipulate the seeds in this situation.

In these two conditions ('Distracted & Unwilling'), birds were expected to interact with the bottle caps. We thought that they could interact with the toys as a behavioural displacement. In the first case they could play with the bottle caps as they observed the experimenter playing with the objects and in the second case we thought that they may throw them to the floor, as they sometimes do if frustrated. However, these behaviours did not occur during testing.

As expected, none of our parrots left the testing zone during the sessions. It seems that in the 'Distracted condition' they were not interested in the action (they spent more time looking away) and did not expect to receive any food, as the experimenter was already engaged in playing with bottle caps. In the 'Unable condition' they focused their attention on the human unsuccessful attempts and tried to solve the problem whereas in the 'Unwilling condition' they displayed behaviours of frustration and tried to attract the human's attention.

These three African grey parrots were hand-raised and received food from us every day. Because of our diverse and frequent interactions we are considered as social members of their group. They are used to see us eating and ask for food most of the time (which we usually share with them). This could influence their ability to distinguish between different behavioural cues provided by the caretaker according to his intentions. This could be linked to the socialization hypothesis proposed for hand-reared primates: human experience could only modify existing social interactions and intentional skills rather than creating new ones (Tomasello & Call, 2004).

Our observations have been made on three hand-reared African grey parrots so that our conclusions can not be applied to the species as a whole Boesch, 2007; Tomasello & Call, 2008; Boesch, 2008). Our positive results suggest the need to study different abilities defined as part of the theory of mind in several individuals of several species. The vast majority of the data concerning cognitive and communicative abilities of African grey parrots came from a single individual: Alex (Pepperberg & Brezinsky, 1991; Pepperberg, 1993; Pepperberg, 1994a; Pepperberg, 1999). There is no doubt that in nature parrots have to face complex social situation during which they need to rely on conspecific behavioural cues.

Regarding our parrots, the abilities demonstrated in this study enhance the human–animal interactions as both partners are able to distinguish between the intentional actions of the other, which in turn improves the efficiency of the communication. Previous studies undertaken on heterospecific language acquisition showed that even if our birds had difficulties learning rapidly new words, they were able to use our labels for their own purpose such as food requests (Giret et al., 2009b). Moreover, several studies confirm the necessity of interactions with humans for referential learning (Pepperberg, 1994b; Pepperberg & McLaughlin, 1996; Pepperberg & Wilkes, 2004).

These results suggest that some birds adapt their behaviour according to the intentional actions of a human experimenter. With this single experiment it is not possible to assess whether they understand that others have mental representations that drive their actions (Penn & Povinelli, 2007; Penn & Povinelli, in press). Nevertheless, data from Pepperberg's (2008) experiment suggest that Alex had some expectations about others representations when questioning experimenters about objects characteristics.

It is the first time to our knowledge that a study shows that a bird species may recognize and distinguish between humans' intentional actions using behavioural cues.

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DISCUSSION

Etude de la coopération

Au cours des expériences de coopération, nous avons pu remarquer que les trois perroquets gris du Gabon avaient le même objectif et ont été capable de résoudre la tâche en tirant sur la ficelle. Le nombre de tirs simultanés augmente au cours du temps car ils réalisent des actions similaires au même instant. Cette capacité (niveau 1 de la coopération selon Boesch & Boesch 1989, similarité) a été observée chez d'autres espèces (tamarins, Cronin et al. 2005 ; marmouset, Werdenich & Huber 2002 ; capucins, Mendres et de Waal 2000 ; bonobos, Hare et al. 2007 ; chimpanzés, Melis et al. 2006a ; corbeaux freux, Seed et al. 2008 ; loups, Möslinger et al. 2009 ; hyènes, Drea & Carter 2009), et cela permet de conclure que les individus parviennent à résoudre la tâche mais non qu'ils comprennent le rôle du partenaire. En effet, il est possible que les oiseaux aient été simplement attirés par la récompense sans compréhension de la nécessité de coopérer (Visalberghi et al. 2000). Les trois oiseaux tirent plus la ficelle quand le partenaire est présent (comme les capucins, Mendres & de Waal 2000) mais seul Shango semble réellement s'ajuster au partenaire en retardant son premier tir de ficelle. Hauser et al. (1999) suggèrent qu'il est difficile d'inhiber une réponse motrice une fois que les sujets ont été entrainés à la réaliser. Qui plus est, une étude réalisée avec ces mêmes oiseaux et concernant le self-control a révélé qu'ils n'étaient pas capables d'attendre plus de deux secondes dans une tâche de récompense retardée (Vick et al. 2009) et que par conséquent le fait de retarder le partenaire de 15 secondes représente un délai trop long, de telle sorte qu'ils ne sont pas capables de se retenir de tirer malgré l'éventuelle compréhension de la nécessité d'un partenaire. Par la suite, ces mêmes perroquets ont été capables de tirer avantage de la présence d'un partenaire pour accéder à une récompense plus grande, contrairement aux corbeaux freux (Seed et al. 2008). Ainsi, les perroquets ont su coordonner leurs actions, comme les hyènes et les chimpanzés, avec cependant une précision importante :

ils étaient amenés à proximité des dispositifs et donc avaient moins d’efforts à fournir pour participer, contrairement aux corbeaux par exemple qui devaient d’eux-mêmes changer de volière. Léo et Zoé, en présence d’un partenaire, ont montré une nette préférence pour le dispositif Duo suggérant ainsi qu’ils comprenaient l’avantage de coopérer. Cependant Léo choisit au hasard quand il est seul ce qui pourrait laisser à penser qu’il ne comprend pas la tâche et que le partenaire (quand il est présent) agit comme un stimulus attractif. Durant des expériences conduites précédemment, ces mêmes oiseaux ont montré qu’ils étaient capables de se servir d’indices fournis par un partenaire (conspécifique ou humain) afin de trouver la récompense cachée (Giret et al. 2009 a, b). Il est possible que Léo prenne simplement en compte la présence d’un partenaire pour faire son choix et qu’il ne fasse pas de distinction entre Zoé et Shango car il peut obtenir la récompense avec les deux. Zoé, quant à elle, se comporte très différemment en fonction du partenaire présent : alors qu’elle choisit de coopérer à chaque fois quand Léo est présent, elle préfère aller vers le dispositif Solo quand Shango est le partenaire. Le fait que Shango soit dominant et agresse parfois Zoé explique ce choix. De plus, il est possible que Zoé se souvienne que lorsque Shango est en position de choisir entre les deux solutions, il ne coopère jamais. Il semble préférer une récompense moins importante mais pour laquelle il n’a pas besoin d’attendre après un partenaire qui en plus pourrait refuser de coopérer. Au cours de cette expérience, les oiseaux ont amélioré leur self-control et ont appris à attendre l’arrivée du partenaire. Cependant lors de l’expérience suivante (collaboration) Zoé tire souvent la ficelle avant l’arrivée de Léo et ce d’autant plus quand ce dernier est retardé. Shango quant à lui préfère quitter le dispositif plutôt que d’attendre. Dans cette dernière expérience, les oiseaux ont appris à agir de manière complémentaire ; cependant, après avoir échangé leurs places nous n’avons observé que trois tentatives de collaboration (toutes trois infructueuses) : bien qu’ils aient été entraînés individuellement pour les deux actions ils n’ont pas su s’adapter ni même échanger leurs places. Il est donc probable qu’ils n’aient pas compris le rôle du partenaire. Ceci est différent de ce qui peut être observé lors de la chasse collective des chimpanzés (Boesch & Boesch 1989) ou des lions (Stander 1992) par exemple. Durant les expériences nous n'avons pas enregistré de tentative de recrutement (vocalisation par exemple) qui aurait pu faciliter la coordination des individus ou la résolution d'un conflit d'intérêts lors de l'expérience de négociation, cependant ne nous savons pas si un tel comportement existe à l'état naturel. Par ailleurs, bien que les chimpanzés soient capables de recruter le meilleur partenaire (Melis et al. 2006a), ils n'ont pas produit de signaux de communication lors de l'expérience de négociation (Melis et al. 2009). Nous avons pu noter que les oiseaux orientaient leur tête vers le partenaire quand ce dernier était retardé, néanmoins vu la position anatomique des yeux il est difficile d'évaluer la direction du regard chez les oiseaux (Dawkins 2002) à moins de faire appel à du matériel particulier comme un laser (Anders et al. 2008). Ces expériences de coopération apportent de nouvelles données pour comprendre comment les oiseaux gèrent leurs relations. Il est certain que l'apprentissage a joué un rôle majeur dans les performances observées et bien que les sujets semblent avoir compris la nécessité d'un partenaire, on aurait probablement pu aboutir à la même conclusion en conditionnant le succès de la tâche à n'importe quel stimulus, comme une lumière par exemple (Noë 2006). Néanmoins, cette capacité à associer de tels stimuli peut éventuellement permettre aux oiseaux vivant à l'état naturel d'apprendre à coopérer de manière efficace. L'étude de plusieurs groupes d'individus serait nécessaire afin de confirmer d'une part les capacités cognitives de l'espèce mais aussi de pouvoir observer d'éventuelles différences en fonction de l'organisation sociale et des types de dispositifs comme ce que l'on peut voir avec l'exemple des kéas (Tebbich et al. 1996 ; Huber et al. 2008) (**Article 1**). En ce qui concerne le groupe de perruches, nous avons observé qu'elles parvenaient à résoudre les tâches de coopération mais avec un faible taux de succès et sans indice suggérant une compréhension du rôle du partenaire. Nous observons que les individus les plus subordonnés tendent à se percher plus sur le dispositif à bascule (rôle d'acteur) parce que les dominants monopolisent la place permettant d'accéder à la récompense. Les oiseaux qui actionnent le levier en général interagissent plus avec l'autre dispositif (tir à la ficelle coopératif). Il est possible que les individus subordonnés soient également les plus explorateurs ou peut-être aussi les plus tolérants permettant ainsi une proximité lors de la résolution du dispositif où ils doivent tirer une ficelle. Les oiseaux ont formé de nombreuses dyades de telle sorte que nous n'observons pas d'influence du sexe ou de l'âge sur les performances. Cependant les juvéniles interagissent de manière plus importante avec les dispositifs, ce qui est certainement dû à un comportement exploratoire exprimé de façon plus importante que chez leurs aînés (**Article 3**). Par contre, nous observons que les dyades formés par les trois perroquets ne sont pas équivalentes et que certaines sont plus performantes que d'autres. Ainsi la probabilité que les individus coopèrent, leur efficacité et l'issue de l'interaction sont influencées par le degré de tolérance entre les participants. Les études conduites avec les rats (Schuster 2002; Rutte & Taborsky 2008), montrent que l'issue influence la prochaine action conjointe et ici, nous observons que le degré de tolérance augmente au cours du temps, peut-être par le fait que la proximité soit récompensée (lorsque les individus parviennent à accéder à la nourriture). De même, dans l'expérience où les sujets avaient le choix du partenaire nous retrouvons l'influence des préférences sociales (tolérance et dominance) sur le choix de coopérer ou non. Il semble que la personnalité des oiseaux soit également un facteur important comme ce qui a pu être observé chez les corbeaux freux (Scheid & Noë 2010) mais ici le faible nombre d'individus ne permet pas de faire des analyses.

Durant cette étude, nous avons occasionnellement observé chacun de nos trois oiseaux passer d'une table à l'autre quand leur plus proche voisin refusait de coopérer ou alors se diriger vers l'autre dispositif. Ainsi les individus se sont parfois adaptés à la situation en se rendant à la position qui permettrait de coopérer. On remarque cependant que leurs choix ne sont pas toujours pertinents. Ainsi Shango continue de tenter de coopérer avec Zoé bien que cette dernière refuse, alors qu'il aurait dû préférer travailler avec Léo (Théorie du marché biologique ; Noë & Hammerstein 1994). Dans l'expérience de négociation, les deux perroquets, loin de se comporter de manière altruiste, ont tout de même su tirer profit de la situation en coopérant et en partageant la nourriture. Contrairement aux loups où seul le dominant accède à la récompense et ne partage pas, nous avons observé que Léo, le subordonné, n'accepte pas toujours les propositions injustes et parvient à faire changer Shango de dispositif (mais celui-ci ne partage pas non plus). Lors de l'expérience avec les chimpanzés, Melis et al. (2009) n'ont pas observé de partage de nourriture, peut-être parce que même dans l'option inéquitable, il y avait une récompense de chaque côté (mais pas la même quantité). Bien que les perroquets soient capables de communiquer de manière référentielle, très peu de communication vocale ou gestuelle ont été observées au cours des expériences. Lors des actions conjointes le fait de communiquer ses intentions aux autres, de les recruter, permettrait pourtant de synchroniser et de coordonner les actions ou encore de résoudre un conflit d'intérêt comme par exemple lors de l'expérience de négociation. Néanmoins, durant ces expériences conduites chez les primates, les individus n'ont pas non plus communiqué (**Article 2**).

Etude de la prosocialité

Au cours de nos expériences avec les 11 individus (de quatre espèces différentes), nous avons observé, comme chez les chimpanzés (Silk et al. 2005 ; Vonk et al. 2008) et les tamarins (Cronin et al. 2009), que les oiseaux ne profitaient pas de l'opportunité de délivrer de la nourriture à un congénère sans coût supplémentaire pour eux-mêmes. Ils ont tous arrêté de choisir le bouchon qui ne les récompensaient pas (nul ou altruiste). Comme les chimpanzés (Brosnan et al. 2005), les oiseaux n'ont pas maximisé le gain total possible en choisissant le bouchon prosocial qui aurait permis de recevoir une récompense à chaque essai, que l'individu soit testé ou partenaire. Comme les chimpanzés, les individus n'ont pas non plus développé des interactions réciproques (Brosnan & de Waal 2004; Brosnan et al. 2009; Pelé et al. 2010). Nous avons noté également que le mâle canindé a volé à deux reprises la récompense de la femelle après avoir choisi le bouchon prosocial. Il est possible que dans la situation où la récompense est répartie entre les individus (lorsqu'ils choisissent le bouchon prosocial) cette même récompense soit perçue comme moins importante, comparée aux situations où l'oiseau reçoit la totalité (en choisissant le bouchon égoïste). D'ailleurs on observe que Griffin émet des signaux de frustration dans cette condition prosociale, plus que dans la condition égoïste mais moins que dans la condition altruiste. Contrairement à nos prédictions, les oiseaux testés n'ont pas développé de préférence pour l'item prosocial et les perroquets gris de Nanterre ne se sont pas comportés différemment en fonction du partenaire avec lequel ils étaient testés. Ainsi, les individus n'ont pas prêté attention au sort de leur partenaire sauf peut-être Griffin qui en fin d'expérience a choisi à de multiples reprise l'item prosocial (dans le cas où il était le second à choisir) (**Article 4 et 5**).

Lorsque nous avons modifié la valeur de l'item prosocial en créant une situation inéquitable, les oiseaux testés n'ont pas réagi (comme les chimpanzés ; Braüer et al. 2006; Braüer et al. 2009) contrairement à ce qui avait pu être observé chez les capucins (Brosnan et al. 2010a) par exemple qui arrêtaient d'être prosociaux quand la différence entre la qualité (ou la quantité) des récompenses était trop grande (**Article 4**).

Dans l'expérience où un oiseau doit transférer un bouchon à l'autre, nous avons observé de nombreuses actions réussies même si les transferts directs de bec à bec ont été très rares. Encore une fois, Léo ne développe pas de préférence entre l'item égoïste et prosocial bien qu'en choisissant le premier il rend Shango réticent à coopérer. En effet, on observe que Shango arrête de transférer le bouchon égoïste à l'expérimentateur de telle sorte qu'aucun oiseau ne reçoit de récompense et il va parfois même jusqu'à prendre le bouchon égoïste et à le jeter par-dessus la table (**Article 4**).

Le fait que Léo n'ait pas de préférences vis-à-vis du sort de son partenaire se retrouve au niveau de l'absence de discrimination faite entre les items égoiste et prosocial, les individus testés ne considérant que leur propre situation. Des essais supplémentaires auraient pu permettre à Léo d'observer l'issue plus favorable provoquée par le choix de l'item prosocial. Ici, le peu d'essais, mais aussi le fait que parfois (et surtout au début) Shango transférait le bouchon égoïste a pu retarder l'apprentissage.

Dans l'expérience où les deux perroquets gris du Gabon jouaient avec des humains aux stratégies différentes (égoïste, altrusite ou imitateur), nous observons que les oiseaux tendent à suivre la stratégie de l'humain. Ainsi les oiseaux choisissent le bouchon égoïste quand l'humain est égoïste (aussi avec l'imitateur pour Arthur), hésitent entre les deux avec l'imitateur pour Griffin et avec le généreux pour Arthur. Griffin choisit préférentiellement le bouchon prosocial avec le généreux. Dans cette expérience on ne peut pas écarter le simple fait que les oiseaux imitent l'humain, ce qui dans tous les cas les conduient à recevoir une récompense. La préférence pour l'un ou l'autre des items peut également venir du fait que l'humain l'ait choisi au préalable. En effet, en fonction de la relation qu'un individu entretient avec un congénère, celle-ci peut l'amener à l'imiter même si il ne reçoit pas de récompense comme ce qui a été montré chez les capucins (Bonding-identification and Observationnal Learning ; Bonnie & de Waal 2007). De plus ces oiseaux ont l'habitude d'assister à des séances de Modèle/Rival durant lesquelles les humains leur montrent quoi faire (**Article 5**).

Nous avons testé plusieurs espèces de psittacidés avec des relations différentes entre les individus en pensant que la nature (frère, partenaire sexuel) et/ou la qualité (tolérance) de la relation influenceraient les résultats. Compte-tenu du faible nombre d'individus, il nous est difficile de généraliser les résultats aux espèces. Cependant l'absence de considération pour la situation du partenaire, observée chez nos 11 individus, tend à montrer que de façon spontanée, les psittacidés ne se comportent pas de manière prosociale dans des tâches artificielles, bien que nous observions des régurgitations entre les individus appartenant à des couples (mais aussi des paires de même sexe). Même si tester plus d'individus et lors de la période de reproduction pourrait peut-être conduire à d'autres données, la différence entre le comportement génétiquement prédéterminé de régurgitation et les réponses produites au cours des tâches artificielles est importante et nécessite des études en conditions contrôlées en laboratoire.

Etude de l'attribution de perception et d'intentions

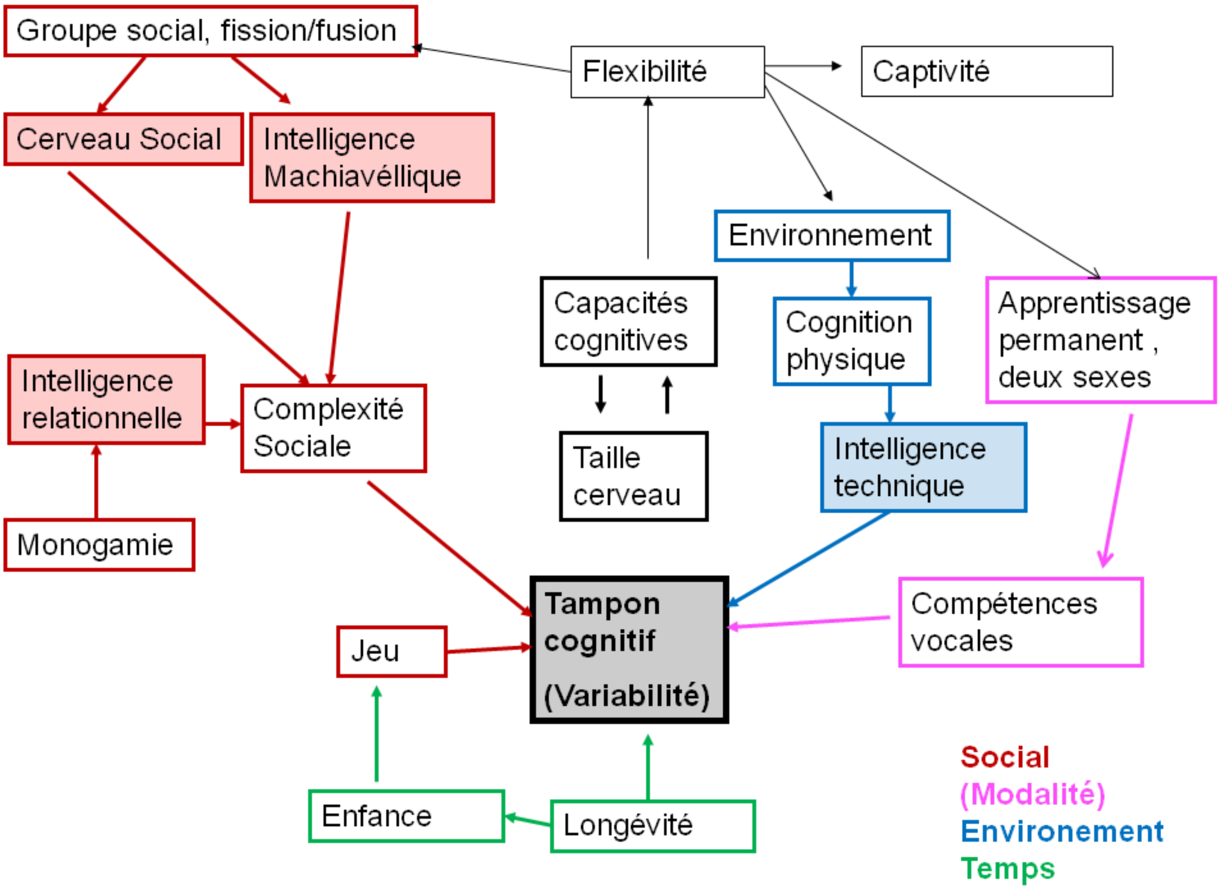
Comme les chimpanzés, il est possible que dans la tâche de négociation, les perroquets (surtout Shango) aient attribué des intentions à leur partenaire qui pouvait ne pas être disposé à coopérer parce qu'il aurait préféré l'autre solution (équitable). En effet, comme les primates, nos oiseaux ont réagi différemment en fonction des indices comportementaux disponibles lors des différentes situations. Néanmoins ces quelques données ne sont pas suffisantes pour conclure si les perroquets comprennent que les autres puissent avoir des états mentaux qui guident leurs actions (Penn & Povinelli, 2007; Penn & Povinelli, in press). Cependant, quelques anecdotes concernant le comportement d'Alex laissent à penser qu'il avait quelques attentes concernant la représentation des autres lorsqu'il leur demandait le nom d'un nouvel objet (ou une de ses caractéristiques). Ainsi nos trois perroquets, au cours de l'expérience d'attribution d'intentions, mordent le grillage quand l'humain n'est pas capable de leur donner une récompense et expriment leur frustration et émettent des cris de quémande quand ce dernier n'y est pas disposé. Dans le premier cas, il semble que les perroquets essayent de résoudre le problème en s'attaquant à l'obstacle alors que dans la seconde situation ils essayent d'attirer l'attention de l'expérimentateur. Les chimpanzés (Call et al. 2004) et les capucins (Philipps et al. 2009) n'ont pas montré de différence entre la condition « nargue » et la condition « bloqué » en ce qui concerne le temps de latence avant de quitter le dispositif et pour ce qui est de notre expérience, utilisant le temps de regard, nous n'avons pas mis en évidence de différence non plus. Les oiseaux ont cependant regardé ailleurs plus souvent dans la condition où l'expérimentateur était distrait et donc ne manipulait pas les graines. Ces oiseaux ont été élevés à la main et interagissent quotidiennement avec leurs soigneurs qu'ils considèrent comme faisant partie de leur groupe social. Ils sont habitués à nous voir manger et à réclamer (et à recevoir) de la nourriture et par conséquent cela peut expliquer pourquoi il est pertinent pour eux de distinguer les intentions humaines. Cette étude montre que les relations qui peuvent exister entre le propriétaire et l'oiseau sont complexes et soulignent l'importance des signaux de communications mais aussi leur diversité (**Article 7**). Dans l'expérience où les individus avaient le choix entre deux sets d'objets placés l'un derrière un écran transparent et le second derrière un écran opaque, les trois perroquets ont montré la même tendance, à savoir préférer l'écran transparent dans la condition contrôle (nourriture) et au contraire aller vers l'autre écran dans la situation test (objets interdits), mais seul le sujet le plus âgé a choisi significativement plus la solution de se cacher. Ceci peut éventuellement s'expliquer par une plus grande expérience de ce genre de situation. En effet, il a été observé chez les corneilles la nécessité d'avoir des expériences (de pillage notamment) pour pouvoir améliorer leur technique de cache et donc tromper leurs observateurs (Schloegl et al. 2007; Bugnyar et al. 2007). De manière générale les oiseaux ont pris leur décision plus rapidement dans la condition Contrôle que dans la condition Test, qu'il s'agisse de se rendre derrière l'écran transparent ou opaque. Ceci pourrait s'expliquer par le fait que l'oiseau comprend le risque encouru à interagir avec les objets ou alors qu'il est plus attirés par de la nouriture que par des objets. L'expérience va être poursuivie avec d'autres perroquets gris afin d'une part, de pouvoir confirmer les résultats mais également de différencier l'attribution de facultés de perceptions chez l'observateur (il ne me voit pas) de la simple perception de l'individu (je ne le vois pas). Ainsi nous voyons que les signaux employés au sein d'un système de communication hétérospécifique sont multiples et complexes (**Article 6**).

CONCLUSION ET PERSPECTIVES

Au cours des différentes expériences réalisées nous avons observé la capacité des psittacidés à s’adapter à leur environnement physique et social et à apporter des réponses comportementales parfois inattendues lors de la conception de l’expérience. Nous avons également observé les modulations d’expression des comportements en fonction du contexte. Pour ce qui est des comportements de coopération observés, plusieurs hypothèses peuvent apporter une explication à commencer par le fait que ces espèces vivent longtemps au sein de groupes stables et avec le même partenaire sexuel tout au long de leur existence, ainsi ils doivent faire au mieux pour préserver cette relation (Emery et al. 2007). De plus il n’est pas impossible qu’au cours de leur vie, les oiseaux puissent être amenés à agir de manière réciproque bien qu’il semble que cela ne soit pas volontaire. Dans le cadre de nos expériences, il est évident que l’apprentissage à jouer une rôle important dans les perfomances observées.

La flexibilité comportementale, selon Sol (2009), serait permise par un support neuronal développé et donc un gros cerveau. En ce qui concerne les psittacidés je propose ici une version adaptée de cette hypothèse en tenant compte plus précisément des caractéristiques de ces espèces. Le schéma reprend les diverses hypothèses et les interactions éventuelles qu’elles développent entre elles. J’ai considéré à la fois les facteurs sociaux tels que la vie en groupe, les dynamiques sociales de fission-fusion et la monogamie mais aussi les caractéristiques environnementales (explorations en trois dimensions, carte cognitive des lieux de fructification, travail pour accéder à la nourriture). Les autres éléments caractéristiques sont la communication vocale qui concerne males et femelles et le fait que les individus peuvent apprendre tout au long de leur vie, ensuite la durée de vie des animaux qui sont donc amenés à interagir de façon répétée avec leurs congénères, qui présentent une période juvénile importante et des comportements de jeux.

Schéma récapitulatif des différentes hypothèses avancées pour expliquer l'origine d'un cerveau plus développé



Les zones colorées correpondent aux hypothèses proposées. Le sens des flèches a été choisi afin d'illustrer les caractères qui étaient pris en considération dans les hypothèses évoquées. Les couleurs correspondent aux différents paramètres qui peuvent, selon moi, être à l'origine d'une variabilité des informations à traiter et par conséquent de la diversité des réponses comportementales à apporter. Ainsi on retrouve les interactions avec l'environnement physique (en bleu) et social (en rouge) mais aussi le facteur temps (en vert) et une des modalités de communication à savoir les vocalisations (en rose).

Bien entendu le support neuronal et les capacités cognitives sont liées et interagissent l'une sur l'autre. En effet, la taille du cerveau influence les performances mais les les interactions avec l'environnment modifie également la structure cérébrale. La flexibilité comportementale permise par les connexions neuronales permet d'expliquer les comportements observés lors des expériences.

Bien évidemment des variations peuvent exister en fonction des espèces compte tenu de la diversité des lieux et mode vie : ainsi le kakapo est solitaire, nocturne et ne vole pas, le kéa vit dans des conditions environnementales plus contraignantes ensuite la taille des groupes sociaux peut varier de quelques individus (essentiellement des familles) pour les aras, à plusieurs centaines chez les gris du Gabon et plusieurs milliers pour les perruches ondulées par exemple.

Ces études ont permis de mettre en évidence que différentes espèces de psittacidés étaient capables de résoudre des tâche physiques nécessitant l'intervention de deux individus. Cependant de manière générale, les oiseaux semblent préférer agir seuls autant que possible plutôt que coopérer. Bien souvent ils ont des difficultés à prendre en compte leur partenaire.

On remarque que les relations entre les individus peuvent influencer le résultat. Bien souvent la plupart de nos expériences n'étaient pas pertinentes d'un point de vue écologique car 1) les animaux vivent dans un milieu où la nourriture est abondante et facilement accessible pour un individu seul et 2) il s'agit d'espèces sauvages apprivoisées qui n'ont pas été sélectionnées pour communiquer avec des êtres humains. Cependant au cours de nos travaux, nous avons mis en évidence des comportements soulignant des capacités latentes similaires à ce qui peut être mis en œuvre à l'état naturel. En effet, les oiseaux interagissent avec leurs congénères et doivent être capables de tirer de l'information pertinente à partir de l'observation des individus et de leurs interactions (comme lors de l'apprentissage de la communication vocale par exemple). De même des comportements de coopération existent chez ces oiseaux, qu'il s'agisse de l'élevage des jeunes ou de la défense du territoire, bien que des actions conjointes puissent être réalisées sans considération pour le comportement des congénères. De même les individus d'un couple ou d'une famille se toilettent mutuellement réalisant ainsi des comportements réciproques et enfin les males régurgitent aux femelles lors de la période de reproduction (altruisme à court terme, l'investissement permétant de maintenir la relation avec la partenaire et donc d'assurer la paternité à la prochaine ponte).

Il semble que les actions coopératives observées chez les espèces testées étaient la conséquence de l'expression de leur flexibilité comportementale ; c'est-à-dire le résultat d'actions individuelles basées sur une motivation propre de l'oiseau qui par le fait que les animaux partagent le même objectif et supporte la proximité, conduisent à une coopération. Cependant quelques éléments laissent à penser que les individus comprennent parfois la nécessité d'un partenaire. En effet, au cours des différentes tâches, les oiseaux ont montré qu'ils prenaient en considération la présence du partenaire (mais non pas son rôle).

Concernant les perroquets gris du Gabon, il s'agit d'individus éclos en captivité et élevés à la main, ils ont tendance à développer des relations privilégiées vis-à-vis d'un être humain en particulier et considèrent les personnes constituant l'environnement social comme faisant partie du groupe social. C'est ainsi que les oiseaux peuvent entrer dans des processus de compétition pour obtenir l'attention ou une récompense, de même ils sont capables d'adapter leurs comportements en fonction des indices fournis par l'humain comme le pointage, le regard (où trouver ou éviter une ressource) ou encore de déterminer les intentions d'un expérimentateur (distrait, pas capable, pas décidé, prosocial, égoïste).

Limites de l'étude

Le nombre d'individus étudiés constituent la limite majeure de notre travail. En effet, les résultats obtenus ne sont pas extrapolables au reste de l'espèce (et de la famille) néanmoins nous pouvons tout de même conclure quant à leur capacité à résoudre ces tâches artificielles. Dans le domaine de la cognition, il suffit que l'on mette en évidence une capacité chez un seul individu pour conclure qu'elle existe au sein de l'espèce . En cas d'échec rien ne peut être affirmé. Il est important également de préciser que les connaissances actuelles sur ces animaux proviennent en grand majorité de quelques individus ; Alex (et quelques autres) pour l'utilisation du langage humain et les trois individus de l'université de Nanterre pour les études de cognition sociale. Détenir des psittacidés en captivité constitue une source d'interrogation d'un point de vue éthique (tout comme beaucoup d'animaux sauvages) de par les besoins en termes d'activités et d'espace de ces espèces pour une expression normale et complète de leur répertoire comportemental. Par conséquent, augmenter l'effectif passe par l'établissement de collaborations évitant ainsi d'introduire de nouveaux individus. De même, de manière plus pratique ces oiseaux demandent de l'espace et représentent un coût à l'achat et à l'entretien et les soins quotidiens sont contraignants pour la recherche.

Le faible nombre d'individus et de groupes fait que des variables telles que le sexe, l'âge ou les différences de relations sociales (hiérarchie par exemple) n'ont pas pu être testées. En effet, les primatologues observent des différences entre des groupes de chimpanzés dans la manière dont ils coopèrent ou encore si ils partagent de la nourriture par exemple. De même, des études réalisées avec les kéas (*Nestor notabilis*) montrent également que la résolution de tâches dépend du groupe. Ainsi dans l'étude de Tebbich et al. (1996), la non-linéarité de la hiérarchie permet aux oiseaux de trouver un subordonné qui sera alors contraint de coopérer. Ce comportement de menace n'a pas été observé dans les deux autres études (voir revue de Huber et al. 2008).

Nous manquons également de données concernant le fonctionnement des groupes de perroquets gris du Gabon, l'organisation sociale précise mais aussi l'existence d'une hiérarchie ou encore de la défense d'un territoire par exemple. Il serait également pertinent de tester des couples et des dyades (non appariées) afin de mettre en évidence d'éventuelles différences comme le fait de ne coopérer qu'avec son partenaire sexuel par exemple, comme cela a été observé chez les aras chloroptère (Spitzhorn 2009). En effet, la monogamie semble être un élément à considérer également chez les psittacidés comme facteur influençant le développement du substrat neuronal. De même, il serait intéressant d'observer la coopération des individus dans le cadre d’une compétition avec d’autres congénères comme ce que pourrait expérimenter un couple qui cherche un creux d’arbre pour établir son nid. Le nombre d’espèces testées constitue également une limite en ce qui concerne les modèles d’organisation sociale. En effet, il aurait été souhaitable de tester des oiseaux présentant quelques caractéristiques particulières dans leur mode de vie tel que des espèces polyandrique ou encore des perroquets qui coopèrent à plus de deux pour élever les petits. Cependant, ceci est toujours possible notamment dans le cadre d’un projet plus large. Les oiseaux ont été testés dans des tâches artificielles et dans le cadre d’interactions hétérospécifique (avec l’Homme). Bien que cette approche ne soit pas pertinente en ce qui concerne la biologie des espèces, elle permet néanmoins d’étudier, dans des conditions controlées, les capacités cognitives de ces oiseaux en nous affranchissant des comportements pré-déterminés génétiquement (comme la régurgitation ou le harcèlement de prédateur). Ensuite le fait d’avoir testé des oiseaux élevés à la main (dans le cas des perroquets gris du Gabon) constitue un biais concernant les résultats obtenus cependant, comme pour les primates, les interactions avec l’homme sont inévitables en captivité et ne peuvent que modifier l’expression de compétences déjà existantes aussi bien vis-à-vis des interactions sociales que des compétences liés à l’attribution d’états mentaux. Des différences entre les individus sauvages et imprégnés peuvent survenir notamment lors de l’emploi d’un système hétérospécifique de communication référentielle. Ainsi nos trois perroquets utilisaient un même son (élément du répertoire vocal, spécifique du groupe) pour réclamer un item (alimentaire ou non) alors qu’ils utilisaient des labels différents en fonction de la catégorie de l’objet tels que ‘stylo’ ou ‘rouleau’ pour désigner un objet ou ‘cacahuète’ ou ‘raisin’ pour désigner un aliment (Giret et al. 2009 c).

Projet PReCog (Parrot Research group on Cognition)

A partir de 2009, j'ai débuté mon projet de créer une base de données regroupant les travaux sur les psittacidés et ce dans le domaine de la cognition physique et sociale mais aussi de la communication. Afin de développer une approche intégrative des psittacidés nous aborderons aussi la biologie, la conservation et les pathologies. Il s'agit de mettre à disposition des chercheurs les articles, photos, vidéos, protocoles et fichiers sons concernant ces espèces. Le projet prévoit également de développer un réseau de collaborations réunissant des équipes et des laboratoires différents, partout dans le monde afin d'améliorer nos recherches en augmentant le nombre d'individus (ce qui est très souvent reproché lors de la soumission d'articles) mais aussi de comparer des espèces ou des conditions de vie.

C'est dans cet esprit que j'ai réalisé mes travaux de thèse, notamment en mettant en place des collaborations, puis des protocoles de recherches. Ainsi je me suis rendu dans les universités de Prague, de Vienne, d'Hambourg et d'Harvard pour des périodes plus ou moins longues (une à six semaines) grâce à l'obtention de financements. Certaines de ces collaborations ont donné lieu à des publications. Un site internet est en cours de création afin de faciliter les échanges mais aussi de mettre à disposition des autres chercheurs et du public les connaissances actualisées.

Ce projet va se poursuivre par la suite grâce à la participation de structures d'accueils (Ferme de Conservation zoologique à Vierzon, France) et de collaborateurs (Dr. Lindova, Dr. Pepperberg). Un projet Egide en collaboration avec l'Université de Prague a été déposé pour 2011 afin de poursuivre nos travaux sur les capacités cognitives des psittacidés dans des conditions sociales.

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Compétences informatiques et linguistiques

- Anglais et Espagnol: lu, écrit et parlé (diplômes du CLES 2 et du DELE)
- Avisoft, Excel, Powerpoint, SigmaStat, The Observer, Word

Autres diplômes (Ecole Nationale Vétérinaire d'Alfort)

En cours -Certificat d'Etudes Supérieures en pathologie aviaire

2008 -Certificat d'Etudes Supérieures en expérimentation animale niveau 1 (agrément préfectoral pour l'expérimentation sur vertébrés n°92-380)

Stages de Formation

2010 -Séjour recherche à **l'Université d'Harvard** (Dr I. PEPPERBERG) Octobre. Etude de la cognition physique et sociale des perroquets gris d'Afrique (*Psittacus erithacus*)

2010 -Séjour de recherche à **l'Université d'Hambourg** (Dr R. WANKER) Janvier-Mars. Etude des capacités d'imitation et de coopération des Touis à lunette (*Forpus conspicilliatus*).

2009 -Séjour de recherche à **l'Université d'Harvard** (Dr I. PEPPERBERG) Juillet. Etude de la cognition physique et sociale des perroquets gris d'Afrique (*Psittacus erithacus*).

2008-2009 -Stage au sein de **l'Agence Française pour la Sécurité Sanitaire des Aliments** de Maisons-Alfort (Dr K. LAROUCAU) dans le cadre du projet de la région Ile-de France : '*Pigeons en ville : Ecologie de la réconciliation et biodiversité urbaine*'. Etude épidémiologique de la prévalence de Chlamyodiophila au sein de la population de pigeons de la région parisienne. Analyses bactériologiques et génotypages.

2008 -Mandat sanitaire (Ecole Nationale Vétérinaire d'Alfort).

2007 -Stage vétérinaire au Biodôme de Montréal (Septembre).

2005-2006 -Erasmus à l'Université Autonome de Barcelone.

2005 -Stage vétérinaire au zoo de Sydney (Juillet).

Appartenance à des sociétés savantes

Membre des Conseils d'Administration de la Société Française pour l'Etude du Comportement Animal (SFECA) et de la Société Européenne d'Ethologie Vétérinaire des Animaux Domestiques (SEEVAD).

Membre de l'Association for the Study of Animal Behaviour (ASAB; **membre du comité d'éthique**), l'International Society of Applied Ethology (ISAE), l'European Society of Veterinary

Clinical Ethology (ESVCE), l'Association Française des Sciences et Techniques des Animaux de Laboratoire (AFSTAL), la Société Française d'Acoustique (SFA), l'Association pour la Recherche Cognitive (ARCo).

Encadrement et jury

Hélène Normand (stage facultatif M2), Lauriane Rat-Fischer (stage obligatoire M2), Mathilde Lalot (stage obligatoire M1), Eléonore de Meyrignac (stage obligatoire véto 2), Julie Simon (stage facultatif M1), Sophie Duhautois (stage facultatif M1), Paul Maître (stage facultatif M1), Sara Hoummady (stage obligatoire véto 2), Franz Heidocker (stage facultatif M2), Stephane Peyregne (stage facultatif L3), Nastia Mauny (stage obligatoire L3), Agathe Colléony (stage obligatoire M1), Agatha Liévin (stage obligatoire M1), Vanessa André (stage obligatoire L3), Cynthia Froc (stage facultatif M1), Raphaelle Malassis (stage facultatif L2), Nicolas Dollion (stage facultatif M1), Christelle Bender (stage facultatif M1), Rémi Aubrun (stage facultatif L3), Laureline Chaise (stage facultatif véto 2), Jeanne Bovet (stage facultatif M1), Anastasia Krasheninnikova (stage facultatif M2), Université d'Hambourg, dans le cadre du projet européen INCORE.

Accueil de lycéens dans le cadre de l'association Paris Montagne, deux étudiants, chacun durant une semaine, pour leur faire découvrir le monde la recherche.

Participation au jury de Zina Skandrani, Master 2 du Cogmaster, réalisé sous la direction du Pr Hauser. (Juin 2010) 'Do dogs (*Canis lupus familiaris*) acquire categories among humans that guide their preferences?'

Activité d'enseignement

Université Paris Ouest Nanterre La Défense

Tutorat/TD : Biologie, Neurobiologie, Psychophysiologie, Ethologie, Méthodologie (110h)

TP : Psychobiologie comparée (132h) et CM : Ethologie (10h)

Université Paris Descartes et Ecole Nationale Vétérinaire d'Alfort

CM : Ethologie (12h)

Activités de Recherche et de Développement :

Recherche dans le domaine de l'éthologie fondamentale :

-Etude de la cognition sociale chez les psittacidés (Prague, Vienne, Hambourg, Boston).

-Evaluation du bien être animal par l'étude des biais cognitifs.

Recherche dans le domaine de l'éthologie appliquée :

-Aménagement du milieu pour les psittacidés.

-Développement de produits olfactifs pour les chiens (ENVA/Paris 13/Nat'Ex Biotech).

-Etude de l'occupation de l'espace au sein d'un groupe de chien (AVA).

Recherche dans le domaine de la clinique vétérinaire :

-Pathologies aviaires (Chlamydiophilose, Virose des psittacidés) (ENVA/AFSSA).

-Méthodes de contentions et prélèvements chez les psittacidés.

-Etude de la Desloréline pour prévenir les tumeurs mammaires de la rate (Virbac).

Implication scientifique

Projets en cours

-**Fondateur du projet PreCog** (Parrot Research group on Cognition): Création d'une base de données regroupant l'ensemble des connaissances disponibles concernant les psittacidés et mise en place de collaborations internationales pour la réalisation de projets communs.

-Collaboration avec le Dr Irene PEPPERBERG de **l'Université d'Harvard,** le Dr Ralf WANKER de **l'Université d'Hambourg,** le Dr Jitka LINDOVA de **l'Université de Prague** et le Pr Shigeru WATANABE de **l'Université de Tokyo** sur la cognition physique et sociale des psittacidés.

-Membre du Projet Odeur, développé en collaboration avec l'ENVA (Pr DEPUTTE, Dr REYNAUD), l'Université Paris 13 (Dr FERON) et l'entreprise Nat'Ex Biotech.

-Collaboration avec le Dr GROSSET et le laboratoire Virbac pour l'étude pharmacologique de la Desloréline dans la prévention des risques de tumeur mammaire chez la rate.

-Membre du pôle identitaire n°5 de l'Université Paris Ouest Nanterre la Défense : 'L'humain en
devenir' ; atelier 'Cognition et Emotion' sous la direction de Gérard LEBOUCHER.

-**Co-organisateur du 1er Symposium d'éthologie vétérinaire, 10-11 Septembre 2011, ENVA.**

Projets passés

-Membre du **projet européen 'What does it mean to be human'** (6th PCRD ; Origins of referential communication ; projet achevé fin 2008) et **INCORE (Integrating Cooperation Research Across Europe** ; projet achevé fin 2010) sous la direction de Dalila BOVET.

-Membre du projet ‘L e Pigeon en ville : Ecologie de la réconciliation et gestion de la nature’ de la région Ile-de-France (Partenaires : Orsay, MNHN, LPO, AERHO).

-**Organisateur du symposium ‘Cooperation : cognitive processes, tolerance & efficiency’ durant le congrès de l’European Conference of Behavioural Biology 2010, Ferrara, Italie.**

Expertise

-**Ethic reviewer pour *Animal Behaviour***

-**Membre du comité d’éthique pour l’expérimentation animale Charles Darwin** (enregistré auprès du CNREEA sous le numéro 05)(6 dossiers par mois environ).

-Membre du comité scientifique de la **Fondation Droit Animal, Ethique et Sciences.**

-Membre du comité scientifique de la **Ferme de Conservation Zoologique**.

-Consultant pour le magazine ‘*Science & Vie*’ sur les questions de comportement et de bien-être animal (Les poissons ressentent-ils de la douleur ? Consultation du 17 mars 2010)

-Membre du groupe de travail pour une commission éthique à l’Université Paris Ouest Nanterre la Défense pour la recherche en psychologie humaine.

-Membre du groupe de travail pour la création d’un groupe d’étude spécialisé en bioacoustique au sein de la **Société Française d’Acoustique**.

Communications scientifiques

Publications dans des revues internationales à comité de lecture

Articles acceptés ou en révision

3) **Péron F**. Rat-Fischer L., Nagle L. & Bovet D. 2010 **Unwilling versus unable: Do grey parrots understand human intentional actions?** *Interaction Studies* **11** (3) 428-441

2) Giret N., **Péron F**., Lindovà J., Tichotová T., Nagle L., Kreutzer M., Tymr F. & Bovet D. 2010 **Referential learning of French and Czech labels in African grey parrots (*Psittacus erithacus*): different methods yield contrasting results.** *Behavioural Processes,* **85** (2) 90-98

1) Giret N., **Péron F**., Nagle L., Kreutzer M. & Bovet D. 2009 **Spontaneous categorization of vocal imitations in African grey parrots (*Psittacus erithacus*).** *Behavioural Processes,* **82** (3) 244-248

-**Guidelines for the treatment of animals in behavioural research and teaching** *Animal Behaviour* (revised in 2010, will be publish in 2011)

-**Péron F**., Rat-Fischer L., Lalot M., Nagle L. & Bovet D **Cooperative problem solving in African grey parrots (*Psittacus erithacus*).** In revision *Animal Cognition*

Articles soumis ou en preparation

-**Péron F**., Rat-Fischer L., Lalot M., Nagle L. & Bovet D **Social preferences and negotiations during a cooperative task in African grey parrots (*Psittacus erithacus*).** Submitted

-**Péron F.**, Colléony A., Liévin A., Nagle L. & Bovet D. **Do psittacids take others' welfare into account?** Submitted

-**Péron F.**, Liévin A., Colléony A., Nagle L. & Bovet D. **Cooperative problem solving in budgerigars (*Melopsittacus undulatus*)** Submitted

-**Péron F.**, Chardard C., Nagle L. & Bovet D. Do African grey parrots (*Psittacus erithacus*) know what an experimenter does and does not see? Submitted

-**Péron F**., John M., Sapowicz S., Bovet D. & Pepperberg I. **Do grey parrots learn prosociality?** Submitted

Publications dans autres revues

-**Péron F. Capacités cognitives des perruches** soumis. *Revue des oiseaux exotiques*

-**Péron F.** & Grosset C**. Dilatation du proventricule : États actuel des connaissances** soumis. *Revue des oiseaux exotiques*

6) **Péron F**. 2011 **Les animaux sont-ils sensibles à l'injustice?** *Revue de la Fondation Droit Animal, Éthique et Sciences*. (accepté)

5) **Péron F**. 2011 **Les interactions hommes-perroquets: comment communiquer?** *Revue de la Fondation Droit Animal, Éthique et Sciences*. (accepté)

4) **Péron F**. 2011 **Travailler ensemble pour obtenir plus: la coopération chez les perroquets**. *Revue de la Fondation Droit Animal, Éthique et Sciences*. (accepté)

3) **Péron F**. 2010 **Critères d'évaluations de la douleur chez les rongeurs**. *Revue de la Fondation Droit Animal, Éthique et Sciences*. Oct

2) **Péron F**. 2010 **L'identification des rongeurs en laboratoire : une cause potentielle de douleurs**. *Revue de la Fondation Droit Animal, Éthique et Sciences.* Oct

1) Grosset C. & **Péron F**. 2010 **Viroses des Psittacidés, actualités diagnostiques et thérapeutiques**. *L'Essentiel*, **176,** 33-35.

Autres publications

-**Péron F**. Coopération et compétition chez les psittacidés : Implication des processus cognitifs. 2010 (thèse de doctorat en éthologie)

-Chateigner C., **Péron F**. & Zebdi R. 'Les journées de la recherche en Psychologie'. Sous la direction de G. Leboucher et P. Attigui. Université Paris Ouest Nanterre. 2009.

-**Péron F**. Apprentissage référentiel chez les perroquets gris du Gabon (*Psittacus erithacus*): Approche expérimentale. 2008 (thèse de doctorat vétérinaire)

Conférences en tant qu'invité

1) **Péron F**. **Le perroquet: une cervelle d'oiseau?** ENVA 25/11/08.

2) Péron F. **Intéractions homme-perroquet**. ENVA 21/01/10

3) Péron F. Social Cognition of African grey parrots Evolution and development of logic and sensibility. Université de Keio, Tokyo, Japon**,** 7-10/03/10.

Invité à des séminaires

1) **Péron F**. **The social brain hypothesis in psittacids**, Université de Vienne, 29/10/08.

2) **Péron F**. **Communicative and cognitive abilities of African grey parrots (*Psittacus erithacus*),** Université de Prague, République Tchèque, 11/05/09.

Communications orales

1) **Péron F**., Giret N., Nagle L., Kreutzer M. & Bovet D. **Comparison of three methods for referential communication learning in African grey parrots (*Psittacus erithacus*)**. Fourth meeting Ecology & Behavior, Toulouse, France, 15/03/08.

2) **Péron F**., Giret N., Nagle L., Kreutzer M. & Bovet D. **Referential communication learning with human words in African grey parrots (*Psittacus erithacus*).** 5ième GDR d'Ethologie, Villetaneuse, France, 15/05/08.

3) Giret N., **Péron F**., Nagle L., Kreutzer M. & Bovet D. **Referential acquisition of human labels in African grey parrots (*Psittacus erithacus*): efficiency of a new learning method**; 4th European Conference on Behavioural Biology, Dijon, France, 18-20/07/08.

4) **Péron F**., Giret N., Nagle L., Kreutzer M. & Bovet D. **Spontaneous categorization in African grey parrots (*Psittacus erithacus*) during referential communication learning**. Vocal Communication in birds and Mammals, St Andrews, Scotland, 31/07 – 2/08/08.

5) Rat-Fischer L., **Péron F**., Nagle L & Bovet D. **Avian social cognition: Tolerance, synchronization, coordination and cooperation in African grey parrots (*Psittacus erithacus*).** 5th Meeting Ecology & Behavior. Lyon, France, 6-10/04/09.

6) **Péron F**., Lalot M., Nagle L & Bovet D. **Do African grey parrots (*Psittacus erithacus*) show prosocial behaviour?** Social genes, social brain and socials minds; Compcog Budapest, Hongrie, 13-16/05/09.

7)**Péron F**. **Coopération et sélection naturelle: une réelle contradiction?** Module pluridisciplinaire: l'évolution en chantier. Université de Nanterre, France, 3/06/09.

8) Rat-Fischer L., **Péron F**., Nagle L., Bovet D. **Capacités cognitives des perroquets gris du Gabon (*Psittacus erithacus*) dans une tâche de coopération.** Supporting engagement of female researchers, 2nd Incore workshop. Université de Nanterre, France, 1-3/07/09.

9) **Péron F**., Nagle L & Bovet D. **African grey parrots: an avian model for social intelligence studies**. Symposium: The use of vertebrate model systems to study social evolution, Adelboden, Suisse, 15-18/08/09.

10) **Péron F**. **Un perroquet peut en cacher un autre : les aléas de la recherche en cognition sociale**. 15ième congrès des étudiants-chercheurs du Muséum National d'Histoire Naturelle, Paris, France, 14-15/12/09.

11) **Péron F**., Giret N., Lindovà J., Tichotová T., Nagle L., Kreutzer M., Tymr F. & Bovet D. **Referential learning of words in African grey parrots (*Psittacus erithacus*): different methods yield contrasting results** The 5th topical meeting of the Ethologische Gesellschaft, Berlin, Allemagne, 21-23/02/10.

12) **Péron F**., Rat-Fischer L., Heidocker F., Nagle L. & Bovet D. **Coordination and negotiation during a cooperative task in African grey parrots**. ECBB, Ferrara, Italie, 15-18 Juillet 2010.

13) **Péron F**., Wanker R., Nagle L. & Bovet D**. From social manipulation to altruism: flexible cooperation in psittacids.** Final TECT-INCORE School: 'Cooperators since life began', Budapest, Hongrie, 11-15 Septembre 2010

14) **Péron F**., Rat-Fischer L., Lalot M., Simon J., Duhautois S., Maître P., Heidocker F., Nagle L. & Bovet D. **Cooperation in African grey parrots: dealing with the apparatus and the partner**. INCORE conference. Cooperation: an interdisciplinary dialogue. Budapest, Hongrie, 17-18 Septembre 2010.

Communications affichées

1) **Péron F.**, Giret N., Nagle L., Kreutzer M. & Bovet D. **How parrots (*Psittacus erithacus*) say the words**. Umwelt: How living beings perceive the world, Paris, France, 18/02/08.

2) **Péron F.**, Giret N., Nagle L., Kreutzer M. & Bovet D. **Catégorisation spontanée chez des perroquets gris du Gabon (*Psittacus erithacus*)**. L'environnement périnatal : incidences sur le développement psychobiologique, Rouen, France, 20/03/08.

3) **Péron F.**, Giret N., Nagle L. & Bovet D. **Pterotillomania**. 5ème GDR d'éthologie, Villetaneuse, France, 15/03/08.

4) **Péron F.**, Giret N., Nagle L., Kreutzer M. & Bovet D. **Catégorisation spontanée d'items chez des perroquets gris du Gabon (*Psittacus erithacus*)**. 5ème GDR d'éthologie, Villetaneuse, France, 15/03/08.

5) **Péron F.**, Giret N., Nagle L. & Bovet D. **Est-il éthique de garder des perroquets en captivité? L'exemple de la pterotillomanie chez des perroquets gris du Gabon (*Psittacus erithacus*)**. 34^{e} Colloque de l'AFSTAL, Strasbourg, France, 4-6/06/08.

6) **Péron F.**, Giret N., Nagle L., Kreutzer M. & Bovet D. **African grey parrots (*Psittacus erithacus*) are able to categorise items spontaneously using human words**. 4th European Conference on Behavioural Biology, Dijon, France, 18-20/07/08.

7) **Péron F.**, Giret N., Nagle L., Kreutzer M. & Bovet D. **Les facteurs influençant l'apprentissage d'une communication référentielle chez des perroquets gris du Gabon (*Psittacus erithacus*)**. Société Française de Psychologie, Bordeaux, France, 10-12/09/08.

8) **Péron F.**, Giret N., Nagle L., Kreutzer M. & Bovet D. **Convergences des mécanismes d'apprentissage et d'emploi des mots chez des perroquets gris du Gabon (*Psittacus erithacus*) et chez l'homme ?** Systématique et comportement, journées annuelles SFS, Paris, France, 1-2/10/08.

9) Rat-Fischer L., **Péron F**., Nagle L., Giret N., Al Aïn S., Kreutzer M., Vick S.J., Anderson J.R. & Bovet D. **Etude de la cognition chez les perroquets gris du Gabon (*Psittacus erithacus*).** Cognivence, forum des sciences cognitives, Paris, France, 23/03/09.

10) **Péron F**., Rat-Fischer L., Nagle L & Bovet D. **Cognition sociale chez les Psittacidés: le comportement de coopération.** Colloque Jeunes Chercheurs en Sciences Cognitives. Toulouse, France, 09-11/06/09 (Prix du meilleur poster).

11) Rat-Fischer L., **Péron F**., Nagle L & Bovet D. **Coopération pour la résolution d'un problème chez les Gris du Gabon (*Psittacus erithacus*).** Société Française de Psychologie. Toulouse, France, 17-19/06/09.

12) **Péron F**., Rat-Fischer L, Nagle L & Bovet D. **Social interactions in Psittacidae during a cooperative task.** 31th International Ethological Conference. Rennes, France 19-24/08/09. (Bourse de la SFECA)

13) Bovet D., Giret N., **Péron F**., Albert A., Nagle L., MiklÓsi A. & Kreutzer M. **Functionally referential communication skills in African grey parrots (*Psittacus erithacus*)** 31th International Ethological Conference. Rennes, France, 19-24/08/09.

14) **Péron F**., Rat-Fischer L., Nagle L. & Bovet D. **Le rôle du partenaire dans la résolution d'une tâche de coopération.** PIRSTEC, Paris, France, 23/10/09.

15) **Péron F.** & Bovet D. **Le perroquet gris du Gabon : interprète et messager universel.** Cognifiction - PIRSTEC, Paris, France, 23/10/09.

16) **Péron F**., Duhautois S., Simon J., Rat-Fischer L., Nagle L. & Bovet D. **Different role taking in a cooperative task in African grey parrots (*Psittacus erithacus*): specialisation or task misunderstanding.** ASAB winter meeting, London, UK, 3-4/12/09.

17) Péron F., Liévin A., Colleony A., Malassis R., Dollion N., Nagle L. & Bovet D**. Testing cooperative abilities in budgerigars (*Melopsittacus undulatus*)** INCORE conference. Cooperation: An Interdisciplinary Dialogue. Budapest, Hungary. 17-18/09/10

18) Péron F., John M., Sapowicz S. & Pepperberg I.M**. African grey parrots did not maximize the payoff when they play at a token exchange task successively.** INCORE conference. Cooperation: An Interdisciplinary Dialogue. Budapest, Hungary. 17-18/09/10

19) Péron F., Colleony A., Liévin A., Malassis R., Dolion N., Nagle L. & Bovet D. **Prosocial behaviour as a condition to maintain cooperation in a token exchange task in African grey parrots.** INCORE conference. Cooperation: An Interdisciplinary Dialogue. Budapest, Hungary. 17-18/09/10

20) Péron F., Lalot M., Simon J., Duhautois S., Froc C., Aubrun R., Nagle L. & Bovet D **Testing prosociality in psittacids** INCORE conference. Cooperation: An Interdisciplinary Dialogue. Budapest, Hungary. 17-18/09/10

21) Péron F., Giret N., Nagle L., Kreutzer M. & Bovet D. **Human-parrot interactions: How to communicate?** ASAB winter meeting, London, 2-3/12/2010

Financements obtenus

Allocation ministérielle *(49000 euros),* Monitorat (*10000 euros*), Bourse de l'Université Kéio de Tokyo (*3200 euros*), Bourse INCORE *(2750 euros),* Fondation Dufrenoy *(2400* *euros)*, Bourse ED 139 *(2000 euros)*, Bourse Aires culturelles 09 *(1500 euros)*, Financement LECC (*580 euros*), Financement UFR SPSE *(250 euros)*, Bourse SFECA *(250 euros)*, Bourse ESF-Compcog *(250 euros)*.

Compétition et coopération chez les psittacidés : implication des processus cognitifs

Résumé –Les animaux vivant au sein de groupe sociaux doivent gérer des interactions diverses et multiples avec leurs congénères. L’objectif de ma thèse portait sur les comportements sociaux chez les pisttacidés et plus précisément l’évaluation de leur aptitude à adapter leurs comportements vis-à-vis d’un congénère ou d’un humain, qu’il s’agisse d’actions conjointes, d’attributions d’états mentaux ou de comportements prosociaux. Les oiseaux testés (perruche et gris du Gabon) ont été capables de coopérer et les perroquets ont appris à attendre le partenaire et à prendre en compte la nécessité de la présence d’un partenaire mais pas son rôle. Les quatre espèces de psittacidés testées n’ont pas profité de l’opportunité de récompenser un partenaire sans coût supplémentaire. Les gris du Gabon ont montré qu’ils étaient capables d’adapter leurs comportements en fonction de l’état attentionnel et des intentions d’un expérimentateur.

Mots clés *: Cognition sociale, Coopération, Comportement prosocial, Théorie de l’esprit.*

Competition and cooperation in psittacids: cognitive processes implication

Abstract-Animals living in social groups have to manage divers and multiple interactions with their conspecifics. My thesis dealt with social behaviours in psittacids and more precisely the valuation of their ability to adapt their behaviours according to a partner whether it was cooperative actions, mental states attribution or prosocial behaviours. Tested birds (budgerigars and grey parrots) were able to cooperate and grey parrots learned to wait for the partner and took into account the necessity of the presence of a partner but not his role. The four psittacids species tested did not take the advantage to deliver food to a partner at no supplementary cost. Grey parrots showed that they were able to adapt their behaviours according to the attentional state and the intentions of an experimenter.

Keywords*: Social cognition, Cooperation, prosocial behaviour, Theory of mind.*