Stratégies comportementales et cinématiques de la préhension chez les primates

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Stratégies comportementales et cinématiques de la préhension chez les primates

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"L’intelligence animale n’est pas une intelligence humaine *moins évoluée* que celle de l’homme, mais tout simplement une intelligence *différente*."

Dominique Lestel

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INTRODUCTION GÉNÉRALE

La "préhension" du latin *prehensio,* lui-même dérivé de *prehendere,* se définit comme l'action de prendre ou de saisir un objet à l'aide d'un organe. Selon les espèces, plusieurs organes comme la bouche, la langue, le bec, le pied, la queue ou la trompe peuvent être impliqués dans la saisie de proie, d'outil, de progéniture, de parasite dans l'épouillage ou encore de support pour se déplacer (Iwaniuk & Whishaw, 2000; Schwenk, 2000). La préhension intervient donc dans des activités diverses de prise de nourriture, d'interaction sociale ou de locomotion et constitue ainsi une fonction essentielle dans le quotidien des espèces et leur survie. Cette étude se focalise essentiellement sur la préhension de nourriture avec le membre supérieur, en l'occurrence la main, chez les primates.

Origines de la main préhensile chez les Primates

La main préhensile des primates actuels à la fois engagée dans la locomotion et la manipulation représente un véritable compromis évolutif. Seule la main humaine a perdu sa fonction locomotrice depuis l'émergence de la bipédie permanente. Dès les premiers primates, les espèces possèdent déjà des capacités préhensiles impliquées dans la locomotion, mais les causes de l'émergence de ces capacités restent mal connues (Wood Jones, 1916; Le Gros Clark, 1934; Cartmill, 1972, 1974a, b, 1992; Rasmussen, 1990; Sussman, 1991). L'hypothèse la plus répandue et la plus ancienne suggère que les mains préhensiles, faisant partie des principaux caractères du morphotype primate (au même titre que les pieds préhensiles, le rapprochement des yeux dans le plan frontal et la vision stéréoscopique, l'accroissement du cerveau et la présence d'ongles à la place de griffes) seraient liés à des adaptations à la vie arboricole (Darwin, 1871; Smith, 1913; Wood Jones, 1916; Le Gros Clark, 1934, 1959).

Cependant Cartmill (1972, 1974a, b) montre que l'arboricolie ne peut expliquer à elle seule l'émergence de ces adaptations. Il relève en effet de nombreux contre-exemples chez des espèces non-primates parfaitement arboricoles mais n'ayant pas évolué vers des adaptations primates. D'après lui, le développement des extrémités préhensiles caractéristiques des primates (longs doigts, pouce opposable, ongles) pourrait constituer une adaptation au milieu arboricole certes, mais plus spécifiquement au milieu de fines branches. Les extrémités auraient ainsi accru leurs forces préhensiles et développé de longs doigts et des ongles en s'enroulant entièrement autour de la branche. De plus, la vision stéréoscopique, autre caractère spécifique aux primates, pourrait, selon l'auteur, s'expliquer davantage par un comportement de prédation visuelle plutôt que par une simple adaptation au milieu arboricole. Il s'inspire des prédateurs non-primates tels que les félidés ou les rapaces possédant une excellente vision stéréoscopique leur permettant de mieux appréhender leur proie. Enfin, la combinaison du comportement de prédation associé au milieu de fines branches pourraient selon lui rassembler un ensemble de facteurs à l'origine du morphotype primate. En effet, la saisie de fines branches par les pieds constituant un facteur de stabilité et libérant ainsi les mains pour la capture de proies repérées au préalable à l'aide de la vision, expliquerait les principaux traits primates: à la fois la vision stéréoscopique, le développement des capacités préhensiles et le remplacement des griffes, devenues gênantes dans la saisie de branches fines et de capture de proies avec la main, par des ongles (Cartmill, 1972). Sur la base de cette hypothèse, soit le milieu de fines branches (Hamrick, 1998, 1999, 2001; Lemelin, 1999, 2000; Schmitt & Lemelin, 2002), soit la prédation (Godinot, 1991, 2007) sont privilégiés l'une par rapport à l'autre pour expliquer l'émergence du morphotype primate. Ces deux tendances considèrent aussi bien l'adaptation à la prédation que l'adaptation au milieu de fines branches comme faisant partie des conditions de l'émergence des primates, mais dans les deux cas l'une apparait secondaire par rapport à l'autre.

Un autre auteur, Sussman (1991) remet l'hypothèse de Cartmill (1972) en question sur la base du constat que tous les primates ne sont pas omnivores ou insectivores alors que tous sont frugivores. Il propose donc une coévolution entre l'émergence des premières angiospermes modernes (plantes à fleurs et à fruits) et celle des premiers primates. L'exploitation des fruits et des fleurs impliquant de se déplacer sur des fines branches terminales pour aller les consommer, et non la prédation visuelle, aurait favorisé l'apparition des caractéristiques proprement primates.

Finalement, Rasmussen (1990) concilie ces trois hypothèses majeures sur l'origine des primates (arboricolie, prédation et frugivorie-folivorie) en s'inspirant du vivant et particulièrement d'un marsupial arboricole (*Caluromys derbianus*) de petite taille similaire à celle des premiers primates. Sur la base de ce modèle, il propose un "premier primate" adapté à la vie arboricole de fines branches, doté d'un régime alimentaire varié impliquant à la fois la capture de proies avec les mains comme la consommation de fruits et de fleurs. Cette plasticité aurait été un facteur déterminant pour le développement de ces espèces.

Parallèlement aux hypothèses articulées autour de l'arboricolie, de la prédation et de la frugivorie-folivorie, d'autres sont discutées comme celle de Szalay & Dagosto (Szalay & Dagosto, 1980; Dagosto, 1988). Sur la base de caractères morphologiques de fossiles et d'actuels (*e.g.* ongles, pieds hypertrophiés comparés aux mains, pouce opposable du pied puissant, anatomie pelvienne et du membre inférieur), les auteurs proposent une adaptation aux sauts "explosifs" et arboricoles combinés avec la capacité de saisir des branches fines lors du grimper et de l'atterrissage ("grasp-leaping").

Les causes de l'émergence des caractères primates sont encore largement débattues (Crompton, 1995; Ross & Martin, 2007; Ravosa & Dagosto, 2007). Il est ainsi suggéré que ces caractères ont pu apparaître successivement. La fonction préhensile de la main est alors souvent proposée comme se développant tardivement ou dans un second temps, bien après le pied préhenseur et l'adaptation locomotrice arboricole (Cartmill, 1972, 1974a, 1992; Szalay & Dagosto, 1988; Gebo, 2004; Sargis *et al.*, 2007). En outre, la main est généralement circonscrite aux activités locomotrices (*e.g.* atterrissage, grimper de fines branches). De plus, l'hypothèse de la prédation visuelle (Cartmill, 1972, 1974a, b), fait davantage référence à la convergence oculaire favorisant une vision en trois dimensions ou la perte des griffes pour des ongles. Selon l'auteur, l'émergence des mains préhensiles serait originellement liée à la locomotion sur fines branches (rappelé dans Kirk *et al.*, 2003) qu'à une réelle implication de la main dans la capture de proies.

Sur la base des différentes hypothèses décrites ci-dessus, plusieurs questions se posent:
- Quel rôle a pu jouer l'arboricolie ainsi que la prédation dans la mise en place des capacités de préhension non locomotrices du membre supérieur chez les premiers primates?
- Plus spécifiquement, comment l'exploitation d'un milieu de fines branches ainsi qu'un type de régime alimentaire, qu'il soit frugivore ou omnivore, a pu favoriser l'utilisation de la main des premiers primates dans d'autres activités que celles strictement locomotrices?

Evolution de la main préhensile chez les Primates

Outre les origines de la préhension, l'évolution des capacités de préhension des primates a longtemps été abordée uniquement à travers le prisme des spécificités humaines. La préhension d'objets comme d'outils chez l'humain ont depuis longtemps fasciné et ont été désignées comme un des facteurs fondamentaux de l'émergence et de l'évolution de la lignée humaine (Napier, 1956, 1964; Susman, 1988, 1998; Marzke, 1997). En particulier, la saisie de précision (entre le pouce et l'index) a longtemps été considérée comme étant le propre de l'humain. Le primatologue et paléoanthropologue John Russel Napier écrivait en 1960 : "*The acme of precision in man is the ability to pick up small objects between thumb and index finger and hold them delicately and securely between the opposed pulp surfaces*". Il est vrai que la préhension humaine peut être caractérisée par une grande dextérité et précision de mouvement mais ces capacités sont encore parfois considérées comme étant propres à l'humain, autrement dit, unique dans le monde animal (Napier, 1956, 1961, 1993; Marzke & Marzke, 2000; Young, 2003; Rolian *et al.*, 2011). Des études ont pourtant montré depuis plusieurs décennies que les capacités manuelles humaines se retrouvaient chez d'autres espèces, notamment chez celles étant les plus proches génétiquement (hominoïdes et cercopithécoïdes) et, de manière insoupçonnée encore à l'époque, chez d'autres espèces plus éloignées (singes capucins) (Costello & Fragaszy, 1988; Christel, 1993; Jones-Engel & Bard, 1996; Pouydebat *et al.*, 2005, 2008; Crast *et al.*, 2009). En conséquence, de nombreuses capacités manuelles de préhension d'objets et d'outils chez l'humain sont aujourd'hui reconnues pour ne plus lui être spécifiques mais plutôt partagées avec d'autres espèces (Costello & Fragaszy, 1988; Butterworth & Itakura, 1998; Christel, 1998; Christel & Fragaszy, 2000; Pouydebat, 2004a; Pouydebat *et al.* 2005, 2006, 2008, 2009; MacFarlane & Graziano, 2009). Ainsi, l'intérêt pour l'évolution et la compréhension des capacités préhensiles des primates et particulièrement celles de l'humain, a autant impliqué des études neurologiques, morphologiques et cinématiques que des recherches sur les postures manuelles de saisie.

La variabilité des postures manuelles au sein des primates est souvent associée à la phylogénie de ce groupe (à l'exception des capucins: genres *Cebus* et *Sapajus*). En effet, chez les platyrhiniens (singes du Nouveau Monde) et les prosimii ou strepsirhiniens (lémuriformes et lorisiformes), la saisie de puissance impliquant tous les doigts et la paume de la main (Napier, 1956) est fréquente, et ce, quelle que soit la taille de l'objet. A notre connaissance, aucun auteur n'a fait mention jusqu'à présent d'utilisation de saisie de précision (hormis *Cebus* et *Sapajus*) chez ces deux grands groupes primates, même si la "pince de précision" peut s'observer chez les lémuriens de manière passive (observation personnelle). Ils présentent une plus faible variabilité de postures manuelles, une absence d'individualisation des doigts et une plus forte implication de la bouche plutôt que de la main dans les saisies de nourritures statiques (platyrhiniens: Rothe 1971; Hershkovitz, 1977; Singer & Schwibbe, 1998; strepsirhiniens: Petter, 1962; Bishop, 1964; Pollock, 1977; Ward & Hopkins, 1993; Ward, 1995; Reghem *et al.*, 2011; Scheumann *et al.* 2011). Toutefois, plusieurs d'entre eux utilisent fréquemment la main en saisie de puissance dans la capture de proies (invertébrés et petits vertébrés). Les galagidés, cheirogaléidés, lorisidés et callichitridés capturent des insectes en milieu naturel avec une ou deux mains selon les espèces (Martin, 1972a, b; Charles-Dominique, 1977; Hershkovitz, 1977; Nekaris, 2005). Le très spécialisé lémurien Aye Aye (*Daubentonia madagascariensis*) présente un cas particulier puisqu'il est le seul lémurien à posséder une individualisation du troisième doigt qu'il utilise pour extraire des larves et insectes des troncs d'arbre et des branches (Erickson, 1991, 1994; Milliken *et al.*, 1991b; Erickson *et al.*, 1998). Par ailleurs, les platyrhiniens (y compris les capucins) utilisent aussi une saisie décrite comme "saisie en ciseau" entre l'index et le majeur (Lemelin & Grafton, 1998; Spinozzi *et al.*, 2004; Pouydebat *et al.*, 2009). Ce type de saisie n'a à ce jour jamais été répertorié chez les strepsirhiniens.

A l'inverse, les singes de l'Ancien Monde ou catarhiniens (hominoïdes et cercopithécoïdes) et les genres *Cebus* et *Sapajus* (singes capucins) appartenant aux singes du Nouveau Monde ou platyrhiniens, sont connus pour utiliser leur main dans la prise de nourriture en utilisant des postures manuelles de saisies très variées (Christel, 1993; Spinozzi *et al.*, 2004; Pouydebat *et al.*, 2008). Toutes ces espèces montrent une individualisation des doigts de la main leur permettant d'effectuer des saisies dites de "précision", entre l'extrémité de tous les doigts sans intervention de la paume (Cutkosky, 1989), et en particulier la pince de précision entre les extrémités du pouce et l'index (Napier, 1956). Les catarhiniens et les genres *Cebus* et *Sapajus* présentent ainsi une forte variabilité de types de saisies alors que l'humain en utilise beaucoup moins (Christel *et al.*, 1994; Pouydebat, 2004a). Les orangs outans, par exemple, présentent jusqu'à 15 types de saisies entre pouce-index (Christel, 1993). La saisie en "ciseau" entre l'index et le majeur est également répertoriée chez ces primates. L'utilisation d'un type de saisie est bien souvent dépendant de la taille de l'objet (Christel *et al.*, 1993, 1994, 1998; MacFarlane & Graziano, 2009; Pouydebat *et al.*, 2009). Les petites tailles d'objets impliquent majoritairement des saisies entre deux doigts (pouce-index et index-majeur pour les plus fréquentes) chez les grands singes (chimpanzés, gorilles, orang-outans, bonobos), les cercopithèques (macaques, babouins, geladas, mangabeys) et les capucins (*Sapajus apella*). En revanche, la taille de l'objet augmentant, les saisies entre tous les doigts impliquant ou non la paume sont plus fréquentes chez toutes ces espèces (Pouydebat *et al.*, 2004b, 2009). Cette tendance est également présente chez les humains (Castiello *et al.*, 1992; Gentilucci *et al.*, 1991; Pouydebat *et al.*, 2009).

Du point de vue neurologique, même si toutes les espèces primates possèdent des adaptations permettant de saisir des objets avec la main, certaines espèces capables d'individualiser les doigts présentent des organisations spécifiques comme cela a été démontré chez le capucin (*Sapajus apella*), le macaque (*Macaca fascicularis* et *nemestrina*), le chimpanzé (*Pan troglodytes*) et l'humain. En effet, ces espèces possèdent des systèmes cortico-motoneuraux et des terminaisons cortico-spinales denses et étendues assurant le contrôle fin des doigts (Kuypers, 1963,1981; Nathan *et al.*, 1990; Bortoff & Strick, 1993). En outre, une plus grande différenciation des connexions proximo-distales du poignet et des muscles des doigts permet une utilisation plus indépendante de la main (Shinoda *et al.*, 1981; Illert & Kümmel, 1999; Nakajima *et al.*, 2000; Davare *et al.*, 2006). Ces caractères contrôlant les mouvements de la main semblent davantage expliquer les capacités manuelles de ces espèces que certains critères morphologiques présentés ci-dessous.

Du point de vue morphologique, de très nombreuses études sur le membre supérieur sont destinées à comprendre la locomotion et non la préhension dans le cadre de la prise d'objet. En outre, la préhension d'objet est abordée essentiellement par l'étude anatomique de la main, et non du membre supérieur dans sa totalité, et qui plus est, basée sur les caractères humains. L'opposabilité du pouce long et robuste, la longueur relativement réduite des doigts, la présence de muscles développés du pouce dont le *flexor pollicis longus*, l'extrémité distale élargie des doigts, et l'asymétrie des têtes métacarpiennes et des os du carpe orientés vers le pouce font partie des critères proposés pour qualifier la préhension humaine et notamment inférer certaines capacités fonctionnelles (saisie de précision, utilisation et fabrication d'outils lithiques) des mains fossiles (Napier, 1956, 1961, 1993; Susman, 1988, 1998; Marzke, 1997; Marzke & Marzke, 2000; Young, 2003; Kivell *et al.*, 2011). Toutefois, certains de ces caractères sont absents chez des espèces actuelles qui utilisent pourtant la saisie de précision et des outils en milieu naturel (capucin:Westergaard & Fragszy, 1987; chimpanzé: Boesch & Boesch, 1990; Orang outan: van Schaik *et al.*, 2003; gorille: Breuer *et al.*, 2005; babouin: Oyen, 1979). Le capucin possède en effet un pouce en pseudo-opposabilité, les grands singes ont un pouce bien plus court que l'humain et n'ont pas de *flexor pollicis longus* (à l'exception des gibbons).

De plus, la présence des proportions humaines (*i.e.* long pouce et doigts courts) a été retrouvée chez des fossiles précédant de plus d'un million d'années la découverte des premiers outils lithiques façonnés, remettant considérablement en question ces caractéristiques morphologiques attribuées à la fabrication d'outils (Semaw, 2000; Alba *et al.*, 2003, 2005; Green & Gordon, 2008; Almécija *et al.*, 2012). Bien que certains auteurs cherchent des critères associés à la fabrication régulière d'outils (Kivell *et al.*, 2011), il n'en demeure pas moins que les caractères morphologiques souvent associés aux saisies de précision et à l'utilisation et fabrication d'outils doivent être confrontés à des données comportementales et fonctionnelles issues du vivant. En effet, certains caractères ne sont pas suffisants pour définir la capacité à fabriquer des outils et ainsi déterminer si des fossiles sont de potentiels ancêtres de la lignée humaine. Dans ce contexte, il devient de plus en plus difficile d'inférer les comportements fossiles sur la base de caractères morphologiques strictement humains.

Outre les postures manuelles, la neurologie et la morphologie, l'étude cinématique du mouvement de préhension tente également d'apporter un éclairage sur l'évolution de la préhension et les spécificités humaines. La cinématique de la préhension est très largement étudiée chez l'humain et porte particulièrement sur la partie distale du membre supérieur. La préhension est décomposée en deux phases définies à partir de la vitesse du poignet (phase d'approche) et de l'ouverture de la pince (phase de saisie) (Jeannerod, 1981, 1984). La première phase se caractérise par l'avancée de la main jusqu'à la cible. La vitesse du poignet dessine une courbe en cloche asymétrique avec un pic de vitesse intervenant à environ 40% de la durée totale du mouvement. L'amplitude de ce pic ainsi que l'instant où il se produit sont dépendants des caractéristiques intrinsèques (*e.g.* taille) et extrinsèques (*e.g.* distance, position) de l'objet à saisir (Jeannerod, 1981, 1984; Marteniuk *et al.*, 1990; Bootsma *et al.*, 1994; Kudoh *et al.*, 1997). La décélération du poignet est cependant toujours plus longue que l'accélération. La seconde phase, phase de saisie, se définit par l'ouverture de la pince évaluée par la distance entre le pouce et l'index. L'ouverture maximale se produit généralement entre 70-80% de la durée totale du mouvement pour se refermer ensuite sur l'objet (Jeannerod, 1986). Ce paramètre est aussi dépendant des caractéristiques de l'objet. Depuis près de 20 ans, les études cinématiques de la préhension chez l'humain sont réalisées en 3D selon des normes bien spécifiques définies par l'International Society of Biomechanics (ISB) (Wu & Cavanna, 1995; Wu *et al.*, 2002; Wu *et al.*, 2005). Ces normes optimisent les méthodes d'analyses sur toutes les articulations du membre supérieur et inférieur, du tronc et des doigts.

Chez les primates non-humains, les études cinématiques sur la préhension n'utilisent pas ces normes ISB et ont analysé jusqu'à présent qu'un seul genre, le macaque (*M. nemestrina*, *M. mulatta*, *M. fascicularis*). Les mêmes invariants cinématiques que l'humain ont été mis en évidence chez cette espèce pour les phases d'approche et de saisie (Roy *et al.*, 2000, 2002; Christel & Billard, 2002). L'humain et le macaque sont donc les deux seuls primates pour lesquels des données cinématiques de la préhension existent, principalement sur l'aspect distal du membre supérieur et en posture assise (*humain*: *e.g.* Jeannerod, 1981, 1984; Castiello *et al.*, 1992; Bootsma *et al.*, 1994; Kudoh *et al.*, 1997; Paulignan *et al.*, 1997; Santello *et al.*, 2002; *macaque*: *e.g.* Georgopoulos, 1981; Scott & Kalasha, 1997; Roy *et al.*, 2000, 2002, 2006; Christel & Billard 2002; Graham *et al.*, 2003; Jindrich *et al.*, 2011). En outre, le macaque n'est étudié en 3D que depuis cette dernière décennie et les conditions d'expérimentation sont alors très souvent contraignantes, impliquant un entraînement intensif de la tâche de préhension à effectuer dans le cadre d'un dispositif expérimental imposant une posture corporelle aux individus et contraignant les articulations proximales. Néanmoins, une étude a été menée dans des conditions non-contraintes, c'est à dire sans apprentissage où les individus étaient libres de choisir leurs postures corporelles et par conséquent libres de leurs mouvements (Christel & Billard, 2002). Dans les conditions expérimentales de cette étude, les macaques ont privilégié la posture assise pour saisir et ont été comparés à l'humain dans cette même posture corporelle. Les auteurs présentent les spécificités de chacune de ces espèces, humain et macaque, en tenant compte à la fois de la cinématique du poignet et de l'ouverture de la pince mais aussi des variations articulaires du membre supérieur au cours du mouvement, aspect quasiment inexploré jusqu'à présent (ou seulement en milieu contraint: Scott & Kalasha, 1997; Jindrich *et al.*, 2011). Ainsi, les travaux de Christel & Billard (2002) ont permis d'aborder l'étude du geste spontané de préhension et de ce fait des questions évolutives. Il est proposé par les auteurs que le contrôle moteur de la préhension aurait pu évoluer du contrôle moteur primitif générant la locomotion. Dans ce cadre, comme cela a déjà été abordé pour l'origine des capacités préhensiles de la main, l'arboricolie peut être aussi proposée comme favorisant l'élaboration de la préhension chez les primates, tous capables de saisir des branches pour se déplacer. Néanmoins, aucune étude n'a encore comparé ce mouvement entre plusieurs espèces dans différentes postures corporelles et selon les normes définies par l'ISB pour comprendre l'influence de l'arboricolie sur le développement de la préhension chez les primates.

Ainsi, des questions émergent quant à l'évolution des capacités de préhension des primates, notamment de l'humain:

- Les capacités préhensiles actuelles des humains ont probablement émergé chez un ancêtre arboricole mais lui sont-elles spécifiques?

- Quelle a pu être l'influence du rôle locomoteur du membre supérieur sur celui de la préhension d'objet chez les primates non-humains?

- Quels rôles ont pu jouer les postures corporelles dans l'élaboration de certaines capacités préhensiles de la main?

- Peut-on retracer une évolution de la préhension des primates en lien avec la cinématique du membre supérieur?

Problématique et objectifs

Afin de mieux comprendre l'origine de l'utilisation de la main dans les activités de prise de nourriture des premiers primates et l'évolution conduisant à la diversité des capacités préhensiles des primates actuels, deux principales questions sont abordées dans ce travail:

- Quels sont les facteurs écologiques (propriétés de la nourriture et du substrat) conduisant à une plus grande utilisation de la main chez les premiers primates?

- Quels sont les facteurs fonctionnels (posture corporelle, cinématique du membre supérieur) impliqués dans l'évolution de la préhension des primates?

Pour répondre à ces questions, nous nous sommes inscrits dans la perspective d'étudier des espèces actuelles primates dont les humains. Ces espèces ont été observées et filmées dans des conditions non-contraintes signifiant que tous les individus étaient libres de se déplacer dans leur espace habituel et de choisir leur posture corporelle pour aller saisir la nourriture comme ils le souhaitaient. Six espèces issues de différents groupes phylogénétiques actuels ont été sélectionnées pour aborder deux objectifs majeurs.

Le premier objectif est de tester différents facteurs écologiques impliqués dans l'émergence des capacités préhensiles des primates. Pour cela, trois études comportementales (chapitres 1 à 3) ont été menées chez un modèle primate actuel présentant des convergences écologiques et comportementales avec les premiers primates: *Microcebus murinus* (Martin, 1972a, b; Cartmill, 1974a, b; Rasmussen, 1990; Crompton, 1995; Gebo, 2004).

Le second objectif est de tester différents facteurs fonctionnels impliqués dans l'évolution de la préhension des primates. Dans ce cadre, deux études comportementales et cinématiques en 3D suivant les normes ISB (chapitres 4 et 5) comparent cinq espèces de primates, dont l'humain (*Lemur catta*, *Sapajus xanthosternos*, *Gorilla gorilla*, *Pan troglodytes*). La phase d'approche a été abordée d'un point de vue cinématique à travers la vitesse du poignet et les amplitudes articulaires de tout le membre supérieur et du tronc. Les postures manuelles de saisie ont également été considérées.

Composition du mémoire

Ce travail s'organise en plusieurs chapitres écrits sous forme d'articles scientifiques, respectivement publiés (chapitres 1 et 2), soumis (chapitres 3 et 4) et en préparation (chapitre 5):

Chapitre 1. Prise et manipulation de nourriture chez *Microcebus murinus* (Prosimii, Cheirogaleidae)

La première étude évalue les capacités préhensiles du microcèbe dans les mêmes conditions que les espèces analysées en cinématique. Cette espèce est étudiée dans la prise de nourriture statique (morceaux de pomme) de petite taille sur substrat plat (sol). La petite taille de nourriture impliquant seulement une saisie bouche pour tous les individus de l'étude, deux autres tailles ont été sélectionnées afin de tester s'il existait une variabilité dans le comportement de prise de nourriture du microcèbe et si ces tailles faisaient davantage intervenir la main lors de la saisie.

Certains résultats ont montré que le microcèbe n'utilisait pas la main seule pour saisir des fruits et ne pouvait donc pas être étudié dans les mêmes conditions cinématiques que les autres espèces. Nous avons donc cherché à déterminer les contextes dans lesquels le microcèbe était susceptible d'utiliser la main. Pour cela, deux autres études basées sur les hypothèses du milieu de fines branches et des régimes alimentaires (frugivore/omnivore) ont été conduites. L'étude du chapitre 2 aborde les postures manuelles de préhension de substrat lors de la locomotion du microcèbe. L'étude du chapitre 3 teste à la fois les propriétés du substrat et celles de la nourriture sur les capacités de saisie de nourriture de ce primate.

Chapitre 2. - Posture de la main du *Microcebus murinus* au cours de la locomotion arboricole sur fines branches

La deuxième étude quantifie les postures de saisie de la main du microcèbe pendant la locomotion sur deux diamètres différents (1 et 3 cm) pour deux orientations (verticale et horizontale). Ici, nous testons l'influence du substrat arboricole sur les capacités préhensiles du microcèbe. Dans le cadre de l'hypothèse du milieu de fines branches dans lequel seraient apparus les premiers primates, cette étude discute et propose de considérer l'orientation du substrat en plus de son diamètre pour comprendre les facteurs écologiques impliqués dans l'origine des capacités préhensiles des primates. En outre, des relations sont proposées entre prise de nourriture et prise de substrat en discussion générale.

Cette étude nous conduit au chapitre 3 où sont testés l'effet des propriétés du substrat et de la nourriture, sur l'implication de la main dans les stratégies de préhension de nourriture.

Chapitre 3. Stratégies de préhension de nourriture statiques et mobiles sur substrats arboricoles chez *Microcebus murinus* (Prosimii, Cheirogaleidae)

La troisième étude quantifie la fréquence d'utilisation de la main et les stratégies de saisie du microcèbe pour des nourritures statiques (morceaux de banane), semi-mobiles (vers de farine) et mobiles (crickets) sur substrats arboricoles horizontaux de différents diamètres (0.2 et 2 cm). Ainsi l'influence à la fois des propriétés de la nourriture et du substrat arboricole sur l'implication de la main dans la prise de nourriture est testée. Les résultats sont discutés dans le cadre des hypothèses sur l'émergence des premiers primates et plus particulièrement sur l'influence du milieu de fines branches en lien avec le comportement de prédation.

Suite à ces réflexions sur l'origine de la préhension chez les primates, nous abordons dans les deux chapitres suivants les aspects évolutifs de cette fonction.

Chapitre 4. Influence de la posture corporelle sur la cinématique de la préhension chez l'humain et le gorille (*Gorilla gorilla*)

La quatrième étude quantifie les stratégies cinématiques et comportementales de préhension chez l'humain et le gorille dans deux postures corporelles: assise et quadrupède. La posture assise a été choisie car elle est la plus utilisée dans les études sur la cinématique de la préhension de l'humain et du macaque. La posture quadrupède présente un autre intérêt car elle est l'une des plus employées chez les primates non-humains en conditions non-contraintes. Les deux espèces ont saisi au sol ou sur substrat plat une nourriture de type statique et de petite taille (raisin sec). Cette étude teste l'influence de la posture corporelle sur les paramètres cinématiques (*e.g.* vitesse du poignet, amplitudes articulaires) et comportementaux (*e.g.* postures manuelles de saisie, préférences manuelles) de la préhension, au sein de la même espèce et entre les espèces. Les résultats sont discutés en lien avec la fonction locomotrice du membre supérieur, le degré d'arboricolie et de terrestrialité des espèces, et leur morphologie.

Chapitre 5. Convergences et spécificités cinématiques de la préhension chez cinq primates: *Lemur catta*, *Sapajus xanthosternos*, *Gorilla gorilla*, *Pan troglodytes*, *Homo sapiens*

Cette dernière étude aborde une comparaison cinématique et comportementale de la préhension de cinq espèces primates dans une même posture, la posture quadrupède. Seul l'humain est comparé à la fois en posture assise et quadrupède. Ces cinq espèces sont issues de grands groupes phylogénétiques primates (strepsirhinen: lémurs; platyrhinien: capucins; hominidés: gorilles, chimpanzés, humains). Tous les individus de l'étude ont saisi au sol une nourriture de type statique et de petite taille (raisin sec), à l'exception du lémur qui l'a saisie avec la bouche. Pour cette espèce seulement, la taille du fruit (morceaux de pomme) a été augmentée afin qu'il utilise la main. Les résultats permettent de déterminer s'il existe des invariants et des stratégies particulières selon les espèces à partir de l'analyse cinématique (*e.g.* vitesse du poignet, amplitudes articulaires) et comportementale (*e.g.* types de saisie, préférences manuelles). Les résultats sont discutés dans le cadre de l'écologie des espèces et de l'évolution de la préhension au sein des primates.

Annexes

En annexes sont définis des points méthodologiques liés à l'étude cinématique ainsi qu'une brève description des espèces. Enfin, les articles en tant que co-auteur sont ajoutés à la fin du mémoire.

Chapitre 1 - Prise et manipulation de nourriture chez *Microcebus murinus* (Prosimii, Cheirogaleidae)

Food Prehension And Manipulation In *Microcebus murinus* (Prosimii, Cheirogaleidae)

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Abstract

Among primates, apes and monkeys are known to use their hands and to exhibit independent control of their fingers. In comparison, prosimii (strepsirhines) are thought to have less digital individualization and to use their mouth more commonly for prehension. Unfortunately, prehension and manipulation studies in strepsirhines have been conducted in conditions constraining the subject to grasp with the hand. Moreover, the effect of food size remains unexplored, even though it could affect the use of the hands *versus* the mouth. Thus, whether prosimians use the hand or the mouth to grasp and manipulate food items of different sizes in unconstrained conditions remains unclear. To address this question, we characterized the eating and manipulation patterns of *Microcebus murinus* in unconstrained conditions, using three food sizes. The results showed that *M. murinus* showed (i) an eating pattern similar to that of rodents with smaller food items being grasped with the mouth, (ii) a greater tendency to use the hands for prehension of larger foods, and (iii) plasticity during food manipulation similar to that which has been observed in rodents. These results are discussed in the framework of grasping in mammals and are used to discuss the origins of prehension in primates.

Key words: Primate, *Microcebus* murinus, Grasping, Repositioning, Evolution, Feeding

Introduction

Tetrapods employ three major modes of food grasping in terrestrial and arboreal environments: lingual, mouth and/or hand prehension (Iwaniuk & Whishaw, 2000; Schwenk, 2000). Among primates, apes and numerous monkeys (in the subfamily Cercopithecinae and the genera *Cebus* and *Sapajus*) are known to use their hands for grasping food using various grip postures. Moreover, there are known to exhibit a degree of independent control of the fingers (Christel, 1993, 1994; Byrne *et al.*, 2001; Fragaszy *et al.*, 2004; Spinozzi *et al.*, 2004; Macfarlane & Graziano, 2009; Pouydebat *et al.*, 2009) and to manipulate tools (Boesch & Boesch, 1990; Van Schaik *et al.*, 2003; Fragaszy *et al.*, 2004; Pouydebat *et al.*, 2005; Visalberghi *et al.*, 2009). In comparison, strepsirhines (lemuriformes and lorisiformes) are thought to be less variable in grip posture, to show no digital individualization and to use the mouth for grasping more often (Bishop, 1964). In order to grasp static foods, the lemuriformes appear to prefer to grasp with the mouth as shown both by observations in the wild (Petter, 1962) and studies on manual preference (Larson *et al.*, 1989; Ward *et al.*, 1990; Milliken *et al.*, 1991a; Dodson *et al.*, 1992; Ward & Hopkins, 1993; Ward, 1995; Leliveld *et al.*, 2008; Nelson *et al.*, 2009; Scheumann *et al.*, 2011). However, these studies on manual preference often adopted protocols forcing the subjects to take static food through a wire mesh or a slot with their hand. In contrast, in order to grasp mobile prey and during manipulation, the hand seems to be used spontaneously. For example, the specialized aye-aye *(Daubentonia madagascariensis)* is known to use the third finger to pry insects from holes in tree trunks or branches (Erickson, 1991, 1994; Milliken *et al.*, 1991b; Erickson *et al.*, 1998). In addition, Galagidae and Cheirogaleidae catch insects with one or both hands (Bishop, 1964; Martin, 1972a, b; Charles-Dominique, 1977; Hladik, 1979; Lemelin, 1996) as do several lorisiformes (Oates, 1984; Nekaris, 2005). Finally, other studies have described variation in hand manipulative capacities in lemurs (Jolly, 1964; Sussman & Tattersall, 1976; Sussman, 1977; Torigoe, 1985; Schöneich, 1993).

However, even though several studies have analyzed grasping and manipulative patterns in strepsirhines, they were often conducted in conditions constraining the subject to grasp with the hand. Moreover, these studies did not test different sizes of food, although this could affect the use of the hand *versus* the mouth, raising the question of whether prosimians use the hand or the mouth to grasp and manipulate foods of different sizes in unconstrained conditions. To address this question, we quantified the grasping and manipulative patterns in the lemuriforme *Microcebus murinus* in unconstrained conditions, using three sizes of static food. The small, arboreal, nocturnal *M. murinus* is one of the most distantly related primates to humans (fig. 1). It is suggested that it represents the most ancient ancestral primate condition (Martin 1972a, b; Cartmill, 1974b; Rasmussen, 1990; Crompton, 1995; Gebo, 2004) (see Appendix A for details) and thus to possess a prehensile pattern which is phylogenetically conservative (Bishop, 1964). Therefore, this species is of particular interest in assessing the origins of grasping in primates. Our results are discussed with those obtained from other primates and mammals (rodents, carnivores, marsupials) and may contribute to the understanding of the origins and evolution of grasping and manipulation in primates.

Material and Methods

Animals and Husbandry

The mouse lemur *M. murinus* (Miller, 1777) is nocturnal and endemic to Madagascar. It is characterized by its small size (mass: 95.5±15.7 g; snout-tail length: 24.5±2.08 cm) and its quadrupedal arboreal locomotion along fine terminal branches (Napier & Napier, 1967).

Four adult males (2-3 years old) were housed individually in 100x50x30 cm enclosures with branches and a wooden nest box (fig. 2). The cages were placed in a maintenance room recreating natural environmental conditions: (i) a 12-hour light/dark cycle, (ii) ambient temperature of 24–26 ° C and (iii) 55% relative humidity. The animals received fruits, insects and water ad libitum (Genin & Perret, 2003). All data were obtained in unconstrained conditions. The daily recording sessions occurred at the beginning of the activity period of individuals in low light levels, lit by a dim red light (20 mW/cm 2 , equivalent to 0.002 lx) not perceived by the animals yet allowing us to film using a digital camera at 50 Hz (Sony, x 40 Digital Zoom, Carl Zeiss, Vario Sonnar). During each session, a cube of apple was placed on a Plexiglas platform. Three sizes of food (size 1: 0.5x0.5x0.5 cm, size 2: 1x1x1 cm, size 3: 2x2x1.5 cm) were offered in different instances. The data were quantified from video recordings obtained with the camera filming three mirrors inclined at 45° allowing us to obtain simultaneous lateral, dorsal, ventral and frontal views (fig. 2). Each animal was food deprived for 24 h before filming. The weight of the animals was regularly controlled, and additional food was provided after filming to avoid any experimental effect on the mass of the animals. The research adhered to the legal requirements of the European Union.

Behavioural Analyses

A series of more than 25 feeding sessions was recorded for each individual. Seven variables were measured during prehension and manipulation events (table 1). The grasp and the lift of the food involved the following grip categories: one hand, both hands, mouth alone, and both mouth and hand(s). The hand manipulations were quantified using two variables: the number of hand repositionings on the food during the grasp (*i.e.* these manipulations adjusting the food position in order to grasp and lift it) and the number of hand repositionings after the grasp, during the initial chewing.

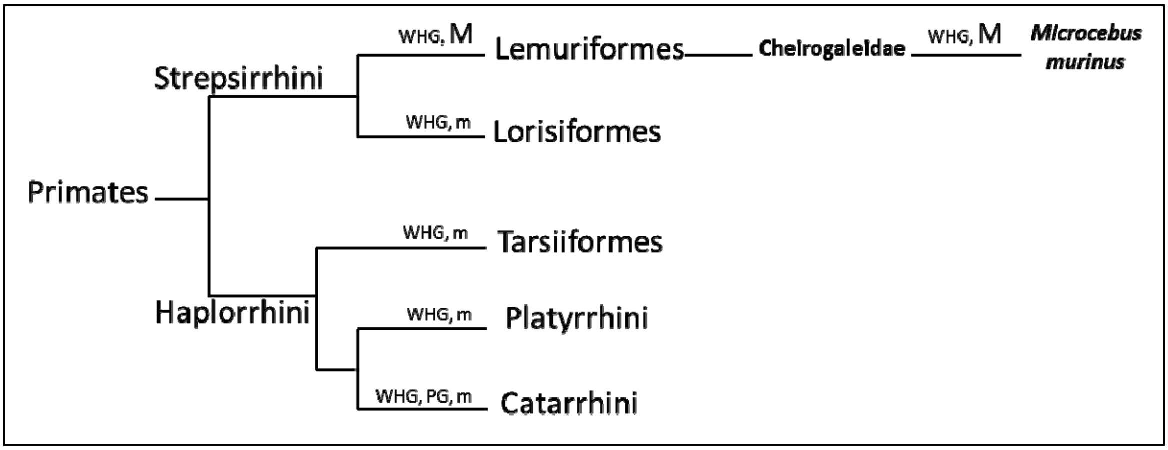

Figure 1. Primate phylogeny (based on Groves, 2001): Catarrhini (Christel *et al.*, 1994; Pouydebat *et al.*, 2008; MacFarlane & Graziano, 2009), Platyrrhini (the capuchin is alone in using the precision grip among this group) (Fragaszy *et al.*, 2004; Spinozzi *et al.*, 2004; Pouydebat *et al.*, 2009), Tarsiiformes (MacKinnon & MacKinnon, 1980; Niemitz, 1984; Lemelin, 1996), Lorisiformes (Bishop, 1964; Oates, 1985; Nekaris, 2005), and Lemuriformes (Bishop, 1964; Charles-Dominique, 1977; Lemelin, 1996; Lemelin & Jungers, 2007). PG = Use of the precision grip (between index and thumb); WHG = use of the whole-hand grip (between all the fingers and the palm); m = some use of the mouth; M = considerable use of the mouth.

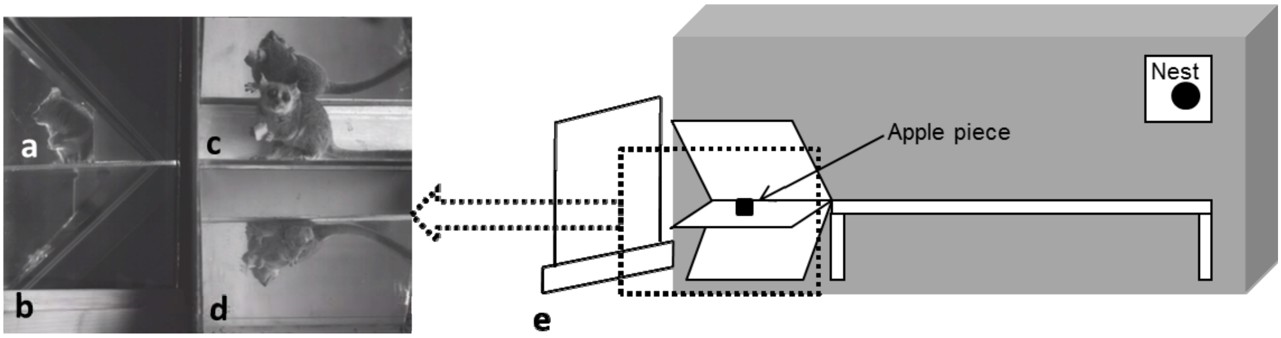

Figure 2. Experimental set-up. **a** *M. murinus* on the platform, with front view (**b**), lateral and dorsal view (**c**) and ventral view (**d**). **e** Diagram of the Plexiglas enclosure used for the experience.

Statistical Analyses

First, the G test was used to test the effect of food size and individual on grasping strategies (one hand, both hands, mouth, one hand and mouth, both hands and mouth) (Sokal & Rohlf, 1995). Second, the non-parametric Kruskal-Wallis (KW) test was used to explore the effect of food size and individual, on the number of hand repositionings during and after the grasp. Multiple comparisons were implemented using the kruskalmc function (Siegel & Castellan, 1988) of the pgirmess R package to specify which variable combinations showed significant differences. Statistical significance was set at 0.05.

Table 1. Abbreviations and definitions of the qualitative and quantitative variables analysed during food prehension and manipulation by *M. murinus*.

Variables	Type of event	Definition
Qualitative		
1H	Grasp	One Hand contact without mouth
2H	Grasp	Both Hands contact without mouth
M	Grasp	Mouth contact alone
1HM	Grasp	One Hand and Mouth contact
2HM	Grasp	Both Hands and Mouth contact
Quantitative		
RepDGr	Food lift	Number of hand Repositioning events During the Grasp
RepAGr	Manipulation	Number of hand Repositioning events After the Grasp

Results

General Feeding Session

For the two larger food sizes, a complete feeding session included 6 successive phases (fig. 3): (1) the food was sniffed, (2) the mouth and the hand approached the food, or the mouth alone approached the food with the hand remaining on the substrate, (3) the food was grasped by one or two hands, by the mouth alone or by both, (4) during the grasp, the first sequence of hand repositioning occurred in order to seize the food correctly and lift it, (5) the food was lifted by both hands and mouth, the animal straightened the trunk, sat down or adopted a bipedal or tripedal posture, then (6) the second sequence of hand repositioning occurred during eating. When handling food items of smaller size, some differences were observed (fig. 4). There was no hand repositioning during the grasp, and the lift of the food always occurred with the mouth alone.

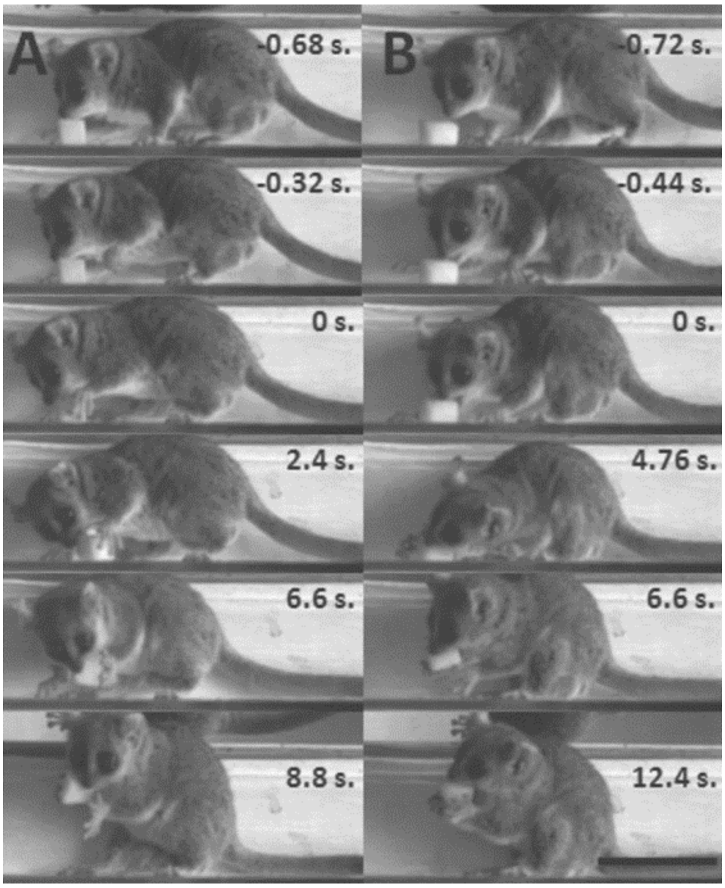

Figure 3. Lateral view of food prehension and manipulation in *M. murinus* (intermediate food size): hand grip (**A**), mouth grip (**B**). T0 = First contact with the mouth or the hand. Black scale bar = 5 cm.

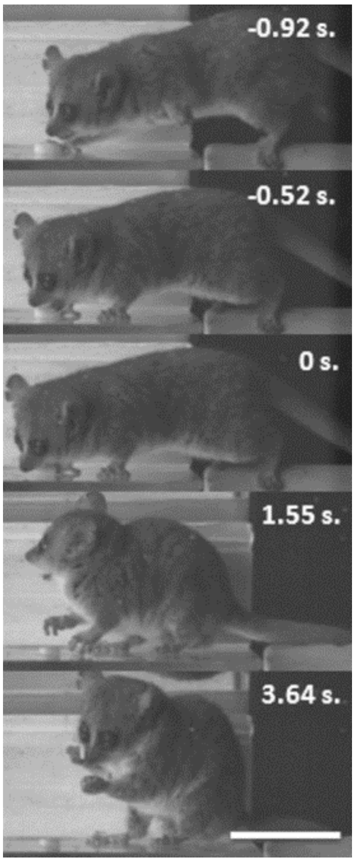

Figure 4. Lateral view of food prehension and manipulation in *M. murinus* (small food size). T0 = First contact with the mouth. White scale bar = 5 cm.

Prehension Strategies and Effect of the Food Size

Before a mouse lemur left the nest box, it always started by turning its head in the direction of the food, then jumped outside toward the food and advanced its head close to the food before grasping it. During the reaching phase, the forelimb advanced while pronated or semisupinated. The fingers were adducted and placed under the wrist. When the hand approached the food, the fingers showed a progressive opening until maximum abduction, followed by a gradual closure to the grasp. This classic biphasic grip (fig. 3) involved a flexion-extension of the metacarpophalangeal, interphalangeal and wrist joints, and an abduction-adduction of the fingers. The hand grasping itself involved a whole-hand grip by one or both hands. During the mouth grasping strategy (figs. 3, 4), the head advanced and the mouth displayed a maximal opening to seize the food. Finally, the grasping strategy concerning both hand(s) and mouth presented a combination of the two previous behaviours.

The statistical analyses showed an effect of food size on grasping strategies ($G=46.30$, X^2 d.f.=8, $p<0.001$) but no interindividual variability ($G=9.78$, X^2 d.f.=12, $p=0.64$). Indeed, all the individuals used only the mouth to grasp the small food (size 1), in contrast to the larger food samples (sizes 2 and 3) which involved use of the hand in a greater proportion in addition to several grip postures (table 2). No significant differences in grasping strategy between the intermediate and the large size food items were detected ($G=5.84$, X^2 d.f.=8, $p=0.66$). However, the grips involving one hand without the mouth represented 45% of the grip used for the intermediate food size (size 2) *versus* 75% for the large food size (size 3). Finally, the use of the mouth alone decreased with an increase in food size (small size: 100%, intermediate size: 35%, large size: 10%) and the bimanual grip was rarely used in comparison to the unimanual grip (table 2).

Table 2. Proportions (%) of the different behavioural strategies used during food grasping by *M. murinus*.

Grasping strategy	Size 1	Size 2	Size 3
One hand (1H)	-	45	75
Two hands (2H)	-	10	10
Mouth and one hand (1HM)	-	5	5
Mouth and both hands (2HM)	-	5	0
Mouth alone (M)	100	35	10

Repositioning Strategies

The hand and finger movements contributed to grasping the food firmly, lifting and manipulating it during eating. In the first sequence of hand repositioning (during gripping), the food was still in contact with the substrate (fig. 5). The hands were placed alternatively in pronation on the superior face of the food and in semisupination on the vertical face of the food. We noted that the food size, but not the individual, had an effect on the number of hand repositioning events (size: KW=43.05, d.f.=2, p<0.001; individuals: KW=1.44, d.f.=3, p=0.69) as the smallest food items were grasped with the mouth and the two others manipulated by the hands (figs. 3-5).

In the second sequence of hand repositioning (after gripping), the movements and postures of the hands and fingers were more variable. *M. murinus* exhibited unimanual or bimanual behaviours to hold small-sized items and bimanual behaviours for larger-sized items. The hands were placed below the food in supination or in semisupination (figs. 3-5). There was neither a food size nor an individual effect on the number of hand repositioning events (size: KW=1.31, d.f.=2, p=0.51; individual: KW=3.87, d.f.=3, p=0.27).

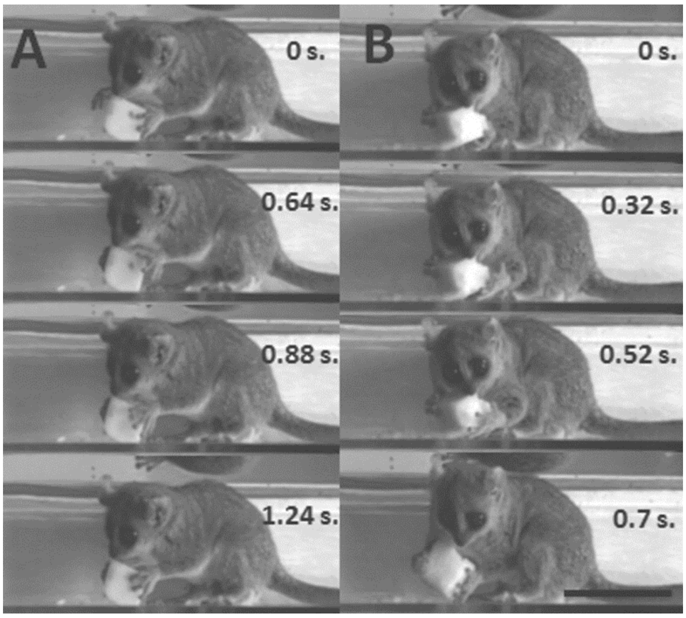

Figure 5. Lateral view of a food repositioning in *M. murinus* (large food size): repositioning before the grasp (**A**) and repositioning after the grasp (**B**). T0 = Beginning of a food repositioning. Black scale bar = 5 cm.

Discussion

This study addresses the question whether in unconstrained grasping conditions, *M . murinus* uses its hands or mouth to grasp and manipulate foods of different sizes.

When grasping small food items, *M. murinus* exhibited an eating pattern close to that observed for rodents. Indeed, both rodents and *M. murinus* sniff the food, grasp it with the mouth alone, sit down most of the time and then hold the food between their hands. This grasping behaviour has been described by Whishaw *et al.* (1998) using the term "rodent-common eating pattern". *M. murinus* differed from other primates, from the most skilled carnivorous mammals (raccoon, kinkajou) (MacClearn, 1992; Iwaniuk & Whishaw, 1999), carnivorous marsupials (opossum, glider) (Ivanco *et al.*, 1996; Landy, 1997) and two rodent species (gerbil and beaver) (Whishaw *et al.*, 1998) which most of the time use unimanual grips when confronted with small static food items.

During the grasping of larger food items, the hands were used extensively by *M. murinus*. During the reaching phase, the hand showed the biphasic grip already described for other primates and rats when constrained (Jeannerod, 1984; Christel and Fragaszy, 2000; Roy *et al.*, 2000; Christel & Billard, 2002; Sacrey & Whishaw, 2009). In addition, *M. murinus* essentially exhibited a whole-hand grip between the palm and all the fingers and preferred one hand in its first contact with the food. Therefore, the mouth was not always involved in the process of static food grasping, in contrast to what has been reported previously (Bishop, 1964; Dodson *et al.*, 1992; Ward & Hopkins, 1993; Scheumann *et al.*, 2011). The nature of the food and the omnivorous diet of *M. murinus* may be linked to the degree of hand use. Indeed, *M. murinus* is known to catch mobile prey using its hands in the wild. However, the static food items offered in this study elicited the use of both mouth and hands, yet are less frequently eaten in the wild (Martin, 1972a, b; Charles-Dominique, 1977; Hladik, 1979; Lemelin, 1996).

Our results can also be discussed in the context of food detection. Indeed, *M. murinus* moved its head close to the food in all the hand grasping strategies, prior to any limb movements, as has been previously observed for raccoons (Iwaniuk & Whishaw, 1999), gerbils and beavers (Whishaw *et al.*, 1998). Several factors can explain this behaviour such as its quadrupedal posture, the vertical orientation of the trunk and the nocturnal activity involving a well-developed olfactory sense typical of *M. murinus* (Epple & Moulton, 1978; Schilling, 1979; Siemers *et al.*, 2007). In addition to the use of olfaction, *M. murinus* seemed to use visual cues to detect food, as previously suggested (Piep *et al.*, 2008). Indeed, before leaving the nest, the lemur turned its head in the direction of the food. This visual detection of food in this species sets it apart from many rodents which invariably locate and reach their food by sniffing (Whishaw & Tomie, 1989; Whishaw *et al.*, 1998; Hermer-Vazquez *et al.*, 2007).

During food repositioning, *M. murinus* exhibited unimanual and bimanual behaviours involving the mouth as has been observed for other primates (Torigoe, 1985, 1987; Crast *et al.*, 2009) and rodents (Whishaw *et al.*, 1998) during object and food manipulation. In addition, this lemur shared characteristics with rodents during manipulation (Whishaw & Coles, 1996; Whishaw *et al.*, 1998; Ballermann *et al.*, 2000). The movements of the fingers were convergent, abducted or adducted and placed on different parts of the food to orient a corner of the food item into the mouth. This differs from behaviours in carnivores (except the kinkajou) which essentially roll static foods between the palms of both hands and hold it with the fingers parallel (MacClearn, 1992; Iwaniuk & Whishaw, 1999).

Finally, in comparison to apes and numerous monkeys, the diversity of hand postures used by *M. murinus* was relatively low when holding small objects. *M. murinus* always showed a whole-hand posture, whereas other primates use two or three fingers (Elliott & Connolly, 1984; Torigoe, 1987; Fragaszy & Adams-Curtis, 1991; Exner, 1992; Byrne *et al.*, 2001; Braido & Zhang, 2004; Crast *et al.*, 2009). In contrast, the body posture of *M. murinus* was more variable than observed in rodents, alternating between crouched, tripedal or bipedal postures as in other primates. It will be interesting to test the effect of the food properties (forms, textures, mobility) on the variability in grasping and manipulative strategies in *M. murinus*, similar to what has been done in rats and primates (Ivanco *et al.*, 1996; Whishaw & Coles, 1996; Crast *et al.*, 2009; MacFarlane & Graziano, 2009; Pouydebat *et al.*, 2009) in order to enrich future discussions on the evolution of grasping and manipulation in mammals.

In conclusion, this study quantified the grasping and manipulative patterns in the lemuriform *M. murinus* in unconstrained conditions using three sizes of food. We found that its grasping, manipulation and detection strategies share common characteristics with both rodents and primates. Indeed, its greater use of the hand than expected and its visual food detection are characteristic of primates. In contrast, the mouth grasping and hand repositioning behaviours in *M. murinus* are more similar to those observed in rodents. This intermediate position of *M. murinus* supports the hypothesis that rodents and primates share a common ancestral pattern of motor action of skilled forelimb movement (Whishaw *et al.*, 1998). However, these assumptions remain to be tested by additional experimental observations taking into account the context (in unconstrained feeding conditions), and the intrinsic (shape, texture, mobility) and extrinsic (function) properties of the food.

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We wish to thank the three anonymous reviewers for helping us to improve the manuscript. We also thank Dr. A. Herrel and Dr. A. Borel for their help and comments, and Dr. M. Perret for providing the grey mouse lemurs used in this study. All the study animals were born in a laboratory breeding colony at Brunoy (Department of Ecology and Management of Biodiversity, MNHN, France) under Agreement No. 962773. This colony was established with animals originally caught on the south-west coast of Madagascar. We finally thank the technical staff at the MNHN, particularly H. Clamouze, E. Pellé and L. Dhennin for their assistance during this study.

SYNTHÈSE CHAPITRE 1

Titre: Prise et manipulation de nourriture chez *Microcebus murinus* (Prosimii, Cheirogaleidae).

Question: La taille de la nourriture influence-t-elle les stratégies comportementales de la préhension?

Modèle: Microcèbe (*Microcebus murinus*)

Résultat: La taille de la nourriture a un effet sur les stratégies de préhension et la main n'est jamais utilisée seule pour la saisir.

Discussion: La saisie de fruit ne nécessite pas l'implication de la main chez cette espèce et les facteurs susceptibles de favoriser son utilisation restent à comprendre.

Perspective: Etudier des contextes dans lesquels le microcèbe est susceptible d'utiliser la main (saisies de substrats: chapitre 2 / saisies de proies: chapitre 3).

SUMMARY CHAPTER 1

Title: Food prehension and manipulation in *Microcebus murinus* (Prosimii, Cheirogaleidae).

Question: Does the size of the food influence the behavioural strategies of prehension?

Model: The mouse lemur (*Microcebus murinus*)

Result: The size of the food has an effect on the strategies of prehension and the hand alone is never used to grasp it.

Discussion: Fruit grasping does not require the implication of the hand in this species and the parameters to favor its use remain to be understood.

Perspective: Study the contexts in which the mouse lemur may use the hand (substrate grasping: chapter 2 / prey grasping: chapter 3).

Chapitre 2 - Posture de la main du *Microcebus murinus* au cours de la locomotion arboricole sur fines branches

Hand Postures Of The Grey Mouse Lemur During Arboreal Locomotion On Narrow Branches

Journal of Zoology (2012) 288, 76-81

Abstract

Primates are typically subdivided into two fundamentally different groups: Strepsirrhini and Haplorrhini. These two suborders are differentiated by several anatomical characteristics, among which are features of the wrist and hand. Whereas strepsirhines are characterized by an ectaxonic hand with a longer fourth digit, haplorhines display a mesaxonic hand with a longer third digit. Two complementary studies suggest that (1) an ulnarly deviated hand with respect to the forearm during locomotion is typical for ectaxonic hands and thin branches whereas mesaxonic hands display a less-deviated posture in relation to a more terrestrial type of locomotion; (2) ulnar deviations are not always produced by ectaxonic hands and may rather be associated with locomotion in an arboreal environment. The aim of this study was to explore how arboreal substrates influence the posture of the hand and the wrist in contact with the substrate. In this context, we assessed the grasping ability of the strepsirhine *Microcebus murinus*, a highly arboreal species. Here we tested the effect of branch diameter (1 and 3 cm) and orientation (horizontal and vertical) on grasp choice during arboreal locomotion. Our results show that two hand postures were observed on horizontal substrates *versus* three hand postures on vertical substrates. When ulnar deviation was observed, it was typically observed on vertical substrates, particularly on thick ones. In conclusion, our data show that vertical substrates increase the variability in grasping hand postures for *M. murinus* and include the use of uncommon grasps compared with horizontal substrates. We suggest that more than the arboreal substrate, the frequent use of vertical supports may influence the hand biomechanics towards ulnar deviation as observed for lorisids, indriids and gibbons.

Key words: *Microcebus murinus*, Primates, Manual Grasping, Locomotion, Ulnar Deviation

Introduction

The function and morphology of the hand in extant primates is diverse, with the grasping hand divided into two broad morphological groups correlated to taxonomic categories. Strepsirhines are characterized by an ectaxonic hand with an anatomical axis located along the fourth and longest digit, long digits, short metacarpals and large ulnae that have extensive contact with the carpal bones. Haplorhines display a mesaxonic hand with an anatomical axis along the third and longest digit, short digits, long metacarpals, radial elements that are more prominent than ulnar ones and reduced carpoulnar contacts (Jouffroy, 1962; Jouffroy & Lessertisseur, 1979; Jouffroy *et al.*, 1991; Preuschoft *et al.*, 1993).

The question of origins for morphology and movements in the primate wrist and hand are debated and often discussed in relation to the substrates used during locomotion. This study addresses the influence of arboreal substrates on wrist and hand postures in primates. In order to interpret the differences in the two major morphologies in primates (ectaxony and mesaxony), Preuschoft *et al.* (1993) proposed a biomechanical model that relates these hand morphologies and taxonomy (strepsirhine/haplorhine) to the type of substrate used (arboreal/terrestrial). These authors suggested that the peculiar features of the strepsirhine ectaxonic hand could be explained by a significant degree of ulnar deviation with respect to the forearm well suited for locomotion on thin branches. The ulnar deviation of the hand involves a hand oriented towards the ulna at the wrist joint. The haplorhine mesaxonic hand is, on the other hand, thought to show less ulnar deviation and to be adapted to locomotion on wide, large supports or to over ground locomotion (*i.e.* the hand remained in a more neutral posture without deviation). However, the observations of Lemelin and Schmitt (1998) revealed that this model is not accurate. They quantified the degree of ulnar deviation in 27 species of primates belonging to both haplorhines and strepsirhines and observed that the deviation of the hand was independent of morphology (*i.e.* ectaxonic and mesaxonic hands) or infraorder affinity (*i.e.* strepsirhine and haplorhine). Indeed, the authors observed that some haplorhine species with mesaxonic hands used ulnar deviation, and some strepsirhine species did not. Rather, ulnar deviation of the hand was correlated with the use of arboreal substrates. Thus, both studies (Preuschoft *et al.*, 1993; Lemelin & Schmitt, 1998) suggest that an arboreal context favours ulnarly deviated hand postures. One species in particular, the grey mouse lemur, does use neutral hand postures on branches despite its highly arboreal lifestyle.

This small nocturnal strepsirhine (*Microcebus murinus*, Miller, 1777) has an ectaxonic hand (Jouffroy *et al.*, 1991) and moves preferentially on narrow branches in the wild (Petter, 1962; Martin, 1973; Tattersall, 1982). Several authors have indicated that *M. murinus* preferentially uses a grasp that places the substrate between digits 2 and 3 (grasp 2–3), or along the third digit (grasp 3), when moving on horizontal branches (Cartmill, 1974b; Lemelin & Schmitt, 1998). These grasp types are considered neutral with respect to wrist and hand posture (*i.e.* non-ulnarly deviated). In contrast, Bishop (1964) observed the same grasp types (grasp 2–3 and grasp 3) on thick horizontal substrates, but a preferred grasp between digits 1 and 2 (grasp 1–2) on narrow horizontal substrates suggesting a more ulnarly deviated hand.

Based on these prior observations, we test whether certain hand postures (that define a range of hand deviation) are preferred on different arboreal supports and whether the hand of the mouse lemur shows more ulnar deviation on narrow substrates as predicted by both previous studies (Preuschoft *et al.*, 1993; Lemelin & Schmitt, 1998) and suggested by Bishop (1964). To do so, we compare the effect of substrate orientation (horizontal vs. vertical) and diameter (narrow vs. thick) on hand posture in *M. murinus* during locomotion. Moreover, we explore whether ulnar deviation is a response to arboreality and if so, which aspects of arboreality may influence ulnar deviation using *M. murinus* as a model system. Finally, considering that this species is often viewed as a potential model to represent early primate behaviour and ecology (Martin 1972a,b; Cartmill, 1974b; Rasmussen, 1990; Crompton, 1995; Gebo, 2004) (see appendix A for details), our results are discussed in relation to the origins of primate-like grasping during locomotion.

Material and Methods

Animal subjects and care

All experiments were carried out using the grey mouse lemur *M. murinus* from the breeding colony located in Brunoy, France (MNHN, France, Agreement 962773). The experimental protocols used here adhered to the legal requirements of the European Union and the American Association of Physical Anthropologists Code of Ethics. The general conditions of captivity were maintained constant and as natural as possible with respect to ambient temperature (24–26°C), relative humidity (55%), *ad libitum* food availability and a photoperiodic regimen highly synchronized with the biological rhythms of the individuals (Genin & Perret, 2003). The subjects (all male) were of average mass (86.8±7.29 g) and length (24.5±2.08 cm).

Experimental procedure

Six male adults were filmed during quadrupedal locomotion using three high-speed video cameras set at 200 fps (Prosilica GE680, Allied Vision Technologies, Stadtroda, Germany). Cameras were placed along the sagittal, frontal and transverse planes relative to the dowels on which animals were moving and were zoomed in to allow a characterization of the grasp type. The animals moved along stiff horizontal and vertical wooden poles fixed at both ends within a Plexiglass enclosure (1 m long x 0.5 m high x 0.3 m wide). To study the effects of substrate diameter, two sizes (1 and 3 cm) were used for each orientation (vertical and horizontal). Several studies reported that narrow terminal branches are preferred by *M. murinus* (Petter, 1962; Martin, 1973; Tattersall, 1982). Unfortunately, exact substrate diameter used by *M. murinus* in the wild is unknown. The narrow (1 cm) and the thick (3 cm) diameters were chosen according to the ability of individuals to grasp the branch. The digits were able to wrap around the narrow substrate, a diameter usually used in the wild by *M. murinus*. However, the digits were unable to enclose around the thick substrates that were rarely used in the wild compared with the narrow ones. A total of 672 grasps were obtained from recordings of locomotion with 28 grasps for each subject (n=6) and each branch size (n=2) and orientation type (n=2).

A grasp implied some digits opposed to some others to hold onto a branch so we report the position of the digits relative to the substrate. According to digit position, a grasp indicates the degree of ulnar deviation in the wrist (Lemelin & Schmitt, 1998). The different grasps used can be classified into four categories based on the postural axis of the hand (Jouffroy, 1962; Cartmill, 1974b):

(a) Grasp 1–2 (telaxonic): substrate between the digit 1 (thumb) and the digit 2 (index);
(b) Grasp 2 (entaxonic): substrate along the digit 2;
(c) Grasp 2–3 (schizaxonic): substrate between digits 2 and 3;
(d) Grasp 3 (mesaxonic): substrate along the digit 3.

These postures represent a hand with progressively less ulnar deviation. In other words, the grasps between the digits 1–2 and along the digit 2 reflect an ulnarly deviated hand and a thumb individualized from the other digits, whereas the grasps between the digits 2–3 and along the digit 3 reflect a more neutral posture of the hand.

Statistical analysis

First, we calculated the basic statistics (percentages, means and standard deviations) for each grasp type per substrate (figs 1, 2). Second, a chi-squared test was performed between grasp type and three variables: orientation, diameter and individual in order to statistically define the dependence of grasp type on these variables as well as to assess interindividual variability.

Results

Substrate influences

No significant individual effects were noted on grasp type (X^2=8.5, degrees of freedom (d.f.)=15, p>0.05), independent of the diameter and the orientation of the substrate. Effects of substrate diameter on grasp type were significant, independent from the effects of orientation (X^2=86.94, d.f.=3, p<0.001). Grasp type 2 (entaxonic) and grasp type 2–3 (schizaxonic) were used on narrow substrates; grasp type 1–2 (telaxonic) was used exclusively on thick vertical substrates (figs. 1, 2). Moreover, the orientation of the substrate had a significant effect on grasp type, independent of the diameter of the substrate (X^2=380.67, d.f.=3, p<0.001). Indeed, during vertical climbing, grasp types 1–2 and 2 were used whereas they were never employed during horizontal walking (figs. 1, 2). Grasp type 3 (mesaxonic) was used during horizontal walking, and not vertical climbing, regardless of the diameter. As a result of these grasp choices, ulnar deviation was rather noticeable on vertical substrates and increased during locomotion on the thick vertical diameter involving a decrease in the use of grasp type 2–3 and an increase in the use of grasp type 1–2. By contrast, the wrist on horizontal substrates mainly appeared in a neutral posture. Overall, grasp type 2–3 is the most preferred posture (grasp 2–3: 43.4% *vs*. grasp 1–2: 9.5%, grasp 2: 19.8%, grasp 3: 27.2%) during quadrupedal locomotion on branches (fig. 3).

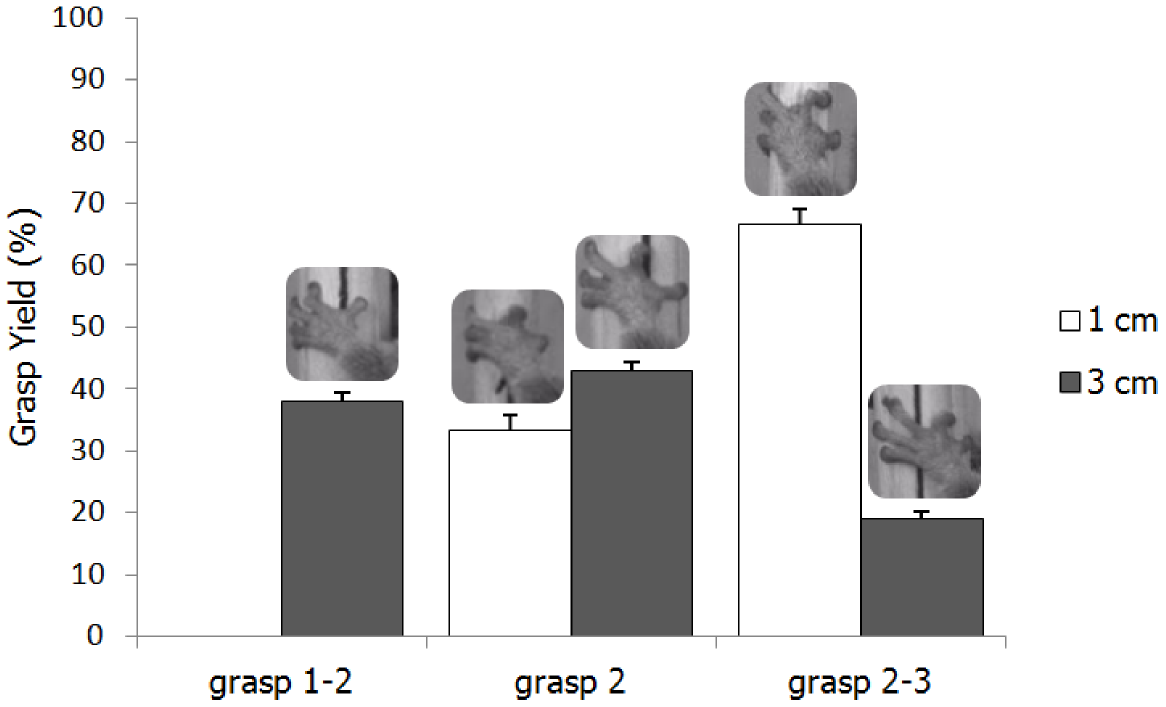

Figure 1. Representation in percentages of each grasp type used by *Microcebus murinus* for the vertical substrates.

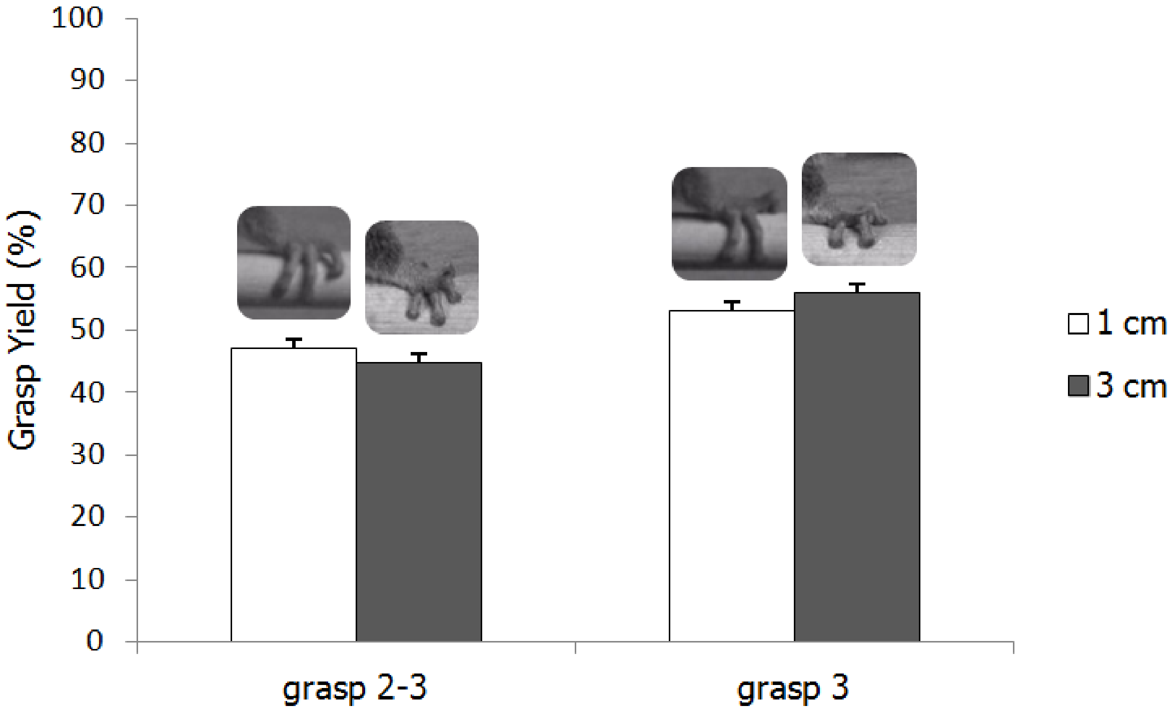

Figure 2. Representation in percentages of each grasp type used by *Microcebus murinus* for the horizontal substrates.

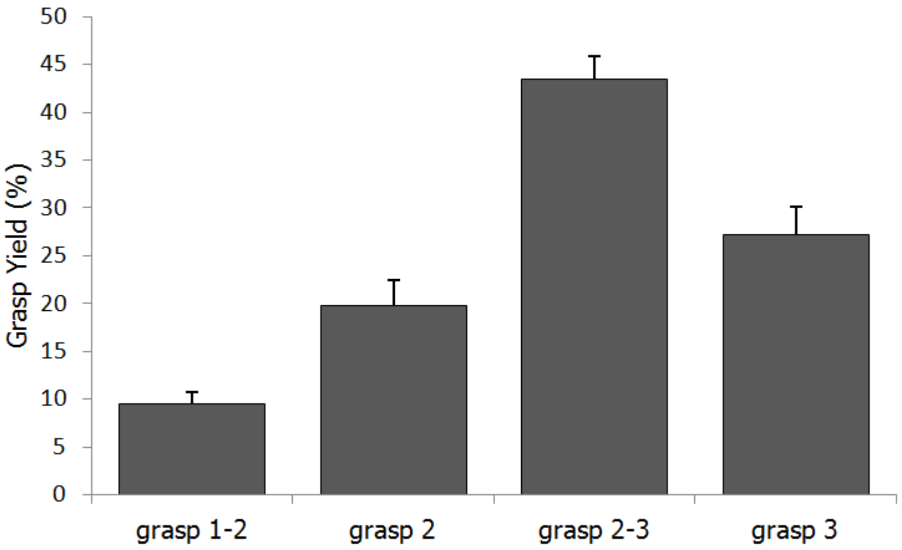

Figure 3. Representation in percentages of each grasp type used by *Microcebus murinus* for all the substrates analysed.

Discussion

The aim of this study was to assess the relationship between substrate use and preferred manual grasp type in the mouse lemur during locomotion on perches. The grasp categories emphasized functional aspects of hand posture and digit use. Six adult males were used here, and individuals did not differ from each other in their grasp preference. There were significant effects of substrate orientation and diameter on hand posture. For locomotion on horizontal substrates, there was a preference for schizaxonic and mesaxonic grasps where the substrate was positioned between more lateral digits. During these hand postures, the first digit is accompanied by the second digit in opposition to more lateral digits 3–5. Our results obtained using thick horizontal substrates were in agreement with observations by Lemelin and Schmitt (1998), Bishop (1964), and Cartmill (1974b) that schizaxonic (2–3) and mesaxonic (3) grasping is preferred by mouse lemurs and not telaxonic (1–2) and entaxonic (2) postures. Bishop (1964) observed a majority of grasping between digits 1–2 on narrow horizontal substrates of 1.2 cm diameter (similar to the small one used in our study) involving an ulnarly deviated hand. These results are inconsistent with those of Lemelin and Schmitt (1998), Cartmill (1974b), and with our analyses where grasp type 2–3 prevailed on all horizontal substrates.

During locomotion on narrow vertical substrates, grasp types 2 and 2–3 were also observed and involved a more ulnar-deviated hand. On thicker vertical substrates, schizaxonic grasps (2–3) were rarely used. Entaxonic (2) and telaxonic (1–2) grasps and ulnar deviation were most utilized. The grasp type 1–2 was dominant on thick vertical substrates but never used by the mouse lemur on other substrates. This suggests that the hand is more deviated on vertical substrates than on horizontal ones. The most important changes in grasp type occurred on vertical substrates and particularly on thick vertical substrates that could be considered extreme for the size of the *M. murinus* hand. Indeed, the mouse lemur usually moves on narrow and horizontal branches in the wild rather than on thick vertical supports, which suggests a pretext for the grasp differences observed here (Petter, 1962; Martin, 1973; Tattersall, 1982). This diversity in grasp use for *M. murinus* on vertical substrates relates to branch thickness and speaks to the challenge of subtending a larger central angle with a given hand span (Cartmill, 1974b). When climbing vertical substrates that are relatively thick, very secure grasping is hypothetically needed to generate more powerful forelimb action. Perhaps, entaxonic and telaxonic grasping that involve ulnar deviation are recruited for this reason. A schizaxonic grasp posture (2–3), also called zygodactylous, was reported in several studies on arboreal and semi-arboreal mammals but mainly as anecdotal observations (Pocock, 1920, 1925; Haines, 1958; Hershkovitz, 1977; Sargis, 2001) except for the howler monkey *Alouatta seniculus* and the woolly opossum *Caluromys philander* (Youlatos, 1999, 2010). It is interesting to note that for these animals, their preferred grasps occurred between digits 2 and 3, and this preference decreased with increases in substrate diameter involving a greater need for ulnar deviation as observed for *M. murinus* in this study.

In conclusion, ulnar deviation observed in the mouse lemur appears related to telaxonic and entaxonic grasping of thick substrates in combination with vertical orientations. This emphasizes the flexibility of hand posture use in small-bodied primates and may be similar in other tiny-sized climbing rodents as suggested by Byron *et al.* (2011). It is relevant here to address the evolution of primate-like grasping because *M. murinus* is often viewed as a potential model to represent early primate behaviour and ecology, and rodents may be considered informative of a precursor stage in primate evolution (Cartmill, 1974b; Martin, 1972a, b; Gebo, 2004; Byron *et al.*, 2009, 2011). We suggest that early primates exhibited a preference for above-branch activity on horizontal perches using mostly schizaxonic grasps (similar to Cartmill, 1974b) and displayed greater ulnar deviation when challenged by vertical supports that require more secure grasping. Vertical climbing more than an arboreal context per se, may favour ulnarly deviated postures because grasping between digits 1 and 2 and along digit 2 provide greater security. These postures are favoured when hand span is challenged with branches that are thicker and vertically aligned. If this assertion is correct, enlarging hand span between digits 1 and 2 (*e.g.* Cartmill, 1974b) by elongating digits in particular, may represent a critical adaptation for primate-like arboreality. This suggestion is congruent with observations on other strepsirhines, indriid and lorisid species and haplorhines such as gibbons. They all share a deep morphological separation between digits 1 and 2. The first are classified as vertical clingers and leapers (Napier & Walker, 1967) and mainly used grasp type 1–2 (Jouffroy *et al.*, 1991; Lemelin & Jungers, 2007) revealing an ulnar deviation of the hand. The second are typically referred to as slow climbers (Napier & Napier, 1967) presenting kinematic adaptations on vertical substrates (Hanna, 2006) and are

known to exhibit extreme ulnar deviation with a preferential use of grasp type 1–2 (Jouffroy & Lessertisseur, 1979; Nieschalk & Demes, 1993; Lemelin & Schmitt, 1998). The third are known as brachiators, but also climb frequently large vertical substrates in the wild with the telaxonic grasp (Napier & Napier, 1967; Van Horn, 1972; Fleagle, 1976). In contrast, the tarsiers and galagos are also defined as vertical clingers and leapers (Napier & Walker, 1967), but do not exhibit a wide span between digits 1 and 2. Studies reported that they principally use thin branches like *M. murinus* (Crompton & Andau, 1986; Dagosto & Gebo, 1997; Niemitz, 1984; Off & Gebo, 2005), but unfortunately, very few data exist on grasp postures in tarsiers and galagos during locomotion that can help to clarify this morphological issue. In galagos, Bishop (1964) reported that grasp types differed between two species (*G. senegalensis* and *G. crassicaudatus*) but both of them displayed various grasps on horizontal branches of different diameters (grasp types 1–2, 2–3 and 3). The same author added that galagos and tarsiers presented a variability of hand posture in locomotion. These observations are related to the idea of flexibility of hand posture in small-bodied species, but need further quantifications. In tarsiers, it is clear that phalangeal elongation is extremely relative to the metacarpus. In fact, tarsiers have such long finger segments relative to their metacarpals that they are closer to gliding mammals such as Dermoptera and *Petauroides*, rather than most other primates (Kirk *et al.*, 2008). Besides, some authors interpret the hand morphology of tarsiers rather as an adaptation to their specialized prey acquisition, and others suggest that their long hand enhances the contact with thick and smooth vertical substrates to help body support (Bishop, 1964; Niemitz, 1984; Lemelin & Jungers, 2007).

Our data on *M. murinus*, when contrasted to data on other species, may suggest that (1) a schizaxonic grasp was the main grasp used by the early primates and (2) ulnar deviation and a telaxonic grasp may have occurred with a preferential use of vertical climbing. These observations and hypotheses need to be expanded upon by further studies on the use of different grasp types in relation to substrate characteristics such as diameter and orientation in a greater number of species if we want to better understand the influence of substrate on the origins of primate grasping during locomotion.

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SYNTHÈSE CHAPITRE 2

Titre: Posture de la main de microcèbe au cours de la locomotion arboricole sur fines branches.

Question: Le diamètre et l'orientation du substrat influencent-ils les stratégies comportementales de la préhension?

Modèle: Microcèbe (*Microcebus murinus*)

Résultat: Le diamètre et l'orientation du substrat influencent fortement les stratégies de préhension se caractérisant par une variabilité des postures manuelles.

Discussion: La diversité du milieu arboricole a probablement favorisé l'élaboration des capacités de préhension.

Perspective: Tester si les propriétés du substrat sur lequel se déplace l'individu influencent les stratégies de préhension de nourriture.

SUMMARY CHAPTER 2

Title: Hand posture of the grey mouse lemur during arboreal locomotion on narrow branches.

Question: Do the size and the orientation of the substrate influence the behavioural strategies of prehension?

Model: The mouse lemur (*Microcebus murinus*)

Result: The diameter and the orientation of the substrate strongly influence the strategies of grasping being characterized by a variability of the manual postures.

Discussion: The diversity of the arboreal environment probably favored the elaboration of the capacities of grasping.

Perspective: Test if the properties of the substrate on which moves the subject influence the strategies of food grasping.

Chapitre 3 - Acquisition de nourriture sur substrats arboricoles chez *Microcebus murinus*

Food Acquisition On Arboreal Substrates By The Grey Mouse Lemur: Implication For Primate Grasping Evolution

Journal of Zoology (Submitted)

Abstract

The use of the hand in food grasping is a shared characteristic of primates. However, the factors involved in the elaboration of this function remain unclear. Current hypotheses concerning the origin of primates agree that grasping hands may have evolved in an arboreal habitat consisting of fine branches. However, several authors suggest an association with different types of feeding such as insect predation, fruit and flower exploitation, or both. One final hypothesis assumes that a specialization for insect predation in the context of the fine branch milieu was important in the origins of primates. No study has tested the importance of arboreal conditions and diet (*e.g.* frugivorous, omnivorous) on the use of the hand in food grasping. Yet, both of them likely impose important selective pressures on the origin and evolution of manual grasping strategies in food acquisition. To test these factors, we quantified whether i) substrate diameters (narrow, wide) and ii) food properties (static, slow moving, fast moving) influence the food grasping of a small primate, *Microcebus murinus*, which is currently considered as a good model to infer the behaviour of the first primates. Our results show that the narrow substrate increases the use of hands in prey grasping. Moreover, the mouth is preferentially used to grasp static food (banana) whereas the hands are preferred to grasp moving prey (mealworm and cricket) regardless of the substrate. These results show that the fine branch niche may be an important selective pressure on the emergence of manual food grasping in primates, but that predation, independent of the substrate, probably also played a key-role.

Keywords: *Microcebus murinus*, Grasping, Hand, Mouth, Food Properties, Substrate Diameter.

Introduction

Among many other features, the primates are characterized by a clawless grasping hand used both for moving and climbing on arboreal substrates and for grasping food items. Even if numerous non-primate species use also the hand in arboreal locomotion, very few use it in food acquisition whereas all the primates do so. Moreover, a wide diversity of manual grasp types exists among primates (Bishop, 1964; Christel, 1993; Pouydebat et al., 2009). Yet, the factors involved in the evolution of manual grasping in the context of food acquisition in primates remain unclear. As this trait was presumably selected for near the origins of primates, the factors suggested important in the context of primate origins could be tested in the context of the use of the hand in food grasping. Many authors consider the exploitation of an arboreal niche of fine branches at the root of the primate tree (for a review see Ross & Martin, 2007; Ravosa & Dagosto, 2007), and four major ones associate this adaptation to feeding activities in order to explain the origins of primates, including the development of prehensile hands (Cartmill, 1972, 1974a, b; Rasmussen, 1990; Sussman, 1991; Godinot, 1991; 2007). First, the visual predation hypothesis suggests that the prehensile hands of primates with long and clawless fingers were originally an adaptation for locomotion on fine branches and were exploited subsequently for visually guided manual predation on insects (Cartmill, 1972, 1974a, b; Kirk *et al.*, 2003). Indeed, the long fingers and the claw loss of primates were likely associated to the habitual feeding and foraging among the small-diameter branches, whereas the visual and manual insect predation better explain orbital convergence. Second, the angiosperm exploitation hypothesis suggests that these traits are also correlated with exploitation of the fine branches but with a visually guided grasping of fruits and flowers, not related to insect predation (Sussman, 1991). This author insists on the grasping extremities being adapted to move among the tips of fine branches to get hold of small fruits and flowers. Third, Rasmussen (1990) combines these hypotheses considering the fine branch niche in which the first primates foraged for both fruits and insects. Fourth, even if Cartmill (1972) and Rasmussen (1990) consider the insect predation in their hypothesis, Godinot (1991, 2007) focused on it as a determinant factor in the origin of primates. He suggested that the primate hand with long and clawless fingers would be more adapted for insect predation than for the use of fine branches, even if this author considers that the first primates probably evolved in this habitat. Indeed, several extant non-primate species such as *Caluromys* and *Ptilocercus* are adapted to the fine branch niche and show long fingers and prehensile hands but they do not possess nails (Sargis, 2001; Schmitt & Lemelin, 2002).

Moreover, these species are able to catch insects with their hands but are not specialized as the first primates are thought to be. Specializations for insect predation consisting of jumping onto the prey and grabbing hold with the hands while remaining attached by the feet on the branch, based on the behaviour of extant galagos and tarsiers (Charles-Dominique, 1977; Niemitz, 1984), were considered to represent the foraging in basal primates (Godinot, 1991). Even if some extant non-primates display this behaviour, they do not show a high degree of specialization. According to Godinot (1991), this specialization is consistent with long fingers which enhance the surface for catching, and the broadened distal parts of the finger which enhance a stable grasp. Although all of these authors suggest that the grasping clawless hand of primates would have arisen in correlation with functional demands, the ecological context of the use of the hand in food grasping remain poorly understand.

Indeed, the effect of the substrate on the abilities for manual food grasping remains untested. Yet, the arboreal milieu in which the first primates likely evolved probably constituted an important selective pressure in the development of food acquisition strategies. In contrast, the food properties have been investigated and have been shown to influence the use of the hands in grasping for primates and non-primates (Castiello *et al.*, 1992; MacFarlane & Graziano, 2009; Pouydebat *et al.*, 2009; Ivanco *et al.*, 1996). One or both hands are used to catch fast moving foods (*e.g.* insects) particularly in some platyrhines, strepsirhines, rats and opossums, (Petter 1962; Martin, 1972a, b; Charles-Dominique, 1977; Niemitz, 1984; Ivanco *et al.*, 1996; Nekaris 2005), whereas many of them preferentially use the mouth to grasp static food (*e.g.* fruits) (Rothe, 1971; Pollock, 1977; Singer & Schwibbe, 1998; Whishaw *et al.*, 1998; Reghem *et al.*, 2011; Scheumann *et al.*, 2011). However, the quantification of the substrate use during food grasping is rarely considered.

In this study, we test the influence of both substrate diameter and food properties on the grasping strategies used by *Microcebus murinus* (Strepsirhini, Cheirogaleidae). This species is often viewed as a good potential model to represent the behaviour and ecology of basal primates (Martin, 1972a, b; Cartmill, 1974a, b; Crompton, 1995; Gebo, 2004) (see Appendix A for details). Indeed, a small sized, generalist, omnivorous and nocturnal animal exploiting a fine branch niche such as *M. murinus* was proposed to adequately describe the first primates (Martin, 1972b; Charles-Dominique, 1977; Gebo, 2004). The fine branch niche described for *M. murinus* and for the first primates consists of branches of small diameter relative to the size of the animal on which the fingers are able to close around (Gebo, 2004; Dagosto, 2007). Concerning the food grasping strategies, *M. murinus* uses its mouth in high proportion for small static food like piece of fruits (Ward & Hopkins, 1993; Reghem *et al.*, 2011; Scheumann *et al*., 2011), but demonstrates an increase of hand use while catching prey in the wild (Martin, 1972a, b; Charles-Dominique, 1977; Siemers *et al*., 2007). The food properties and the substrate used are often discussed in the context of primate origins but, to our knowledge, no study has yet quantified both in the context of food grasping strategies. Therefore, in this study, we test the corollaries of the four major hypotheses on primate origins outlined above by exploring whether grasping strategies are affected by substrate diameter (wide and narrow) and food properties (static: banana, slow moving: mealworms and fast moving: crickets). Consequently, we tested whether and how these factors may have played a role in the hand use in food grasping.

First, we predict that substrate diameter will have an influence on the stability of the individuals and thus on their grasping strategy. The narrow diameters should result in an increase of the use of the hand in food grasping. Indeed, *M. murinus* being a specialist of fine branches and possessing a powerful pedal grasping, should be more stable in grasping narrow substrates rather than wide ones. Consequently, attached by its feet on narrow substrates, it will have its hands free to be used during prey grasping. Second, we predict that the presence of moving food should increase the use of manual grasping. Indeed, some studies have observed this trend in platyrhines and strepsirhines.

Material and Methods

Species and Husbandry

Microcebus murinus (Miller, 1777) is a small arboreal, nocturnal, and omnivorous strepsirhine species endemic to Madagascar (Martin, 1972a, b). This species is classified as a branch walker and runner and prefers to move on narrow horizontal substrates in the wild (Petter, 1962; Martin, 1972a). The individuals of the study were all born in captivity in the captive colony of the UMR 7179 of the Muséum National d'Histoire Naturelle (Brunoy, France, Agreement 962773). Their cages and the experimental enclosure were placed in a maintenance room recreating natural environmental conditions with a constant ambient temperature of 24–26 ° C and 55% humidity. The individuals were exposed to a 12-hour light/dark cycle (night: 2pm-2am, day: 2am-2pm). The animals received foods and water *ad libitum* as usual. The experimental protocols used here adhered to the legal requirements of the European Union and the American Association of Physical Anthropologists Code of Ethics.

Experimental set up

Five adult males (mean age: 4±1 years old; mean mass: 82±2 g) were recorded individually with two cameras at 30 fps (Sanyo X Acti Full HD 1920x1080) in a transparent experimental enclosure (51x25x26 cm) (fig. 1). A wooden nest was mounted inside the enclosure with one horizontal substrate.

Two diameters of substrate were selected in order to obtain relevant, yet different constraints. As the precise diameter of the substrate used by the mouse lemurs in the wild is unfortunately unknown we considered a narrow diameter as one where the hands and feet are able to wrap around the substrate. The narrow substrate used in this study was 2 mm wide. We hypothesize that this sort of diameter corresponds to the definition of the fine branch milieu or fine terminal branch niche used by the mouse lemurs in the wild and described by many authors (Petter 1962; Cartmill, 1972; Martin, 1972a; Rasmussen, 1990; Sussman, 1991). We characterized as a wide diameter one where the hands and feet are unable to close around the substrate. The wide substrate measured 20 mm. This substrate diameter is likely less frequently used in the wild compared to the narrow substrate.

We selected three properties of food on the basis of type of movement exerted by the food itself: a static fruit, a slow moving mealworm and a fast moving cricket. The static fruit consisted of a piece of banana with a volume of approximately 1 cm^3. The slow moving food consisted of a crawling mealworm with a size in between 1 and 1.5 cm in length. These prey move not at all or very slowly on both substrates. The fast moving food consisted of crickets between 1 and 1.5 cm in length. These prey moved rapidly across both substrate types.

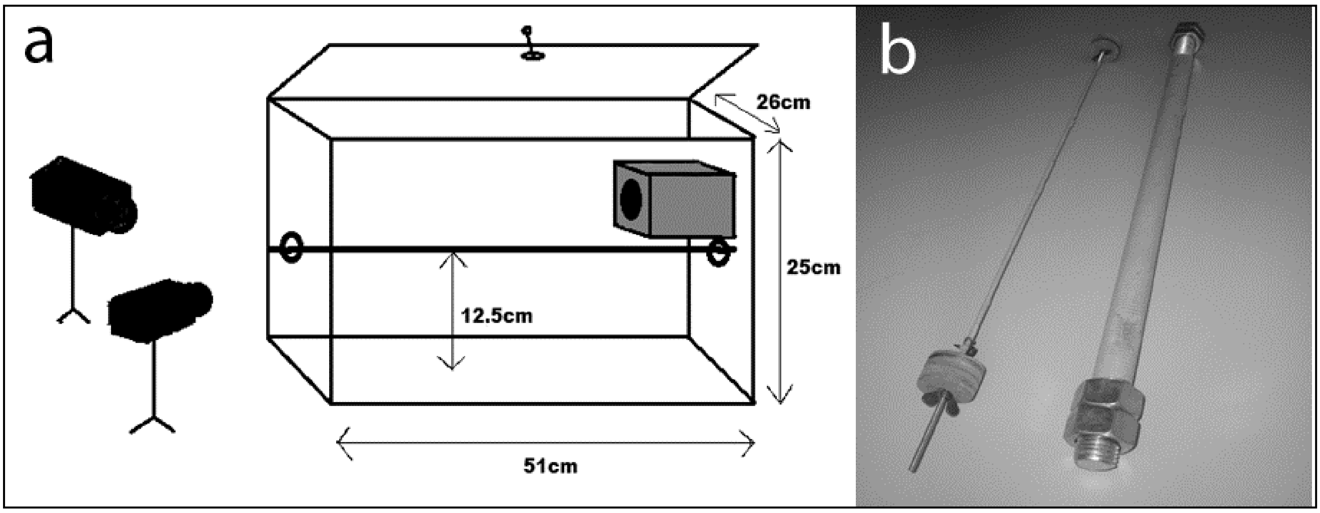

Figure 1. Experimental set up (a) and the two substrates (b) (diameters of 2 mm and 20 mm).

Procedure

Before recordings, a period of two days of habituation for each individual in the experimental enclosure to familiarize the mouse lemurs to the experiment was implemented. The daily recording sessions started at the beginning of the activity period in low light levels, with the experimental set-up lit by a dim red light (20 mW/cm 2 , equivalent to 0.002 lx) not perceived by the animals. During the first hour or the first two hours of the dark cycle (2 pm to 3 or 4 pm) individuals were the most active.

For each session, one piece of banana, one mealworm or one cricket was placed on the substrate inside the enclosure. The mealworm and the cricket placed on the substrate moved freely but banana was pinned onto the substrate. The session started as soon as the food was placed on the substrate and finished when the individual grasped the food. The individuals were always in their nest box within the enclosure when the food was placed on the substrate and returned to their nest boxes after grasping or after having eaten the food. We collected 10 grasps per type of food for each substrate and for each individual (n=60 grasps per individual). However, one individual refused to eat crickets. A total of 280 grasps were recorded and analyzed. Each individual needed between three to five days to execute all the grasps.

All data were obtained in unconstrained conditions meaning that the individual was totally free to move out to the nest in order to climb on the substrate and to grasp the food. The individuals were not trained in this task prior the experimental trials.

Table 1. Abbreviations and definitions of the type of grasps identified during food grasping by *M. murinus*.

Type of grasps	Abbreviations	Definitions
Mouth grasp	M	The **M**outh alone grasps the food without use of the hands
Hand alone grasp	1H	**One H**and alone grasps the food without the mouth and the 2nd hand
Bimanual grasp	2H	The **both H**ands at the same time grasp the food without the mouth
Mouth and one hand grasp	M+1H	The **M**outh firstly grasps the food followed almost instantaneously by **one H**and
One hand and mouth grasp	1H+M	**One H**and firstly grasps the food followed almost instantaneously by the **M**outh
Mouth and bimanual grasp	M+2H	The **M**outh firstly grasps the food followed almost instantaneously by the **both H**ands
Bimanual and mouth grasp	2H+M	The **both H**ands firstly grasps the food followed almost instantaneously by the **M**outh

Data analysis and grasping strategies

The different grasping strategies were defined and quantified after frame by frame analyses of the videos. We observed seven strategies or grasp types: the mouth grasp (M), the hand alone grasp (1H), the bimanual grasp (2H), the mouth first with one hand (M+1H), the hand first with the mouth (1H+M), the mouth first with the both hands (M+2H), and the both hands first with the mouth (2H+M) (table 1).

Statistical analysis

We tested for differences in grasping strategies using chi-square tests using the data for each individual separately as well as the data for all individuals combined. First, we tested for the effect of food properties within each substrate type. Second, we tested the effect of substrate within each food property type. All analyses were performed using the R graphical and statistical package v.2.9.0.

Results

Effect of the substrate diameter on the grasping strategies

For the whole group, the substrate diameter had a significant effect on the grasping strategies when grasping moving foods (mealworm and cricket), but not in the context of static foods (banana: $X^2=8.7132$, d.f.=4, $p<0.06$; mealworm: $X^2=15.4624$, d.f.=4, $p<0.003$; cricket: $X^2=10.0407$, d.f.=3, $p<0.01$).

Moreover, inter-individual differences appeared (table 2). Indeed, a modification of strategies used according to the substrate was significant for at least one individual for each food type. For crickets, the individual 1 preferentially used both hands to catch the prey on the narrow substrate, but a combination of one or both hands with the mouth on the wide substrate. Similarly, for mealworm capture, the individual 2 typically grasped mealworms with both hands on the narrow substrate, but added the mouth on the wide substrate. For banana, a different trend occurred with the individual 5 using the mouth to grasp the fruit on narrow substrate, but involved one or both hands in addition to the mouth on the wide substrate yet the other individuals still preferred the mouth alone.

Overall, the individual trends for crickets and mealworms reflected the trends for the group as a whole. First, the frequency of mouth use combined with one or both hands increased on the wide substrate for prey (fig. 2) and the mouth grasping remained similar for static food on both substrates (88±3.3% on the narrow substrate, 84±6.1% on the wide one). Second, more variability in grasp types was observed on the wide substrate than on the narrow one (fig. 2). Indeed, the individuals on the wide substrate exhibited one additional type of grasp for banana (2H) and two additional types of grasp for mealworm (M, 1H+M) in comparison with the narrow substrate. In addition, the bimanual grasp without the mouth (2H) was widely preferred for catching prey on the narrow substrate (78±2.2% for mealworm; 62.5±9.3% for cricket) and less on the wide substrate (46±2.7% for mealworm; 37.5±5.3% for cricket). Therefore, no single one strategy was preferred (<50%) for prey on wide substrate and this was more pronounced for crickets (fig. 2).

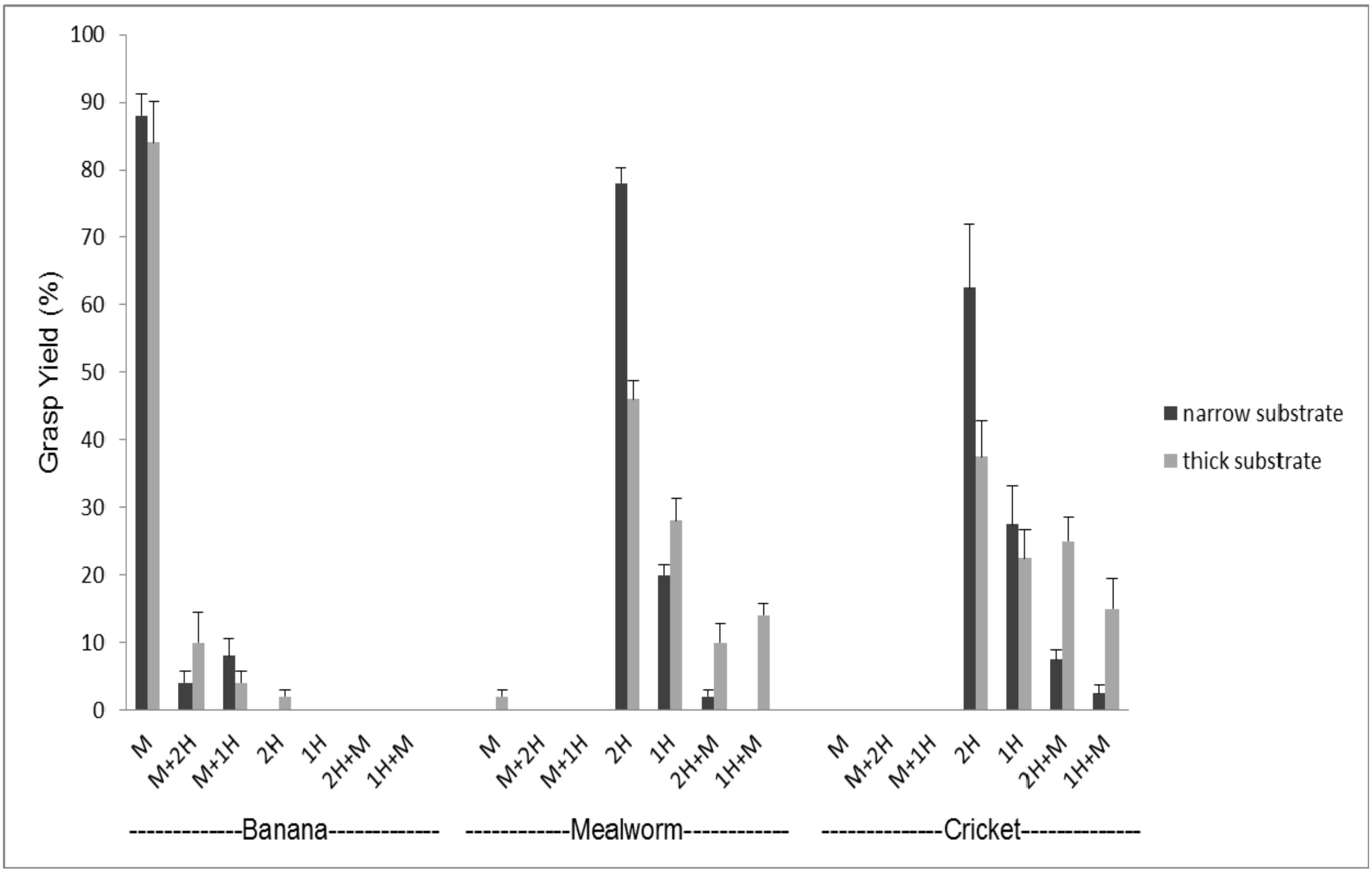

Figure 2. Frequency of grasping strategies used as function of the food properties and the substrate diameters for the whole group. For abbreviations see table 1.

Effect of food properties on the grasping strategies

A significant effect of food properties on the grasping strategy was observed for both substrates, both when testing each individual (table 3) and when testing the whole group (narrow substrate: $X^2=146.2984$, d.f.=12, $p<0.001$; wide substrate: $X^2=137.2069$, d.f.=12, $p<0.001$). No inter-individual differences were noted.

The grasping strategies were defined by the use of several types of grasp which were different in function of food properties (table 3, fig. 2). Four types of grasp (M, M+2H, M+1H, 2H) were observed for static foods (banana). The most commonly used one was the mouth grasp (M) (more than 80%) whereas the other types of grasp were very rarely used (less than 10%). Five types of grasp (2H, 1H, 2H+M, 1H+M, M) were observed in the context of slow moving and fast moving foods. The bimanual grasp (2H) without the mouth was preferentially used for both foods (more than 35%). Moreover, the hand alone was the second type of grasp also widely used for these prey (more than 20%) followed by the hands-mouth combination (2H+M, 1H+M). The mouth alone was never used except one time by one individual for catching mealworms.

Interestingly, when mouth and hands were both used to grasp food, the individuals preferred the mouth to initiate the grasping of banana (M+2H, M+1H); yet, the same individuals used the hands first to grasp prey (2H+M, 1H+M).

Table 2. Statistical tests of the effect of substrate diameter on the grasping strategies per individual for each food type.

Individual	banana	mealworm	cricket
1	$X^2 = 4.25$, d.f. = 2, $p<0.1$	$X^2 = 1.48$, d.f. = 2, $p<0.47$	$X^2 = 10.4$, d.f. = 3, $p<0.01$*
2	$p<1$	$X^2 = 5.72$, d.f. = 2, $p<0.05$*	-
3	$p<1$	$X^2 = 6.47$, d.f. = 3, $p<0.09$	$X^2 = 0.86$, d.f. = 2, $p<0.64$
4	$p<1$	$X^2 = 3.54$, d.f. = 3, $p<0.31$	$X^2 = 3.61$, d.f. = 3, $p<0.30$
5	$X^2 = 8.93$, d.f. = 3, $p<0.03$*	$X^2 = 6.28$, d.f. = 3, $p<0.09$	$X^2 = 6.47$, d.f. = 3, $p<0.09$

* Significant at 0.05

Table 3. Statistical tests for the effect of food properties on the grasping strategies per individual for both substrates.

Individual	Narrow substrate	Thick substrate
1	$X^2 = 32$, d.f. = 8, $p<0.001$*	$X^2 = 41.2667$, d.f. = 8, $p<0.001$*
2	$X^2 = 22$, d.f. = 2, $p<0.001$*	$X^2 = 20$, d.f. = 2, $p<0.001$*
3	$X^2 = 31$ d.f. = 6, $p<0.001$*	$X^2 = 33.75$, d.f. = 8, $p<0.001$*
4	$X^2 = 36$ d.f. = 8, $p<0.001$*	$X^2 = 36.381$, d.f. = 8, $p<0.001$*
5	$X^2 = 30$ d.f. = 8, $p<0.001$*	$X^2 = 36.8$ d.f. = 12, $p<0.001$*

* Significant at 0.05

Discussion

The aim of the present study was to assess whether substrate diameter and food properties influenced the food grasping strategies of a small primate, *M. murinus*. As food grasping with the hands is one of the main characteristic of primates, this trait was presumably selected for near the origins of the group. Based on the factors suggested in the hypotheses of primate origins and on the behaviour of extant species, we predicted 1) that narrow substrate should increase the use of manual grasping to pick up foods because the feet can more easily close around this substrate compared to wide one and enhance the stability, allowing the hands to remain free, 2) and that the presence of moving food should increase the use of manual grasping. The main results supported these two hypotheses. A behavioural pattern appeared for the group associating different strategies with different substrate diameters and food properties, especially for the capture of live prey. Indeed, the mouse lemurs modified their strategies and preferentially caught the slow moving and fast moving prey (respectively mealworm and cricket) with one or both hands, consistent with previous observations in the wild (Petter 1962; Martin, 1972a, b; Charles-Dominique, 1977; Siemers *et al.*, 2007). The preferred use of one or both hands without the mouth for capturing prey appears common to the mouse lemurs and other primates including platyrhines (callithrichids, capuchins), strepsirhines (galagids, cheirogaleids, lorisids), tarsiers and non-primate species as rats and opossums (*strepsirhines*: Petter 1962; Martin, 1972a, b; Charles-Dominique, 1977; Nekaris 2005; *tarsiers*: Niemitz, 1984; *platyrhines*: Singer & Schwibbe, 1998; Pouydebat *et al.*, submitted; *rats and opossums*: Ivanco *et al.*, 1996). Therefore, the trend in prey grasping strategy as observed for the mouse lemurs is supported by other extant primates and non-primate mammals. Moreover, the use of hands prevailed on narrow substrate for catching prey and the use of mouth was rarely involved on the same substrate. In contrast, the use of the mouth combined with the hands increased for catching prey on the wide substrate. One study seems to support our findings. Indeed, in a previous study the mouth-hand combination used by *M. murinus* for catching mealworms put on a food bowl was the most use (mouth-hand combination: 69%) followed by the mouth alone (28.1%) and finally by very few one hand alone (2.9%) (Scheumann *et al.*, 2011). The wide substrate seems to favor the use of the mouth for prey capture. The modification of grasping strategies according to substrate may be related with the habitual environment of *M. murinus*. Indeed, the mouse lemurs possess a powerful pedal grasp with a divergent hallux particularly adapted to grasp small branches improving security and stability (Cartmill 1974a, b; Sargis *et al.*, 2007) (Martin, 1972a). Considering that the feet of the mouse lemurs are able to grasp and encircle the narrow substrate but not the wide substrate used in the present study, we suggest that their stability is enhanced on the narrow substrate allowing them to free their hands for food grasping. Therefore, the narrow substrate likely allows the mouse lemurs to increase the use of the hands for prey capture. However, quantified observations of prey grasping behaviour on arboreal substrates in other species are still missing and the influence of this substrate on prey grasping must be improved by further studies.

Concerning the grasping of static foods (banana), the main type of grasp used was the mouth alone, regardless the substrate. The use of both mouth and hands or hands alone was always less prominent. This is consistent with previous studies on the grasping of small sized fruits (Ward & Hopkins, 1993; Reghem *et al.*, 2011; Scheumann *et al.*, 2011). Moreover, grasping static foods with the mouth as observed here for mouse lemurs is commonly observed for other species, yet always on non-arboreal substrates (strepsirhines: Pollock, 1977; Ward & Hopkins, 1993; platyrhines: Singer & Schwibbe, 1998; and non-primate species as rodents: Whishaw *et al.*, 1998; opossums: Ivanco *et al.*, 1996 and tupaia: Joly *et al.*, 2012). As is the case for prey grasping, quantitative data do not exist for arboreal substrates and are needed in order to confirm this trend for other species.

In summary, the use of the hand in food grasping was different between static and moving foods (both slow and fast moving) and between substrate diameters. Both the narrow substrate and the moving food increased the use of the hand in food grasping and suggest that prey capture associated with the use of fine branches may have been an important selective force increasing prehensile capacities in the first primates. These results are consistent with the hypotheses on primate origins which propose adaptations to both fine branch environment and visually directed prey capture with hands (Cartmill, 1974a, b; Rasmussen, 1990; Godinot, 2007). However, for both the mouse lemur as well as other species, prey grasping involves the use of the hand independent of substrate diameter (narrow and wide). Therefore, this behaviour suggests that predation potentially is even more important than the fine branch niche per se in driving the use of the hand among the first primates. Thus, the hypothesis that essentially considers the fine branch niche in association to grasping fruits and flowers (Sussman, 1991) appear insufficient to explain the origins of primate hand use in food grasping. Our results supported the insect predation specialization hypothesis suggested by Godinot (1991, 2007), Cartmill (1972, 1974a, b) and Rasmussen (1991). Our results do not refute existing hypotheses on primate origins but emphasize predation as potential determinant factor in the elaboration of manual ability and the use of the hands in food grasping in the first primates. However, the study of the factors implicated in the increased use of the hand in grasping and manipulation needs further attention and must be complemented by studies on other model species. Indeed, comparisons of primate (tarsiers, galagos, cheirogaleids) and non-primate models (rodents, soricids, carnivorans, marsupials, tupaias, anurans) with various locomotion (arboreal and terrestrial) and dietary (omnivorous and frugivorous) habits will likely provide new insights into the factors that may have driven an increased use of the hands and their prehensile capacities among primates.

Acknowledgments

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SYNTHÈSE CHAPITRE 3

Titre: Acquisition de nourriture sur substrats arboricoles chez *Microcebus murinus*.

Question: La saisie de proies sur différents substrats influence-t-elle les stratégies comportementales de la préhension?

Modèle: Microcèbe (*Microcebus murinus*)

Résultat: La saisie de proies implique une utilisation de la main (contrairement aux fruits saisis avec la bouche), plus fréquente encore sur petits substrats.

Discussion: La prédation a probablement eu un effet sur l'implication de la main et sa fréquence d'utilisation, indépendamment du milieu.

Perspective: Tester différents types de proies et la reproductibilité de ce résultat chez d'autres primates voire d'autres tétrapodes.

SUMMARY CHAPTER 3

Title: Food acquisition on arboreal substrates by the grey mouse lemur: Implication for primate grasping evolution.

Question: Does the prey grasping on various substrates influence the behavioural strategies of grasping?

Model: The mouse lemur (*Microcebus murinus*)

Result: The prey grasping involves a use of the hand (contrary to fruit grasped with the mouth), more frequent on small substrates.

Discussion: The predation probably had an effect on the implication of the hand and its frequency of use, independent of the environment.

Perspective: Test different types of prey and the reproducibility of this result among other primates and other tetrapods.

CONCLUSION DES CHAPITRES 1, 2 & 3

Question: Quels sont les facteurs écologiques (propriétés de la nourriture et du substrat) susceptibles de favoriser l'utilisation de la main chez les premiers primates?
Modèle: Microcèbe (*Microcebus murinus*)
Résultat: La saisie sur petits substrats et la capture de proies favorisent l'utilisation de la main.
Discussion: L'hypothèse de l'implication du milieu de fines branches dans l'élaboration des capacités de préhension se confirme mais la prédation, indépendamment du milieu, a probablement joué un rôle clé dans l'utilisation de la main pour se nourrir chez les premiers primates.
Perspective: Comprendre les facteurs fonctionnels (postures corporelles: chapitre 4 / cinématique du membre supérieur: chapitre 5) impliqués dans l'évolution de la préhension.

CONCLUSION OF THE CHAPTERS 1, 2 & 3

Question: What are the ecological factors (food and substrate properties) which could favor the use of the hand among the first primates?
Model: The mouse lemur (*Microcebus murinus*)
Result: The food grasping on small substrates and the prey capture favor the use of the hand.
Discussion: The hypothesis of the implication of fine branch niche in the elaboration of the capacities of prehension is supported, but the predation, independent of the environment, probably played a key-role in the use of the hand in food grasping among first primates.
Perspective: Understand the functional factors (body postures: chapter 4 / kinematics of the forelimb joints: chapter 5) involved in the evolution of the prehension.

Chapitre 4 - Influence de la posture corporelle sur la cinématique de la préhension chez l’humain et le gorille (*Gorilla gorilla*)

The Influence Of The Body Posture On The Kinematics Of Prehension In Humans And Gorillas (*Gorilla gorilla*)

American Journal of Physical Anthropology (Submitted)

Abstract

The origins, evolution, and mechanisms of human prehension can be better understood through comparisons with non-human primate models. However, most non-human primates are arboreal, and adopt a variety of body postures compared with humans, strictly terrestrial and bipedal. Much of our current understanding of human prehension in a comparative context is only based on macaque models in a sitting, constrained body posture. Thus, knowledge of prehension kinematics in primate that are more closely related to humans and knowledge of how different body postures influence prehension kinematics is critical to understand how prehension evolved in humans. This study compares humans and gorillas during an unconstrained food prehension task in two body postures, a sitting and a quadrupedal posture. The objective is to determine the behavioural and kinematic strategies as well as differences and invariants of trunk and forelimb motions between species. Our results show that (1) despite significantly influences of body postures on ranges of motion in gorillas and humans, species preserve their specific forelimb joint and trunk contribution independent of the posture; (2) body posture has a small effect on the basic pattern of wrist velocity. Our study indicates that different primate species have specific kinematic features of limb coordination during prehension, which do not alter with change in postural positioning. Therefore, across varying species it is possible to compare limb kinematics irrespective of postural constraints. Kinematic analyses of other primates differing in the degree of terrestriality/arboreality and from different phylogenetic groups are needed to better understand common and specific strategies in the context of the evolution of primate prehension.

Key words: Prehension, Primates, Gorilla, Kinematics, Evolution

Introduction

The human prehension was first defined kinematically by Jeannerod (1981) who subdivided it into two phases: reaching and grasping. The first phase is characterized by the spatiotemporal variability of the wrist velocity and the second phase is defined by the grip aperture between thumb and index. Primates are known for their agile manual prehension, in particular apes including humans, but how these skills appeared and evolved still remains unclear. The origins, evolution, and mechanisms of human prehension can be better understood by comparisons with non-human primate models. In this context, the macaque is one of the most commonly investigated genus in kinematic studies (*e.g.* Scott & Kalasha, 1997; Roy *et al.*, 2000; Fogassi *et al.*, 2001; Christel & Billard, 2002; Jindrich *et al.*, 2011). This genus shows basic kinematic similarities with humans (Scott & Kalasha, 1997; Roy *et al.*, 2000; Fogassi *et al.*, 2001), but also specific differences (Christel & Billard, 2002). Not only are macaques the only non-human primate in which prehension have been investigated, but macaques are most often analyzed only under constrained conditions, such as repetitive, intensive learning of a specific movement, grasping through a slot, or grasping while parts of the body are constrained in movement. Such conditions induce stereotyped movements and postural modifications. In addition, most of the studies concentrated on the distal forelimb and very few quantified the degrees of freedom at the shoulder and the elbow (Scott & Kalaska, 1997; Christel & Billard, 2002). However, only one study filmed macaques on the ground in totally unconstrained conditions and revealed differences to humans in the duration of forelimb movement and the trunk-shoulder-elbow movement ranges (Christel & Billard, 2002). The authors invoked variation in motor control, posture and morphology to explain differences as these would all likely have a strong influence on the kinematics of prehension.

Moreover, prehension is essentially studied in a single body posture, the sitting posture, for both humans and macaques (*humans*: Jeannerod, 1981, 1984; Marteniuk *et al.*, 1990; Paulignan *et al.*, 1997; *macaques*: Scott & Kalasha, 1997; Roy *et al.*, 2000, 2002; Jindrich *et al.*, 2011). While studies have documented the kinematics of prehension in a standing posture in humans (*e.g.* Gardner *et al.*, 2001; Thomas *et al.*, 2005), none has explored the influence of various body postures across species. Compared with terrestrial and bipedal humans, most primates are arboreal or semi-arboreal, use a great variety of body postures and their forelimbs are used during locomotion. Therefore, understanding how body posture affects the kinematics of prehension is critical for making cross-species comparisons. Indeed, how did the primate forelimb transition from being one used in locomotion to one used for prehension of objects? Moreover, did body posture and arboreality play a role in the emergence and evolution of primate prehensile skills?

To better understand the evolution and mechanism of human prehension, analyses in different body postures in unconstrained conditions should be conducted for several species. Here, we compare humans with gorillas in both sitting and quadrupedal postures, two postures commonly used by wild gorillas (Remis, 1995; Tuttle & Watts, 1985; Doran, 1996) (see Appendix A for details). Gorillas represent a relevant comparative model to humans considering their phylogenetic proximity (Arnold *et al.*, 2010), their similarity in grasping ability (Pouydebat *et al.*, 2005; Pouydebat *et al.*, 2008), and their locomotor mode as the most terrestrial among the non-human apes (Tuttle & Watts, 1985; Hunt, 2004). This study aims to test the influence of body posture on the trunk and forelimb kinematics during an unconstrained food prehension task in humans and gorillas. Moreover, the behavioural strategies were considered such as the type of grasp used, the handedness, the position relative to the food and the distance of the food. Only the reaching phase was kinematically considered and grasping was defined by grasp postures. This original approach allows us to emphasize invariants between both species as well as the human and gorilla specific features independent of posture.

Material and Methods

Subjects

Seven male and female human adults (age: 33±7.3) were all right-handed for this task. The study was carried out in accordance with "The ethical codes of the World Medical Association" (Declaration of Helsinki).

For gorillas (*Gorilla gorilla*), the experimental protocol adhered to the legal requirements of the European Union. Three adults (two females and one male, 17.6±4.1) were filmed in the zoological park La Palmyre (France). For this task, the females were significantly left-handed (Ibana: HI=-0.21; Yola: HI=-0.37, according to the Handedness Index based on hand responses from our data, see Hopkins, 1999) and the male was significantly right-handed (Bongo: HI: 0.36).

Experimental set up

Food size

Small sized food (raisin) was used for humans and gorillas in order to involve precision grasp between thumb and index tips. Indeed, several studies on the manual grasp postures in humans and gorillas during prehension reported that the precision grasp is mainly used for small sized food (Christel, 1993, 1994; Pouydebat *et al.*, 2009). Therefore, forcing the use of precision grasp through the prehension of small sized foods in both species may shed light on the evolution of this ability. The size of the food was standardized according to the length of the hand calculated between landmarks of the wrist and those of the metacarpal heads. The size of the raisin was 1/4th of this length for each species, respectively 1.5 cm for humans and 1.7 cm for gorillas.

Humans

Reaching movements were recorded (100 Hz) using a Motion Analysis® system (LMBC, Lyon, Motion Analysis Corporation, Santa Rosa, USA). Subjects received no particular instruction except to reach, grasp, and move the raisin to the mouth. In sitting posture, participants sat on a stool with the hands rested on the table. In the quadrupedal posture, body weight was supported by the knees and the palms of the hands. Raisins were scattered on a surface of 50 cm^2 in front of the subject. Twelve infrared reflective markers used in both postures were positioned on anatomical landmarks of the forelimb and the trunk (fig. 1) as recommended by the ISB (Wu *et al.*, 2005).

Gorillas

Five video cameras filmed gorillas (60 Hz) (Sanyo® X-Acti Full HD 1920x1080). Cameras were synchronized with a manually operated flashlight. Raisins were scattered on the ground on a surface of 50 cm^2. In sitting posture, gorillas sat on the ground and they were with only their feet and hands in contact with the substrate in quadrupedal posture. Gorillas were recorded in unconstrained conditions meaning that they were in their habitual enclosure where they were totally free to move and choose their body postures to grasp. Furthermore, as no markers were allowed to be placed on the animals in zoos for ethical reasons (see Aerts *et al.*, 2000, Isler *et al.*, 2005), twelve landmarks were manually digitized frame by frame approximately at the same location than those of humans.

Behavioural analysis of gorillas

Five variables were quantified from the 300 grasps for each subject (total=900 grasps) recorded during sessions of 20 minutes/day: body postures, position of the gorilla relative to the food location (in front, at left or at right), successful grasps, handedness and preferred grasp types. A grasp was considered as successful when it occurred at the first contact between fingers and food. Grasp types were defined by the contact surface between each finger and the food (see Pouydebat *et al.*, 2006). These behavioural variables helped us to select comparable trials between gorillas and humans for the movement analysis.

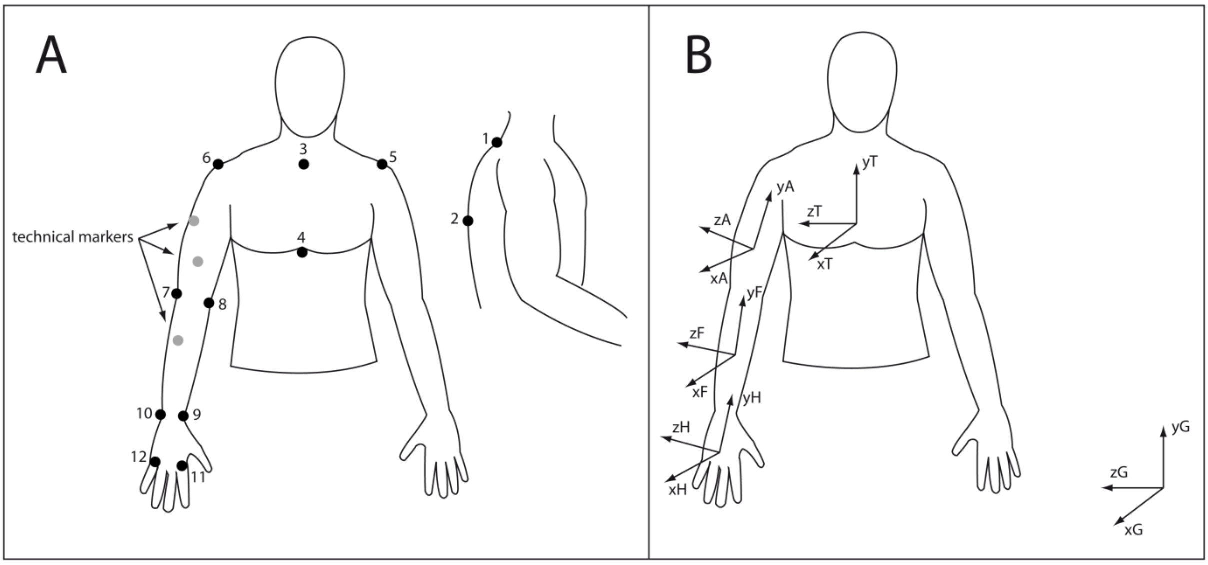

Figure 1. Position of the landmarks (A) and the segments' coordinate systems (B) on the forelimb of the species. Two additional reflective markers placed on the arm and one on the forearm helped to reconstruct the motion of forelimb for humans. For both species (humans and gorillas), the trunk landmarks [1] and [2] were used to calculate the kinematic variables in quadrupedal posture whereas in sitting posture we considered the trunk landmarks [3] and [4], in both cases for visibility reasons. Indeed, both species are positioned with the trunk vertically oriented in sitting. In the quadrupedal posture, four limbs support the body weight and the trunk is horizontally oriented.

Landmarks' legend (A): [1] processus spinosus of the 7th cervical vertebra, [2] 8th thoracic vertebra, [3] suprasternal notch, [4] xiphoid process, [5, 6] left and right dorsal point on the acromio-clavicular joint, [7, 8] medial and lateral epicondyles of humerus, [9, 10] radial and ulnar styloid processes, [11, 12] head of 2nd and 5th metacarpus.

Segments' coordinate systems legend (B): G: Ground, T: Trunk, A: Arm, F: Forearm, H: Hand.

Kinematic analysis

Kinematics (wrist velocity, movement duration and ranges of motion of forelimb joints and trunk) was analyzed on five trials per subject and each posture (30 sequences for gorillas; 70 for humans). First, as gorillas preferentially grasped food in front of them (see results), we retained prehension movements in front of the subjects for both postures and both species with the hand leaving the substrate at the movement onset to standardize the tasks. Second, the calculation of the ratio of the gorillas' forelimb length (arm+forearm) to the food distance (between initial position of the wrist until the food) allowed standardizing food distances for humans according to their forelimb length (ratio in sitting: 0.6, ratio in quadrupedal posture: 0.9 for both species).

For gorillas, video calibration, manual digitization of the landmarks and 3D coordinate's reconstruction were performed using a custom-written Matlab® routine (Loco 3.3). A precision test of three digitizations of the same gorilla's prehension trial revealed fairly constant body segment lengths (trunk, arm, forearm, hand) suggesting that the method is accurate enough to quantify the movement kinematics (see Isler, 2005) (variability±1.24 cm) (see Appendix B for details).

For human subjects, the software EvaRT® 5.0 reconstructed and extracted the 3D coordinates of the markers. For both species, kinematic data were processed with Matlab®. Data were low-pass filtered at a frequency of 6 Hz with a second order dual-pass Butterworth filter (see Appendix C for details). In both species, onset and offset (grasp) of the reaching phase were defined as the time when wrist velocity reached 5% of its peak velocity for each trial (Santello *et al.*, 2002; Graham *et al.*, 2003).

First, we calculated the wrist velocity and the movement duration which was the time from movement onset to the grasp. The wrist velocity was computed from the mid-point of the two wrist landmarks (Kudoh *et al.*, 1997). Then we calculated the mean, the maximal amplitude and the time to the velocity peak. The mean of curves of wrist velocity were interpolated for each species allowing resampling on 100 points in order to represent the patterns relative to the overall movement duration. Furthermore, a typical pattern of wrist velocity of gorillas was presented relative to the time for both body postures.

Second, local joint coordinate systems were defined on the basis of the ISB recommendations (Wu *et al.*, 2005) for the trunk segment, shoulder, elbow and wrist joints to calculate their range of motion (see Appendix D for details). Ten degrees of freedom were quantified: (a) trunk flexion-extension (forward/backward motion in sitting; upward/downward motion in quadrupedal), (b) trunk inclination (lateral motion of the trunk on the left or right side), (c) trunk rotation, (d) shoulder flexion-extension, (e) shoulder abduction-adduction, (f) shoulder rotation, (g) elbow flexion-extension, (h) elbow rotation, (i) wrist flexion-extension, (j) wrist abduction-adduction. In order to quantify the variation of the species for all the variables, the coefficient of variation was calculated (CV=SD/Mean).

Statistical Analysis

All analyses were performed using the R statistical package v.2.9.0. For behavioural data, a t-test was performed on the distance chosen by gorillas to test the body posture effect. A Kruskall-Wallis test was used on the three positions of gorillas relative to the food to determine if differences existed between these positions. On the kinematic data, a multivariate analysis of variance (MANOVA) tested the effect of two factors: body postures and species. A Shapiro-Wilks' test tested the normality of the data and the Bartlett-test for homogeneity of variances. The F statistics were estimated from the Pillai's trace as recommended by Hand and Taylor (1987). In order to better understand the variability of each species for each posture, an ANOVA was performed on the variables to determine which ones differed.

Results

Behaviour

For gorillas, 96.3% of grasps are successful. Through the filmed sessions, gorillas are approximately in 50% in sitting posture (S) and 50% in a quadrupedal posture (Q) while grasping raisins (Ibana: Q=57.7%; S=42.3%; Bongo: Q=55%; S=45%; Yola: Q=37.3%; S=62.7%). The position of gorillas relative to the food remains relatively invariant between postures. They are preferentially placed in front of the food in 63.6% of cases independent of body posture rather than on the left (22.1%) or right (14.2%) (KW=882, d.f.=2, $p< 0.001$). The distance chosen by the gorillas between the initial position of the wrist and the raisin to grasp is significantly shorter while sitting compared to a quadrupedal posture ($t=-3.06$, d.f.=14, $p<0.008$). In both postures, they mainly use precision grasps (more than 90%) due to the small food items presented.

Kinematics

Ranges of motion

Firstly, the ranges of motion of forelimb joints and trunk segment relative to the ground are all significantly different for both species in both postures (table 1, see all the tables at the end of the study).

Secondly, for gorillas, no significant differences in the motion of trunk and forelimb joints exist between postures with the exception of the shoulder abduction and elbow extension which are significantly smaller in sitting (tables 2-3). Moreover, all their ranges of motion are smaller in a sitting posture compared to quadrupedal posture even if they are not significantly different. By contrast, humans show many significant differences between sitting and quadrupedal postures (table 2). The ranges of trunk flexion and elbow extension are smaller in a quadrupedal posture, but all other ranges of motion in the same posture are higher or close to those in a sitting posture as was observed for gorillas (tables 3-4).

Thirdly, the comparison between both species in a sitting posture exhibits significant differences for all variables except trunk rotation (table 2). In this sitting posture, humans and gorillas show an inverse trend of forelimb joint and trunk motion (tables 3-4). Indeed, humans use smaller trunk flexion and shoulder-elbow rotation but wider shoulder flexion and elbow extension than gorillas. On the contrary, gorillas seem to compensate the smaller amplitudes of their shoulder flexion and elbow extension by greater movements of the trunk flexion and shoulder-elbow rotation (fig.2).

Fourthly, the comparison between both species in a quadrupedal posture shows significant differences in most variables except for trunk inclination and shoulder abduction (table 2). The same contribution of the trunk motion and the forelimb joints as described for sitting is found in both gorillas and humans (*i.e.* wider trunk flexion, shoulder and elbow rotation in gorillas *versus* lower trunk flexion but wider shoulder and elbow flexion-extension for humans) (tables 3-4).

Finally, compared to humans, the variability of gorillas (CV: Coefficient of Variation) is not always the greater in both postures (tables 3-4). Surprisingly, humans exhibit wide CV close to gorillas for most of the motions (table 3) emphasized by thevariability between the subjects (table 4).

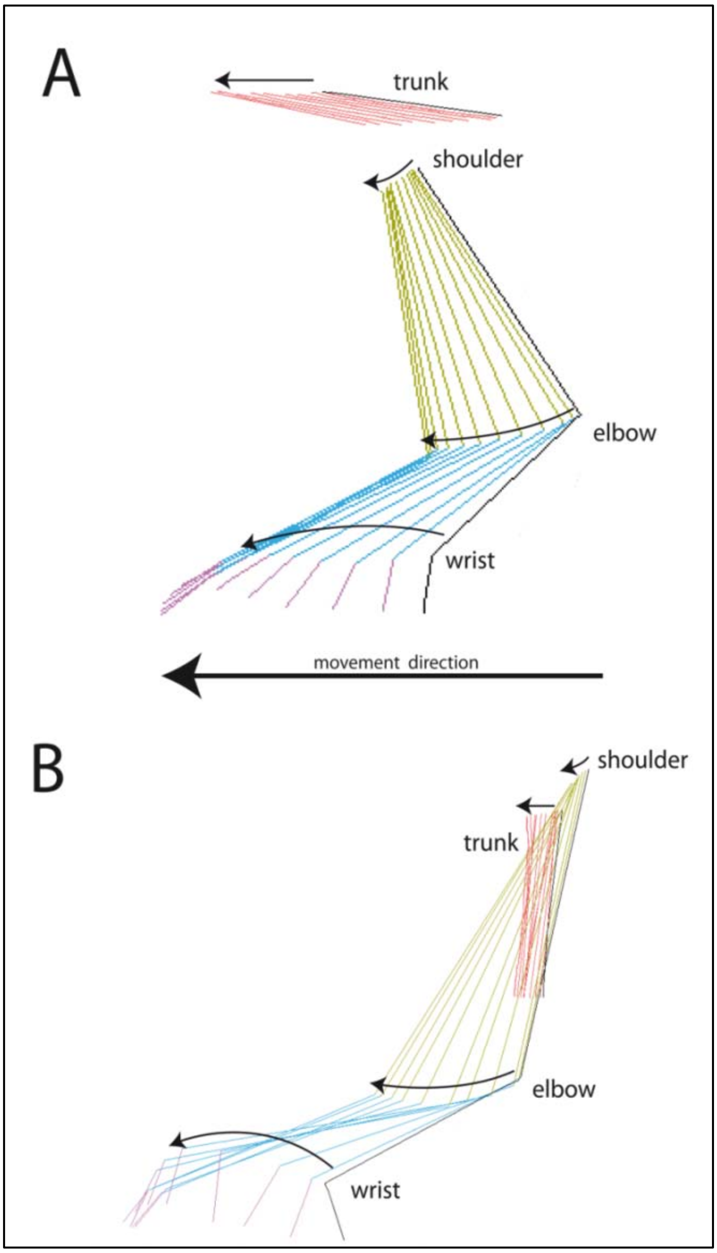

Figure 2. Kinograms in lateral view representing the advance of the trunk, arm, forearm and hand segments of one single gorilla subject in the quadrupedal (**A**) and sitting (**B**) postures during a typical movement prehension. The highlighted black line on each segment defines the onset of the movement.

Wrist velocity

The wrist velocity profile is bell shaped and typically single-peaked with a longer deceleration than acceleration phase in both species and postures (fig. 3). However, all variables related to the wrist velocity, are significantly different in both species and postures (table 5). Only the time to the wrist velocity peak is similar (not significantly different) in all conditions (tables 6-7). The mean of wrist velocities and the amplitude of the wrist velocity peak are significantly higher in gorillas than humans but both species are slower while sitting compared to when being in a quadrupedal posture (tables 6-7). All the results observed from the means of gorilla and human groups are also found for each subject of species (table 8).

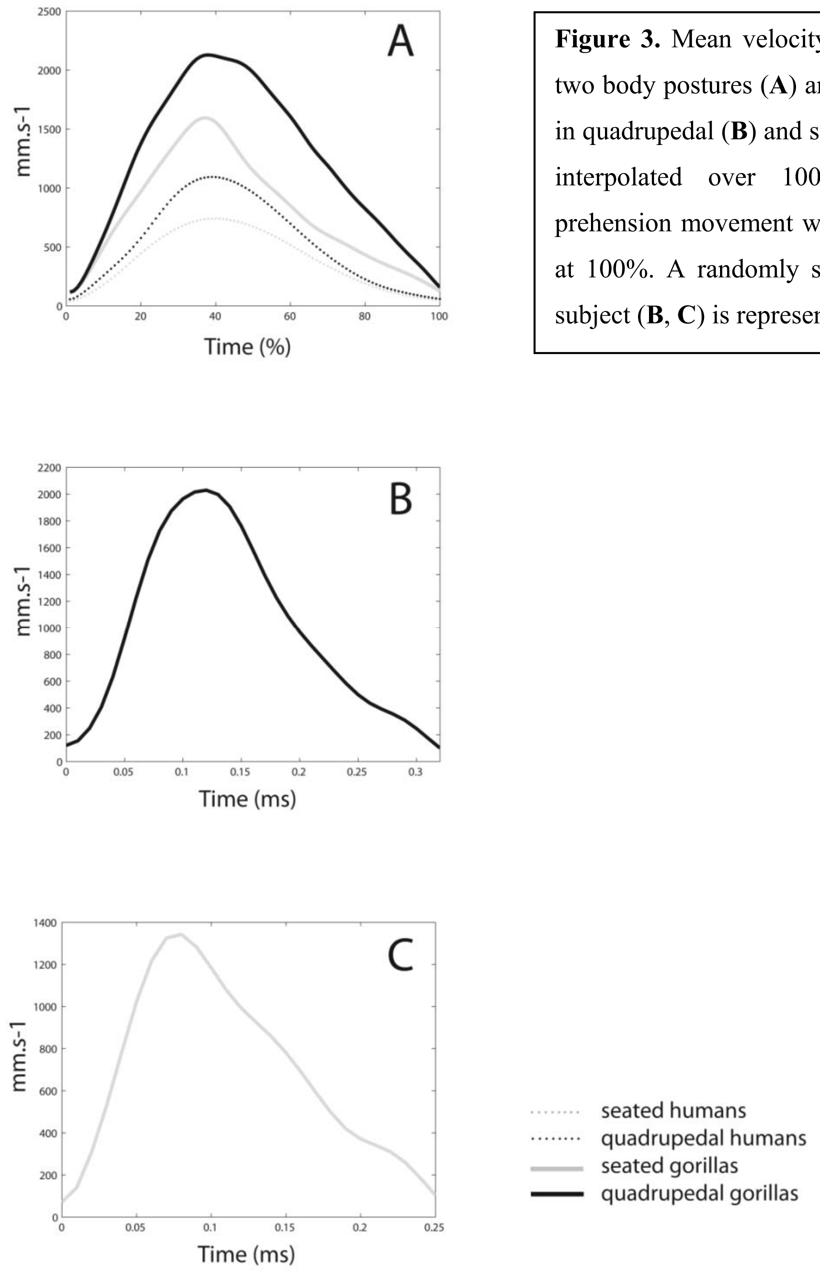

Figure 3. Mean velocity of the wrist for both species in two body postures (**A**) and typical wrist velocity of gorilla in quadrupedal (**B**) and sitting (**C**) postures. The means are interpolated over 100 points defining the overall prehension movement with the onset at 0% and the grasp at 100%. A randomly selected movement in one gorilla subject (**B**, **C**) is represented according to the time (ms).

Discussion

The aim of this study is to explore strategies between humans and gorillas during reaching and grasping in both sitting and quadrupedal body postures. The effect of the postures and species is significant when considering the range of motion of the trunk segment and the forelimb joints. The quadrupedal posture is associated with greater ranges of movement in both species. Sitting is a strictly static posture whereas a quadrupedal posture involves some displacements during the grasp, thus increasing the joint motions.

Moreover, the results obtained when testing for differences between species reveal two different prehensile strategies based on the ranges of motion of forelimb joints and trunk.

Independent of the body posture, gorillas use wider trunk flexion and shoulder-elbow rotation whereas humans favor flexion-extension of these same forelimb joints with a lower trunk flexion. The greater trunk displacement (in flexion) observed in gorillas is a common motor implication shared with the macaques in order to compensate reduced shoulder flexion (Christel & Billard, 2002). However, macaques essentially compensate with the trunk and elbow rotation whereas gorillas also involve an increase in the abduction and rotation of the shoulder and elbow. Macaques have a terrestrial morphology limiting shoulder motion (scapula laterally oriented) whereas gorillas, like humans, retain a more arboreal morphology allowing greater shoulder mobility in both abduction and rotation (scapula dorsally oriented) (Chan, 2007; Larson, 1993). Despite Chan (2008) found no significant differences in passive shoulder circumduction between gorillas, humans and macaques, prehension movements exhibit marked differences in their shoulder motion. It is interesting to note that passive and active movement reflect different ranges of motion underlining differences in forced movement (*i.e.* constrained) and spontaneous responses in the natural gesture. Similarly, Scott & Kalasha (1997) reported that macaques were able to execute high shoulder abduction while constraining but spontaneously they were not. Moreover, a higher range of motion in the shoulder joint requires less assistive motion of the trunk for humans. This low contribution of the human trunk and greater shoulder motion during reaching was previously reported (Christel & Billard, 2002). Thus, each species exhibits a specific strategy of prehension. Indeed, the specific trunk-shoulder motion strategy of gorillas and humans observed here is preserved independent of body posture as well as the specific contribution of each forelimb joint. The strategy of trunk-shoulder motion shared by gorillas and macaques, despite a different general morphology, is surprising. Indeed, we would expect that gorillas and humans exhibit a more similar trunk-shoulder motion because they present more similar shoulder morphology than macaques. However, the forelimbs in gorillas and macaques are used during locomotion which might necessitate further shoulder stability during motion involving a higher contribution of the trunk compared to humans. Furthermore, gorillas retain arboreal locomotor abilities that humans have lost completely. Given that the flexor muscles are widely used during arboreal locomotion, the limited shoulder flexion may be also a consequence of the strength and limited flexibility of these muscles.

The bell-shape wrist velocity profile, and the velocity peak occurring at the same time around 40% of the movement duration in both species for both postures are recognized as classical invariants in human and macaque prehension while sitting (humans: Jeannerod, 1981, 1984; Marteniuk *et al.*, 1990; Paulignan *et al.*, 1997; macaques: Roy *et al.*, 2000;

Christel & Billard, 2002). Therefore, these invariants mean that humans, macaques and gorillas responded in the same way to the same stimulus and indicate a common motor control in monkeys and apes. Moreover, in humans and gorillas, quadrupedal postures involve faster movements of the wrist despite the greater food distances and ranges of motion. This result could be related to the fact that a quadrupedal posture allows the execution of more free movements with some displacements compared to the strictly static sitting posture, even in humans for which the quadrupedal posture might be considered as being more constrained. Finally, since all subjects within each group displayed a distinct, species-specific kinematic pattern, variation in handedness (found in gorillas only) had little effect on determining the general trends in prehension mechanics in this study.

To conclude, as the joint strategy and the pattern of wrist velocity are preserved in both postures for each species, a comparison of the kinematics of prehension between species in different body postures is possible and relevant. The limited effect of body posture on the general pattern of prehension in gorillas and humans also suggests that the study of the body posture alone is not sufficient to explain the differences in strategy. Further kinematic analyses on species with different degrees of arboreality/terrestriality will enrich our understanding of the influence of these adaptive contexts on the trunk and forelimb motion during prehension. Finally, comparison with primates from different phylogenetic groups is needed to better understand the evolution of prehension in primates as well as those elements specific to human.

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TABLES 1-8 OF THE STUDY

Table 1. Results of a MANOVA on the ranges of motion testing for differences between species and body postures.

	d.f.	**Pillai's trace**	***F***	**num d.f.**	**den d.f.**	***P***
species	1	0.84	29	15	82	<0.001
body postures	1	0.78	19	15	82	<0.001
species × body postures	1	0.62	9	15	82	<0.001
residuals d.f.	96					

Table 2. Results of ANOVA's on the ranges of motion comparing both postures and species.

	Comparison between postures for a same species		**Comparison between species for a same posture**	
	Comparison between postures in humans	Comparison between postures in gorillas	Comparison between species in sitting	Comparison between species in quadrupedal
Trunk flexion	$F_{1,567}=27,p<0.001$	$F_{1,10}=0.09,p<0.75$ NS	$F_{1,341}=6,p<0.016$	$F_{1,1659}=46,p<0.001$
Trunk inclination	$F_{1,3741}=243,p<0.001$	$F_{1,70}=0.9,p<0.33$ NS	$F_{1,796}=35,p<0.001$	$F_{1,85}=2,p<0.1$ NS
Trunk rotation	$F_{1,633}=13,p<0.07$ NS	$F_{1,0.6}=0.003,p<0.95$ NS	$F_{1,0}=0.001,p<0.98$ NS	$F_{1,405}=6.8,p<0.01$
Shoulder flexion	$F_{1,650}=4.7,p<0.03$	$F_{1,308}=0.95,p<0.33$ NS	$F_{1,1774}=10,p<0.002$	$F_{1,1689}=8,p<0.006$
Shoulder abduction	$F_{1,2343}=36,p<0.001$	$F_{1,526}=6,p<0.02$	$F_{1,738}=27,p<0.001$	$F_{1,282}=2.4,p<0.1$ NS
Shoulder rotation	$F_{1,43}=0.4,p<0.4$ NS	$F_{1,593}=0.6,p<0.44$ NS	$F_{1,10821}=45,p<0.001$	$F_{1,19027}=38,p<0.001$
Elbow extension	$F_{1,1464}=14,p<0.001$	$F_{1,1194}=7.7,p<0.009$	$F_{1,1549}=12,p<0.001$	$F_{1,971}=9,p<0.004$
Elbow rotation	$F_{1,1036}=15,p<0.001$	$F_{1,904}=0.9,p<0.32$ NS	$F_{1,25345}=120,p<0.001$	$F_{1,28848}=70,p<0.001$
Wrist extension	$F_{1,4312}=108,p<0.001$	$F_{1,1198}=1.9,p<0.16.$ NS	$F_{1,18366}=92,p<0.001$	$F_{1,15779}=76,p<0.001$
Wrist deviation	$F_{1,21}=0.7,p<0.4$ NS	$F_{1,431}=1.2,p<0.28$ NS	$F_{1,5424}=44,p<0.001$	$F_{1,10360}=77,p<0.001$

NS: not significant

Table 3. Mean (M), Standard Deviation (SD) and Coefficient of Variation (CV) of the ranges of motion (in degrees) of the trunk, shoulder, elbow and wrist in gorillas and humans during the prehension (reaching) in both body postures (sitting and quadrupedal).

	Sitting				**Quadrupedal**			
	humans (N=7)		gorillas (N=3)		humans (N=7)		gorillas (N=3)	
	M, SD	CV	M, SD	CV	M, SD	CV	M, SD	CV
Trunk flexion	9.4±6.2	66	15.1±9.8	64.9	3.7±2.1	56.8	16.3±10.6	65
Trunk inclination	3.5±1.9	54.3	12.2±8.4	68.9	18.1±5.2	28.7	15.3±8.8	57.5
Trunk rotation	18.5±7.2	39	18.4±15.2	82.6	12.5±6.7	53.6	18.7±9.7	51.9
Shoulder flexion	42.7±10.3	24.1	29.7±18.4	62	48.8±12.9	26.4	36.1±17.4	48.2
Shoulder abduction	8.2±3.9	47.6	16.6±7.4	44.6	19.8±10.7	54	25±11.2	44.8
Shoulder rotation	23.7±9.7	40.9	55.8±24.2	43.4	22.1±11.8	53.4	64.7±37	57.2
Elbow extension	41.8±10.6	25.4	29.6±12.8	43.2	32.6±9.6	29.4	42.2±12	28.4
Elbow rotation	14±5.7	40.7	63.1±25.5	40.4	21.7±10.1	46.5	74.1±34.2	46.2
Wrist extension	18.1±7.2	39.8	59.9±23.6	39.4	33.7±5.3	15.7	72.5±25.4	35
Wrist deviation	10.2±7	68.6	32.9±17.5	53.2	9.1±3.8	41.8	40.5±20.6	50.9

Table 4. Mean and Standard Deviation of the ranges of motion (in degrees) of the trunk, shoulder, elbow and wrist in each subject of gorillas and humans during the prehension (reaching) in sitting and quadrupedal postures.

Body postures	Species	Subjects	Trunk flexion	Trunk inclination	Trunk rotation	Shoulder flexion	Shoulder abduction	Shoulder rotation	Elbow extension	Elbow rotation	Wrist extension	Wrist deviation
Sitting posture	gorillas	1	15±11.2	12±3.8	16.9±9	15.5±3.7	15.4±9.5	48.9±22.1	23.7±12.1	49.7±17.2	56.3±32.2	37.7±23.9
		2	14.9±5.3	12.2±10.5	25.1±21.1	29.6±14.1	18.3±4.7	48.8±24.3	28.7±11.7	76.7±26.9	59.9±24	36.1±12.9
		3	15.4±13.4	12.4±10.9	13.3±13.7	44.1±21.6	16.2±8.7	69.7±24.9	36.6±13.7	63±17.5	63.5±17.5	24.9±14.4
	humans	1	13.9±6.6	1.4±0.6	23±7.8	39.6±9	7.9±5.2	13.5±7.9	37.8±5.5	12.2±3.7	14±2.1	5.4±1.2
		2	5.1±4.3	4.4±2	21±8.3	41.6±8.7	7.9±2.7	30.4±8.2	48.2±11.4	17.8±5.8	27±8.6	24.1±4.4
		3	6±4.6	3±1	18.9±8	38.3±9.7	6±2.4	19±8.1	44.6±11.5	10.3±4.5	10.6±1.9	7.9±2.5
		4	6.2±3.6	4.6±1.7	14.4±7.2	43.3±15.8	11.6±5.2	28.3±8.2	39.2±17.3	15.5±7.8	12.4±3.7	6±0.6
		5	11.1±4.1	3.6±1	19.2±5.7	42.4±6.9	6.7±3	19.2±7	36.5±5.2	17.1±2.9	22.1±3.6	12.3±4.1
		6	9.6±5.5	4.4±2.3	15.8±7.2	52±11.6	8.3±4	35.6±3.3	48.1±10.6	9.8±5.4	19.3±4.2	8±5.4
		7	14±8.6	3.1±2.4	17.4±6.6	41.9±8.3	9.3±3.5	19.9±4.5	38.2±5.5	15.4±5.4	21.3±6.7	7.9±4.6
Quadrupedal posture	gorillas	1	21.4±14.6	19.8±12.2	13.6±8.2	48±16.9	20.6±9.7	74.4±33	39.1±11.3	80.3±23	76.5±41.2	50.3±26.2
		2	14.9±9.3	14.7±7.8	24.6±7.4	28.1±15.1	29.8±11.4	82.3±45.7	46.4±4.7	85.6±52.7	74.8±18.4	45±16.6
		3	12.6±6.6	11.4±4.2	32.3±11.3	32.3±16.6	24.6±12.7	37.4±13.6	41.3±18	56.5±13.7	66.4±12.4	26.2±11.3
	humans	1	6.8±1.9	16.7±6.6	13.2±4.8	60.5±16.8	24.3±13.6	27.7±12.8	35.4±4.5	29.8±15.4	38±2.9	6.1±2.7
		2	3.4±0.6	17.3±5.6	14.5±4.6	55.2±15.3	20.2±11.7	14.7±7.5	41.2±8.5	21.8±6.8	36.8±2.6	14.8±3.6
		3	2.5±0.9	18.3±4.4	7±2.7	40.4±9.8	16.2±9.3	21±9.6	32.6±2.4	26.8±3.5	32±5.2	8.4±1.8
		4	2.1±0.8	20.1±5.6	18.9±6.7	51.7±12.7	22±8.7	33.4±10.7	43.7±6.9	16.7±8.9	33.3±5.2	8.8±0.9
		5	2±0.7	14.2±4.6	5.6±2.8	40.1±4.6	13.3±10.7	13.6±3.3	18.3±0.9	19.5±5.9	39±3.9	6.5±1.4
		6	3.2±1.2	21±4	17.8±7.1	51.9±8.3	26.9±11.7	32.8±7.6	31.6±5.7	21.8±15.4	30.1±2.1	7.8±4.8
		7	6±2.1	19.5±5.4	10.5±5.4	41.7±7.4	15.9±8.1	11.7±7.7	25.6±4.9	15.5±4	27.4±3.2	11.4±2.7

Table 5. Results of a MANOVA on the wrist kinematics and the movement duration testing for differences between species and body postures.

	d.f.	Pillai's trace	*F*	num d.f.	den d.f.	*P*
species	1	0.7	43	5	92	<0.001
body posture	1	0.3	8	5	92	<0.001
species × body postures	1	0.4	11	5	92	<0.001
residuals d.f.	80					

Table 6. Results of ANOVA'S performed on the velocity of wrist and the movement duration comparing both species and body postures.

	Comparison between postures for a same species		**Comparison between species for a same posture**	
	Comparison between postures in humans	Comparison between postures in gorillas	Comparison between species in sitting	Comparison between species in quadrupedal
Mean of the wrist velocity	$F_{1,38343}$=28,p<0.001	$F_{1,13622}$=10,p<0.003	$F_{1,15733}$=58,p<0.001	$F_{1,46470}$=65,p<0.001
Amplitude of the wrist velocity peak	$F_{1,20992}$=45,p<0.001	$F_{1,26621}$=4.11,p<0.52 NS	$F_{1,11354}$=68,p<0.001	$F_{1,17454}$=63,p<0.001
Time to the wrist velocity peak	$F_{1,38}$=1.02,p<0.3 NS	$F_{1,11.5}$=0.17,p<0.6 NS	$F_{1,8.8}$=0.2,p<0.67 NS	$F_{1,34}$=0.8,p<0.37 NS
Movement duration	$F_{1,41503}$=9,p<0.003	$F_{1,0.03}$=0.03,p<0.051 NS	$F_{1,217482}$=49,p<0.001	$F_{1,759163}$=24,p<0.001

NS: not significant

Table 7. Mean (M), Standard Deviation (SD) and Coefficient of Variation (CV) of the velocity of the wrist and the movement duration in gorillas and humans during the prehension (reaching) in sitting and quadrupedal postures.

	Sitting				**Quadrupedal**			
	humans (N=7)		gorillas (N=3)		humans (N=7)		gorillas (N=3)	
	M, SD	CV	M, SD	CV	M, SD	CV	M, SD	CV
Mean of the wrist velocity (mm.s-1)	389±123	31.6	776±237	30.5	537±112	20.9	1202±465	38.7
Amplitude of the wrist velocity peak (mm.s-1)	779±215	27.6	1819±675	37.1	1125±214	19	2415±916	37.9
Time to the wrist velocity peak (%)	40.7±7	17.2	39.8±7	17.6	39.2±5	12.8	41±9	22
Movement duration (ms)	1034±243	23.5	578.8±182	31.4	880±95	10.8	611.1±165	27

Table 8. Mean and Standard Deviation of the velocity of the wrist and the movement duration in each subject of gorillas and humans during the prehension (reaching) in sitting and quadrupedal postures.

Body postures	Species	Subjects	Mean of the wrist velocity (mm.s-1)	Amplitude of the wrist velocity peak (mm.s-1)	Time to the wrist velocity peak (%)	Movement duration (ms)
Sitting posture	gorillas	1	791.5±428.4	2047.1±1160.3	35.9±4.8	633.3±108.7
		2	761±87.1	1632.7±197.5	42.7±9.3	536.7±66
		3	775.4±73.6	1777.5±315.3	40.7±7	566.7±97.2
	humans	1	333.2±90.3	707±178.4	35.5±3.7	1156±44.5
		2	488.7±85.9	947.2±165.4	50±3.9	832±92.3
		3	538.1±124.4	977.1±252.3	44.4±5.2	670±64
		4	259.6±84.8	543.1±144.2	37.7±6.2	1238±73.3
		5	399.5±45.6	797.5±99.9	42.4±3.5	982±102.8
		6	298.7±51.7	623.5±113.5	40.9±8.3	1364±169.4
		7	404.1±100.8	859.1±164.4	34.1±2.3	996±116.3
Quadrupedal posture	gorillas	1	991.1±302.9	2079.6±604.7	39.1±11.6	766.7±178
		2	1466.2±381.4	2902.1±776.4	43.3±8.9	546.7±112.7
		3	1149.1±611	2263±1225.5	40.6±7.7	520±72
	humans	1	616.2±80.4	1236.5±154	42.1±2.2	734±62.7
		2	604.8±101.2	1226.5±191.5	38.8±1.9	762±40.9
		3	637±114.5	1363.5±193.9	40.4±3	686±73.7
		4	439.5±53	953.6±125.5	46.7±5.7	1038±148.1
		5	506.5±81	1003.4±143	34.8±2.4	866±82.6
		6	416.2±59.5	916.1±123.1	34.4±3.2	1160±102.7
		7	537.7±76.4	1179.4±172.9	37.5±4.1	914±97.4

SYNTHÈSE CHAPITRE 4

Titre: Influence de la posture corporelle sur la cinématique de la préhension chez l'humain et le gorille (*Gorilla gorilla*).

Question: La posture corporelle influence-t-elle les stratégies cinématiques de préhension ?

Modèles: Humain & Gorille (*Gorilla gorilla*).

Résultat: La posture corporelle (assise et quadrupède) n'a pas d'influence sur la vitesse du poignet ni sur les stratégies articulaires et implication du tronc.

Discussion: La posture corporelle n'a peut-être pas joué un rôle essentiel dans l'élaboration des stratégies cinématiques de préhension.

Perspective: Explorer la variabilité interspécifique des stratégies cinématiques de la préhension chez d'autres espèces.

SUMMARY CHAPTER 4

Title: The influence of the body posture on the kinematics of prehension in humans and gorillas (*Gorilla gorilla*).

Question: Does the body posture influence the kinematic strategies of prehension?

Models: Human & Gorilla (*Gorilla gorilla*).

Result: The body posture (sitting and quadrupedal postures) has no influence on the velocity of the wrist, on the joint strategies, and on the trunk contribution.

Discussion: The body posture may not have played an essential role in the elaboration of the kinematic strategies of prehension.

Perspective: Investigate the interspecific variability of the kinematic strategies of the prehension in other species.

Chapitre 5 - Convergences et spécificités de la préhension chez cinq primates: *Lemur catta*, *Sapajus xanthosternos*, *Gorilla gorilla*, *Pan troglodytes*, *Homo sapiens*

Convergences And Specificities Of The Prehension In Five Primates: *Lemur catta*, *Sapajus xanthosternos*, *Gorilla gorilla*, *Pan troglodytes*, *Homo sapiens*

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Abstract

Primates are known for their use of the hand in many activities including food grasping. Yet, how their prehension ability evolved remains unclear. Moreover, the human specificities in comparison to other species remain poorly understood. Most studies concentrate on the distal component of prehension and the kinematics of the whole forelimb in food prehension have not been studied with the exception of humans and macaques. In order to improve our understanding of the prehension movement in primates, we study the behavioural strategies (*e.g.* handedness, types of grasp, body postures) as well as the 3-D kinematics of the whole forelimb and the trunk during the prehension of small static food items in five primate species in unconstrained conditions. All species preferred the quadrupedal posture and grasp small food with one hand, except lemurs which grasp it with the mouth but use one hand for larger sized food. Whereas the apes display a similar bell-shaped profile of the wrist velocity, capuchins and lemurs exhibit a later peak in the wrist velocity profile. The non-human apes used more rotation movement than flexion-extension at the shoulder and elbow. Yet this was inversed for humans, capuchins and lemurs. The trunk is a major contributor in the displacement of the forelimb to the food in sitting humans and in quadrupedal posture for non-humans. In conclusion, the human prerequisites of food prehension with the hand are present in primates, yet lemurs show less hand plasticity. Wrist velocity and joint motion are discussed in relation to morphological, locomotor, and arboreal adaptations from ecological and evolutionary perspectives.

Keywords: Prehension, Primates, Behaviour, Kinematics, Forelimb, Evolution

Introduction

The hand can be involved in multiple activities including food grasping, locomotion, social interactions, and is particularly often used in primates. All the members of the order primates share the characteristic ability to grasp with one or both hands (Wood Jones, 1916; Napier, 1960; Bishop, 1964; Costello & Fragaszy, 1988; Christel, 1993; MacFarlane & Graziano, 2009; Pouydebat *et al.*, 2009; Reghem *et al.*, 2011). Primates fascinate humans because of their remarkable and highly developed prehensile abilities especially when grasping food or objects. This ability is a key trait implied in daily activities in both humans and non-human primates. Although all primates are able to grasp, different food prehension strategies have been identified in both manual grasp postures (Bishop, 1964; Christel; 1994; Spinozzi *et al.*, 2004; Pouydebat *et al.*, 2009) as well as for the kinematics of the forelimb (Scott and Kalasha, 1997; Roy *et al.*, 2000, 2002; Christel & Billard, 2002).

Considering the manual grasp postures, many authors attempted to define and classify them for humans (for a review see MacKenzie & Iberall, 1994). Napier (1956, 1960) determines two main categories of grasp types in both humans and non-human primates: the precision grasp and the power grasp (*i.e.* whole hand grasp). Both categories consist of many variants and have been described in detail for several primate species (Christel, 1998; MacFarlane & Graziano, 2009; Pouydebat *et al.*, 2008, 2009). Indeed, precision grasps exhibit many forms such as between the thumb and index tips or between several finger tips (Spinozzi *et al.*, 2004). Moreover, precision grasps can occur between many other areas of contact than the tip and include the pulp and lateral side of fingers (Christel, 1993). In humans, Napier (1960) already divided the precision grasp into the “tip-to-tip” grasp and the “pad-to-pad” grasp. The whole hand grasps involve all or some fingers and the palm (Boesch & Boesch, 1994; Spinozzi *et al.*, 2004). These studies often quantify manual grasp postures in unconstrained conditions for the species implying that nothing influences or disturbs the subjects which are able to move freely in their habitual enclosure. The Old World monkeys (the catarhines: hominoids and cercopithecoids) and two genera of New World monkeys (the platyrhines capuchins: *Sapajus* and *Cebus*) show individuation of the fingers and a wide variety of manual postures during grasping such as precision grasps between thumb and index, scissor grasps, and whole hand grasps according to the food size (Costello & Fragaszy, 1988; Christel, 1993, 1994; Jones-Engels & Bard, 1996; Christel *et al.*, 2000; Pouydebat *et al.*, 2008, 2009; MacFarlane & Graziano, 2009). Similarly, for chimpanzees a wide variety of in-hand postures has been documented and the independent movement of fingers has been emphasized (Crast *et al.*, 2009). By contrast, most of the platyrhines (except capuchins) and strepsirhines show less individuation of the fingers and principally use whole hand grasps (Bishop, 1964; Fragaszy, 1983). Several platyrhines are also able to grasp food using a scissor grasp (Bishop, 1964; Lemelin & Grafton, 1998).

In kinematic studies, the movement of prehension is often described as consisting of two phases. The first one is the transport phase where the hand is transported to the object to be grasped. The second one is the grasping phase where the grasp aperture between thumb and index opens and ultimately closes around the object (Jeannerod, 1981, 1984). The kinematics of food prehension has been essentially investigated in humans and macaques. Macaca is the only one genus of non-human primates studied with respect to the kinematics of food prehension. In addition, most studies focus on the kinematical invariants between humans and macaques (Scott & Kalasha, 1997; Roy *et al.*, 2000; Fogassi *et al.*, 2001; Roy *et al.*, 2002, 2006). Indeed both species show a similar bell-shaped pattern of the wrist velocity with a longer deceleration phase than acceleration one, a straightness of the wrist trajectory and a grasp aperture varying according to the object size. However, these results were obtained for macaques in constrained conditions (*e.g.* intensive learning of the movement, grasping through a slot, parts of the body attached, head immobilized) that induce stereotyped movements, a bias in elbow motion and an immobility of the shoulder motion whereas these proximal joints are important in the forelimb movement. In part because of these constrained conditions, many studies focus only upon the distal component, *i.e.* the wrist kinematics and grasp aperture. One study (Christel & Billard, 2002) has investigated macaques in unconstrained condition (*i.e.* in their group within their habitual enclosure) and quantified the ranges of motion of the trunk and the forelimb joints in comparison to humans. Despite the fact that similar results were obtained in comparison with prior studies on wrist velocity, wrist trajectory, and grasp aperture, they emphasized differences in kinematic strategies of both species. Indeed, macaques are faster than humans and show more variability. Moreover, humans and macaques perform opposite movements. During the reaching phase, macaques adopt a larger elbow, wrist and trunk motion and a smaller shoulder motion, contrary to what is observed in humans. Therefore, the trunk of macaques contributes in a large proportion to the prehension movement and compensates for the lower excursion of the shoulder. The authors suggested that variation in motor control, posture and morphology could explain the differences. Indeed, macaques use their forelimb in locomotion which may imply a different shoulder joint morphology, muscular strength, body posture and a change in the control system. Furthermore, the authors suggest that prehension control would evolve from primitive motor centers of locomotion.

Whether these kinematic parameters are specific to monkeys or general features of non-human primates remains, however, unclear. Moreover, the evolution of the primate prehension still remain poorly understand in many aspects. Indeed, very few kinematic studies have been conducted under unconstrained conditions involving spontaneous and free gestures. These conditions appear, however, fundamental to understand both the source of variation in movement and the prehension mechanism, and to address evolutionary questions pertaining to the evolution of prehension and the human specificities. In this study the following questions are addressed: How do different forelimb joints and the trunk segment contribute to the prehension movement in several primate species of different phylogenetically distinct taxa? Are the invariants observed in humans and macaques, such as wrist velocity profiles, shared by all primates? Are there specific strategies for each of the species? Do the closest relatives of humans show similar wrist velocities and forelimb joint kinematics during prehension? Does the study of prehension reveal relevant differences or similarities related to the morphology or locomotion of the species? In other words, are forelimb joint amplitudes and trunk motion observed during prehension movements correlated to the degree of arboreality and terrestriality or locomotor modes?

In order to address these questions and to better understand the evolution and mechanisms implicated in human and non-human prehension, the present study examines unconstrained prehension in five species. We selected species representative of several groups of primates: the ring-tailed lemurs (*Lemur catta*, strepsirhine), the yellow-breasted capuchins (*Sapajus xanthosternos*, platyrhine), and three catarhines, gorillas (*Gorilla gorilla*), chimpanzees (*Pan troglodytes*) and humans (*Homo sapiens*). From a phylogenetic perspective the lemur is the most distantly related primate relative to humans, followed by the capuchin, and the hominids including the gorilla and chimpanzee (Groves, 2001; Arnold *et al.*, 2010; Chatterjee *et al.*, 2010). These species present different morphologies and degrees of arboreality *versus* terrestriality and different locomotor modes. Indeed, humans are permanent terrestrial bipeds. The lemur catta is an arboreal quadruped and one of the most terrestrial of the strepsirhines (Ward & Sussman, 1979; Jolly, 2006). The gorilla is a brachiator but spends a lot of its time as a terrestrial quadrupedal knuckle walker (Tuttle & Watts, 1985; Remis, 1995; Hunt, 2004). Finally, the capuchin is an arboreal quadruped (Fleagle & Mittermeier, 1980; Wright, 2007; Schmidt, 2011) and the chimpanzee is a knuckle walker and brachiator (Doran, 1993; Hunt, 2004). Both capuchins and chimpanzee spend most of their time in an arboreal context even if they are at ease on the ground. All these species, except the lemur, use the precision grasp and a wide variability of grasps (Bishop, 1964; Christel, 1993; Ward & Hopkins, 1993; Fragaszy *et al.*, 2004; Pouydebat *et al.*, 2009).

Here we quantify the 3D-kinematics of the reaching and the type of grasp during a prehension task in unconstrained conditions. Reaching is addressed by the ranges of motion of the forelimb joints and the trunk, and by the wrist velocity profile. Grasping is here defined by grasp postures. Moreover, the behavioural strategies during prehension were quantified such as the body posture, the handedness, the position of the subjects relative to the food and the distance of the food. The relationships among these behavioural and kinematic variables are examined in order to extract the invariants across species and the strategies and specificities of each species. Finally, we discuss prehension in primates from an ecological and evolutionary perspective.

Material and Methods

Species

Seven human adults (two women and five men, mean age: 33±7.3 years) were investigated. The study was carried out in accordance with "The ethical codes of the World Medical Association" (Declaration of Helsinki). For the non-human primates, the experimental protocol used adhered to the legal requirements of the European Union and the American Association of Physical Anthropologists Code of Ethics. Three untrained adults were recorded for each species. Chimpanzees (*Pan troglodytes*, three females, mean age: 19.66±3.8 years), gorillas (*Gorilla gorilla*, two females and one male, mean age: 17.6±4.1 years), and capuchins (*Sapajus xanthosternos*, two females and one male, mean age: 7.6±5.6 years) were filmed in the zoological park of La Palmyre, France. Lemurs (*lemur catta*, three males, mean age: 3 years) were filmed in the zoological park of Jardin Zoologique Tropical, France. Gorillas were the heaviest (mean of 120.3±47.5 kg), followed by humans (mean of 63.8±7.5 kg), chimpanzees (mean of 44.6±10 kg), capuchins (mean of 2.8±0.7 kg) and lemurs (mean of 2.6±0.3 kg).

Food selection and food size

Lemurs are considered frugivorous, gorillas as folivorous-frugivorous, capuchins, chimpanzees and humans as omnivorous (Harding, 1981; Jolly, 2003; Fragaszy *et al.*, 2004). We selected raisin because all consume fruits as part of their diet. Moreover, this small food size was also chosen to test an accuracy task of prehension, relevant from an evolutionary perspective because some species use precision grasping and some others do not (Bishop, 1964; Costello and Fragaszy, 1988; Pouydebat *et al.*, 2009). The size of the food was standardized according to the length of the hand calculated between landmarks of the wrist and those of the metacarpal heads. The size of the raisin was 1/4th of this length for each species (table 1). However, the lemur was different in raisin grasping compared to the other species in systematically grasping the raisins with the mouth. The objective of this study being to test the kinematics of manual prehension, we decided to increase the size of the food to a size for which the lemurs used the hand to grasp. This food size corresponded to an apple morsel representing 2 cm^3 and was distributed for this species instead of raisins.

Experimental set up for humans

Reaching and grasping movements were recorded at 100 frames/sec using a Motion Analysis® system (LBMC, Lyon; Motion Analysis Corporation, Santa Rosa, USA) with eight Eagle® cameras surrounding the subject. This protocol is detailed in the chapter 4. Twelve infrared reflective markers were positioned on anatomical landmarks of the forelimb and the trunk (fig. 1) as recommended by the International Society of Biomechanics (ISB) (Wu *et al.*, 2005).

Experimental set up for non-human primates

Data were acquired using five video cameras for chimpanzees and gorillas and four video cameras for capuchins and lemurs (Sanyo® X-Acti Full HD 1920x1080). All the non-humans were recorded at 60 frames/sec. Cameras were located in semi-circle around the subject and were synchronized with a manually operated flashlight. The food was scattered on the ground on a surface of 50 cm^2. All the non-humans were in unconstrained conditions meaning that they were not trained prior the recordings, they were in their habitual enclosure and totally free to choose their body posture and their distance relative to the food. Spontaneous grasping mainly occurred in a quadrupedal posture (see results) with only the feet and hands in contact with the substrate. As no markers could be placed on the animals in zoos for ethical reasons (see Aerts *et al.*, 2000, Isler *et al.* 2005; Vereecke *et al.*, 2006), ten landmarks were manually digitized at the same location as those digitized in humans.

Behavioural analysis of non-human primates

Four behavioural variables were collected using frame-by-frame analysis for 100 grasps per subject (total = 1200 grasps) from video recordings (sessions of 20 minutes/day): body postures, position of the subject relative to the food (in front, at left or at right), handedness, and preferred grasp type (*i.e.* manual grasping postures). Grasp types were defined by a grasp with the hand or with the mouth. For manual grasping, the contact surface between each finger and the food was recorded (*e.g.* Christel, 1994; Spinozzi *et al.*, 2004; Pouydebat *et al.*, 2009). Precision grasps are defined here by a grasp between the thumb and index tips on the lateral, pulp or medial side of the distal part of the fingers. The whole hand grasp describe a grasp with the palm and all the fingers. These behavioural variables helped us to select comparable trials between all the species for the movement analysis. Only the principal grasp used by each subject was used for subsequent kinematic analysis.

Kinematic analysis

Kinematics were analyzed for five trials in each subject (15 grasp sequences per species for the non-humans and 35 grasp sequences for humans). First, as the non-humans preferentially grasped food in front of them (see results), we retained prehension movements in front of the subjects for all the species to standardize the comparison. Indeed, it is well-documented both in macaques and humans that object location affects the wrist kinematics (Paulignan *et al.*, 1997; Roy *et al.*, 2002). Second, we know that distance directly affects the wrist kinematics in humans (Jeannerod, 1981, 1984; Marteniuk *et al.*, 1987; Jakobson & Goodale, 1991). In order to select food distance for humans comparable with those preferred by non-humans, we created a large database of prehension sequences for humans with numerous food distances in front of the subjects. The calculation of the ratio of each species forelimb length (arm + forearm) to the food distance allowed to standardize food distances and to select ones proportional for all species according to their forelimb length. The length of the arm was measured from the video recordings as the distance between the acromio-clavicular joint and the mid-point of the two elbow landmarks (lateral and medial epicondyles of humerus). The length of the forearm was measured between the mid-point of the two elbow landmarks and the mid-point of the two wrist landmarks (ulnar and radial styloid processes). In the large database of humans, we obtained ratios between 0.4 and 1.2. The food distances obtained for the non-humans during spontaneous grasping mainly included ratios between 0.9 and 1. Thus these ratios (between 0.9 and 1) were selected from the database of humans. Indeed, the selection of a comparable distance between species, limited the effect on the forelimb kinematics. Finally, for all the sequences selected, the hand was on the ground in a stationary position before being moved forward to reach.

For non-humans, video calibration, manual digitization of the anatomical landmarks and the reconstruction of the 3D coordinates were performed using a custom-written Matlab® routine (Loco 3.3, P.A. Libourel, MNHN). The accuracy of the software reconstruction was tested by digitizing the four corners of a checkerboard and showed less than 1% of error (see Appendix B for details). A precision test of three digitizations of the same prehension trial for each of the non-human species revealed a fairly constant arm and forearm segment length suggesting that the method is accurate enough to quantify the movement kinematics (see Isler, 2005) (see Appendix B for details). For human subjects, the software EvaRT® 5.0 reconstructed the markers trajectories and extracted their coordinates in 3D.

For all the species, kinematic data were processed using Matlab® (The MathWorks, Inc., Natick, MA). Data were low-pass filtered at a frequency of 6 Hz with a second order dual-pass Butterworth filter (see Appendix C for details). Onset and offset of the reaching phase (*i.e.* between the movement onset and the grasp) were identified based on the wrist velocity profile and were defined as the time when wrist velocity reached 5% of its wrist peak velocity (Alstermark *et al.*, 1993; Santello *et al.*, 2002; Graham *et al.*, 2003). All variables were obtained in a trunk-centered frame of reference. The X axis was oriented toward the food, the Y axis was upward and the Z axis was directed laterally (fig.1).

From the digitizations, we quantified several variables for the wrist kinematics. The wrist velocity (also referred to as the wrist tangential velocity) was calculated from the filtered three dimensional Cartesian coordinates (x, y, z) of the mid-point of the two wrist landmarks (Kudoh *et al.*, 1997). The wrist velocities were converted to dimensionless units in order to reduce the effect of the size of the species for comparisons (Hof, 1996; Vereecke *et al.*, 2006). Dimensionless velocities were obtained from velocities divided by the mean of the arm and forearm length of all the subjects for each species. The velocity mean, the maximal amplitude and the time to the velocity peak were measured. The first two variables are reported both in absolute values and in dimensionless values. The mean of dimensionless wrist velocity curves were interpolated for each species allowing resampling on 100 points in order to represent the patterns relative to the overall movement duration. This interpolation was done using the standard spline function in Matlab®. Based on this method, the data could be compared preserving their species- and method-specific characteristics. The movement duration was the time measured from movement onset to the grasp.

The ranges of motion of the trunk (relative to the ground) and the forelimb joints (shoulder, elbow, wrist) were computed using the ISB recommendations (Wu *et al.*, 2005) (see Appendix D and fig. 1 for details). The aim of these recommendations is to standardize the methods of calculation, involving a standardization of joint motions in order to facilitate comparison, and thus discussion between studies, and in order to obtain movements close to the functional reality. Ten degrees of freedom were quantified: (a) trunk flexion-extension (forward/backward motion in sitting; upward/downward motion in quadrupedal), (b) trunk inclination (lateral motion of the trunk on the left or right side), (c) trunk rotation, (d) shoulder flexion-extension, (e) shoulder abduction-adduction, (f) shoulder rotation, (g) elbow flexion-extension, (h) elbow rotation, (i) wrist flexion-extension, (j) wrist abduction-adduction.

The ranges of motion, as well as the absolute differences between minimal and maximal angles, were calculated for the trunk segment, the shoulder, the elbow, and the wrist joints. The curves of the ranges of motion were averaged for the subjects of each species and interpolated over 100 points to represent the patterns relative to the overall movement duration. The positive values obtained on figure 2 represented flexion, right inclination and right rotation of the trunk, and flexion, adduction, internal rotation for all the forelimb joints movements. For elbow, internal rotation corresponded to the pronation and external rotation corresponded to supination. We use pronation and supination in our descriptions below. For the wrist, adduction implies radial deviation and abduction implies ulnar deviation. In order to quantify the variation of the species for all the variables, the coefficient of variation was calculated using the following formula: CV= SD/Mean.

Statistical analyses

All analyses were performed using the R graphical and statistical package v.2.9.0 (R Development Core Team, 2009). The hand preference (Hopkins, 1999) was determined for reaching in all the species studied in order to conduct kinematic analyses on the preferred hand of each subject. The degree of manual asymmetry was calculated for each subject via the handedness index (HI) using the formula (R-L)/(R+L) where R and L represent the total number of right and left responses. The HI values ranging from +1.0 to -1.0 indicate for positive values a right hand preference and negative values, a left-hand preference. Then, the binomial z-score determined if the manual preference (handedness) is significant. The subjects were classified with z score, $z \leq -1.96$ as right-handed, $z \leq 1.96$ as left-handed, and $1.96 < z < 1.96$ as ambipreferent.

Analyses of variance (ANOVA) with one factor (species) and Tukey's HSD post-hoc tests were used to test for differences in kinematics between species. The absolute values of angular displacements, the time to wrist velocity peak (in % and ms), the duration of the deceleration phase (in % and ms), the movement duration, and the dimensionless values of wrist velocity were tested. A Shapiro-Wilks' test was used to test the normality of the data and the Bartlett-test was used to check for homogeneity of variance.

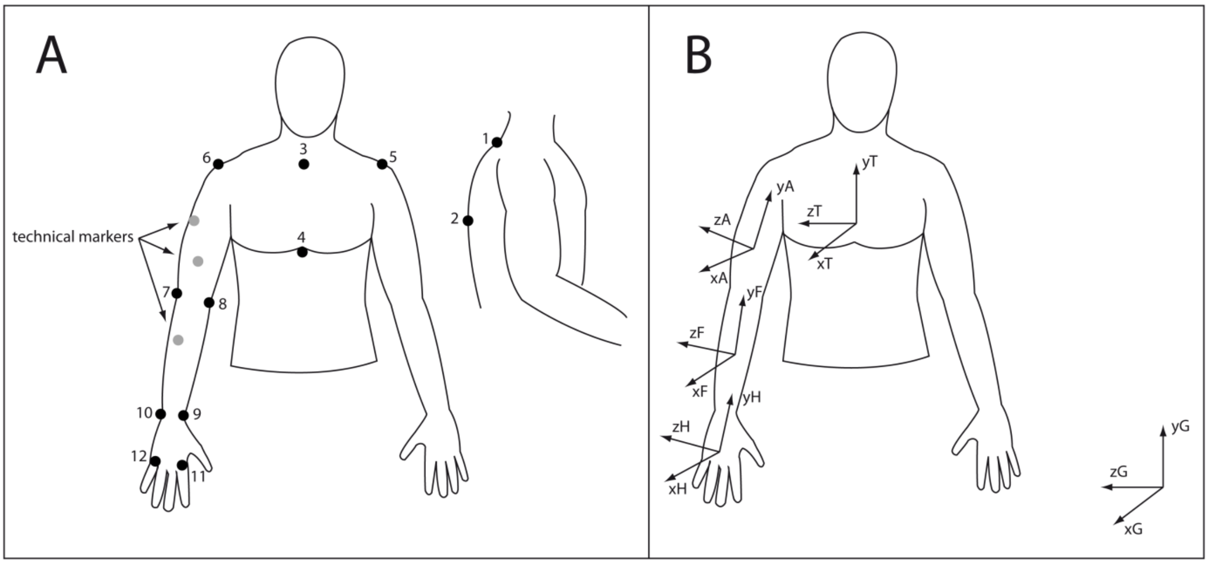

Figure. 1. Position of the landmarks (A) and the segment coordinate systems (B) on the forelimb.

Two additional reflective markers placed on the arm and one on the forearm helped to reconstruct the motion of forelimb in humans. For the five species (humans, chimpanzees, gorillas, capuchins, lemurs), only the trunk landmarks [1] and [2] were used for visibility reasons.

Landmark legend (A): [1] processus spinosus of the 7th cervical vertebra, [2] 8th thoracic vertebra, [3] suprasternal notch, [4] xiphoid process, [5, 6] left and right dorsal point on the acromio-clavicular joint, [7, 8] medial and lateral epicondyles of humerus, [9, 10] radial and ulnar styloid processes, [11, 12] head of 2nd and 5th metacarpus.

Segment coordinate system legend (B): G: Ground, T: Trunk, A: Arm, F: Forearm, H: Hand.

Results

Behaviour

The hand preference varied among the subjects of the same species and between the species except for humans which were all right-handed (table 2). All species showed a hand preference except two chimpanzees. Moreover, all the species, except lemurs, showed precision grasps. Humans used only this type of grasp, whereas all other species showed two or three types of grasp (table 3). Chimpanzees and gorillas adopted precision grasps. Gorillas used few scissor grasps (precision grasps: 95.66%, scissor grasps: 4.33%) compared to chimpanzees which used both in the same proportion (precision grasps: 56.66%, scissor grasps: 42.33%). Moreover, chimpanzees used only precision grasps involving the thumb pulp and medial side of the index. Humans used only precision grasps between the thumb pulp and index pulp, and gorillas used only precision grasps between the thumb tip and the index tip. Capuchins and lemurs were the only ones to use whole hand grasps. Capuchins mainly used the whole hand grasps (65.33%) compared to precision grasps (30%) and the mouth grasps (5.66%). Lemurs mainly used the whole hand grasp (87%) and also the mouth grasps (13 %). Lemurs showed the widest use of mouth grasps, whereas capuchins rarely used it and apes, including humans very rarely employed it (1% for chimpanzees, 0% for the other species).

Considering the body posture adopted during grasping, the quadrupedal posture was preferred in all the species. Lemurs and capuchins were always in quadrupedal posture (lemurs: 98%, capuchins: 99.66%) whereas gorillas or chimpanzees diversified their postures between the sitting and the quadrupedal ones. Gorillas and chimpanzees were respectively 52.6% and 65.6% of the time in quadrupedal posture against 47.4% and 34.4% in a sitting posture. For the position of the subject relative to the food location, all the subjects preferentially placed themselves in front of the food (lemurs: 90.7%, capuchins: 61.3%, gorillas: 70.3%, chimpanzees: 44%) rather than at the left (lemurs: 4%, capuchins: 19%, gorillas: 17%, chimpanzees: 24.3%) or at the right relative to the food location (lemurs: 5.3%, capuchins: 19.7%, gorillas: 12.7%, chimpanzees: 31.7%).

The above behavioural information was used to select prehension sequences for the kinematic analyses. Hand preferences were considered for subjects who had a significant z-score (table 2). Therefore, food prehension sequences with the preferred hand, type of grasp (*i.e.* precision grasp for chimpanzees, gorillas and humans; whole hand grasp for lemurs and capuchins), quadrupedal posture with food located in front of them were retained for the kinematic study.

Kinematics

Wrist velocity

The statistics and the means of the values of the wrist velocity variables for all the species were reported in the tables 4, 5 and 6. Figure 2 shows the dimensionless curves of the wrist velocity for each species. Two groups were identified and showed no significant differences for most of the variables: the first being the non-human apes (gorillas and chimpanzees), the second being the smaller species (capuchins and lemurs) (table 4).

Moreover, humans always showed significant differences with the smaller species and some ones with the non-human apes. The group of the non-human apes was significantly different from the smaller species in some variables.

Humans in both body postures (HS: Humans in a Sitting posture, HQ: Humans in a Quadrupedal posture) displayed a similar time to peak wrist velocity as chimpanzees (C) and gorillas (G) (HS: 40.7±6 %, HQ: 39.2±5 %, C: 42.2±9 %, G: 41±9 %) and earlier peaks than capuchins (S) and lemurs (L) (S: 47.8±2 %, L: 48.4±7 %) (fig. 2) (table 4). Consequently, apes including humans exhibited a longer deceleration phase, but all the species showed a longer deceleration phase than the acceleration phase. When considering absolute velocities (means and peak amplitudes), the non-human apes displayed the highest velocities. In contrast, when the velocities were rendered dimensionless, capuchins and lemurs presented the highest ones (table 5 and fig. 2). The dimensionless values helped us to reduce the influence of the size and allowed inter-specific comparisons. However, no change occurred in humans who showed the lowest velocities in both absolute and dimensionless terms.

The smaller species exhibited a shorter movement duration compared to apes. Humans exhibited the longest ones (table 5). Concerning the variability of the species (table 6), the non-humans primates were more variable than humans for the wrist velocity means and amplitudes. By contrast, they all displayed similar variability for the time to peak wrist velocity, the duration of the deceleration phase, and the movement duration.

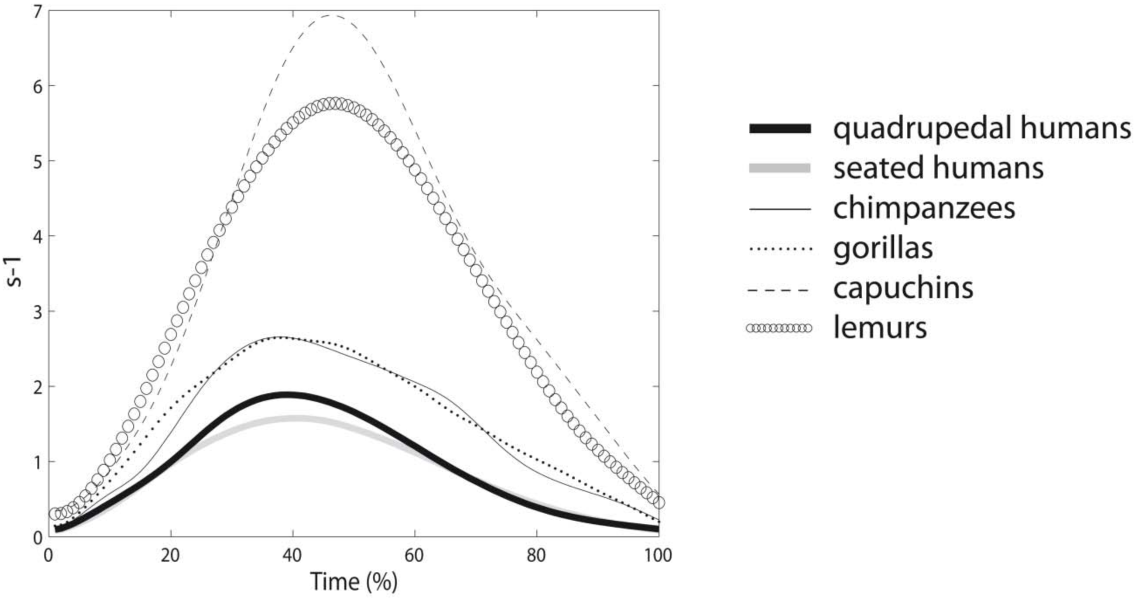

Figure 2. Dimensionless wrist velocity curves during the entire movement for the five species. The movement is initiated at 0% and grasping occurs at 100%.

Profiles of trunk and forelimb joint motion

The unconstrained prehension movements with the forelimb toward the food involved for all species a trunk, shoulder and elbow flexion rather than extension, a shoulder abduction rather than adduction, an elbow supination rather than a pronation. For the other joint movements, different profiles occurred according to the species (fig. 3).

Trunk

Concerning the trunk flexion relative to the ground, humans in a sitting posture presented the trunk in the most upward vertical orientation (around 20-30°) (fig. 3A). In contrast to a sitting posture, the quadrupedal posture implied a trunk in a horizontal position (around 90°). Gorillas were the ones which had the trunk the most oblique upward direction (around 80°-90°), followed by the quadrupedal humans (around 90°-100°), the chimpanzees (around 100°), the capuchins (around 110°-120°) and the lemurs (around 130°-140°) . The latter presented the trunk the most flexed downward (fig. 3A) which was related to the need to smell the food during prehension (fig. 4). None of the other species displayed this behaviour. Their head remained distant from the food even if they looked at it.

Humans showed trunk rotation and trunk inclination (relative to the substrate) directed to the left side whereas the other species were in a more neutral posture (fig. 3B-C). The inclination might be related to the hand preferences of the subjects. As all the humans were right-handed for this task, the trunk mainly inclined and rotated on the left side during the lifting of the right hand to reach. Similarly, capuchins were all left-handed and presented an inclination toward the right side. As the subjects of the other species showed different hand preferences, the means exhibited more neutral rotation and inclination of the trunk.

Shoulder

Helped by trunk movements, the proximal forelimb joint widely contributed to the transport of the forelimb. This unconstrained prehension involved an increase of the shoulder flexion with maximal values at the grasp (fig. 3D). Humans exhibited the lowest angular values of flexion in a sitting posture and the widest ones in a quadrupedal posture. The angular values of the lemurs in their start position demonstrated a small flexion compared to the other non-humans. The angular values of gorillas and chimpanzees were very close. Despite some differences, the shoulder flexion profiles of the five species were similar. Moreover, the shoulder was in internal rotation, principally in gorillas (fig. 3E). Another strategy was adopted by the lemurs which essentially execute external rotation. Species shared a similar profile except humans while sitting. Finally, all species abducted the shoulder during the movement (fig. 3F).

Elbow

The elbow remained in flexion and formed a bell-shaped profile during the movement with a smaller angle of flexion at the beginning and the end of the movement for all the species when in a quadrupedal posture (fig. 3G). However, humans in a sitting posture exhibited an elbow in flexion changing towards extension during the prehension. More specifically, gorillas and chimpanzees displayed a similar profile with lower degrees of flexion than capuchins and lemurs. The apes, including quadrupedal humans, presented a smaller angular flexion of the elbow than the smaller species. The elbow remained supinated for all the species, especially for the chimpanzees and the gorillas which displayed maximal values of supination (fig. 3H). The movement of elbow supination was very similar in lemurs and humans in both postures.

Wrist

The wrist moved both in flexion and in extension according to the species (fig. 3I). The pattern of the chimpanzees, gorillas and lemurs was the same and forms a bell-shaped curve but the angular values differed. The non-human apes show a flexed wrist throughout the movement whereas lemurs exhibited a more extended wrist which reached a neutral posture at mid-course and re-extended at the end of the movement. Humans in a quadrupedal posture and capuchins exhibited a similar profile but the wrist of the capuchins was less extended than that of humans and lemurs. Humans in a sitting posture showed a particular pattern with the lowest variation close to a neutral wrist position. For wrist deviation, lemurs and capuchins began in abduction (*i.e.* ulnar deviation) and finished in small abduction close to a neutral posture (fig. 3J). Chimpanzees and humans displayed a more pronounced ulnar deviation. Humans in both postures exhibited the same pattern of movement with very little variation compared to gorillas and chimpanzees.

General quadrupedal body postures

In summary, lemurs had the most downward inclined trunk involving less shoulder flexion, especially at the start of movement. Their elbow and their wrist were respectively in pronounced flexion and extension (fig. 4). The trunk and forelimb segments of lemurs were very compact and in a Z position compared to the other species. The position of their head near the food on the ground influenced the general posture of their trunk and forelimbs. Indeed, the other species showed a more distant position of the head relative to the food involving an opposite angular position with a more upright trunk, flexed shoulder and reduced elbow flexion. However, a major difference appeared for the hand posture at start which changed according to the species. Indeed, non-human apes showed a knuckle walking posture meaning that they supported body weight on the back of phalanges whereas humans, capuchins and lemurs used palmigrade postures with the palm and the finger tips in contact with the substrate (fig. 4).

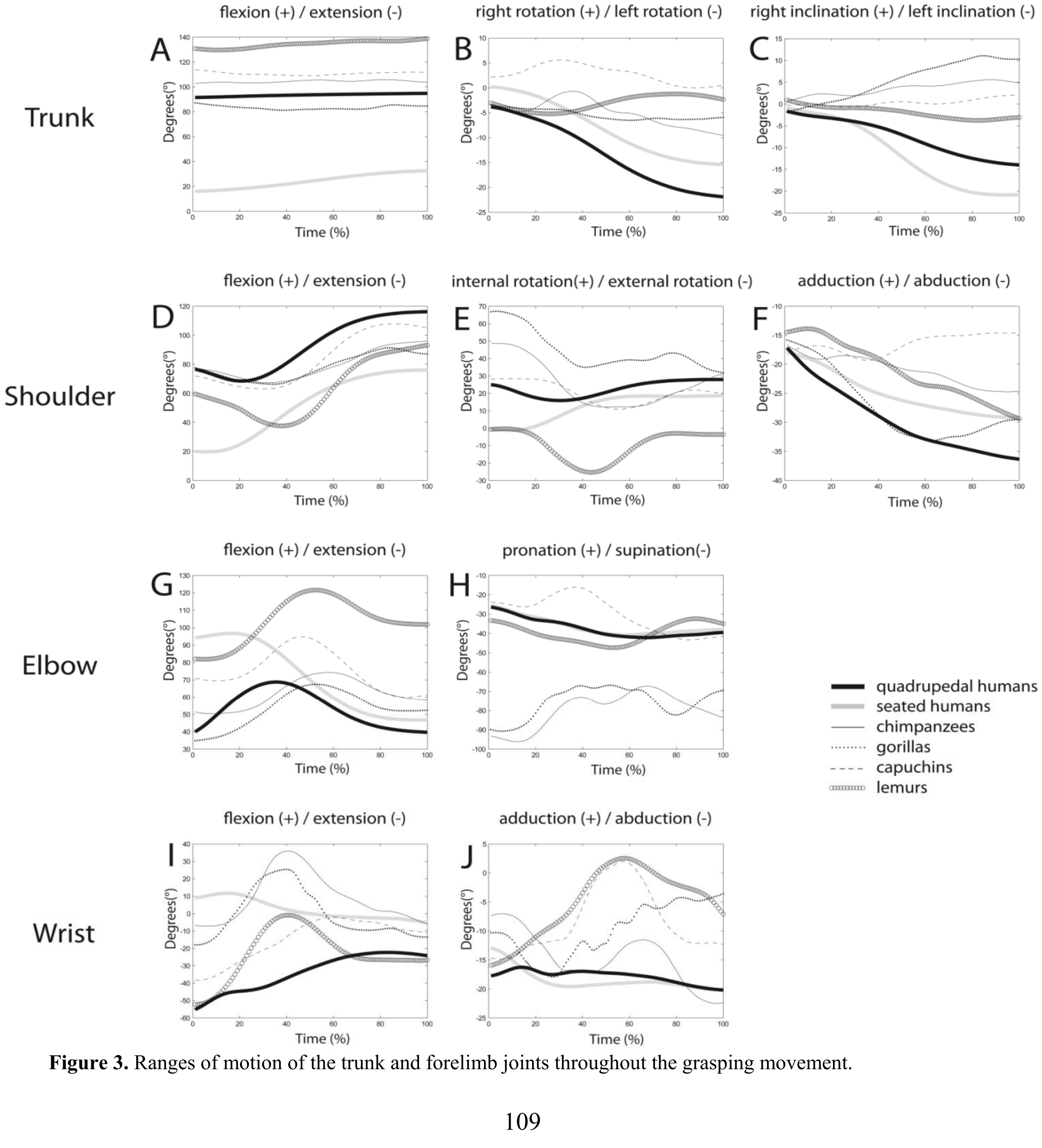

Figure 3. Ranges of motion of the trunk and forelimb joints throughout the grasping movement.

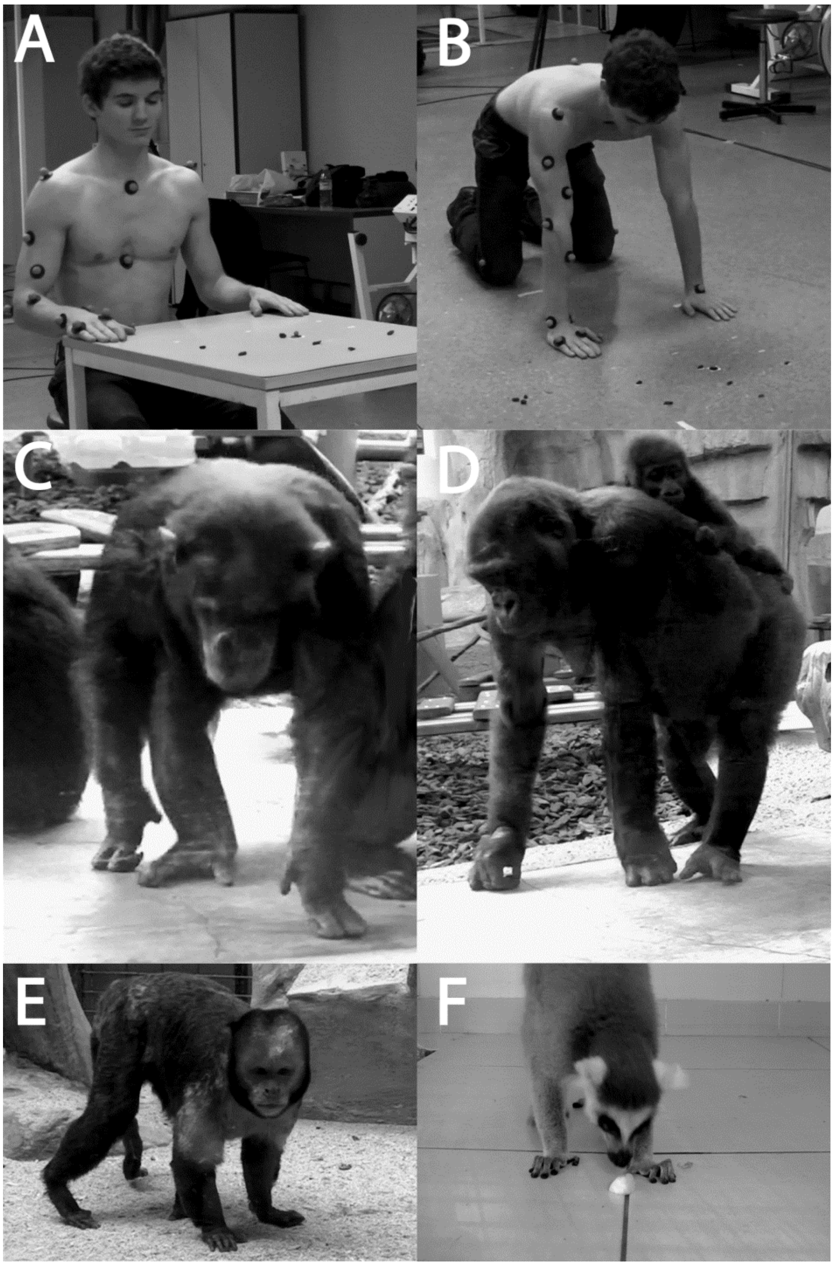

Figure 4. Posture of the different species prior to prehension movements in unconstrained conditions. Note the palmigrade hand posture of humans (A, B), capuchins (E) and lemurs (F) and the knuckle walking posture of chimpanzees (C) and gorillas (D).

Ranges of motion of forelimb joints and trunk

Concerning the range of motion of trunk and forelimb joints, the statistical and absolute values are presented for all the species in the tables 7, 8 and 9. Each value represents the mean for across all subjects.

First, when we compared humans in both postures with the non-humans in a quadrupedal posture, humans showed the most significant differences independent of body postures (table 7). Their shoulder and elbow rotation and all their wrist motions (flexion/extension and deviation) were significantly lower compared to the non-humans. Although no significant differences were detected for the other ranges of motion, humans often presented low ranges of motion especially in a quadrupedal posture, and showed few coefficient of variations lower than non-humans (tables 8-9). Moreover, humans exhibited inverse their strategy compared to non-humans with respect to the ranges of motion of trunk flexion and shoulder abduction depending on body posture. In a sitting posture, the human trunk flexion was as pronounced as that of non-humans and showed no significant differences. Yet, the human shoulder abduction was significantly lower than that of non-humans. In contrast, the range of trunk flexion of humans in a quadrupedal posture was significantly lower than that of the non-humans, but the shoulder abduction was not significantly different from that in non-humans (tables 7-8).

When we compared the non-humans between them, they did not present significant differences concerning their ranges of motion with the exception of shoulder flexion (lemurs *versus* gorillas and chimpanzees) and elbow rotation (lemurs *versus* gorillas) (table 4). Indeed, the range of shoulder flexion in lemurs (65.3±26.9°) was significantly greater than in chimpanzees (41.8±23.8°) and gorillas (36.1±17.4°). Moreover, only lemurs and gorillas were significantly different in terms of elbow rotation with wider ranges observed in gorillas (74.1±34.2°) compared to lemurs (41.6±18.2°). More generally, gorillas and lemurs presented the more extreme ranges of motion for most of the forelimb joints (table 8).

Despite the fact that non-humans exhibited no significant differences, they did exhibit two different strategies of motion during prehension. Compared to gorillas and chimpanzees, capuchins and lemurs displayed an inverse trend in shoulder and elbow motion. The ranges of flexion-extension of the smallest species were greater compared to the non-human apes but the ranges of rotation of the former were lower than the latter (table 8). When we compared humans in both postures with the non-humans, humans appeared closer to lemurs and capuchins as they all display greater flexion-extension motion than rotation at the shoulder and elbow (table 8). Moreover, concerning the abduction of the shoulder, the non-humans presented similar values (ranges between 22.4° and 25.6°) and humans the lowest values in both postures (HS=12.3±6.6°, HQ=19.8±10.5°). Similarly, for the wrist motion, the non-humans exhibit angular ranges that were nearly twice those of humans both in flexion-extension and in their deviation (table 8).

Concerning the contribution of the trunk in flexion relative to the ground, the lemurs exhibited the widest range of all the non-humans (22.3±11°) and capuchins the lowest (14.5±13.5°). Apes, including humans, shared a similar trunk flexion (around 16°, table 8), except humans in quadrupedal posture which displayed very small ranges of flexion (3.7±2.1°). Finally, the coefficients of variation of humans were not always lower than those of the non-humans (table 9). Except for the trunk motion of capuchins, the intraspecific variability (CV) was relatively similar for all species.

Discussion

The aim of this study was to identify the behavioural and 3D-kinematic specificities of each species but also to explore the invariants between the species during a food prehension task in unconstrained conditions. The study shows two major results: the main characteristics of the wrist velocity appear as an invariant between the studied species whereas the motion strategies of the forelimb joints and the trunk show different pattern according to the species.

Behaviour

The behavioural data reveal that all species choose similar positions prior to reaching for and grasping food. They position themselves mainly in front of the food at a distance which can be described as comfortable. Indeed, the calculated ratios of each species mainly included similar ranges (between 0.9 and 1). Moreover, all the subjects prefer to use a quadrupedal posture to grasp whereas Christel & Billard (2002) quantified macaques in unconstrained condition mainly in a sitting posture to grasp. This suggests that the body stability may differ according to the species. Indeed, even in our samples, different frequencies of body postures are quantified according to the species: chimpanzees and gorillas exhibit more sitting postures than lemurs and capuchins. The assessment of this behaviour during prehension needs further investigations to be interpreted in relation with motor control or morphology of the species.

Concerning the types of grasp used by the species, apes always use a grasp between two fingers (precision and scissor grasps) like macaques in the study of Christel & Billard (2002) and as it was observed in previous studies for apes and macaques (Christel, 1993, 1994; Pouydebat *et al.*, 2009). The variability of type of grasp in this study is very low compared to that quantified by previous studies (Christel, 1993, 1994; Pouydebat *et al.*, 2009). The variability of grasps could also depend on the studied group and not only of species. Similarly, the capuchins can use a precision grasp (Costello & Fragaszy, 1988) but preferred a whole hand grasp in this study. As for the lemurs, they always use the whole hand grasp, as described by Bishop (1964), which suggests that they do not have individuation of fingers like the other species of this study.

Concerning handedness, our results are consistent with literature data for humans and non-human primates in the context of a uni-manual food prehension task. There is currently no consensus for non-human primates. Preferences generally occur at the subject-level but not at group-level, and appear to be flexible (Papademetriou *et al.*, 2005; Hopkins, 2006). In contrast, humans always exhibit a preference at the group-level for the right hand (Annett, 1985; Perelle & Erhman, 2005) which is confirmed in this study. As the existence of kinematic differences between the use of the dominant and non-dominant hand is still debated in the literature (Carlson *et al.*, 1993; Elliot & Chua, 1996; Grosskpof & Kuhtz-Buschbeck, 2006), we selected the dominant hand of each subject in our kinematic analysis.

Kinematics

Wrist velocity

For the reaching movements, all the species showed a bell-shaped, single-peaked profile of wrist velocity. Indeed, their velocity profiles show an initial phase of velocity increase to reach a maximal amplitude (*i.e.* peak velocity) followed by a deceleration phase. This profile shape remains invariant across these species is similar to those seen in biomechanical studies in humans (e g. Jeannerod, 1981, 1984; Paulignan *et al.*, 1997 Marteniuk *et al.*, 1987), in macaques (*e.g.* Roy *et al.*, 2000; Christel & Billard, 2002), in cats (*e.g.* Alstermark *et al.*, 1993) and in rats and opossums (Ivanco & Whishaw, 1996). However, it is interesting to note that all subjects included in these studies (except macaques of the study of Christel & Billard, 2002) were trained to complete the prehension movement in constrained conditions (*e.g.* through a slot, with a hand attached). Therefore, our results show that without learning and in unconstrained conditions, the species included in our study execute natural gestures and show basic features of the wrist kinematics. This confirms that the bell-shaped profile of the wrist velocity is a basic component of the object prehension mechanism. Moreover, if the length of the deceleration phase is poorly understood in cats, rats and opposums, the wrist velocity profile in humans (Jeannerod, 1981), macaques (Roy *et al.*, 2000) and the species in our study is asymmetric with a deceleration phase which is always longer than the acceleration phase. This specific wrist velocity profile reveals that these primate species, belonging to various phylogenetic groups, share a similar motor control of prehension.

However, differences appear in both movement duration and in the asymmetry of the wrist velocity profile curve. Indeed, the smallest species, capuchins and lemurs, showed shorter movement durations, a later peak in the velocity profile, and consequently a shorter deceleration phase compared to apes (chimpanzees, gorillas and humans). The later velocity peak can be assigned to the use of their principal grasp type. Indeed, capuchins and lemurs mainly grasped with their whole hand. In humans and macaques, a whole hand grasp has been reported to affect the wrist kinematics and is known to extend the timing of peak velocity and shorten the deceleration phase (Gentilucci *et al.*, 1991; Castiello *et al.*, 1992; Roy *et al.*, 2002). As this grasp needs less accuracy than the precision grasp, it does not need to decelerate as much as the precision grasp does in order to adjust the grasp (Fitts, 1954). Even if capuchins were able to use precision grasps between two finger tips (thumb and index), we selected in this study the type of grasp the most used by each species for the kinematic analyses, which was the whole hand grasp in capuchins and lemurs. Concerning the lemurs, they grasped larger food items than capuchins and the other species and consequently exhibited the latest occurrence of peak velocity and the shortest deceleration phase. Indeed, reaching in humans and macaques also depends on the intrinsic properties of the object such as its size (Bootsma *et al.*, 1994; Roy *et al.* 2002). An increase of the size of the object decreases the need for an accurate grasp and induces a later occurrence of peak velocity, and a shorter deceleration phase (Fitts, 1954; Gentilucci *et al.*, 1991; Castiello *et al.*, 1992). The relationship between the parameters of the wrist velocity and both the grasp posture and food size could explain the lemur results. Thus, wrist velocity in lemurs could be strongly dependent on both the grasp posture and food size but this needs further investigation.

However for a similar sized food item, apes exhibited similar grasp types and wrist velocity profiles. Their wrist velocity peak occurs at the same time although non-human apes are faster than humans. The slower velocity of humans could be explained by the laboratory conditions in which no pressure is exerted on the subjects for access to food, in contrast to all other species. Moreover, the same kinematic features were observed for precision grasps both between the thumb and index tips (principally in humans and gorillas) and between the thumb pulp and medial side of index (principally in chimpanzees). Apes appear more similar in their prehension mechanism, consistent with their phylogenetic proximity and manual ability (*e.g.* individuation of fingers and precision grasps) in food grasping (Christel, 1992, 1993; Jones-Engels & Bard, 1996; Pouydebat *et al.*, 2008, 2009; Crast *et al.*, 2009). Moreover, these invariants are shared with macaques, suggesting that monkeys and apes respond in the same way to the same stimulus, suggesting a common strategy. Although capuchins share many features with apes, especially the frequent use of tools in the wild, and their grasping and manipulation skills (Spinozzi *et al.*, 2004; Fragaszy *et al.*, 2004; Pouydebat *et al.*, 2009), their kinematic strategy in wrist velocity is different. Their principal manual posture used to grasp small food items may explain their different kinematic response with a later wrist velocity peak. Would capuchins display the same kinematical features as those observed in apes and monkeys if they used a precision grasp? This would allow us to determine whether the same manual abilities to grasp involve same kinematic features, independent of phylogeny. Investigating the grasping kinematics of capuchins when using a precision grasp is a question that requires further attention, essential to improve our understanding of the evolution of prehension in primates.

Although we did not compare different conditions (*e.g.* different food sizes and manual postures) in each species, the kinematic characteristics of these conditions found within species (macaques or humans) are also present across species (chimpanzees, gorillas, capuchins and lemurs). Indeed, kinematic features of lemurs and capuchins are consistent with those of the prehension of large objects with the whole hand in humans and macaques. Those of apes are consistent with those of humans and macaques grasping small objects between thumb and index. Finally, this study and the previous ones on spontaneous prehension revealed similarities in kinematics and grasp types for macaques, gorillas, chimpanzees and humans (kinematics: Roy *et al.*, 2000, 2002; Christel & Billard, 2002; grasp types: Christel, 1993; MacFarlane & Graziano, 2009; Pouydebat *et al.*, 2009). This suggests that prehension skills have evolved early-on in cercopithecoids but further analyses are needed to shed light on the abilities of platyrhines like capuchins. However, whether capuchins would exhibit the same kinematic features for precision grasping as cercopithecoids raises the question of the convergence or homology of these features. Pouydebat *et al.* (2009) postulated for a convergent postural grasps with cercopithecoids rather than a homologous ones. This would be supported by the uniqueness of the capuchin's features among platyrhines and remains to be tested.

Motion of forelimb joints and trunk

When we compare humans in sitting and quadrupedal postures, the general description of angular profile reveals differences between the body postures in terms of trunk and forelimb joint profiles during prehension. Only shoulder flexion and abduction exhibit the same movement profile in both body postures. Despite these differences and in comparison to non-humans, humans appear to prefer flexion-extension rather than rotation and abduction irrespective of body posture.This suggests that the body posture in humans has a limited effect on the general strategy of the forelimb joints during prehension, even if the articular profile during prehension is not exactly the same in both postures.

When we compared the quadrupedal species, included humans in this posture, the articular profiles of trunk and forelimb joints are generally similar but exhibit different ranges of motion. Indeed, the forelimb joints contribute to the prehension movement following two strategies of ranges of motion according to the species. Humans, capuchins and lemurs prefer movements in a parasagittal plane (shoulder and elbow flexion-extension) to reach the food, whereas gorillas and chimpanzees favor shoulder and elbow rotation. The two strategies seem to be correlated with the structure of the forelimb joints, especially that of the shoulder joint. Indeed, the overall mobility of the forelimb in primates is affected by scapular and glenohumeral orientation (Larson, 1993; Schmidt *et al.*, 2002; Chan, 2007a, b; Schmidt & Krause, 2010). Previous studies identified several patterns of scapular and humeral ranges of motion that differ in the degree of dorsolateral scapular motion and mediolateral glenohumeral mobility (Jenkins, 1973; Whitehead & Larson, 1994; Chan, 2007a, b; Schmitd & Krause, 2010). Ranges of motion of the shoulder of capuchins and lemurs are not restricted to the parasagittal plane as are those of the cercopithecoids (*e.g.* macaques), but show less movement rotation than chimpanzees and especially gorillas. Lemurs seem to be more constrained by their shoulder morphology than capuchins (Schmidt & Krause, 2010). The shoulder abduction of lemurs could be related more to movements of the scapula rather than the mobility of glenohumeral joint itself. Capuchins, however, display a glenohumeral joint that is more independent from scapula (Schmidt & Krause, 2010). During prehension, lemurs use wider ranges of shoulder flexion than capuchins but their trunk is more inclined downward which may force the execution of greater shoulder movements to advance the arm. However, in our data, both species presented similar ranges of motion in other movements of the shoulder during prehension and also in elbow and wrist with the exception of elbow rotation being higher in capuchins. In contrast, hominoids are known to have the most mobile forelimbs in primates with a dorsal position of the scapula and high degree of motion of the glenohumeral joint which is oriented more laterally and totally independent of the motion of the scapula (Schmidt & Krause, 2010). However, Chan (2007b, 2008) reported that hominoids are more constrained in the glenohumeral joint and did not show higher shoulder circumduction than other primates. These results emphasize the complexity of shoulder joint movements and suggest that the scapula could play a role in the mobility of shoulder even if the species are constrained at the glenohumeral joint. Moreover, while humans show a shoulder morphology similar to that of non-human apes (Corruccini, 1975; Chan 2007a, b), they did not use the same joint motion strategy. They use flexion-extension joint motion than rotation. Some features as their locomotor mode and muscular strength could explain their different joint strategy. Humans which are strictly terrestrial bipeds have a habitual use of the forelimb held below the level of the shoulder and supporting the weight of a pendant limb (MacConail and Basmajan, 1969). Moreover, humans have lost the arboreal abilities and locomotor function of their forelimb, and show smaller muscular masses compared to other apes (Thorpe *et al.*, 1999). Therefore, this could also explain the lesser forelimb joint excursion (especially in abduction and rotation) during prehension compared to non-humans apes.

Hominoids are known to have a generally greater joint excursion than non-hominoids even in elbow and wrist. Their longer forelimb is thought to be adapted to greater movements for climbing and brachiation in an arboreal environment (*e.g.* Lewis, 1969; Tuttle, 1969; O'Connor & Rarey, 1979; Rose, 1989; Swartz, 1989; Thorpe, 1999; Zilhman *et al.* 2011). In elbow motion, apes are recognized to have the maximal ranges of rotation (pronation-supination) followed by capuchins and finally cercopithecoids (Jenkins, 1973; O'Connor & Rarey, 1979; Rose, 1988). Even the wrist morphology is considered to be a specialization facilitating pronation-supination (Lewis, 1969). However, although the functional abilities of humans can display the same joint excursion as non-human apes, they do not use high rotations in prehension and exhibit the smallest one of all the primates in our study. Concerning wrist movements, they are consistent with the functional morphology of the species and more particularly with the start position of the hand movement prior to prehension. Chimpanzees and gorillas use quadrupedalism with knuckle-walking. This hand and wrist posture on the ground induces a mechanical restriction of wrist extension which is reflected in our data (Tuttle, 1969; Tuttle, 1985; Lewis, 1969). Indeed, gorillas and chimpanzees show the widest ranges of wrist motion and the profile of their wrist movement exhibit a flexion rather than an extension. However, the weight-bearing of capuchins, quadrupedal humans and lemurs occurs on the palm rather than the knuckles, and exhibits a wrist extension (Fragaszy *et al.*, 1990; Patel, 2010). Despite the different start position of the hand, all the non-humans exhibit greater ranges of motion of the wrist than humans.

Considering the trunk, its orientation varies according to the species whereas its contribution shows that all the species flexed the trunk in reaching except quadrupedal humans. The orientations of the trunk are related to both the length of the limbs and the behaviour of the species during prehension. Indeed, the inter-membral index, based on the ratio of the length of the forelimb to that of the hindlimb, indicates that the more the index is close to 1 or exeeds it, the more upright the posture (Jungers, 1985; Fleagle, 1999). Apes share an index close to or superior to 1 and have longer forelimbs that orient the trunk in a more upward posture. Capuchins and lemurs have longer hindlimbs than forelimbs orienting the head more downwards. Moreover, the lemurs show the most downward trunk related to a special behaviour. Indeed, lemurs smell the food during prehension as has been previously observed for the grey mouse lemur (Reghem *et al.*, 2011), for carnivores such as raccoons (Iwaniuk & Whishaw, 1999), and rodents such as gerbils and beavers (Whishaw *et al.*, 1998). Therefore, lemurs move the head close to the food increasing the downward posture of the trunk and much affects the forelimb joints. Indeed, especially the shoulder and elbow are pushed towards greater flexion. The ranges of motion of the trunk in lemurs contribute the most to prehension compared to the other species. Our data show that the behaviour of the species must also be considered besides its morphology to understand the kinematic strategy of prehension. Furthermore, food size has an effect on hand use in lemurs. They always grasped small food items with the mouth. The increase of food size enhances the use of the hand in lemurs as already observed in the grey mouse lemur (Reghem *et al.*, 2011). Why these two strepsirhines species tend to grasp small items with the mouth rather than with the hand remains unresolved. The food size has implications on the frequency of the hand use in strepsirhines whereas most of the haplorhines always spontaneously use their hand for small as well as large food items (Costello & Fragaszy, 1988; Christel, 1993, 1994; MacFarlane & Graziano, 2009; Pouydebat *et al.*, 2009).

In conclusion, the mechanical primitives in wrist velocity of human prehension appear to be present in other primates regardless of their phylogenetic affinity, or morphological and locomotor adaptations. However, cercopithecoids share a similar wrist velocity profile with a longer deceleration phase as observed in macaques, humans and non-humans apes. These parameters seem to be influenced by manual grasping and food size, but not by joint movements, morphologies, degrees of arboreality/terrestriality or locomotor modes. In contrast, ranges of joint motion during prehension in the studied primates are consistent with morphological features which are more related to locomotion or to phylogenetic affinity. Moreover, the joint strategies highlighted across species seem to have evolved independently from their prehensile abilities. lemurs remain a special case because they are the only ones among the species studied which grasp small food items with the mouth and use only the whole hand grasp.

On the other hand, we can wonder whether the variability in proximal movements (trunk, shoulder and elbow) of the forelimb such as the type of motion (rotation or flexion) would play a role in the emergence of specific distal grasping abilities such as precision grasps. The variability of the joint contribution and the manual postures during locomotion could have favored the elaboration of the prehension capacities, independent of the degree of arboreality and terrestriality. In addition, the varied use of the forelimb in locomotion combined with other non-locomotor activities could have increase manual abilities of primates. Indeed, a compromise between locomotor and foraging habits would likely drive the evolution of grasping ability. We suggest that arboreal abilities of primates do not alone explain grasping in primates. The use of the forelimb in diverse non-locomotor activities as food or tool prehension and manipulation would have favored the emergence of some morphological features. This idea is also suggested by Schmidt & Krause (2010) and Aversi-ferrarei *et al.* (2010). The latter suggest that a specific activity such as tool use shared by several closely related species may have played an important role in the evolution of some primate forearm muscles.

In order to better understand both the factors at the origin of prehension and those that may have implications in the evolution of manual abilities, especially in catarhines and capuchins, we suggest to test several sizes and food properties to address both kinematic and behavioural questions. Finally, the social context and interactions (*e.g.* self- and social grooming, learning) and their role in manipulation activities and technical practice (*e.g.* fine-scale object manipulations, nest building, tool use, precision grasp) should be investigated in integrative studies with primates and non primates.

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Table 1. Food size according to the species.

Species	**Small food size** (cm)	**Large food size** (cm^3)
humans	1.5	_
chimpanzees	1.7	_
gorillas	1.7	_
capuchins	0.5	_
lemurs	0.5	2

Table 2. List of the subjects of all the species and scores of their handedness (right-handers=R, left-handers=L or Ambidextrous=A). All the non-humans species were in quadrupedal postures and humans in sitting and quadrupedal postures. The score of humans was the same in both postures.

Species	Subjects	Sex	Age in years	Forelimb length (cm)	Mass (kg)	HI	z-score	Handedness
humans	1	male	28	57.5	68	1	10.1≤ -1.96***	R
	2	female	29	58	57	1	10.1≤ -1.96***	R
	3	female	38	59	73	1	10.1≤ -1.96***	R
	4	male	22	57	62	1	10.1≤ -1.96***	R
	5	male	33	57	62	1	10.1≤ -1.96***	R
	6	female	44	57	53	1	10.1≤ -1.96***	R
	7	male	37	60	72	1	10.1≤ -1.96***	R
chimpanzees	1	female	18	65.4	44	0.07	0.73 NS	A
	2	female	17	48.3	35	0.2	2.71≤ -1.96**	R
	3	female	24	67.6	55	-0.06	-0.6 NS	A
gorillas	1	male	21	87.5	150	0.46	4.6≤ -1.96**	R
	2	female	13	72.1	145.5	-0.2	-2≤ 1.96*	L
	3	female	19	81.5	65.5	-0.6	-6≤ 1.96**	L
capuchins	1	male	14	24.8	3.3	-0.24	-2.4≤ 1.96*	L
	2	female	6	19.1	3.1	-0.24	-2.4≤ 1.96 *	L
	3	female	3	18.3	2	-0.34	-3.1≤ 1.96 **	L
lemurs	1	male	3	22.9	2.3	-0.93	-8.9≤ 1.96**	L
	2	male	3	20.7	2.5	1	8.5≤ -1.96**	R
	3	male	3	20.4	3	-1	-9.4≤ 1.96**	L

NS not significant; *: significant at 0.05; **: significant at 0.01; ***: significant at 0.001

Table 3. Types of grasp used by the five species expressed in percentages. Precision grasp = between the thumb and index, scissor grasp = between the index and the third finger, whole hand grasp = between all the fingers and the palm, mouth grasp = the mouth alone. All the non-humans species were in quadrupedal postures and humans in sitting and quadrupedal postures. The score of humans was reported for both postures.

	humans (N=7)	**chimpanzees** (N=3)	**gorillas** (N=3)	**capuchins** (N=3)	**lemurs** (N=3)
Precision grasps	100	56.66	95.66	30	_
Scissor grasps	_	42.33	4.33	_	_
Whole hand grasps	_	_	_	65.33	87
Mouth grasps	_	1	_	4.66	13

Table 4. Results of ANOVA's and Tukey's HSD post-hoc tests on of the variables of the wrist velocity and movement duration during prehension comparing the five species. All the non-humans species were in quadrupedal postures and humans in sitting (S) and quadrupedal (Q) postures.

	Mean of the wrist velocity (s^{-1})	**Amplitude of the wrist velocity peak (s^{-1})**	**Time to the wrist velocity peak (ms)**	**Time to the wrist velocity peak (%)**	**Duration of the deceleration phase (ms)**	**Duration of the deceleration phase (%)**	**Movement duration (ms)**
ANOVA's results							
	$F_{5,21.51}=31.05$ $p<0.001$	$F_{5,474.4}=55.5$ $p<0.001$	$F_{5,1202861}=37.88$ $p<0.001$	$F_{5,1468}=6.8$ $p<0.001$	$F_{5,3989124}=36.25$ $p<0.001$	$F_{5,1468}=6.8$ $p<0.001$	$F_{5,9527451}=47.3$ $p<0.001$
Results of Tukey's HSD post-hoc tests							
humans(S)-humans(Q)	0.99 NS	0.93 NS	0.001	0.94 NS	0.001	0.94 NS	0.001
humans(S)-chimpanzees	0.051 NS	0.02	0.001	0.98 NS	0.001	0.98 NS	0.001
humans(S)-gorillas	0.021	0.013	0.001	0.99 NS	0.001	0.99 NS	0.001
humans(S)-capuchins	0.001	0.001	0.001	0.007	0.001	0.001	0.001
humans(S)-lemurs	0.001	0.001	0.001	0.002	0.001	0.001	0.001
humans(Q)-chimpanzees	0.14 NS	0.13 NS	0.001	0.69 NS	0.001	0.69 NS	0.001
humans(Q)-gorillas	0.06 NS	0.09 NS	0.001	0.94 NS	0.001	0.94 NS	0.001
humans(Q)-capuchins	0.001	0.001	0.001	0.001	0.001	0.001	0.001
humans(Q)-lemurs	0.001	0.001	0.001	0.001	0.001	0.001	0.001
chimpanzees-gorillas	0.99 NS	0.99 NS	0.99 NS	0.99 NS	0.99 NS	0.99 NS	0.99 NS
chimpanzees-capuchins	0.001	0.001	0.22 NS	0.17 NS	0.07 NS	0.17 NS	0.04
chimpanzees-lemurs	0.001	0.001	0.78 NS	0.10 NS	0.17 NS	0.1 NS	0.21 NS
gorillas-capuchins	0.001	0.001	0.08 NS	0.057 NS	0.03	0.057	0.011
gorillas-lemurs	0.001	0.001	0.49 NS	0.03	0.07 NS	0.03	0.07 NS
capuchins-lemurs	0.79 NS	0.41 NS	0.93 NS	0.99 NS	0.99 NS	0.99 NS	0.98 NS

NS: not significant

Table 5. Means and Standard Deviations of the velocity of the wrist and the movement duration in the five species during the prehension. All the non-humans species were in quadrupedal postures and humans in sitting (S) and quadrupedal (Q) postures. Absolute values (mm.-1s and ms), dimensionless values (s^{-1}) and percentages (%) are reported.

	humans (S) (N=7)	**humans (Q)** (N=7)	**chimpanzees** (N=3)	**gorillas** (N=3)	**capuchins** (N=3)	**lemurs** (N=3)
Mean of the wrist velocity (mm.-1s)	486±143	537±112	866±329	1202±465	705±234	652±287
Dimensionless values (s^{-1})	0.83±0.2	0.92±0.2	1.43±0.5	1.49±0.5	3.36±1.1	3.05±1.3
Amplitude of the wrist velocity peak (mm.-1s)	957±248	1125±214	1780±613	2415±916	1459±506	1293±531
Dimensionless values (s^{-1})	1.65±0.4	1.94±0.4	2.94±1	3±1.1	6.95±2.4	6.05±2.5
Time to the wrist velocity peak (ms)	439±107	343±76	239±49	252±91	173±37	201±51
Time to the wrist velocity peak (%)	40.7±6	39.2±5	42.2±9	41±9	47.8±2	48.4±7
Duration of the deceleration phase (ms)	659±227	537±133	339±107	359±111	189±42	211±35
Duration of the deceleration phase (%)	59.3±6	60.8±5	57.8±9	59±9	52.2±2	51.6±7
Movement duration (ms)	1098±304	880±182	578±117	611±165	362±78	412±67

Table 6. Coefficient of Variation of the velocity of the wrist and the movement duration in the five species during the prehension. All the non-humans species were in quadrupedal postures and humans in sitting (S) and quadrupedal (Q) postures. Absolute values (mm.-1s and ms), dimensionless values (s^{-1}) and percentages (%) are reported.

	humans (N=7)	**humans** (N=7)	**chimpanzees** **(N=3)**	**gorillas** **(N=3)**	**capuchins** **(N=3)**	**lemurs** **(N=3)**
Mean of the wrist velocity (mm.-1s)	29.4	20.9	38	38.7	33.2	44
Dimensionless values (s^{-1})	24.1	21.7	35	33.6	32.7	42.6
Amplitude of the wrist velocity peak (mm.-1s)	25.9	19	34.4	37.9	34.7	41.1
Dimensionless values (s^{-1})	24.2	20.6	34	36.7	34.5	41.3
Time to the wrist velocity peak (ms)	24.4	22.2	20.5	36.1	21.4	25.4
Time to the wrist velocity peak (%)	14.7	12.8	21.3	22	4.2	14.5
Duration of the deceleration phase (ms)	34.4	24.8	31.6	30.9	22.2	16.6
Duration of the deceleration phase (%)	10.1	8.2	15.6	15.3	3.8	13.6
Movement duration (ms)	27.7	20.7	20.2	27	21.5	16.3

Table 7. Results of ANOVA's and Tukey's HSD post-hoc tests on the ranges of motion during prehension comparing the five species. All the non-human species were in quadrupedal posture and humans in sitting (S) and quadrupedal (Q) postures.

	trunk flexion	**trunk inclination**	**trunk rotation**	**shoulder flexion**	**shoulder abduction**	**shoulder rotation**	**elbow flexion**	**elbow rotation**	**wrist extension**	**wrist deviation**
ANOVA's results										
	$F_{5,5073}$=13.9 p<0.001	$F_{5,410}$=1.2 p<0.3 NS	$F_{5,1568}$=4.7p <0.001	$F_{5,8942}$=5.4 p<0.001	$F_{5,3211}$=6.2 p<0.001	$F_{5,33769}$=13.8 <0.001	$F_{5,7197}$=10.2 p<0.001	$F_{5,60046}$=26.8 p<0.001	$F_{5,51944}$=32.1, p<0.001	$F_{5,23706}$=33.3, p<0.001
Results of Tukey's HSD post-hoc tests										
humans(S)-humans(Q)	0.001	0.80 NS	0.0016	0.47 NS	0.02	0.99 NS	0.001	0.95 NS	0.01	0.99 NS
humans(S)-chimpanzees	0.99 NS	0.69 NS	0.08 NS	0.09 NS	0.02	0.001	0.001	0.001	0.001	0.001
humans(S)-gorillas	0.99 NS	0.99 NS	0.99 NS	0.004	0.0012	0.001	0.16 NS	0.001	0.001	0.001
humans(S)-capuchins	0.96 NS	0.35 NS	0.011	0.97 NS	0.004	0.03	0.7 NS	0.001	0.001	0.001
humans(S)-lemurs	0.25 NS	0.96 NS	0.87 NS	0.63 NS	0.001	0.02	0.64 NS	0.003	0.001	0.001
humans(Q)-chimpanzees	0.001	0.99 NS	0.99 NS	0.81 NS	0.96 NS	0.001	0.99 NS	0.001	0.001	0.001
humans(Q)-gorillas	0.001	0.87 NS	0.14 NS	0.21 NS	0.56 NS	0.001	0.09 NS	0.001	0.001	0.001
humans(Q)-capuchins	0.001	0.91 NS	0.99 NS	0.99 NS	0.78 NS	0.056 NS	0.006	0.001	0.001	0.001
humans(Q)-lemurs	0.001	0.99 NS	0.37 NS	0.044	0.43 NS	0.04	0.008	0.03	0.001	0.001
chimpanzees-gorillas	0.99 NS	0.76 NS	0.48 NS	0.95 NS	0.98 NS	0.95 NS	0.44 NS	0.71 NS	0.58 NS	0.84 NS
chimpanzees-capuchins	0.99 NS	0.99 NS	0.99 NS	0.62 NS	0.99 NS	0.43 NS	0.09 NS	0.99 NS	0.99 NS	0.99 NS
chimpanzees-lemurs	0.35 NS	0.99 NS	0.76 NS	0.007	0.95 NS	0.5 NS	0.11 NS	0.06 NS	0.99 NS	0.98 NS
gorillas-capuchins	0.99 NS	0.47 NS	0.18 NS	0.15 NS	0.99 NS	0.11 NS	0.96 NS	0.37 NS	0.75 NS	0.97 NS
gorillas-lemurs	0.39 NS	0.97 NS	0.99 NS	0.001	0.99 NS	0.15 NS	0.98 NS	0.001	0.37 NS	0.47 NS
capuchins-lemurs	0.13 NS	0.91 NS	0.39 NS	0.36 NS	0.99 NS	0.99 NS	0.99 NS	0.22 NS	0.99 NS	0.91 NS

NS: not significant

Table 8. Means and Standard Deviation of angular values (in degrees) of the ranges of motion during prehension in the five species. All the non-humans species were in quadrupedal postures and humans in sitting (S) and quadrupedal (Q) postures.

	trunk flexion	**trunk inclination**	**trunk rotation**	**shoulder flexion**	**shoulder abduction**	**shoulder rotation**	**elbow flexion**	**elbow rotation**	**wrist extension**	**wrist deviation**
humans (S)	16.6±8	15.6±4.5	20.2±6.5	56.6±10.7	12.3±6.6	23.2±11.7	51±10.9	17.3±6.5	19±8	10.1±6.4
humans (Q)	3.7±2.1	18.1±5.2	12.5±6.7	48.8±12.8	19.8±10.5	22.1±11.8	32.6±9.6	21.7±10	33.7±5.3	9.1±3.8
chimpanzees	16.1±7.8	19.3±7.5	13.4±5.2	41.8±23.8	22.4±9.8	58.2±35.3	34.3±16.8	63.1±29.5	61.9±27.6	35.3±17.9
gorillas	16.3±10.6	15.3±8.8	18.7±5.2	36.1±17.4	25±11.2	64.7±37	42.2±12	74.1±34.2	72.5±25.4	40.5±20.6
capuchins	14.5±13.5	20.6±14.5	11.7±11.7	52.2±25.3	23.9±15.1	42.6±19.6	45.8±14.8	58.9±35.2	63.6±29.2	37±17.2
lemurs	22.3±11	17.6±11.7	17.4±10.8	65.3±26.9	25.6±8.4	43.7±25.6	45.4±9.2	41.6±18.2	59.7±19.5	32.7±9

Table 9. Coefficient of Variation of angular values of the ranges of motion during prehension in the five species. All the non-humans species were in quadrupedal postures and humans in sitting (S) and quadrupedal (Q) postures.

	trunk flexion	**trunk inclination**	**trunk rotation**	**shoulder flexion**	**shoulder abduction**	**shoulder rotation**	**elbow flexion**	**elbow rotation**	**wrist extension**	**wrist deviation**
humans (S)	48.2	28.8	32.2	18.9	53.7	50.4	21.4	37.6	42.1	63.4
humans (Q)	56.8	28.7	53.6	26.2	53	53.4	29.4	46.1	15.7	41.8
chimpanzees	48.4	38.9	38.8	56.9	43.7	60.7	49	46.8	44.6	50.7
gorillas	65	57.5	27.8	48.2	44.8	57.2	28.4	46.2	35	50.9
capuchins	93.1	70.4	99.1	48.5	63.2	46	32.3	59.8	45.9	46.5
lemurs	49.3	66.5	62	41.2	32.8	58.6	20.3	43.7	32.7	27.5

SYNTHÈSE CHAPITRE 5

Titre: Convergences et spécificités de la préhension chez cinq primates: *Lemur catta*, *Sapajus xanthosternos*, *Gorilla gorilla*, *Pan troglodytes*, *Homo sapiens sapiens.*

Question: Quelle est la variabilité cinématique de la préhension chez les primates et existe-t-il des convergences interspécifiques ou au contraire des spécificités?

Modèles: Humain, Gorille (*Gorilla gorilla*), Chimpanzé (*Pan troglodytes*), Capucin (*Sapajus xanthosternos*), Lémur (*Lemur catta*).

Résultat: Des invariants interspécifiques n'impliquent pas les mêmes espèces selon le paramètre étudié (vitesse du poignet *versus* amplitudes articulaires). Deux stratégies articulaires divisent les espèces favorisant les rotations (gorilles et chimpanzés) de celles privilégiant les flexion-extension (lémurs, capucins, humains).

Discussion: Il est difficile de proposer un scénario évolutif fonctionnel de la préhension compte tenu de l'échantillonnage et de la variabilité des paramètres (*e.g.* intra-individuelle, morphologique, locomotrice). En revanche, la variabilité de l'implication des articulations et des postures manuelles pendant la locomotion a peut-être favorisé l'élaboration des capacités de préhension, indépendamment du degré d'arboricolie et de terrestrialité.

Perspective: Reproduire le protocole sur davantage d'espèces, tester l'effet des contraintes locomotrices sur les stratégies cinématiques de la préhension et mettre en évidence les corrélations entre les paramètres cinématiques et morphologiques.

SUMMARY CHAPTER 5

Title: Convergences and specificities of the prehension in five primates: *Lemur catta*, *Sapajus xanthosternos*, *Gorilla gorilla*, *Pan troglodytes*, *Homo sapiens sapiens.*

Question: What is the kinematic variability of the primate prehension and are there interspecific convergences or, conversely, specificities?

Models: Human, Gorilla (*Gorilla gorilla*), Chimpanzee (*Pan troglodytes*), Capucin (*Sapajus xanthosternos*), Lemur (*Lemur catta*).

Result: Interspecific invariants do not involve the same species according to the studied parameter (wrist velocity *versus* joint motion). Two joint strategies divide the species favoring the rotations (gorillas and chimpanzees) and those using more the flexion-extension (lemurs, capuchins, humans).

Discussion: It is difficult to propose a functional evolutionary scenario of the prehension considering the sampling and the variability of the parameters (*e.g.* intra-individual, morphological, locomotor). On the other hand, the variability of the joint implications and the manual postures during the locomotion could have favored the elaboration of the prehension capacities, independent of the degree of arboreality and terrestriality.

Perspective: Reproduce the protocol on more species, test the effect of the locomotor constraints on the kinematic strategies of the prehension and highlight the correlations between the kinematic and morphological parameters.

CONCLUSION DES CHAPITRES 4 & 5

Question: Quels sont les facteurs fonctionnels (posture corporelle, cinématique du membre supérieur) impliqués dans l'évolution de la préhension ?

Modèles: Humain, Gorille (*Gorilla gorilla*), Chimpanzé (*Pan troglodytes*), Capucin (*Sapajus xanthosternos*), Lémur (*Lemur catta*).

Résultat: La posture corporelle n'a pas d'effet sur les vitesses du poignet et les stratégies articulaires. Il existe des spécificités et des invariants cinématiques ainsi qu'une forte variabilité se traduisant par des regroupements d'espèces qui diffèrent selon le paramètre étudié.

Discussion & perspective : L'influence du mode locomoteur et de la morphologie doit être approfondie et l'étude poursuivie sur d'autres espèces afin de mieux comprendre le transfert de l'utilisation puissante du membre supérieur pendant la locomotion quadrupède vers son utilisation précise pendant la saisie de nourriture.

CONCLUSION OF THE CHAPTERS 4 & 5

Question: What are the functional factors (body posture, kinematics of the forelimb) involved in the evolution of the prehension?

Models: Human, Gorilla (*Gorilla gorilla*), Chimpanzee (*Pan troglodytes*), Capuchin (*Sapajus xanthosternos*), Lemur (*Lemur catta*).

Result: The body posture has no effect on the velocity of the wrist and the joint strategies. There are specificities and kinematic invariants as well as strong variability as showed by groupings of species which differ according to the studied parameter.

Discussion & perspective: The influence of the locomotor mode and the morphology must be explore and the study pursued on the other species in order to understand better the transfer of the powerful use of the forelimb during the quadruped locomotion towards its precise use during the food grasping.

Discussion Générale

DISCUSSION GÉNÉRALE

L'objectif de ce travail était d'aborder l'origine et l'évolution de la préhension chez les primates au travers deux grandes questions:

-Quels sont les facteurs écologiques (propriétés de la nourriture et du substrat) conduisant à une plus grande utilisation de la main chez les premiers primates?
-Quels sont les facteurs fonctionnels (posture corporelle, cinématique du membre supérieur) impliqués dans l'évolution de la préhension des primates?

Pour répondre à ces questions, ce travail s'est divisé en deux grandes parties:

Les trois premiers chapitres ont traité de l'origine de la fonction de préhension chez les premiers primates à travers l'espèce *Microcebus murinus*.

Les deux chapitres suivants ont abordé l'évolution de la préhension en comparant plusieurs espèces issues des grands groupes primates (*Lemur catta*, *Sapajus xanthosternos*, *Gorilla gorilla*, *Pan troglodytes* et l'humain).

Ces études ont toutes été menées dans des conditions non-contraintes (individus libres de se déplacer et d'aller saisir la nourriture) suivant deux approches. Une approche comportementale a été mise en place dans les trois premiers chapitres. Une approche à la fois comportementale et cinématique a été conduite dans les deux derniers chapitres.

Les résultats permettent d'aborder différentes discussions et de proposer de nouvelles hypothèses.

I. Quelles sont les stratégies de préhension de nourriture du modèle microcèbe dans un contexte arboricole et pour des nourritures variées ? Que nous apportent ces observations dans le cadre des discussions sur l'émergence de la préhension ?

Le microcèbe est souvent proposé comme présentant des convergences avec les premiers primates (Martin, 1972a, b; Cartmill, 1974a, b; Rasmussen, 1990; Crompton, 1995; Gebo, 2004). Cette espèce a donc été étudiée comme modèle pour évaluer les facteurs pouvant être à l'origine de l'utilisation de la main dans l'acquisition de nourriture des premiers primates. Généralement, les hypothèses sur l'origine des primates proposent un milieu de fines branches dans lequel aurait évolué les premières espèces (Cartmill, 1972, 1974a, b; Szalay & Dagosto, 1988; Rasmussen, 1990; Godinot 1991, 2007; Sussman, 1991; Crompton, 1995). Certaines lui associent le comportement de prédation (Cartmill, 1972, 1974a, b; Rasmussen, 1990; Godinot 1991, 2007). Ces facteurs ont pu aussi imposer des pressions sélectives sur l'implication de la main dans les activités de prises de nourritures dès l'apparition des premiers primates. Dans ce contexte, **quel rôle a pu jouer l'arboricolie ainsi que la prédation dans la mise en place des capacités de préhension non locomotrices du membre supérieur chez les premiers primates? En d'autres termes, comment l'exploitation d'un milieu de fines branches ainsi qu'un type de régime alimentaire, qu'il soit frugivore ou omnivore, a pu favoriser l'utilisation de la main des premiers primates dans d'autres activités que celles strictement locomotrices?**

La plupart des études analysent le microcèbe dans des conditions forçant les individus à saisir avec la main sans impliquer la bouche (*e.g.* saisie de nourriture à travers un grillage ou dans une boite) (Bishop, 1964; Dodson *et al.*, 1992; Ward & Hopkins, 1993; Ward, 1995; Leliveld *et al.*, 2008; Scheumann *et al.*, 2011). Seule une étude a quantifié des saisies de vers de farine avec la main sans contraindre les individus (Scheumann *et al.*, 2011). Par ailleurs, des observations en milieu naturel ont aussi rapporté l'utilisation spontanée de la main lors de capture de proies mais celles-ci n'ont jamais été quantifiées (Petter, 1962; Martin, 1972a). Dans ce contexte, nous connaissions peu le comportement de préhension du microcèbe pour une variabilité de type de nourritures et de substrats, et en dehors des protocoles contraints.

Des stratégies variées de préhension chez le microcèbe ont pu être mises en évidence. Elles dépendent fortement des propriétés de la nourriture et des substrats utilisés.

Dans la saisie de nourriture statique de petite taille (morceaux de pomme et banane), les microcèbes de cette étude utilisent toujours la bouche (chapitres 1 et 3). Cette stratégie de saisie est identique quel que soit le substrat utilisé (au sol et sur des substrats arboricoles horizontaux de différents diamètres). Ce comportement rejoint les observations faites au cours d'études menées sur la préférence manuelle (Ward & Hopkins, 1993; Ward, 1995; Scheumann *et al.*, 2011) et ressemble fort à celui connu et décrit par Whishaw *et al.* (1998) chez le rat (*i.e.* forte implication de la bouche). **Toutefois, la main du microcèbe intervient dans le mouvement de préhension lorsque la taille de la nourriture statique augmente.** L'utilisation d'une seule main ou des deux mains a été mise en évidence dans les premiers contacts entre le microcèbe et les morceaux de fruits de plus grandes tailles (chapitre 1). Cependant, si le microcèbe se sert de sa main pour saisir et soulever ces morceaux de fruits de grandes tailles, ses saisies sont toujours accompagnées de la bouche. Cette saisie combinée main-bouche a également été observée par Scheumann *et al.* (2011) pour des saisies de vers de farine. Par ailleurs, **lors de la manipulation des fruits et après les avoir saisis, une seule main (pour la petite taille du fruit) ou les deux mains (pour les deux plus grandes tailles) interviennent de manière systématique et portent les fruits à la bouche**. En outre, la préhension et la manipulation des fruits chez cette espèce impliquent un seul type de saisie, la saisie de puissance. Lors de cette saisie, le fruit est en contact avec tous les doigts et la paume. Enfin, les microcèbes s'approchent fortement du fruit pour le sentir et ensuite seulement approchent la main pour entrer en contact avec lui. Ce comportement d'olfaction avant la saisie est systématique chez cette espèce et pourrait expliquer comme l'on suggéré d'autres auteurs l'importance de l'utilisation de la bouche lors de saisie de nourriture (Scheumann *et al.*, 2011).

En comparant le microcèbe au lémur catta, tous deux appartenant au même grand groupe phylogénétique (strepsirhiniens), de nombreux points communs ont été relevés. Les individus lémurs étudiés (chapitre 5) saisissent systématiquement des petites tailles de nourriture statique (raisins secs et petits morceaux de pomme) avec la bouche et s'approchent toujours pour sentir le fruit avant de le saisir. En revanche, dès lors que des morceaux de pomme de plus grandes tailles sont présentés aux lémurs, les individus choisissent préférentiellement la main seule avec une saisie de puissance. La bouche n'intervient plus que dans 13% des saisies. Cette différence est notable puisqu'elle nous a permis de mener une étude cinématique sur le lémur (que nous discutons plus bas) impossible à mettre en place chez le microcèbe dans des conditions non-contraintes puisqu'aucun individu n'a spontanément saisie de nourriture statique avec la main seule, même en augmentant la taille de la nourriture. Par ailleurs, contrairement au microcèbe et au lémur qui utilisent constamment la bouche pour des petites tailles de nourriture, les autres espèces de l'étude (le capucin, le gorille, le chimpanzé et l'humain), emploient presque toujours leur main ou seulement deux doigts (pouce-index, index-majeur).

Chez les microcèbes, l'utilisation de la main seule ou des deux mains intervient uniquement dans la manipulation de la nourriture ou dans la saisie de proies, c'est-à-dire de nourritures mobiles (vers de farine et criquets). Ici encore, seule la saisie de puissance est observée. En revanche, les individus présentent une variété de stratégies de saisies lors de la capture de proies (saisie unimanuelle, bimanuelle, unimanuelle ou bimanuelle combinée avec la bouche et dans de très rares cas la bouche seule) (chapitre 3). Les saisies bimanuelles ou de la main seule sont prépondérantes pour les saisies de vers de farine et de criquets et rejoignent les observations faites en milieu naturel pour la capture de proie volantes (Petter, 1962; Martin, 1972a). De plus, la taille du diamètre du substrat sur lequel le microcèbe se déplace pour aller saisir la proie influence les types de saisie utilisés. En effet, la fréquence d'utilisation d'une ou des deux mains pour saisir les vers de farine et les criquets augmente sur le substrat de faible diamètre pendant que l'implication de la bouche diminue. Les individus stabilisent leur position en saisissant ce substrat avec les pieds. Les doigts de pied se fléchissent autour, ce qu'il est impossible de réaliser sur de plus larges substrat. Ils peuvent ainsi libérer leurs mains pour capturer la proie. D'autre part, la saisie combinée main-bouche pour capturer des proies est plus fréquente sur le substrat de grand diamètre. Cette stratégie augmente l'efficacité de l'individu qui ne peut enserrer par les pieds la totalité du diamètre du substrat. Il ne peut alors libérer pleinement ses mains pour capturer la proie. Cette combinaison main-bouche est aussi largement observée dans l'étude de Scheumann *et al.* (2011) dans laquelle les microcèbes saisissent des vers de farine sur un substrat plat. **Ces résultats montrent que la capture de proie associée à un substrat arboricole de type fines branches augmente l'utilisation des deux mains ou de la main seule dans la préhension.** Ce résultat est cohérent avec la plupart des hypothèses sur l'émergence des premiers primates qui proposent une évolution dans un milieu arboricole de fines branches associé au comportement de prédation visuelle pour expliquer le morphotype primate (*e.g.* préhension puissante du pouce du pied opposé aux autres doigts, présence d'ongles et non de griffes, longs doigts, convergence des yeux) (Cartmill, 1972, 1974a, b; Rasmussen, 1990; Lemelin, 1999; Schmitt & Lemelin, 2002; Godinot, 2007; Lemelin & Jungers, 2007). Cependant, l'une ou l'autre adaptation est privilégiée selon les auteurs. Certaines études s'attachent à démontrer l'importance de l'exploitation d'un milieu de fines branches dans l'émergence des premiers primates (Hamrick, 1998; 1999; 2001; Lemelin, 1999, 2000 ; Schmitt & Lemelin, 2002). La prédation serait une adaptation postérieure (Kirk *et al.*, 2006). En revanche, un autre auteur présente le comportement de prédation comme un facteur déterminant dans l'émergence du morphotype primate, sans pour autant éliminer le rôle de l'adaptation au milieu de fines branches (Godinot, 1991, 2007). Ces résultats sont soutenus par les interprétations de mains fossiles des premiers primates qui présentent souvent de longs doigts (Godinot & Beard, 1991; Jouffroy *et al.*, 1991; Godinot, 1992; Hamrick & Alexander, 1996; Bloch & Boyer, 2002). Or, ces longs doigts sont interprétés comme étant adaptés à la capture de proie (Godinot, 1991, 2007; Gebo *et al.*, 2012) comme au milieu de fines branches (Lemelin, 1999; Schmitt & Lemelin, 2002). Si ces hypothèses ne sont pas en accord sur l'importance du facteur déterminant l'émergence du morphotype des primates, la plupart prennent en considération à la fois l'adaptation à la prédation et aux fines branches. Nos résultats tendent à associer ces deux facteurs pour expliquer l'utilisation de la main dans des activités d'acquisition de nourriture. Toutefois, la prédation semble être plus déterminante que le substrat. Chez le microcèbe, elle fait intervenir majoritairement la main alors que la saisie de fruit se fait principalement avec la bouche quel que soit le substrat (terrestre, arboricole de petit et large diamètres). **L'hypothèse de l'implication du milieu de fines branches dans l'élaboration des capacités de préhension se confirme mais la prédation, indépendamment du milieu, a probablement joué un rôle clé dans l'utilisation de la main pour se nourrir chez les premiers primates.**

Plusieurs études menées sur d'autres primates et non-primates sont susceptibles de fournir davantage de pistes de réflexion sur les éléments discutés ci-dessus autour des origines de la préhension chez les primates. En effet, le comportement d'autres espèces souligne la complexité des facteurs impliqués dans l'élaboration des capacités de préhension manuelle. Le rat (*Rattus norvegicus*) et l'opossum (*Monodelphis domestica*), tous deux omnivores, utilisent la bouche pour acquérir des nourritures statiques et la main pour des insectes (Ivanco *et al.* 1996). Ces espèces sont pourtant considérées comme terrestres même si, comme pour la plupart des petits mammifères, leurs déplacements au sol où s'enchevêtrent racines, pierres et grandes herbes leur confèrent une certaine plasticité locomotrice et quelques habilités arboricoles (Jenkins, 1974). La prédation exerce ainsi pour ces espèces une influence sur l'utilisation de la main, indépendamment de leur adaptation locomotrice (arboricole/terrestre).

En outre, le comportement de prédation impliquant la main montre des convergences avec des grenouilles cette fois arboricoles. En effet, ces dernières vivent en grande partie dans les arbres et présentent une tendance à utiliser la ou les mains seules (*i.e.* sans la langue ou la bouche) pour saisir des proies mobiles (*e.g.* criquets) (Gray *et al.*, 1997). Toutefois, le type de substrat utilisé (orientation, diamètre) par ces espèces est encore mal connu. De plus, les captures de proies ont été observées en laboratoire sur substrat plat (Gray *et al.*, 1997).

Par ailleurs, outre la prédation et l'arboricolie, les techniques d'acquisition de nourriture en milieu naturel peuvent exercer une influence sur l'utilisation de la main pour saisir. En effet, au sein des primates callitrichinés, le marmouset (*Callithrix*) préfère la bouche quel que soit le type de nourriture (statique: banane, mobile: vers de farine et criquet) alors que le tamarin lion (*Leontopithecus*) utilise la main (Singer & Schwibbe, 1999). Les deux espèces consomment des insectes mais le marmouset se nourrit aussi beaucoup d'exsudats végétaux qui impliquent fortement l'utilisation de la bouche alors que le tamarin lion est spécialisé dans l'extraction d'insectes peu mobiles qu'il recueille sous l'écorce ou dans des trous avec ses longs doigts fins (Garber, 1992).

D'autre part, des études sur les grenouilles non arboricoles montrent aussi une relation entre la taille de la nourriture et l'utilisation de la main. Il est rapporté que chez certaines grenouilles (Anuran, *Cyclorana novaehollandiae*) consommant de grosses proies, la main est largement impliquée dans la manipulation même si la langue saisit (Valdez & Nishikawa, 1997). Ce constat est fait aussi chez les grenouilles arboricoles citées plus haut qui utilisent leur main uniquement dans la saisie de larges proies (Gray *et al.*, 1997). En revanche, les grenouilles se nourrissant de petites proies utilisent seulement la langue pour saisir et amener directement la proie dans l'œsophage sans intervention de la main (Anderson, 1996; Valdez & Nishikawa, 1997). L'influence de la taille de la nourriture a aussi été observée chez le microcèbe. Comme nous l'avons vu, ce dernier utilise systématiquement la bouche pour prendre des petits morceaux de fruits (pomme et banane) et la main pour les plus grands morceaux et leurs manipulations.

Ces observations sur l'utilisation de la main chez différentes espèces primates et non-primates montrent que la prédation implique la main malgré des adaptations différentielles au milieu. Toutefois, d'autres facteurs comme les techniques d'acquisition et la taille de la nourriture doivent être pris en compte et soulignent la pluralité des causes pouvant conduire à une utilisation forte de la main dans l'acte de préhension. **La variabilité de l'utilisation de la main a donc probablement favorisé l'élaboration des capacités de préhension.**

Ces observations mettent en évidence l'intérêt d'explorer le comportement d'espèces non-primates afin d'éclaircir les facteurs pouvant favoriser le développement de capacités préhensiles des primates.

II. Dans quel autre contexte le microcèbe utilise sa main ? Le substrat arboricole a-t-il une influence sur les postures locomotrices manuelles du microcèbe ? Ont-elles, à leur tour, une influence sur l'utilisation de la main dans la préhension de nourriture ?

Nous venons de voir que le microcèbe n'utilise pas sa main pour saisir des nourritures statiques mais pour des proies mobiles. Quel autre contexte permet d'évaluer ses capacités préhensiles ? Les hypothèses sur l'origine des primates considèrent toutes le milieu arboricole comme déterminant dans la mise en place des caractéristiques morphologiques propres aux primates, dont la main préhensile (Cartmill, 1972, 1974a, b; Szalay & Dagosto, 1980; Dagosto, 1988; Rasmussen, 1990; Sussman, 1991; Lemelin, 1999; Preuschoft, 2002; Schmitt & Lemelin, 2002; Godinot, 2007; Lemelin & Jungers, 2007). Dans ce contexte, nous avons évalué les postures locomotrices manuelles du microcèbe encore mal connues. L'étude du chapitre 2 a comme point de départ des hypothèses portant sur les caractéristiques morphologiques des mains des primates en lien avec le substrat. Les résultats permettent de discuter la variabilité des postures locomotrices du microcèbe et de l'influence du substrat arboricole sur celles-ci ainsi que des potentielles convergences avec les premiers primates. Une certaine variabilité de saisies a pu être mise en évidence. Ces saisies dépendent à la fois du diamètre et de l'orientation du substrat et reflète une forme de plasticité propre aux espèces de petites tailles (Byron *et al.*, 2011).

Quel que soit le diamètre (1 et 3 cm), les saisies principalement utilisées sur substrats horizontaux sont les saisies schizaxoniques et mésaxoniques (Cartmill, 1974b; Lemelin & Schmitt, 1998; Reghem *et al.*, 2012). Pour ces saisies, le pouce n'est pas individualisé puisqu'il est accompagné de l'index. Le pouce et l'index sont donc en opposition aux autres doigts pour saisir le substrat. Ces types de saisie sont rarement utilisés chez les primates hormis quelques exceptions chez les platyrhiniens (*Chiropotes*, *Cacajao*, *Alouatta*, *Lagothrix*) (Pocock 1920, 1925; Haines, 1958; Youlatos, 1999; Hershkovitz, 1977). La grande majorité des primates adopte toujours une saisie télaxonique (*i.e.* entre le pouce et les autres doigts), pour tous types de substrats arboricoles (Lemelin & Schmitt, 1998). Pour cette saisie, le pouce est divergent et opposé aux autres doigts. Par ailleurs, beaucoup d'espèces arboricoles non primates et de petites tailles semblent utiliser fréquemment la saisie schizaxonique tels que les tupaiidés, les soricidés, les marsupiaux (didelphidés et phalangéridés) et les caméléons (Pocock 1920, 1925; Haines, 1958; Youlatos, 2010, Sargis, 2001; Gebo *et al.*, 2004). **L'utilisation de la saisie schizaxonique chez le microcèbe, peu répandue chez les primates actuels et fréquente chez nombre d'espèces non-primates arboricoles, suggère qu'elle a pu être une saisie fréquemment adoptée par les premiers primates** (Cartmill, 1974b)**.** Si ces postures ont été utilisées chez les premiers primates la question est de savoir quels facteurs ont pu conduire à une utilisation de saisie télaxonique, employée aujourd'hui par la plus grande majorité des primates?

Notre étude nous permet de proposer une hypothèse en lien avec le type de substrat utilisé. En effet, **la saisie télaxonique s'observe chez le microcèbe uniquement sur le substrat vertical de large diamètre** et suggère ainsi que l'utilisation fréquente de ces types de substrats aurait pu avoir une influence au cours de l'évolution sur les saisies locomotrices des primates. Cartmill (1974b) et Van Horn (1972) avaient déjà proposé que le pouce très divergent des propithèques (Lémuriformes) et des gibbons (Hominoïdes) pouvait être une adaptation à la saisie de supports verticaux de larges diamètres. De plus, les lorisidés connus pour adopter une saisie télaxonique avec une forte déviation ulnaire présente aussi des adaptations cinématiques au grimper vertical (Hanna, 2006). Les déplacements sur substrats verticaux larges engendreraient donc une individualisation du pouce opposé aux autres doigts, conséquence des forces de tension exercées sur le substrat pour lutter contre la gravité (Cartmill, 1974b; Preuschoft, 2002). Cartmill (1974b) parle en effet de "first interdigital cleft" ou "séparation entre pouce-index". Cette saisie pourrait générer une plus forte puissance de maintien. **Au cours de l'évolution, l'augmentation de la taille des espèces en lien avec la fréquentation de substrats larges et verticaux a pu être un facteur favorisant l'utilisation de saisies de type télaxonique aujourd'hui largement adopté par les primates actuels.**

D'autre part, sur la base de ces résultats, on peut se demander si les saisies télaxoniques favorisant la divergence du pouce ont pu jouer un rôle dans l'émergence de capacités préhensiles impliquées dans la prise d'objet et de nourriture telles que les saisies entre le pouce et l'index. En effet, de nombreux catarhiniens utilisent la saisie dite de précision pour maintenir un objet entre le pouce et l'index (Christel 1993, 1994; Pouydebat 2004a; Pouydebat *et al.* 2008, 2009; MacFarlane & Graziano, 2009). Toutefois, les strepsirhiniens préfèrent aussi des saisies locomotrices de type télaxonique (Nieschalk & Demes, 1993; Lemelin & Schmitt, 1998; Lemelin & Jungers, 2007) mais n'utilisent pas de saisies de précision (Bishop, 1964; Reghem *et al.*, 2011). Par conséquent, d'autres facteurs associés à la locomotion auraient pu jouer un rôle dans l'émergence de capacités préhensiles propres aux catarhiniens comme l'épouillage ou l'utilisation d'outils, absent par exemple chez les strepsirhiniens.

Ici encore, un facteur ne peut être le seul déterminant d'une fonction et de caractères morphologiques, comme c'est le cas dans la mise en place du morphotype primate et de l'utilisation fréquente de la main des primates dans des activités autres que locomotrices.

Nous venons de voir l'implication du milieu arboricole et du régime alimentaire sur l'utilisation de la main chez le microcèbe, modèle écologique et comportemental des premiers primates. Ceci nous a permis de discuter et de proposer des hypothèses sur l'émergence des capacités de préhension à l'origine des primates.

Par ailleurs, qu'en est-il de l'évolution des capacités préhensiles chez les primates ?

Afin d'apporter des éléments de réponse, un second objectif aborde la question à travers deux analyses comportementales et cinématiques 3D chez plusieurs espèces primates actuelles (chapitres 4 et 5). La première grande fonction abordée par l'analyse cinématique depuis les prémices de la chronophotographie jusqu'à aujourd'hui, est celle de la locomotion humaine et non-humaine (*e.g.* Marey, 1894; Muybridge, 1887; Aerts, 2000; Isler, 2005; Vereecke *et al.* 2006). En comparaison, si l'étude cinématique de la préhension chez l'humain s'est largement développée depuis, très peu d'études ont été menées sur la préhension des primates non-humains. Le macaque est ainsi le seul genre à avoir été étudié et comparé avec l'humain (Roy *et al.*, 2000, 2002, 2006; Christel & Billard, 2002; Scott & Kalasha, 1997). Ces travaux ont montré l'existence de points communs mais aussi de différences. Les points communs permettent de rendre compte de la continuité (*i.e.* proximité) des mécanismes de la préhension entre le macaque et l'humain en posture assise. Quant aux différences, elles questionnent la mise en place des capacités et spécificités de chacun. La perte de la fonction locomotrice du membre supérieur de l'humain, à l'inverse, le rôle locomoteur de celui du macaque, la morphologie de ces deux genres, ainsi que les différentes postures corporelles adoptées, ont pu influencer leur préhension et pourrait expliquer les divergences cinématiques mises en évidence par Christel & Billard (2002). Toutefois, aucune étude n'a été menée sur la cinématique de la préhension d'autres primates que le macaque et l'humain, et aucune n'a comparé ce mouvement entre plusieurs espèces dans différentes postures corporelles. Or, les précédentes études sur la cinématique de la préhension chez l'humain et le macaque ont soulevé plusieurs questions. **Les capacités préhensiles actuelles des humains ont probablement émergé chez un ancêtre arboricole mais lui sont-elles spécifiques? Quelle a pu être l'influence du rôle locomoteur du membre supérieur et de sa morphologie sur celui de la préhension d'objet chez les primates non-humains? Comment le mode locomoteur influence la préhension de nourriture? Quels rôles ont pu jouer les postures corporelles (quadrupède *versus* assis) dans l'élaboration de certaines capacités préhensiles de la main?** Ce second objectif cherche ainsi à déterminer les invariants ainsi que les spécificités cinématiques de la préhension chez cinq espèces primates représentatives de la phylogénie du groupe afin de mieux comprendre son évolution.

Ce mouvement divisé en deux composantes comprend la phase d'approche et la phase de saisie. La première a été abordée par la cinématique de la vitesse du poignet et les amplitudes articulaires du membre supérieur, la seconde par la détermination et la quantification des types de saisie.

III. Quelles sont les stratégies cinématiques liées à la vitesse du poignet pendant la préhension de cinq espèces: lémur catta (*Lemur catta*), capucin (*Sapajus xanthosternos*), gorille (*Gorilla gorilla*), chimpanzé (*Pan troglodytes*) et humain ?

La vitesse du poignet au cours du mouvement d'approche est très étudiée chez l'humain (Jeannerod, 1981, 1984; Marteniuk *et al.*, 1990; Gentilucci *et al.*, 1991; Castiello *et al.*, 1992; Bootsma, 1994; Kudoh *et al.*, 1997; Paulignan *et al.*, 1997). Souvent associée à l'analyse cinématique de l'ouverture de la pince (pouce-index) (Jeannerod, 1986), elle permet de comprendre l'organisation motrice et le contrôle neurologique de ce mouvement, fondamental dans la vie quotidienne. Des invariants cinématiques caractérisant la vitesse du poignet ont ainsi été mis en évidence chez l'humain depuis les premiers travaux de Jeannerod dans les années 1980. Classiquement, la vitesse du poignet forme une courbe en cloche au cours du temps. La première phase décrit la phase d'accélération menant à un pic de vitesse, suivie d'une seconde phase, la phase de décélération. L'asymétrie de cette courbe de vitesse présente une décélération toujours plus longue que l'accélération.

Ces invariants ont été découverts chez un autre primate, le macaque (Georgopoulos *et al.*, 1981; fogassi *et al.*, 2001; Roy *et al.*, 2000; 2002; Christel & Billard, 2002). Notre étude révèle que la même asymétrie de la courbe de vitesse du poignet est également présente chez les cinq espèces de cette étude (chapitres 4 et 5). **Cet invariant caractérisant la vitesse du poignet semble être le prérequis moteur impliqué dans la préhension d'objet, et ce, quelle que soit l'espèce.** Il est intéressant de noter l'existence de ce point commun interspécifique majeur malgré des mouvements du membre supérieur effectués dans des contextes très variés (*e.g.* conditions non-contraintes, postures corporelles, types de saisie et tailles de nourriture variés). De plus, d'autres espèces non primates comme le chat (Alstermark *et al.*, 1993; Martin *et al.*, 1995), le rat et l'opossum (Ivanco *et al.*, 1996) présentent aussi un profil de vitesse en forme de cloche. Toutefois, le moment du pic de vitesse du poignet ainsi que la longueur de la phase de décélération reste à déterminer chez ces espèces. Si le même profil asymétrique (*i.e.* décélération plus longue que l'accélération) venait à être mis en évidence, cette caractéristique actuellement propre aux primates pourrait s'étendre à l'ensemble des espèces qui utilisent leur main pour saisir des objets statiques.

Par ailleurs, si le profil asymétrique des vitesses du poignet est invariant chez les cinq espèces de l'étude, des différences existent dans le moment d'apparition du pic de vitesse et par conséquent dans la longueur de la phase de décélération. **Les grands singes, humains et non-humains (chimpanzé et gorille), présentent un même profil de vitesse du poignet avec un pic autour de 40% de la durée totale du mouvement.** Ces données rejoignent celles précédemment observés chez l'humain et le macaque. **De plus, ce profil est présent chez l'humain et le gorille quelle que soit la posture corporelle adoptée (assise et quadrupède). En revanche, le capucin et le lémur présentent un pic de vitesse plus tardif que les grands singes, autour de 48% de la durée totale du mouvement.** Par conséquent, leur phase de décélération est plus courte. Peut-on attribuer cette différence au type de saisie utilisé par les espèces? La question se pose en effet car le capucin et le lémur ont saisi (majoritairement pour le premier et tout le temps pour le second) avec toute la main (saisie de puissance) tandis que les grands singes non-humains ont principalement saisi entre deux doigts (saisie de précision ou en ciseau). Quant à l'humain, il a présenté une très faible variabilité de types de saisie, cohérent avec les observations de Pouydebat *et al.* (2004a, 2009). Le type de saisie le plus fréquemment utilisé chez chacune des espèces a été retenu pour les analyses cinématiques. Par conséquent, uniquement les saisies de puissance ont été étudiées chez le capucin pour la petite taille de nourriture bien qu'il soit capable de saisir en précision entre le pouce et l'index. Plusieurs études ont montré que le contexte d'enregistrement pouvait influencer l'utilisation du type de saisie chez le capucin (Spinozzi *et al.*, 2004; Pouydebat *et al.*, 2009). Malgré les conditions non-contraintes de notre étude, les individus se trouvaient en concurrence pour l'accès à la nourriture et ont donc optimisé leur saisie en privilégiant des postures manuelles de puissance. On sait que chez l'humain, le type de saisie a une influence sur la cinématique du poignet. Lorsqu'il utilise la saisie de précision, le pic de vitesse de son poignet apparait plus tôt dans le temps et la phase de décélération est plus longue que lorsqu'il utilise la saisie de puissance (Gentilucci *et al.*, 1991; Castiello *et al.*, 1992). Sur la base de ces invariants observés chez l'humain, nous pouvons émettre l'hypothèse que le capucin présenterait la même réponse cinématique que l'humain s'il utilisait une saisie de précision.

Concernant le cas du lémur, tous les individus ont utilisé une saisie de puissance sans jamais présenter de saisie de précision. De plus, la taille de la nourriture présentée aux lémurs était plus grande que celle des autres espèces. En effet, les individus utilisaient uniquement la bouche pour saisir une taille de nourriture proportionnelle à celle des autres espèces (*i.e.* raisin). Nous avons donc dû augmenter la taille pour qu'ils saisissent manuellement. Chez l'humain et le macaque, nous savons que la taille de l'objet présente la même influence que les types de saisie sur la cinématique de la vitesse du poignet. Plus la taille de la nourriture est grande, plus le pic de vitesse intervient tardivement et plus la phase de décélération est courte (Fitts, 1954; Gentilucci *et al.*, 1991; Castiello *et al.*, 1992; Bootsma *et al.*, 1994; Kudoh *et al.*, 1997; Roy *et al.* 2002). La durée de la phase de décélération augmente donc pour ajuster au mieux la prise de l'objet, accommodation nécessaire pour un objet de plus petite taille ou saisi entre seulement deux doigts. En effet, un petit objet comme une saisie en précision (pouce-index) ou en ciseau (index-majeur) fournit moins de surface de contact. Par conséquent, la grande taille de la nourriture saisie par les lémurs ainsi que l'utilisation de la saisie de puissance pourraient expliquer le pic de vitesse tardif et la phase courte de décélération que nous avons quantifié.

Ce qui est connu pour une espèce (l'influence du type de posture manuelle chez l'humain et l'influence de la taille de l'objet à saisir chez l'humain et le macaque) pourrait finalement s'appliquer à l'échelle du groupe étudié et dévoiler l'**existence d'invariants**

cinématiques propres au mouvement de préhension, quelle que soit l'espèce. En effet, le capucin et le lémur utilisent une saisie manuelle de puissance et présentent une cinématique du poignet différente de celle des grands singes qui ont privilégié la saisie manuelle dite de précision. En outre, la saisie de puissance cumulée à une plus grande taille de nourriture chez le lémur pourrait expliquer son pic de vitesse plus tardif encore que celui du capucin. **L'étude cinématique du poignet montre donc des points communs entre les macaques, les grands singes humains et non-humains. Les différences observées chez le capucin et le lémur semblent être liées aux conditions de saisie (type de posture manuelle et taille de la nourriture).** Si ces résultats venaient à se confirmer par de nouvelles études testant diverses conditions de saisie, nous pourrions en déduire que i) les invariants cinématiques de la préhension liés à la vitesse du poignet existent indépendamment des espèces, ii) les invariants cinématiques sont dépendants du comportement de l'espèce puisque dépendants des conditions de saisie, iii) par conséquent, ces réponses cinématiques pourraient être anticipées car elles semblent être directement associées aux postures manuelles de saisie que l'espèce peut produire, iv) des invariants cinématiques pourraient se retrouver quel que soit l'organe qui saisit (exemple du bec chez le pigeon: Klein *et al.*, 1985).

IV. Quelles sont les stratégies articulaires durant la préhension chez ces cinq espèces: lémur catta (*Lemur catta*), capucin (*Sapajus xanthosternos*), gorille (*Gorilla gorilla*), chimpanzé (*Pan troglodytes*) et humain ?

Grâce à l'application des normes méthodologiques recommandées par l'International Society of Biomechanics (ISB) (Wu *et al.*, 2003, 2005) plusieurs degrés de liberté des mouvements du tronc et des articulations du membre supérieur ont pu être quantifiés dans cette étude (chapitres 4 et 5). Cette méthodologie ISB couramment employée en biomécanique humaine, est pour la première fois appliquée à des primates non-humains dans cette étude. Cette méthodologie permet d'avoir accès à des mouvements souvent difficiles à quantifier (*e.g.* rotations, déviations du poignet). Le positionnement des marqueurs ainsi que la construction des repères segmentaires ont été définis selon les recommandations de l'ISB. Les principaux mouvements de l'épaule (flexion-extension, rotation, adduction-abduction), du coude (flexion-extension, rotation) et du poignet (flexion-extension, adduction-abduction ou déviations) ont été comparés entre les espèces. De plus, l'orientation et les amplitudes des mouvements du tronc (flexion-extension, rotation, inclinaison) par rapport au sol a permis d'évaluer sa contribution dans la préhension. Ainsi, **deux stratégies articulaires sont mises en évidence dans les études cinématiques** (chapitres 4 et 5).

Tout d'abord, la comparaison entre le gorille et l'humain en postures quadrupède et assise montre des contributions articulaires impliquant davantage de rotation de l'épaule et du coude pour le premier et de flexion-extension de ces mêmes articulations pour le second (chapitre 4). **Les contributions des mouvements articulaires spécifiques à l'humain et celles spécifiques au gorille restent inchangées dans les deux postures corporelles (assise et quadrupède)**, et ce, malgré des distances de saisie différentes entre la posture assise et quadrupède. En effet, dans les conditions non-contraintes de cette étude, le gorille a saisi à des distances plus proches en posture assise. Les postures ont donc un effet sur la distance de saisie de cette espèce. Nous comparons un groupe de distance plus petite pour les deux espèces en postures assise, et un groupe de distance plus grand pour les deux espèces en posture quadrupède en se basant donc sur le comportement spontané et non-contraint du gorille. Toutefois, une forte variabilité inter-individuelle et intra-individuelle est relevée pour le gorille et en moindre mesure pour l'humain. Malgré cette variabilité, les contributions articulaires des espèces restent inchangées. En outre, de fortes variabilités sont aussi rapportées par Christel & Billard (2002) pour des individus macaques filmés dans les mêmes conditions non-contraintes que les nôtres, ainsi que par Jindrich *et al.* (2011) sur des macaques pourtant entraînés à saisir.

Par ailleurs, les deux stratégies articulaires mises en évidence chez l'humain et le gorille dans les deux postures corporelles se retrouvent dans la comparaison de toutes les espèces de l'étude (humains, gorilles, chimpanzés, capucins, lémurs). Toutes ont été analysées en posture quadrupède et pour des distances proportionnelles (chapitre 5). Lors de l'avancée du membre supérieur, le gorille ainsi que le chimpanzé présentent de plus fortes amplitudes dans leur mouvement de rotation de l'épaule et du coude comparées aux amplitudes de flexion-extension pour ces mêmes articulations. A l'inverse, l'humain ainsi que le capucin et le lémur utilisent davantage de mouvements de flexion-extension pour l'épaule et le coude comparés à leurs rotations. En outre, non seulement ces stratégies sont visibles au sein de chaque espèce mais elles s'appliquent aussi entre les espèces. En d'autres termes, les grands singes non-humains présentent toujours des mouvements de rotation plus importants que l'humain, le capucin et le lémur, et ces derniers utilisent toujours des mouvements de flexion-extension plus grands que ceux des grands singes non-humains. En comparaison, les mouvements de rotation de l'épaule et du coude, ainsi que les flexions du coude des macaques étudiés par

Jindrich *et al.* (2011) présentent des valeurs proches de celles du capucin et du lémur. En revanche, les flexions de l'épaule de ces macaques présentent des amplitudes inférieures à toutes les espèces de notre étude. Ces différences peuvent être en partie attribuées aux conditions de l'étude de Jindrich *et al.*, (2011) puisque leur individus sont entraînés à effectuer la tâche de préhension en posture assise. Outre les rotations et les flexions-extensions, **les amplitudes d'abduction-adduction de l'épaule des cinq espèces de l'étude sont très proches** (chapitre 5), **exceptées en posture assise pour l'humain et le gorille où elles sont plus faibles** (chapitre 4). Pour ce mouvement, il n'y a pas d'effet de l'espèce mais un effet de la posture corporelle. Cet effet est confirmé par l'étude de Jindrich *et al.* (2011) dans laquelle les macaques présentent des amplitudes d'abduction de l'épaule plus faibles que celles des espèces de notre étude en posture quadrupède mais proches de celles du gorille et de l'humain en posture assise. D'autre part, **des différences dans les positions d'appui distal (main) à l'initiation du mouvement existent entre les espèces de notre étude. Néanmoins, elles semblent peu affecter les amplitudes de flexion-extension et de déviations du poignet des primates non-humains**. Le chimpanzé et le gorille débutent leur mouvement de préhension en knuckle walking, c'est à dire en appui sur la face dorsale des phalanges de leurs doigts (Tuttle, 1969; Whitehead *et al.*, 1993). Dans cette position, la main est dans le prolongement de l'avant-bras et le poignet se place en posture neutre ou fléchi. Au contraire, l'humain, le capucin et le lémur qui ont pourtant des morphologies de main variées (Jouffroy *et al.*, 1991) se positionnent en palmigradie avec la paume et les doigts en contact avec le substrat (Whitehead *et al.*, 1993; Patel, 2010). Cette position place le poignet en forte extension dès le début du mouvement. Malgré ces différences, tous les primates non-humains étudiés ici présentent de fortes amplitudes de flexion-extension du poignet, même si des nuances sont quantifiées : les grands singes non-humains présentent les amplitudes les plus importantes, suivis des capucins, puis des lémurs et enfin de l'humain. Pour ce dernier, la position de départ de la main en posture assise implique une faible amplitude, et la posture quadrupède, inhabituelle pour cette espèce, applique des forces sur le poignet pour lesquelles il n'est pas adapté. Enfin, les mouvements de déviation du poignet montrent des amplitudes relativement proches pour tous les primates non-humains, à l'exception de l'humain qui présente des amplitudes beaucoup plus faibles. Le poignet n'a pas été analysé dans l'étude de Jindrich *et al.* (2011) mais Christel & Billard (2002) rapportent des mouvements du poignet plus importants chez le macaque comparé à l'humain. Ainsi, de manière générale, **l'humain présente souvent les plus faibles amplitudes articulaires pour l'épaule, le coude et le**

poignet en posture quadrupède mais conserve d'importantes amplitudes de flexion en posture assise comparé aux primates non-humains.

Ces stratégies articulaires peuvent s'expliquer par le mode locomoteur des espèces et par leur morphologie, particulièrement de l'épaule et du coude. En effet, les grands singes non-humains de cette étude (chimpanzés et gorilles) à la morphologie arboricole (scapula orientée dorsalement, mobilité importante des articulations: Lewis, 1969; Tuttle, 1969; Corruccini, 1975; Swartz, 1989; Chan, 2007; Schmidt & Krause, 2010) sont adaptés à la brachiation, à la suspension et au knuckle-walking (Tuttle & Watts, 1985; Doran, 1993; Hunt, 2004). Ces caractéristiques semblent expliquer leurs importants mouvements medio-latéraux (rotations) comparés aux plus petites espèces étudiées, capucin et lémur catta. Ces dernières montrent également des caractéristiques arboricoles mais sont qualifiées de quadrupèdes arboricoles généralistes. La locomotion du capucin est décrite comme très versatiles (Wright, 2007), alors que le lémur catta est défini comme le plus terrestre des lémuriformes (Ward & Sussman, 1979; Jolly, 2006). Le capucin et le lémur possèdent une orientation plus latérale de la scapula limitant leurs amplitudes médio-latérales (O'Connor & Rarey, 1979; Chan, 2007a; Schmidt & Krause, 2010). La position de la scapula chez le capucin et le lémur en lien avec leurs stratégies articulaires (moins de rotations et davantage de flexions de l'épaule et du coude) sont concordants avec les données sur le macaque. Christel & Billard (2002) quantifient des mouvements importants dans le plan sagittal (flexion-extension) pour tout le membre supérieur du macaque et Scott & Kalasha (1997) mesurent, quant à eux, une faible abduction de l'épaule. Le macaque est en effet un quadrupède semi-terrestre doté d'une scapula en position latérale. Ses articulations du membre supérieur sont également connues pour être beaucoup moins mobiles que celles des grands singes (Corruccini, 1975; Chan, 2007a). Quant à l'humain, il présente davantage de mouvements dans le plan sagittal. Il possède pourtant une orientation dorsale de sa scapula, héritée de ses ancêtres arboricoles et de sa proximité morphologique avec les grands singes non-humains (Corruccini, 1975; Aiello & Dean, 1990; Chan, 2007a). Sa bipédie permanente pourrait expliquer ses différences de stratégies articulaires avec les grands singes non-humains. En effet, son membre supérieur a perdu sa fonction locomotrice arboricole à la différence de tous les primates non-humains.

Concernant le tronc, l'humain ne produit que très peu de mouvement dans le plan sagittal (flexion-extension). Cette différence avec les primates non-humains est particulièrement marquée en posture quadrupède quelle que soit la distance de saisie et en posture assise lorsque les distances sont moins éloignées. Cette faible implication du tronc a précédemment été relevée chez l'humain par Christel & Billard (2002) en comparaison du macaque. Dans cette étude, l'humain est comparé assis sur une chaise à des macaques assis au sol. Les sujets ont saisi à des distances décrites comme des distances de "confort". Les macaques dans les mêmes conditions montraient une forte contribution du tronc comme pour les espèces de notre étude en posture corporelle quadrupède. Les auteurs ont proposé plusieurs explications et hypothèses. Tout d'abord, la morphologie différentielle entre le macaque et l'humain, comme abordée plus haut, est prise en considération. Selon les auteurs, la position de la scapula du macaque limitant les mouvements de l'épaule impliquerait davantage le tronc dans le mouvement de préhension afin de compenser. L'implication du membre supérieur du macaque dans la locomotion induirait une forte stabilisation de l'épaule plus restreinte mécaniquement et un équilibre différent de celui de l'humain. La première hypothèse ne semble pas suffire à expliquer la contribution importante du tronc chez le macaque puisqu'elle a été observée pour tous les primates non-humains de notre étude pourtant de morphologie plus arboricole. En revanche, la seconde hypothèse portant sur la fonction locomotrice du membre supérieur pourrait être une explication applicable aux quatre primates non-humains étudiés ici (chimpanzés, gorilles, capucins, lémurs). Il est intéressant de noter que le fort degré de terrestrialité du gorille n'influence pas ses stratégies articulaires dans le plan sagittal (flexion-extension) comme c'est le cas chez le macaque également très terrestre. De plus, l'arboricolie du capucin ne présente pas non plus d'invariants dans ses stratégies articulaires avec le chimpanzé également arboricole. Plus que le degré d'arboricolie ou de terrestrialité, le mode locomoteur de ces espèces (quadrupédie terrestre, quadrupédie arboricole, knuckle walking et brachiation) ainsi que la morphologie associée expliqueraient davantage ces différences.

Les invariants interspécifiques n'impliquent pas les mêmes espèces selon le paramètre étudié (vitesse du poignet *versus* amplitudes articulaires). En effet, deux stratégies cinématiques liées aux vitesses du poignet séparent les grands singes (dont l'humain), du capucin et du lémur. En effet, les premiers ont un pic de vitesse plus tôt dans le temps et une phase de décélération plus longue. De plus, deux stratégies articulaires divisent les espèces favorisant les rotations (gorilles et chimpanzés) de celles privilégiant les flexions-extensions (lémurs, capucins, humains).

Compte tenu de l'échantillonnage et de la variabilité de certains paramètres (*e.g.* intra-individuel, morphologique, locomoteur), il est difficile de proposer un scénario évolutif fonctionnel de la préhension sur la base des stratégies articulaires. En revanche, la variabilité de l'implication des articulations et des postures manuelles pendant la locomotion a peut-être favorisé l'élaboration de capacité de préhension, indépendamment du degré d'arboricolie et de terrestrialité. Par ailleurs, l'influence du régime alimentaire qui semble jouer un rôle important dans l'utilisation de la main des premiers primates apparait ici moindre. Les études sur les postures manuelles avaient déjà mis en évidence cet aspect. En effet, des espèces aux régimes alimentaires différents montrent des types de saisie similaires (exemple du gorille folivore-frugivore et du chimpanzé omnivore) (Christel, 1993, 1994; Pouydebat *et al.*, 2004a, 2008, 2009). Dans notre étude, aucune corrélation ne peut être proposée à la fois entre les stratégies articulaires, la cinématique des vitesses du poignet et les types de saisie utilisés.

Synthèse et Conclusion

Pour conclure, les principaux résultats de cette étude ont été synthétisés:

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- L'augmentation de la taille de la nourriture statique augmente la fréquence d'utilisation de la main chez le microcèbe et le lémur.

- Indépendamment des substrats, le microcèbe utilise la main seule pour saisir une nourriture mobile mais jamais pour saisir une nourriture statique (le lémur, oui).

- Le substrat influence l'utilisation de la main seulement dans la prise de nourriture mobile et implique une variabilité de postures locomotrices chez le microcèbe.

- A partir des observations du modèle microcèbe, **l'hypothèse de l'implication du milieu de fines branches dans l'élaboration des capacités de préhension se confirme mais la prédation, indépendamment du milieu, a probablement joué un rôle clé dans l'utilisation de la main pour se nourrir chez les premiers primates.** Toutefois, au regard d'autres observations chez des espèces non-primates, l'implication de la main seule dans la capture de proie a été mis en évidence chez des rongeurs (rat) et des marsupiaux (opossum) terrestres (Ivanco *et al.* 1996). Nous pouvons alors nous demander si l'origine arboricole et omnivore des premiers primates aurait suffi à l'élaboration de la préhension dans des activités autres que locomotrices.

Concernant l'évolution de la préhension chez les primates

- Des invariants cinématiques liés à la vitesse du poignet, mesurés à partir des mouvements de prehension sont mis en évidence pour toutes les espèces de l'étude et rejoignent les résultats habituellement obtenus chez l'humain et le macaque (*i.e.* un seul pic de vitesse et une phase de décélération plus longue que la phase d'accélération). Cette même asymétrie de courbe est commune à toutes ces espèces malgré des mouvements du membre supérieur d'une très large variété (*i.e.* espèces, conditions de saisie, conditions non-contraintes).

- Les grands singes non-humains présentent davantage de points communs cinématiques avec l'humain et le macaque que le capucin et le lémur (*i.e.* même moment d'apparition du pic de vitesse de poignet et importante utilisation de saisies de précision entre deux doigts).

- La cinématique de la vitesse du poignet des espèces de l'étude semble corrélée aux conditions de saisies (posture manuelle de saisie, taille de l'objet), résultat déjà connu pour l'humain et le macaque (*i.e.* pic de vitesse tardif et diminution de la décélération pour des saisies de puissance comparées aux saisies de précisions, et pour une grande taille de nourriture comparée à une plus petite).

- Deux stratégies d'amplitude articulaire sont mises en évidence et semblent être associées à la fois au mode locomoteur des espèces (brachiation, quadrupédie arboricole, bipédie terrestre permanente) ainsi qu'à leur morphologie de l'épaule et du coude. L'humain présente un cas à part pour deux raisons. D'une part, malgré une morphologie héritée de ses ancêtres brachiateurs, il utilise une stratégie proche des quadrupèdes arboricoles de cette étude (capucin et lémur). D'autre part, la contribution de son tronc est moindre en comparaison des primates non-humains. La perte de la fonction locomotrice de son membre supérieur pourrait expliquer ces différences majeures.

- La posture corporelle n'a pas d'influence sur la vitesse du poignet ni sur les stratégies articulaires du gorille et de l'humain.

La posture corporelle, en d'autres termes, la bipédie permanente propre à l'humain, n'a peut-être pas joué un rôle essentiel dans l'émergence et l'élaboration des stratégies cinématiques de la préhension. En outre, de plus en plus de travaux montrent que les capacités manuelles de l'humain sont partagées par d'autres primates autant dans les postures manuelles de saisie (Christel, 1993, MacFarlane & Graziano, 2009; Pouydebat *et al.*, 2005, 2009; 2011) que dans la cinématique des vitesses du poignet (Roy *et al.*, 2000; Christel & Billard, 2002; Reghem *et al.*, soumis; Reghem et al, in prep). Ces similarités présentes chez les macaques et les grands singes humains et non-humains suggèrent l'existence d'un lien fort entre ces deux adaptations: postures manuelles et cinématique des vitesses du poignet. En revanche, **les stratégies articulaires mises en évidence chez les espèces de cette étude semblent avoir évoluées indépendamment de leurs capacités préhensiles** et ne peuvent constituer à l'heure actuelle un marqueur phylogénétique exploitable. Il serait intéressant de reproduire le protocole sur davantage d'espèces afin de tester l'effet des contraintes locomotrices et posturales sur les stratégies cinématiques de la préhension et de mettre en évidence les corrélations entre les paramètres cinématiques et morphologiques.

L'implication du membre supérieur dans la locomotion arboricole et dans la prédation a pu favoriser une forte variabilité de mouvements et permettre l'élaboration des capacités de préhension dès les origines des primates et au cours de leur évolution. Toutefois, d'autres facteurs que l'arboricolie et la prédation ont pu leur être associés. L'origine et l'évolution de la préhension apparaissent comme plurifactorielles.

Perspectives

Afin de mieux comprendre à la fois les origines et l'évolution des capacités préhensiles chez les primates, il semble important de 1) reproduire sur d'autres espèces les protocoles expérimentaux appliqués au microcèbe, 2) continuer à développer les études cinématiques chez les non-humains et de tester l'existence d'invariants propres à la préhension, indépendamment des espèces, 3) s'intéresser à d'autres activités où la main est susceptible d'être utilisée et 4) définir et tester des caractères morphologiques en lien avec les capacités préhensiles. Dans ce contexte, il est impératif d'élargir l'étude de la préhension à d'autres groupes de Tétrapodes dans lesquels des espèces utilisent, sans être contraintes, leur main pour acquérir leur nourriture (*grenouilles:* Gray *et al.*, 1997; *rat et opossum:* Ivanco *et al.* 1996; *carnivores:* MacClearn, 1992; *kangourou arboricole:* Iwaniuk *et al.*, 1998; *rongeurs:* Whishaw *et al.*, 1998; *raton-laveur:* Iwaniuk & Whishaw, 1999; *tétrapodes:* Iwaniuk & Whishaw, 2000; Sustaita *et al.*, en révision). En outre, ces nombreux groupes présentent des espèces plus diversifiées que les primates sur le plan locomoteur (strictement terrestres, strictement arboricoles) et comportemental (certains saisissent beaucoup, d'autres moyennement et certains jamais). Ces observations sur les non-primates soulèvent la question de l'implication d'autres facteurs que l'arboricolie et la prédation dans l'élaboration de la préhension. L'utilisation de la main et de tout le membre supérieur dans des activités autres que locomotrices a pu favoriser l'émergence de certaines caractéristiques morphologiques (Schmidt & Krause, 2010; Aversi-ferrarei *et al.*, 2010). Aversi-ferrarei *et al.*, 2010 suggèrent en ce sens que des activités spécifiques comme l'utilisation d'outil chez des primates proches phylogénétiquement (chimpanzés, gorilles, orang-outans) et plus éloignées (capucins et capucins) ont pu jouer aussi un rôle dans l'évolution de certains muscles. Dans ce contexte, d'autres activités où la main est impliquée sont présentes chez certaines espèces comme l'épouillage par exemple. Qui le pratique et ne le pratiquent pas ? Y a-t-il une corrélation entre cette activité et certaines capacités de préhension ? Enfin, les interactions sociales, la manipulation d'objet et les techniques utilisées dans l'acquisition de nourriture (fourragement, outils) ou dans la construction de nids ou autres aménagements sont encore des axes de recherches à développer chez les primates et les non-primates afin de mieux comprendre la mise en place et la diversité des capacités de préhension.

Si les origines et l'évolution de la préhension chez les primates restent encore un vaste champ de recherche à explorer, il apparait de plus en plus clair que les études menées sur les non-humains contribuent à mieux nous connaître et à affirmer cette proximité qui existe entre nous et les autres espèces.

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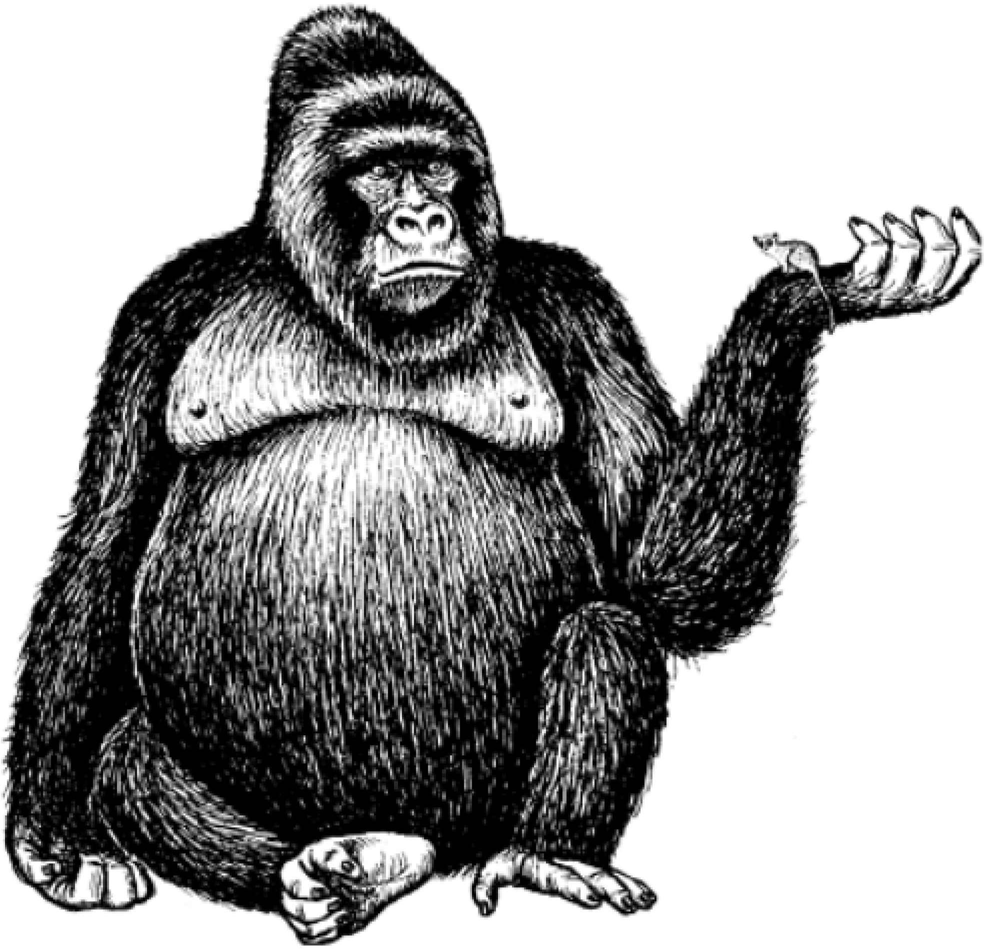
ANNEXES

APPENDIX A

Présentation des espèces de l'étude



La diversité chez les primates :
gorille (200 kg.) et microcèbe (50g.) (Source: Fleagle, 1999)

Prosimiens (Prosimii, Illiger, 1811) ou Strepsirhiniens (Geoffroy Saint-Hilaire, 1812, Pocock, 1918)

Les primates actuels se divisent en deux grands groupes: les prosimiens ou strepsirhiniens et les simiiformes ou haplorhiniens. Les prosimiens rassemblent à leur tour les lémuriformes et les lorisiformes. Les premiers sont endémiques à Madagascar tandis que les seconds vivent en Asie du sud-est et en Afrique. Ces primates au museau allongé munis d'un rhinarium (truffe) et de vibrisses (moustaches) sont quadrupèdes et possèdent une denture entre 36 et 40 dents selon les espèces avec 3 ou 4 prémolaires (*versus* 3 chez les platyrhiniens et 2 chez les catarhiniens). Ils présentent une morphologie des incisives et canines inférieures, longues et orientées horizontalement qui forment le "peigne dentaire". Il sert à arracher les exudats végétaux dont ces animaux se nourrissent ou lors du toilettage, à nettoyer le pelage dont l'action participe au contact et à l'échange social. Leur crâne montre un frontal et une symphyse mandibulaire non fusionnés, ainsi qu'une ouverture post-orbitaire. Ils possèdent une griffe sur le deuxième doigt de pied mais des ongles à tous les doigts. La présence d'ongles fait partie des principales caractéristiques définissant les primates. La morphologie de l'articulation trapézo-métacarpienne du pouce limite les mouvements de rotation du pouce et est considérée comme pseudo-opposable (Jouffoy & Lessertisseur, 1959). A la différence des Platyrhiniens, qui possèdent aussi un pouce pseudo-opposable, le pouce des prosimiens ne se place pas dans le prolongement des autres doigts, il est détaché, particulièrement chez les lorisiformes. De nombreuses espèces de prosimiens sont nocturnes et toutes sont majoritairement restées arboricoles. Leur sens olfactif plus développé que les autres primates joue un rôle important dans la communication (*e.g.* Palagi *et al.*, 2004; Braune *et al.*, 2005; Colquhoun, 2011).

Malgré ces points communs, ce grand groupe présente une grande diversité tant morphologique, comportementale, écologique, alimentaire, que physiologique (*e.g.* taille des espèces, régimes alimentaires, modes locomoteurs, organisations sociales, activités variées). Ils se divisent en deux super-familles, les lémuroïdés (Lemuroidea) endémiques à Madagascar et les lorisoïdés (Lorisoidea) présents sur le continent africain et asiatique. Leur répartition est moins étendue et moins importante que celle des haplorhiniens (platyrhiniens et catarhiniens). Enfin, l'infra-ordre des lémuriformes comprend 12 genres organisés en 4 ou 5 familles selon les auteurs (Groves 2001; Lecointre & Le Guyader, 2006; Mittermeier *et al.*, 2006).

Les espèces choisies pour cette étude et représentatives du groupe lémuriforme sont le microcèbe (*Microcebus murinus*) et le lémur catta (*Lemur catta*).

Microcebus murinus (Miller, 1777)

Spécificités générales

Source: E. Reghem

Le microcèbe est un des plus petits primates au monde. Il est nocturne et hiberne pendant la saison sèche, lorsque les heures du jour diminuent et lorsque les ressources alimentaires sont moins présentes (Martin, 1973; Schmid & Ganzhorn, 2009). A l'inverse, il est particulièrement actif lorsque les jours rallongent (saison humide de reproduction, stockage calorique, etc.). Il connait aussi des torpeurs journalières (Schmid, 2000). **Il est considéré comme étant à la base de la lignée des primates et est souvent proposé comme une des espèces actuelles pouvant représenter un bon modèle pour inférer les premiers primates** (Martin 1972a, b; Cartmill, 1974b; Rasmussen, 1990; Crompton, 1995; Gebo, 2004). En effet, il partage des similitudes avec les premiers primates comme sa petite taille corporelle (moins de 100g.), sa morphologie moins spécialisée que certaines autres espèces primates, son mode locomoteur arboricole assez généraliste (marcheur et coureur sur branche et capable de sauts), sa niche écologique (inféodé aux milieu de "fines branches" quel que soit l'altitude et fréquente des substrats plutôt orientés horizontalement ou obliquement de petits diamètres), son régime alimentaire omnivores et son comportement de prédateur (invertébrés et petits vertébrés, fleurs, feuilles, éxudats) et enfin son hypothermie (qui le fait ressembler à de nombreux autres petits mammifères qui auraient pu être à la base de l'émergence des primates).

Toutefois, il n'est pas la seule espèce à présenter ces caractères ou des caractères proches de ceux des premiers primates et à pouvoir être envisagé comme un potentiel modèle. En effet, les petits marsupiaux arboricoles avec le genre *Caluromys* (Rasmussen, 1990; Schmitt & Lemelin, 2002), les tupaïdés arboricoles avec le genre *Ptilocercus* (Sargis *et al.*, 2001), ainsi que de nombreux petites musaraignes arboricoles notamment avec le genre *Sylvisorex* (Gebo, 2004) peuvent contribuer à une meilleure compréhension des adaptations comportementales, morphologiques et locomotrices des premiers primates.

En effet, le microcèbe ne peut servir de modèle unique puisqu'il possède des spécificités propres liées à son évolution (*e.g.* main ectaxonique avec 4$^{\text{ème}}$ doigt de la main plus long, phénomène de nanisme, etc.) (Genin & Masters, 2011) comme toutes autres espèces actuelles. Rappelons que le microcèbe n'est pas moins évolué que d'autres primates, particulièrement les haplorhiniens. Toutes les espèces actuelles primates ou non-primates sont marquées par des caractéristiques propres à leur histoire phylogénétique et évolutive et aucune ne peut être considérée comme plus évoluée qu'une autre, toutes ont leurs spécificités, d'ailleurs parfois encore difficile à définir comme pour le genre humain (Lestel, 2001).

En revanche, l'étude du microcèbe peut malgré tout contribuer à répondre à certaines grandes questions évolutives ainsi qu'à tester des hypothèses portant sur l'origine des primates. La recherche sur le vivant prend tout son intérêt dans l'étude des convergences possibles et de la pertinence des points communs qui peuvent exister entre les multiples modèles actuels et les fossiles. Enfin, comme le précise Genin & Masters (2011) "c*ertains auteurs font explicitement référence au microcèbe vu non pas comme primate archaïque mais comme un analogue fonctionnel, résultat d'une convergence écologique (Gebo, 2004)*", ce qui est à mon sens plus juste et permet d'envisager cette espèce comme un bon modèle sans pour autant la considérer comme étant la copie conforme d'espèces disparues il y a des millions d'années.

Phylogénie

Le microcèbe (appelé aussi "*the mouse lemur*" en anglais) est un primate arboricole et nocturne endémique à Madagascar appartenant au sous-ordre des prosimiens ou strepsirhiniens, à l'infra-ordre des lémuriformes, à la super-famille Cheirogaleoidea à la famille des Cheirogaleidae, la sous-famille des cheirogaleinae et au genre *Microcebus* (Groves, 2001; Mittermeier *et al.* 2006). En 1994, seulement deux espèces avait été observé, aujourd'hui 16 ont été décrites à Madagascar. Le microcèbe murin a été l'une des premières espèces à être identifiée dans les années 60' par Jean-Jacques Petter, biologiste français et spécialiste des prosimiens de Madagascar. Aujourd'hui, il existe encore à Brunoy la colonie de microcèbe qu'il a fondé il y près de 40 ans.

Description morphologique

Microcebus murinus possède une longue queue de la longueur de leur corps (Rasoloarison, 2000). Le corps porte une fourrure de couleur variant du brun-marron sur le dos au beige sur les flancs et le ventre. Le dessous de leur corps, ainsi que leurs mains et leurs pieds sont blancs. Des patches plus clairs sont visibles près du nez et entre les yeux. Leurs oreilles sont grandes et charnues.

Il n'existe pas de dimorphisme sexuel (Zimmermann *et al.*, 1998). Les mâles et les femelles ont presque la même taille. Ils mesurent en moyenne entre 12-14 cm (de la tête à la croupe) avec une queue de 13-14.5 cm pour une longueur totale de 25-28 cm. Ils pèsent en moyenne entre 58-67g en milieu naturel et peuvent atteindre 100g. en captivité (Rasoloarison, 2000). Le microcèbe peut prendre beaucoup de poids avant d'entrer en léthargie pendant la période d'hiver. Cet engraissement peut être observé au niveau du corps et de la queue. Par ailleurs, ils ont les membres antérieurs plus courts que les postérieurs mais quasiment de la même taille (indice intermembral[1]: 72, Fleagle, 1999).

Espérance de vie

Il peut vivre jusqu'à 12 ans en captivité (Bons *et al.*, 2006), voire même jusqu'à 15 ans (Napier & Napier, 1967) et sa maturité sexuelle est autour de 1 à 2 ans.

Biogéographie

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[1] L'indice intermembral est un ratio basé sur la longueur des membres antérieurs et postérieurs et est souvent corrélé au type locomoteur de l'espèce. En général les sauteurs ont un indice faible (longs membres postérieurs), les brachiateurs ont un indice élevé (longs membres antérieurs), les espèces quadrupèdes terrestres ou arboricoles (non spécialisées sauteurs ou brachiateurs) ont un indice intermédiaire (longueurs des membres antérieurs et postérieurs proches) (Fleagle, 1999).

On trouve cette espèce sur la côte ouest de Madagascar (voir carte IUCN). Il habite en forêt tropical sèche, forêt d'épineux, en forêts galeries, en forêts secondaires et habitats dégradés. Le microcèbe murin est l'espèce mammifère la plus abondante à Madagascar qui s'adapte le mieux aux changements anthropiques et climatiques (Genin & Masters, 2011). Il peut occuper toutes les strates de la forêt entre 0 et 30 mètres dès lors qu'il y trouve ses substrats préférentiels de "fines branches" (Martin, 1972a).

Groupe social

Son système social est quasiment solitaire. La nuit, il fourrage souvent seul et peut dormir avec quelques individus ou seul le jour dans des nids pouvant contenir jusqu'à une dizaine d'individus dont la composition varie selon le genre et les saisons. Les femelles tendent à se répartir en groupe sur un territoire donné tandis que les mâles ont tendance à émigrer du groupe d'origine (Radespiel, 2000).

Régime et techniques de recherche alimentaire

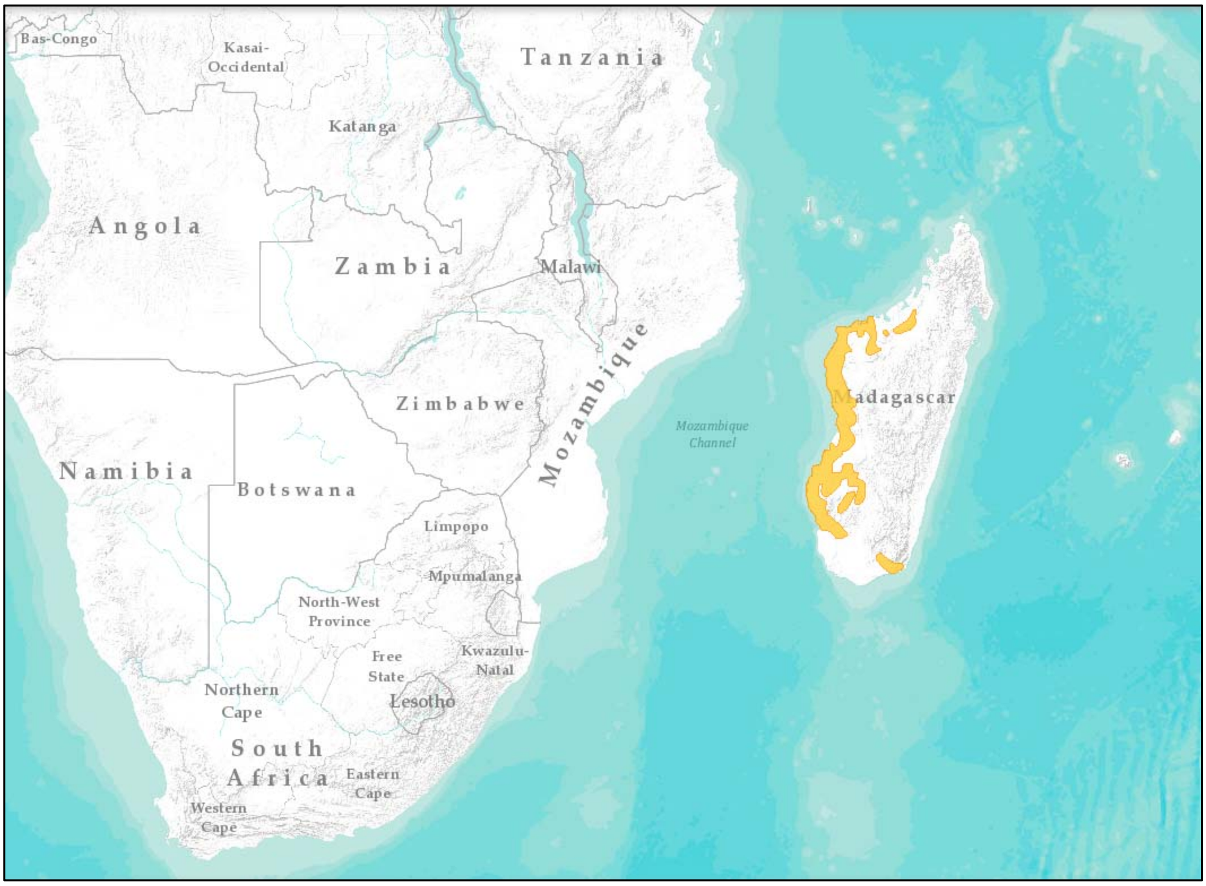
Il est omnivore (Petter, 1962; Corbin & Schmitt, 1995; Reimann *et al.*, 2003) et consomment aussi bien des insectes que des petits vertébrés (amphibiens et reptiles), des fruits, fleurs, gomme, nectars, exudats. Il est solitaire dans sa recherche de nourriture (Martin, 1972a). En milieu naturel, Martin (1972a) et Siemers *et al.* (2007) rapportent que l'information auditive suffirait au microcèbe à la détection d'arthropodes. Siemers *et al.* (2007) ont aussi observé une détection visuelle des insectes et une détection olfactive des fruits cachés. Si l'information auditive semble être prédominante dans la capture de proie, Piep *et al.* (2008) confirme avec une étude en milieu captif que le microcèbe présente une prédisposition visuelle dans sa prédation même si celle-ci dépend évidemment de l'environnement. Ils concluent sur le rôle de la vision dans la prédation comme une modalité clé chez un primate nocturne. Il capture ses proies en utilisant fréquemment les deux mains (Martin, 1972a).

Locomotion

Le microcèbe est arboricole, il vit dans un habitat dense composée de fines branches ("*fine branch niche*") (Petter, 1962; Martin 1972a). De par sa petite taille, il est adapté aux branches de faibles diamètres. Il est classiquement définit comme un marcheur quadrupède et coureur sur branches ("*quadrupedal branch walker and runner*") (Petter, 1962; Martin, 1972a, b; Walker, 1979; Fleagle, 1999). Il est assez généralisé en termes de mouvements (Gebo, 1987, 2004). Parfois il peut descendre au sol pour attraper différents insectes en se déplaçant par petits bonds plutôt qu'en marchant (Martin, 1972a). Ses mains sont à plat sur le sol (palmigradie) quand il se déplace en quadrupédie.

Statut IUCN

"Least Concern" (Préoccupation mineure) (www.iucnredlist.org)



Répartition géographique du *Microcebus murinus* (Carte IUCN)

Lemur catta (Linnaeus, 1758)

Source: M. Perrenoud

Spécificités générales

Le lémur catta est une espèce de prosimiens les plus connues et la plus étudiée, depuis les années 60 et les études d'Alison Jolly (Jolly 1966, 2006). Avec sa queue rayée noir et blanc, le lémur catta ou maki catta est un symbole de la faune de Madagascar.

Phylogénie

Le lémur catta ("*ring-tailed lemur*" en anglais) est un primate arboricole et diurne endémique à Madagascar appartenant au sous-ordre des prosimiens, à l'infra-ordre des lémuriformes, la super famille Lemuroidea, à la famille des Lemuridae, la sous-famille des lemurinae et au genre *Lemur* (Groves, 2001; Mittermeier *et al.* 2006). Une seule espèce a été répertoriée jusqu'à présent.

Description morphologique

Il possède une longue queue rayée blanc et noir. Le corps porte une fourrure de couleur variant entre le gris rougeâtre clair et le brun rougeâtre foncé. Le dessous de leur corps, ainsi que leurs mains et leurs pieds sont blancs. Il a le visage blanc, les yeux brun clairs, chacun entouré d'une zone triangulaire brun foncé ou noire, qui ressemblent à un masque, et le museau noir. Ses oreilles sont blanches et angulaires, semblables à celles des chats. Il existe très peu de dimorphisme sexuel, la femelle étant dominante au sein du groupe peut être plus imposante, mais aucun autre caractère ne les distingue vraiment.

Le mâle et la femelle ont presque la même taille. Ils mesurent en moyenne entre 39-46 cm (de la tête à la croupe) avec une queue de 56-63 cm pour une longueur totale de 95-110 cm. Ils pèsent en moyenne entre 2.3-3.5 kg dans leur habitat naturel (Mittermeier *et al.*, 2006). En captivité, le lémur catta pèse un peu plus: les mâles environ 2.7 kg et les femelles environ 2.6 kg (Kappeler, 1990). Il a les membres antérieurs plus courts que les postérieurs ce qui abaisse son corps vers l'avant en position quadrupède (indice intermembral: 70, Fleagle, 1999).

Espérance de vie

Il peut vivre jusqu'à 30 ans en captivité et sa maturité sexuelle est autour de 3 ans.

Biogéographie

On trouve cette espèce dans le sud-ouest et le sud de Madagascar. Il habite dans des environnements très variés: en forêt galerie humide, forêt tropical sèche, dans des buissons épineux en savane anthropique et dans des canyons rocailleux (voir carte IUCN). La niche écologique qu'il occupe est comparée à celle du babouin et du macaque, particulièrement au vervet qui reste dépendant de la forêt pour la nourriture et pour dormir (Wilson *et al.*, 2010). En effet, le lémur catta passe son temps dans toutes les strates de la forêt mais se nourrit peu au sol. Il est adapté aux conditions climatiques les plus extrêmes de l'île, du plus chaud et sec au plus froid (Massif Andringitra).

Groupe social

Le nombre d'individus au sein d'un groupe varie de 6 à 24, certains groupes pouvant aller jusqu'à 30. La femelle est dominante et reste au sein du groupe natal. Les mâles émigrent à l'âge de la mâturité. Les comportements d'agression entre femelles sont fréquents allant jusqu'à exclure certains individus mais impliquent très rarement de dommages physiques (Jolly 1966; Kappeler 1990; Pereira 2006). Les femelles ont la priorité d'accès aux ressources.

Régime et techniques de recherche alimentaire

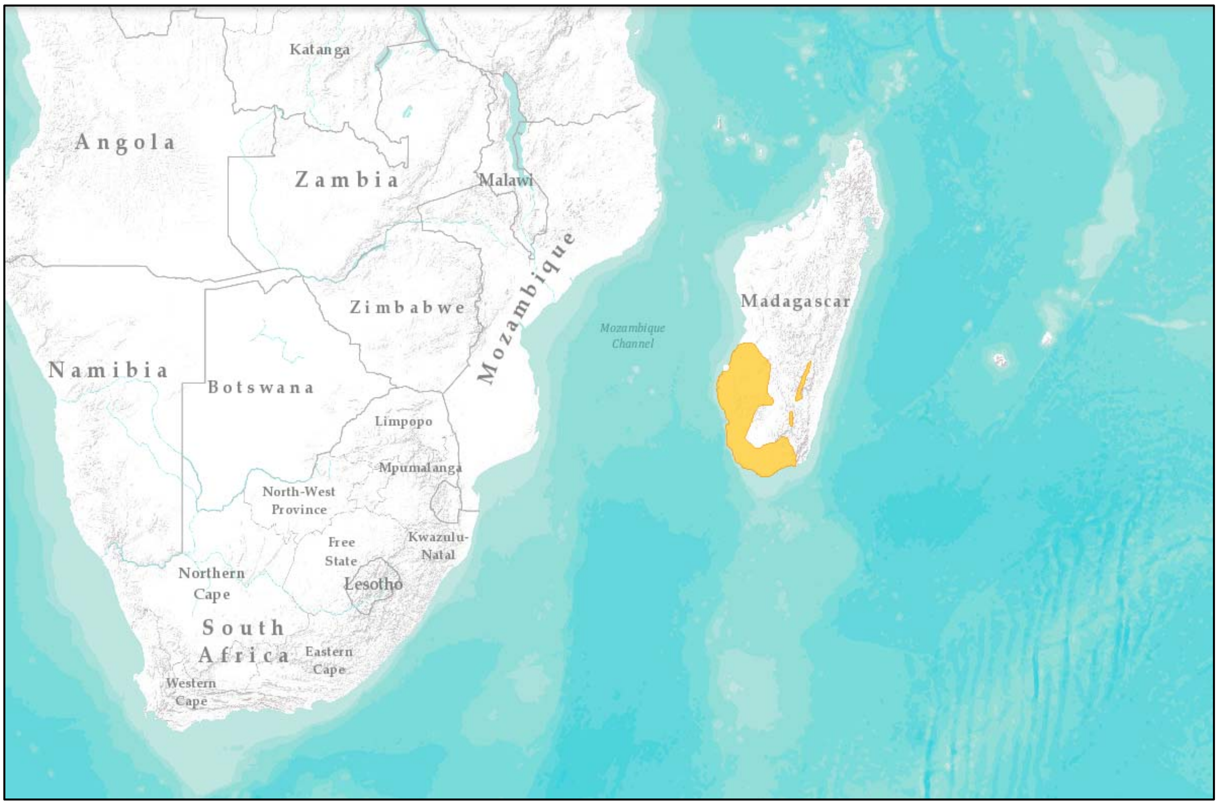
Le catta a un régime diversifié et plutôt omnivore opportuniste, il se nourrit de fruit, feuilles, fleurs, herbes, écorces, exudats. Des consommations de vieux morceaux de bois, de terre, d'insectes (araignées, sauterelles, termites), de petits vertébrés (oiseaux, caméléons) et de plantes agricoles ont été aussi observées en milieu naturel (Jolly, 2006). Nos observations en parcs zoologiques ont plutôt révélé une indifférence pour les insectes (grillons, crickets).

Locomotion

Le lémur catta est le plus terrestre de tous les lémuriens mais conserve des habilités arboricoles. Il est défini comme quadrupède terrestre et arboricole, il se déplace en marchant ou en courant et est capable de sauts de plusieurs mètres (Ward & Sussman, 1979; Fleagle, 1999; Jolly 2006; Mittermeier *et al.*, 2006).

Statut IUCN

"Near Threatened" (Quasi menacé) (www.iucnredlist.org)



Répartition géographique du *Lemur catta* (Carte IUCN)

Simiens, Anthropoïdes (Mivart, 1864) ou Haplorhiniens (Pocock, 1918)

Les haplorhiniens sont donc le deuxième grand groupe (ordre) des primates avec les strepsirhiniens précédemment définis. Les espèces haplorhiniennes ont perdu le rhinarium. Les principaux caractères anatomiques de ces primates sont la présence d'une cloison individualisant l'orbite de la fosse temporale (fermeture post-orbitaire) ainsi qu'un frontal et une symphyse mandibulaire fusionnés. Leur cortex cérébral présente un plissement accentué. Ils se subdivisent en deux autres groupes (sous-ordres), les platyrhiniens et les catarhiniens.

Les platyrhiniens (Hilaire, 1812)

Le groupe des platyrhiniens rassemble les primates d'Amérique centrale et du Sud ou Nouveau Monde. Ils ont une aire de répartition s'étendant du Mexique jusqu'au nord de l'Argentine. Platyrhinien signifie "nez plat" car les narines de ces singes sont écartées et orientées vers l'extérieur. La plupart ont une queue préhensile. La denture est composée de 36 dents avec 3 prémolaires à chaque hémi-mâchoire (*versus* 2 pour les catarhiniens et 3 ou 4 pour les prosimiens). Comme chez les prosimiens, le pouce est pseudo-opposable à l'inverse de la "vraie" opposabilité rencontrée chez les catarhiniens. Seules quelques rares espèces sont nocturnes, sinon toutes sont diurnes. Leur origine proviendrait d'un stock ancestral africain de primates anthropoïdes, il y a environ 30 à 40 millions d'années, et ils partageraient un ancêtre commun avec les singes catarrhiniens de l'Ancien Monde. Ce grand groupe présente aussi une grande diversité tant morphologique, comportementale, écologique, alimentaire, que physiologique (*e.g.* taille des espèces, régimes alimentaires, modes locomoteurs, organisations sociales, activités variées). Certaines espèces portent des griffes non rétractiles (callitrichidés) qui se seraient modifiées à partir de leurs ongles. Ceci signifie que ces espèces auraient possédé des ongles avant le retour à ces griffes particulières et qu'ils n'ont donc pas conservé les griffes ancestrales (Hamrick, 1998). L'utilisation fréquente de larges troncs ou substrat arboricoles pour se déplacer expliquerait ce retour à la griffe. L'infra-ordre des platyrhiniens comprend entre 16 ou 18 genres organisés en 2 ou 4 familles selon les auteurs (Groves, 2001; Lecointre & Le Guyader, 2006; Chatterjee *et al.*, 2009). L'espèce choisie pour cette étude et représentative de ce groupe est le capucin à poitrine jaune (*Sapajus xanthosternos*).

Sapajus xanthosternos (Wied-Neuwied, 1826)

Spécificités générales

Source: E. Reghem

Le capucin qui regroupe les genres *Sapajus* et *Cebus* font partie des seuls primates, hors des cercopithèques et particulièrement des grands singes, à utiliser aussi fréquemment des outils en milieu naturel pour accéder aux ressources alimentaires (Westergaard & Fragaszy, 1987; Jalles-Filho *et al.*, 2008; Liu *et al.*, 2009) et à effectuer la saisie de précision entre le pouce et l'index (Costello & Fragaszy, 1988). Malgré son articulation trapézo-métacarpienne en pseudo-opposition, son pouce et son index sont individualisés et s'opposent pour saisir le plus souvent entre l'extrémité ulnaire du pouce et l'extrémité radiale de l'index. En outre, un grand nombre de postures manuelles entre pouce-index a déjà été répertorié et rejoint la variabilité connus chez les cercopithèques et les grands singes (Christel & Fragaszy, 2000; Pouydebat, 2004; Spinozzi *et al.*, 2004). Pouydebat *et al.* (2004a,b, 2006, 2009) ont mis en évidence une proximité forte concernant la fréquence des saisies de précision utilisées par les humains et capucins. Malgré leur éloignement phylogénétique, ils utilisent leurs phalanges distales de manière quasi exclusive dans la saisie de petits et de plus grands objets. En outre, le capucin manipule énormément et présente des comportements d'onction (utilisation de plantes pour se frotter énergiquement les poils) interprété comme des phénomènes sociaux, d'auto-médicamentation ou comme apaisement après un conflit (Lynch Alfaro *et al.*, 2012a). Ses capacités de manipulation sont souvent reliées à la fréquence des postures adoptées où leurs membres inférieurs ainsi que leur queue préhensile sont utilisés pour libérer la main. Les déplacements bipèdes sur de courtes de distances afin de porter de la nourriture ou un outil percuteur pour casser des noix sont aussi mis en relation avec leur facultés de manipulation.

Phylogénie

Le capucin à poitrine jaune ("*yellow breasted capuchin*" en anglais) est un primate arboricole diurne du Nouveau Monde appartenant au sous-ordre des haplorhiniens, à l'infra-ordre des simiiformes, au groupe des platyrhiniens, à la famille des Cebidae, la sous-famille des Cebinae et au genre *Sapajus* (Groves, 2001; Lynch-Alfaro *et al.*, 2012b). Plusieurs espèces (7 ou 8 selon les auteurs) et sous espèces (26 à 32 selon les auteurs) ont été répertoriés (Groves, 2001). Toutefois, deux sous genres sont reconnus aujourd'hui: *Cebus* et *Sapajus* (Lynch-Alfaro *et al.*, 2012a,b). *Cebus* regroupe les espèces les plus graciles alors que *Sapajus* rassemble des espèces plus robustes (Lynch-Alfaro *et al.*, 2012a, b). Les premières sont plutôt inféodées à la forêt Amazonienne et les seconds à la forêt Atlantique. Des cas de sympatrie existent toutefois depuis une expansion du genre *Sapajus* à la forêt Amazonienne il y a environ 400 000 ans.

Description morphologique

Sa taille est moyenne, il est robuste et possède une queue semi-préhensile. Le capucin à poitrine jaune tient son nom de son pelage. Il est de couleur beige foncé à marron sur tout le corps à l'exception des bras et de la poitrine. Le visage est aplati et dénué de poil de couleur rose à marron variant selon les individus. Un dimorphisme sexuel est visible, le mâle présentant un gabarit plus trapu que la femelle et une crête sagittale sur le crâne. Son pouce est long et dit pseudo-opposable aux autres doigts (Napier, 1961) contrairement aux grands singes. Ses membres postérieurs sont un peu plus longs que les membres antérieurs inclinant le corps légèrement vers l'avant en position quadrupède (indice inter-membral: 81, Fleagle, 1999). Cet indice est moins faible que celui du microcèbe et du lémur catta suggérant des membres postérieurs un peu moins longs en comparaison des membres antérieurs chez le capucin. Le corps peut mesurer entre 35 et 45 cm et la queue 35 à 55 cm et pèse entre 2.5 et 4 kg (IUCN; Fleagle, 1999; Fragaszy, 2004). La longueur de la queue est relativement petite comparée aux autres platyrhiniens.

Espérance de vie

Le capucin peut vivre jusqu'à l'âge de 40 ans, voire plus en captivité. La maturité sexuelle intervient autour de 3-5 ans.

Biogéographie

La zone de répartition de cette espèce de capucin (*Sapajus xanthosternos*) est restreinte à la forêt Atlantique, limitée au sud de la région de Bahia au Brésil, au nord du fleuve Paraguaçú près de la ville Salvador au nord de la région de Bahia (Coimbra-Filho *et al.,* 1992) (voir carte IUCN). Ce capucin (*Sapajus xanthosternos*) occupe les plaines tropicales et les forêts submontagneuses. Il se déplace dans la partie inférieure de la canopée et dans des zones plus sèches de forêt semi-décidues (Fragaszy *et al.,* 2004).

Groupe social

Les deux sexes peuvent être dominants. Les mâles subordonnés sont souvent en périphérie du groupe. A l'âge de leur maturité sexuelle, les mâles quittent leur groupe natal vers d'autres groupes (Fragaszy *et al.,* 2004).

Régime et techniques de recherche alimentaire

Le capucin est omnivore. Il se nourrit à la fois de graines, branches, fleurs, feuilles, d'une grande variété de fruits (dont il affectionne particulièrement la pulpe de fruits mûrs), invertébrés, petits vertébrés (grenouilles, oiseaux, rongeurs, petites espèces primates).

Locomotion

Le capucin est un quadrupède arboricole se déplaçant majoritairement sur de larges supports (6 cm de diamètre) mais utilise aussi de petites branches (3 cm ou moins) lorsqu'il fourrage en se maintenant par la queue (Fleagle & Mittermeier, 1980; Wright, 2007; Schmidt, 2011). Il descend au sol pour accéder à certaines nourritures et notamment pour utiliser des outils ("nut cracking", Liu *et al.*, 2009). Il présente une bipédie occasionnelle, comme dans le transport d'objet. Il peut sauter (1-3 m) en milieu arboricole. Ses mains sont à plat sur le sol (palmigradie) quand il se déplace en quadrupédie.

Statut IUCN

"Critically Endangered" (en danger critique d'extinction) (www.iucnredlist.org)

Répartition géographique de *sapajus xanthosternos* (carte IUCN)

Les catarrhiniens (Hilaire, 1812)

Les catarrhiniens tout comme les platyrhiniens appartiennent au sous-ordre des haplorhiniens qui rassemble les primates ne présentant pas de rhinarium mais un véritable nez individualisé où les narines rapprochées sont dirigées vers le bas et sont séparées par une fine cloison. Les principaux caractères anatomiques de ces primates sont la présence de molaires bi-lophodontes, c’est-à-dire à deux crêtes. Les catarhiniens rassemblent les primates de l'Ancien Monde (Afrique-Eurasie). La denture est constituée de 32 dents avec 2 prémolaires uniquement à chaque hémi-mâchoire (*versus* 3 ou 4 prémolaires pour les prosimiens et les platyrhiniens). L'articulation du pouce (trapézo-métacarpienne) est décrite comme proche de celle de l'humain, et permet l'opposabilité du pouce aux autres doigts. Tous sont diurnes. Ce grand groupe présente aussi une grande diversité tant morphologique, comportementale, écologique, alimentaire, que physiologique (*e.g.* taille des espèces, régimes alimentaires, modes locomoteurs, organisations sociales, activités variées). Par exemple, la sous famille des cercopithécinés présente un corps massif de singes terrestres (babouins, macaques) alors que les colobinés sont arboricoles et plus petits (souvent chassés par les chimpanzés!). Les grands singes comme leur nom l’indique sont les plus grandes espèces primates. Leurs membres supérieurs sont plus longs que leurs membres inférieurs (excepté l’humain), leur scapula est orientée dorsalement et allongée antéro-postérieurement alors qu’elle est orientée et étirée latéralement chez un cercopithécinés comme le macaque. Enfin, les grands singes n’ont plus de queue et les vertèbres caudales s’atrophient pour se souder en un coccyx. L'infra-ordre des catarrhiniens comprend entre 25 et 27 genres (selon les auteurs) organisés en 2 super-familles (cercopithecoidea et hominoidea) et 4 à 6 sous-familles (selon les auteurs) (Groves, 2001; Chatterjee *et al.*, 2009; Arnold *et al.*, 2010). Les espèces choisies pour cette étude et représentatives du groupe des catarhiniens sont les hominidés ou grands singes chimpanzé (*Pan troglodytes*), gorille (*Gorilla gorilla*) et humain (*Homo sapiens*).

Pan troglodytes (Blumenbach, 1799)

Source: E. Pouydebat

Spécificités générales

Le chimpanzé est un des grands singes les plus étudiés et le plus proche génétiquement de l'espèce humaine avec les bonobos (Ruvolo, 1997; Wood & Richmond, 2000). Il utilise très fréquemment des outils en milieu naturel (Boesch & boesch, 1990). Il est décrit pour la première fois par la célèbre Jane Goodall dans les années 60'. Son comportement culturel est riche et largement documenté (McGrew, 2004). Ses capacités d'individualisation des doigts et par conséquent de préhension et de manipulation sont très proches de l'humain (Jones-Engel & Bard, 1996; Butterworth & Itakura, 1998; Pouydebat, 2004a, b; Pouydebat *et al.*, 2006, 2008, 2009; Crast *et al.*, 2009). Il consomme des plantes en milieu naturel susceptibles de contribuer au maintien ou au rétablissement de sa santé. Ce comportement d'automédication n'est pas propre aux grands singes ou aux primates, beaucoup d'autres espèces le pratique. En revanche sa proximité phylogénétique est exploitée en vue d'applications à l'espèce humaine (*e.g.* Krief *et al.*, 2010). Sa population était estimée encore à 1 million dans les années 60', aujourd'hui le nombre d'individus chimpanzés se situe probablement entre 200 000 et 300 000…

Phylogénie

Le Chimpanzé ("*chimpanzee*" en anglais) est un primate grand singe diurne et africain. Il appartient au sous-ordre des haplorhiniens, à l'infra-ordre des catarrhiniens, à la super-famille des Hominoidea, à la famille Hominidae, à la sous-famille des Panines et au genre *Pan*. Ce genre est divisé en deux espèces: *Pan troglodytes*, le chimpanzé commun, et *Pan paniscus*, le bonobo. Ce dernier est plus gracile que le chimpanzé, il présente un crâne plus petit, de morphologie plus ronde avec une face plus aplatie et utilise plus rarement des outils en milieu naturel. Quatre sous-espèces de Chimpanzé sont répertoriés par l'IUCN: *Pan troglodytes verus*, le chimpanzé de l'ouest; *P. t. vellorosus*, le chimpanzé de l'est du Niger à l'ouest du Cameroun; *P. t. troglodytes*, le chimpanzé du centre; *P. t. schweinfurthii*, le chimpanzé de l'est. *Par ailleurs, l*e séquençage du génome d'un chimpanzé commun comparé à celui de l'humain a montré que les deux espèces partage plus de 95% de leurs gènes, faisant du chimpanzé l'espèce la plus proche de l'espèce humaine.

Description morphologique

Le chimpanzé est un primate de grande taille et sans queue. Le corps est recouvert d'un pelage épais noir foncé ou brun brillant mais la face en est dépourvue. Son crâne est allongé avec une face prognathe et possède une plus faible capacité crânienne que l'humain. Le trou occipital (*foramen magnum*) où vient s'insérer la première vertèbre, l'atlas, est positionné plus en arrière du crâne que chez l'humain. Le bassin est étroit et long en comparaison de celui de l'humain. Ses oreilles sont larges, les arcades sourcilières fortes, la face peut être de couleur noire jusqu'à rose selon les individus et il possède de longues mains aux doigts individualisés (Kuypers, 1963) leur permettant de saisir des objets et d'utiliser des outils (Boesch & Boesch, 1990; Butterworth & Itakura, 1998; Pouydebat *et al.*, 2004a,b, 2008, 2009). Son pouce est court et opposable aux autres doigts. En position quadrupède, son corps est incliné vers l'arrière en appui sur les membres inférieurs plus courts que les membres supérieurs (indice intermembral: 106, Fleagle, 1999). Le chimpanzé mâle mesure environ 90-120 cm (jusqu'à 170 cm en station érigée) pour 35-70 kg, la femelle entre 66-100 cm pour 26-50 kg (IUCN; Fleagle, 1999; Goodall, 1986).

Espérance de vie

Son espérance de vie en milieu naturel peut aller jusqu'à 45-60 ans. Les individus sont sexuellement mâture dès l'âge d'environ 7 à 10 ans.

Biogéographie

On rencontre le chimpanzé dans **21 pays africains**, de l'est à l'ouest de l'Afrique, au niveau de la zone équatoriale (voir carte IUCN). Il vit surtout dans la forêt, tropicale humide dense ou en forêt claire, les plaines et la savane arborée.

Groupe social

Il vit dans des petites communautés stables ou des plus grands groupes de 40-60 individus pouvant aller jusqu'à plus de 100 individus. La journée, de petits sous-groupes de 6-7 individus se séparent et vivent ensemble pour un temps (phénomène de fission-fusion). Les mâles restent au sein du groupe, ils ne migrent pas à leur maturité sexuelle et dominent les femelles du groupe (Goodall, 1986).

Régime et techniques de recherche alimentaire

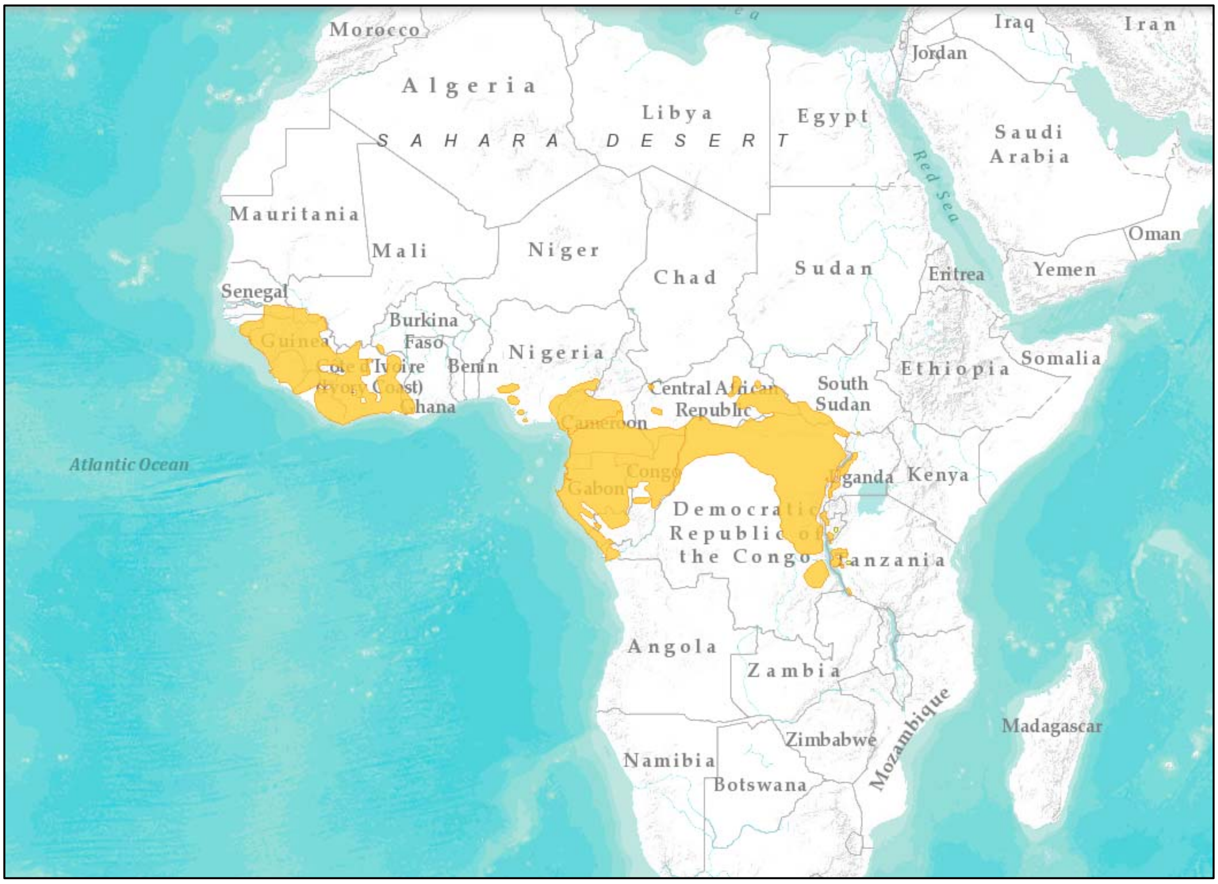
Il est omnivore (fruits, feuilles, graines, insectes-chenilles termites fourmis, miel, œufs d'oiseaux, oiseaux et petits mammifères-antilopes, petits singes ou cochon sauvage) et connu pour chasser d'autres espèces primates (colobes) en milieu naturel et développer des stratégies de chasse en groupe. Il peut consommer aussi de la terre argileuse provenant des termitières et des minéraux dans des roches. Il utilise aussi des outils afin d'accéder à la nourriture comme le percuteur que l'individu brandit pour fendre la noix sur une enclume, ou encore la branche effeuillé pour extraire des insectes des termitières (Boesch & Boesch, 1990; Tutin *et al.*, 1992).

Locomotion

Arboricole et terrestre. Le chimpanzé est quadrupède au sol en appui sur le dos des phalanges de la main, marche couramment dénommée "knuckle-walking" (Tuttle, 1969; Fleagle, 1999). Les pieds sont à plat sur le sol légèrement inclinés sur le bord externe. Dans les arbres il est capable de suspension et de sauts (Doran, 1993; Fleagle, 1999; Hunt, 2004) et adopte la posture bipède dans des cas précis par exemple pour montrer sa domination ou lors de situations d'agressions (Goodall, 1986).

Statut IUCN

"Undangered" (en danger) (www.iucnredlist.org)



Répartition géographique de *Pan troglodytes* (Carte IUCN)

Gorilla gorilla (Savage, 1847)

Source: E. Pouydebat

Spécificités générales

Le gorille est le parent le plus proche de l'humain génétiquement après le chimpanzé. Il utilise des outils (Pouydebat *et al.*, 2005) même si en milieu naturel peu d'observations ont pu être faite comparées aux chimpanzés. On relève par exemple l'utilisation de branche morte afin de sonder la profondeur de l'eau (Breuer, 2005). Le gorille est le grand singe le plus folivore. Il pratique aussi le comportement d'automédication et des comparaisons avec le chimpanzé sont effectuées à l'heure actuelle pour mieux comprendre l'apprentissage de ces pratiques afin d'enrichir nos connaissances sur l'origine de ce comportement chez l'espèce humaine et de découvrir de potentielles molécules exploitables chez notre espèce (*e.g.* Masi *et al.*, 2012) Sa population est menacée de disparition comme la plupart des primates, notamment grands singes. Certaines sous-espèces ne compteraient plus que 200 voire 300 survivants…

Phylogénie

Le gorille ("*gorilla*" en anglais) est un primate grand singe diurne et africain. Il appartient au sous-ordre des haplorhiniens, à l'infra-ordre des catarrhiniens, à la super-famille des Hominoidea, à la famille Hominidae, à la sous-famille des Panines et au genre *Gorilla*. Il existe deux espèces: le gorille de l'ouest africain (*Gorilla gorilla*) et le gorille de l'Est africain (*Gorilla beringei*). *Gorilla gorilla* présente deux sous-espèces: *Gorilla gorilla gorilla* et *Gorilla gorilla diehli*. *Gorilla beringei* présente aussi deux sous-espèces: *Gorilla beringei beringei* et *Gorilla beringei graueri* (IUCN).

Description morphologique

Le gorille est l'espèce primate actuelle la plus grande. L'espèce *Gorilla gorilla* présente un pelage gris sur le dos d'où son appellation en langage courant "gorille au dos argenté". Son crâne est très robuste et montre une crête sagittale plus importante chez le mâle que chez la femelle. Son cou est court et massif et présente à l'arrière du crâne des assises osseuses importantes (os occipital, vertèbres cervicales) permettant l'ancrage d'une musculature puissante maintenant sa tête imposante. Cette espèce partage des caractéristiques aussi présentes chez le chimpanzé: face prognathe, arcade sourcilière forte, trou occipital en arrière du crâne, bassin étroit et long en comparaison du bassin large et court de l'humain. Le gorille possède une main trapue lui permettant de saisir et d'utiliser des outils en milieu naturel comme l'humain, le chimpanzé et le capucin. Son pouce est court et opposable aux autres doigts. Ses membres postérieurs sont courts et inclinent le corps vers l'arrière en appui à l'avant sur les longs membres supérieurs en position quadrupède (indice intermembral: 116, Fleagle, 1999). Le gorille montre un dimorphisme sexuel fort. La femelle peut peser entre 70-80 kg tandis que le poids du mâle peut atteindre près de 200 kg (IUCN; Fleagle, 1999). Cette espèce est plus grande que le chimpanzé et mesure autour de 150 cm (jusqu'à 180 cm en station érigée).

Espérance de vie

Son espérance de vie se situe autour de 40 ans. Il est habituellement reconnu que sa maturité sexuelle intervient autour de 7 à 10 ans.

Biogéographie

La présence du gorille est plus limitée que celle du chimpanzé et a été relevée dans 7 pays africains. La population se répartie principalement du sud de la République Centrafricaine, le long du fleuve Congo jusqu'à la côte ouest (voir carte IUCN). Il vit dans les plaines des forêts tropicales, particulièrement dans les hautes herbes et forêts marécageuses.

Groupe social

Le gorille vit en petits groupes d'environ une dizaine d'individus jusqu'à 20. Le groupe est composé d'au moins un mâle, de plusieurs femelles adultes et de leurs petits. Une intense compétition entre mâles pour le contrôle du groupe est typique.

Régime et techniques de recherche alimentaire

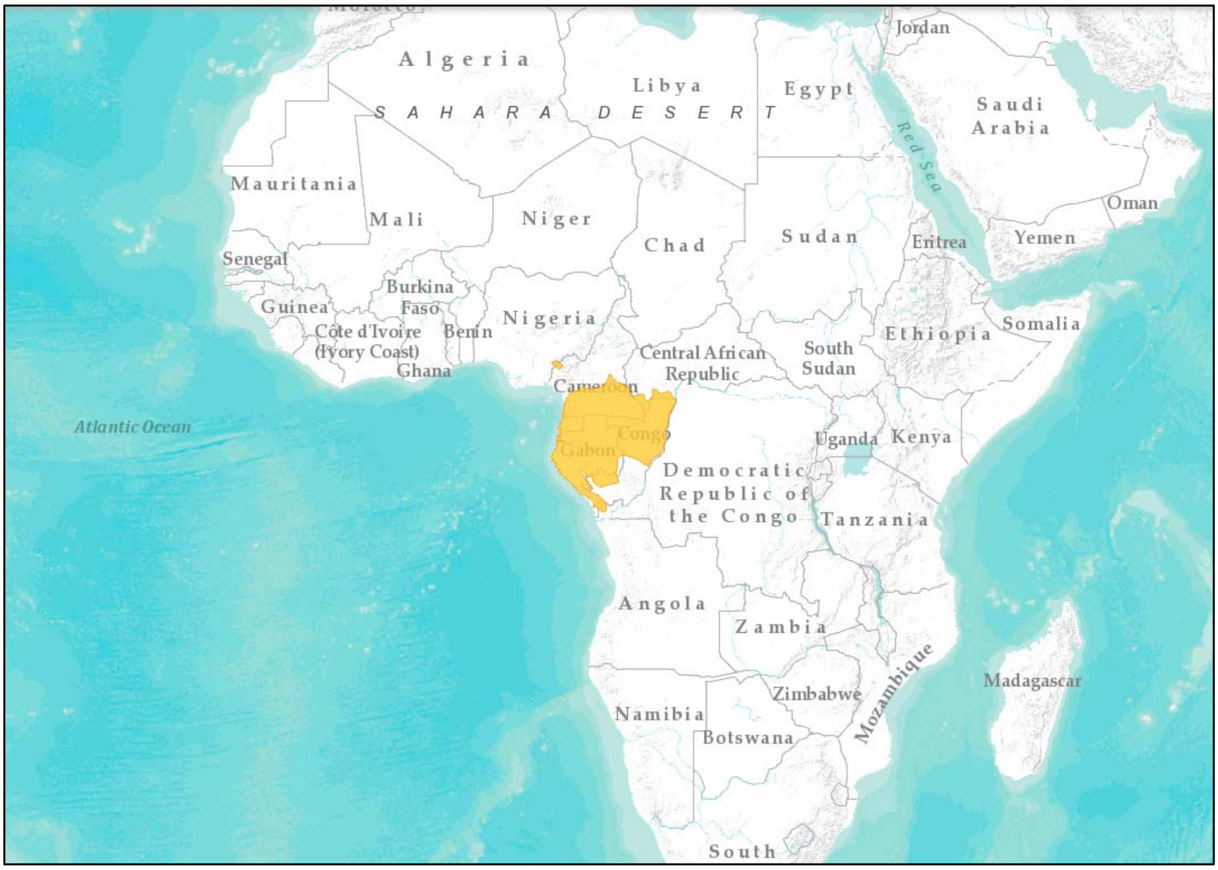
Il est folivore et frugivore. Il se nourrit de feuilles, baies, mais aussi d'écorces, racines, de termites et moelle en fonction des disponibilités des ressources variant selon les saisons (Tutin *et al.*, 1992; Fleagle, 1999).

Locomotion

Majoritairement terrestre, le gorille est capable de se déplacer dans les arbres. Comme le chimpanzé, il est quadrupède au sol en appui sur le dos des phalanges de la main ("knuckle-walking") (Tuttle & Watts, 1985; Fleagle, 1999; Hunt, 2004). Ses pieds sont à plat sur le sol légèrement inclinés sur le bord externe. La bipédie est rare.

Statut IUCN

"Critically endangered" (en danger critique d'extinction) (www.iucnredlist.org)



Répartition géographique de *Gorilla gorilla* (carte IUCN)

Homo sapiens (Linnaeus, 1758)

Source: E. Reghem

Spécificités générales

L'importance écologique d'une seule espèce telle que l'humain est en train de modifier rapidement et profondément la biosphère comme probablement aucune autre espèce ne l'avait fait auparavant. Il est présent sur toute la surface de la Terre et est en pleine explosion démographique. On estime la population humaine à plus de 7 milliards d'individus. Les innovations technologiques sont une des particularités de cette espèce.

Phylogénie

L'humain ("*human*" en anglais) est un primate grand singe répandu à travers le monde, des régions les plus froides aux régions les plus chaudes et les plus hostiles. Il appartient au sous-ordre des haplorhiniens, à l'infra-ordre des catarrhiniens, à la super-famille des Hominoidea, à la famille Hominidae, à la sous-famille des Hominines et au genre *Homo*. Ce genre regroupe une seule espèce actuellement, mais de nombreux fossiles *Homo*, disparus aujourd'hui, ont été mis au jour (pour les plus connus: *Homo habilis*, *H. erectus*, *H. neanderthalensis*, *H. florensis*).

Description morphologique

L'humain se caractérise par sa bipédie permanente. Il présente des membres inférieurs plus longs que les membres supérieurs (indice intermembral: 72, Fleagle, 1999), un trou occipital (*foramen magnum*) sous la calotte crânienne plus en avant que chez les autres espèces primates, une colonne vertébrale en S, des muscles de la région glutéale plus développés que chez n'importe quelle autre espèce et un bassin élargi et court. Son pouce est opposable aux autres doigts. Selon les zones géographiques, un humain de sexe masculin mesure environ 130 et 200 cm pour 40 à 90 kg, un humain de sexe feminin entre 120 et 180 cm pour 30 à 80 kg (Boaz & Almquist, 2002). Leur espérance de vie varie en fonction des pays entre 45 et 80 ans (84,5 ans pour une femme française née en 2009; 77,8 ans pour un homme français né en 2009). Il peut atteindre dans certains cas les 100 ans. La maturité sexuelle varie considérablement avec le niveau nutritionnel des mères et des jeunes et est sous l'influence des pratiques culturelles (Boaz & Almquist, 2002). La présence des menstrues intervenant autour de l'âge de 10 à 14 ans permet une procréation.

Biogéographie

L'espèce humaine présente la plus grande répartition terrestre dans le monde. Elle se retrouve en effet à toutes les latitudes (bien qu'il n'y ait pas d'établissement permanent en Antarctique). Un petit groupe humain a été introduit dans l'espace à la station spatiale internationale.

Groupe social

L'humain est une des espèces animales présentant une forte diversité culturelle, sociale et comportementale. Les premiers humains nomades et chasseurs-cueilleurs ont vu leur système économique et leur démographie totalement changés avec le développement de l'agriculture il y a environ 10 000 ans. Quelques rares sociétés humaines sont encore nomades mais la plupart des individus se sont sédentarisés. L'organisation sociale diffère d'une société à une autre, mais généralement le système patriarcal est largement prépondérant au sein de l'espèce humaine (Boaz & Almquist, 2002).

Régime et techniques de recherche alimentaire

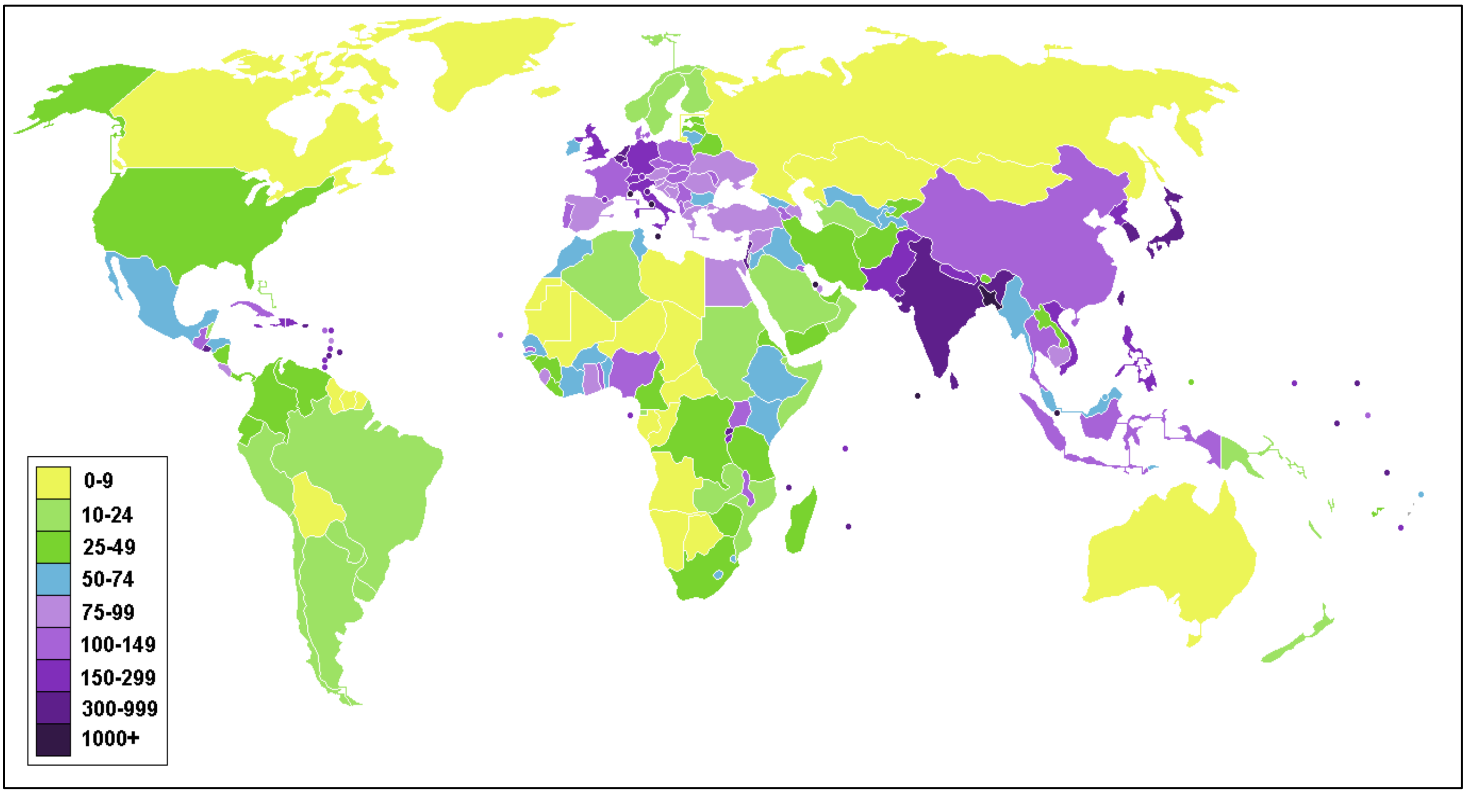
Il est omnivore et connu pour chasser d'autres espèces mais il pratique en grande majorité l'élevage et l'agriculture comme mode de subsistance. Il utilise majoritairement des outils afin d'accéder à sa nourriture.

Locomotion

L’humain est la seule espèce primate à avoir adopté la bipédie permanente et terrestre. Toutefois, jusqu’à l’âge d’environ 1 ans, l’humain es quadrupède et se déplace en appui sur la paume de ses mains et ses genoux. A l’âge adulte, il utilise rarement cette posture à l’exception de rares cas qui pour des problèmes congénitaux se déplacent de façon permanente en quadrupédie en appui sur la paume des mains et la plante des pieds (Ozcelik *et al.*, 2008).

Statut IUCN

"Least concern" (préoccupation mineure) (www.iucnredlist.org)



Densité géographique de *Homo sapiens* (source : http://www.telegraph.co.uk/news/newstopics/politics/2967374/England-is-most-crowded-country-in-Europe.html). Légende : habitants/km².

APPENDIX B

Assessment of instrumental and experimental error of the digitization of landmarks:

When studying kinematics of primates, body markers cannot be used for several reasons (Aerts, 2000; D'Août *et al.*, 2002; Isler, 2005; Vereecke *et al.*, 2006; Bril *et al.*, 2009; Bérillon *et al.*, 2010; Channon *et al.*, 2010). First of all, the practical and ethical guidelines prevent the placement of markers on the animals in zoological parks. Second, in order to address evolutionary questions filming natural behaviour in unconstrained conditions is essential and as such the experimenter tries to disturb the animals as little as possible, especially with untrained animals.

Estimating the effects of different sources of error (instrumental and experimental) is crucial for assessing the reliability of the primate movement analysis presented in this study.

i) First, we tested the **instrumental error** of the set up (cameras, recordings through the Plexiglas enclosures), the software of manual digitization and 3D reconstruction of the landmarks (software Loco 3.3).

ii) Second, we assessed the **experimental error** in terms of accuracy and precision involved in the manual digitization of the twelve landmarks. The unmarked condition used here in the kinematic analysis of primates involves a lower precision than what is usually obtained with humans (who can be marked), yet allows to obtain consistent results with a margin of error calculated and presented here.

i) Assessment of the instrumental error

In this study, the subjects were filmed behind a Plexiglas enclosure by five cameras at 60 Hz (Sanyo® X Acti Full HD 1920x1080), located in semi-circle approximately 3 m from the experimental arena and synchronized with a light signal. Then, the manual frame by frame digitization and the 3D-reconstruction were performed using a custom-written Matlab® routine (Loco 3.3, Libourel P.A., MNHN, Paris).

In order to assess both the set up and the software Loco 3.3, we filmed with the same cameras at 60 Hz a black and white checkerboard (with known dimensions) moving behind and in front of the Plexiglas. Then, manual digitization and 3D reconstruction were obtained using the software Loco 3.3. The recordings and the data analysis were performed exactly in the same conditions as those involving primate subjects. First, we compared the known measures of the checkerboard with the computed measures obtained from the digitization and 3D reconstruction. Second, we compared the data of the checkerboard filmed behind and in front the Plexiglas to assess the effect of the Plexiglas on the data.

Three measures were compared (fig. B-1):
-angle ABC: 90°
-distance AB: 52 cm
-distance BC: 52 cm

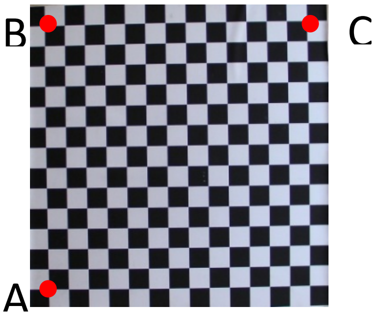


Figure B-1. The black and white checkerboard used to assess the instrumental error and landmarks (A, B, C) digitized.

Thus, we digitized the landmarks A, B, C on ten frames filmed at 60 Hz. The results were reported in table B-1 and showed that the accuracy of the software digitization and reconstruction was less than 1% of error for all the conditions (*i.e.* behind and in front of the Plexiglas). These results validated the set up and the software Loco 3.3 and confirmed that the Plexiglas has no effect on the baseline data.

Table B-1. Results of the assessment of the instrumental error.

Conditions	Type of measure	Real measure	Mean of the computed measures[1]	Standard deviation
Behing the plexiglas	**Angle ABC**	90°	89.94°	±0.2
	Distance AB	52 cm	51.7 cm	±0.002
	Distance BC	52 cm	51.6 cm	±0.002
In front of the plexiglas	**Angle ABC**	90°	89.73°	±0.4
	Distance AB	52 cm	52.9 cm	±0.001
	Distance BC	52 cm	52.5 cm	±0.002

[1] The means of the computed measures were obtained for the ten digitized frames.

ii) **Assessment of the experimental error**

For this study, in order to limit the variation of digitized points on unmarked animals, the same experimenter manually digitized the landmarks for all the trials. The assessment of the experimental error was conducted through the measure of reproducibility. The same experimenter digitized three times the landmarks of a same trial (*i.e.* a prehension sequence) for each primate species in this study. The variation of the experimental error was calculated from the standard deviation (SD) of the length of each body segment (table B-2), of the variables of the wrist velocity and movement duration (table B-3), and of the ranges of motion of the trunk and forelimb joints (table B-4).

The intra-experimenter error revealed a relatively constant error in the comparison of the three digitizations of the same trial. Indeed, fairly constant body segment lengths (trunk, arm, forearm, hand[2]) during the prehension movement suggest that the method is accurate enough to quantify the movement kinematics (see Isler, 2003, 2005). Isler (2003, p.42) found similar results as those described here using five gorillas and four bonobos (means of the SD for the length of the gorillas' arm: ±2.88 cm, the gorillas' forearm: ±2.02 cm; the bonobos' arm: ±0.95 cm, the bonobos' forearm: ±1.44 cm). The error in the variables of the wrist velocity, movement duration, and ranges of motion of the trunk and forelimb joints was acceptable for our movement analysis. Only, the ranges of motion of the trunk and forelimb joints exhibit more variation, and required cautious consideration of the results and interpretations thereof.

In order to visualize the variability we present the graphical representation of the mean and standard deviation of the ranges of motion of the trunk and forelimb joints (figs. B-2, 3, 4, 5) and the wrist velocity curves (fig. B-6) for each species (chimpanzee, gorilla, capuchin, and lemur).

Table B-2. Standard deviation (SD) of the length of body segments of the primate species during prehension (reaching). Data are obtained from the three digitalization of a same trial of each species.

	chimpanzee	**gorilla**	**capuchin**	**Lemur**
	SD	SD	SD	SD
Length of the trunk (cm)	0.97	0.28	0.28	0.24
Length of the arm (cm)	2.17	1.43	1.14	2.16
Length of the forearm (cm)	1.61	1.92	1.29	0.84
Length of the hand (cm)	0.58	1.37	0.97	1.15

Table B-3. Standard deviation (SD) of the wrist velocity and movement duration in each species during the prehension (reaching). Data are obtained from the three digitalization of a same trial of each species.

	chimpanzee	**gorilla**	**capuchin**	**lemur**
	SD	SD	SD	SD
Mean of the wrist velocity (mm.s-1)	21.1	17.18	15.62	12.50
Amplitude of the wrist velocity peak (mm.s-1)	77.71	37.67	22.41	6.69
Time to the wrist velocity peak (%)	2.23	1.52	2.76	0.94
Movement duration (ms)	9.62	9.65	16.67	9.62

---

[2] The length of the trunk is calculated between the both landmarks on the trunk (or on the breast for gorillas and humans in sitting posture). The length of the arm is calculated between the shoulder landmark and the mean of both elbow landmarks. The length of the forearm is calculated between the mean of both elbow landmarks and the mean of both wrist landmarks. The length of the hand corresponds to the back of the hand without fingers. This length is calculated from the means of both wrist landmarks and the means of both landmarks of the metacarpal heads (2nd and 3rd metacarpal heads).

Table B-4. Standard deviation (SD) of the ranges of motion (in degrees) of the trunk, shoulder, elbow and wrist in each species during prehension (reaching). Data are obtained from the three digitizations of the same trial for each species.

	chimpanzee	**gorilla**	**capuchin**	**lemur**
	SD	SD	SD	SD
Trunk flexion (°)	2.50	2.07	0.79	1.63
Trunk inclination (°)	1.25	2.14	0.41	1.21
Trunk rotation (°)	1.64	4.84	0.46	7.46
Shoulder flexion (°)	7.07	4.6	4.38	3.47
Shoulder abduction (°)	0.17	1.56	0.61	7.7
Shoulder rotation (°)	5.03	15.22	5.75	5.37
Elbow extension (°)	1.68	2.55	4.15	0.05
Elbow rotation (°)	7.49	7.97	13.37	6.57
Wrist extension (°)	6.65	13.37	4.14	3.02
Wrist deviation (°)	10.94	2.55	12.28	1.88

WRIST VELOCITY

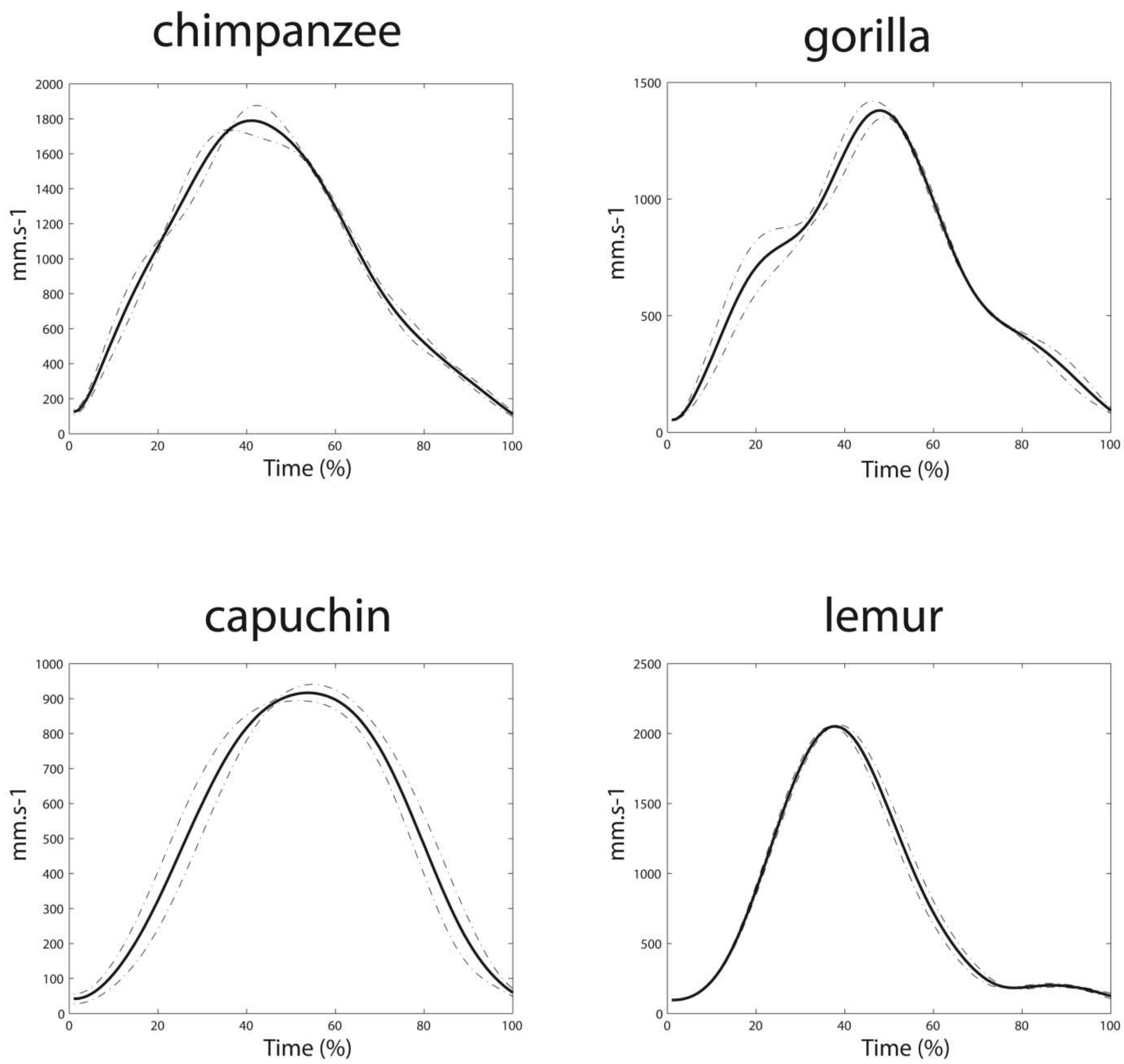


Figure B-1. Representation of the mean and standard deviation (dotted lines) of the **wrist velocity** for each non-human primate during prehension.

TRUNK MOTION

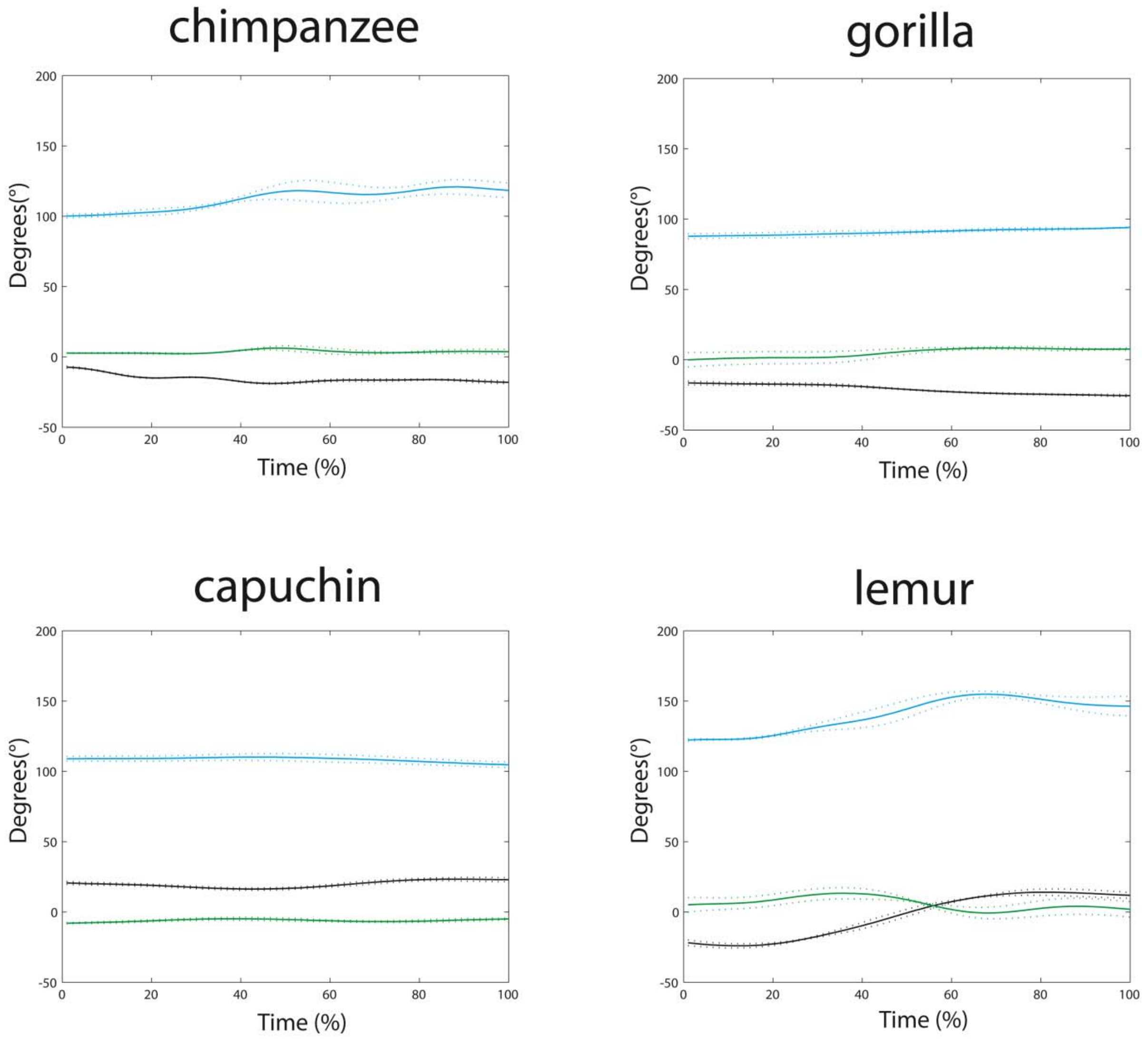


Figure B-2. Representation of the mean and standard deviation (dotted lines) of the **trunk motion** for each non-human primate during prehension. In blue: flexion (+) and extension (-); in black: right (+) and left (-) inclination; in green: right (+) and left (-) rotation.

SHOULDER MOTION

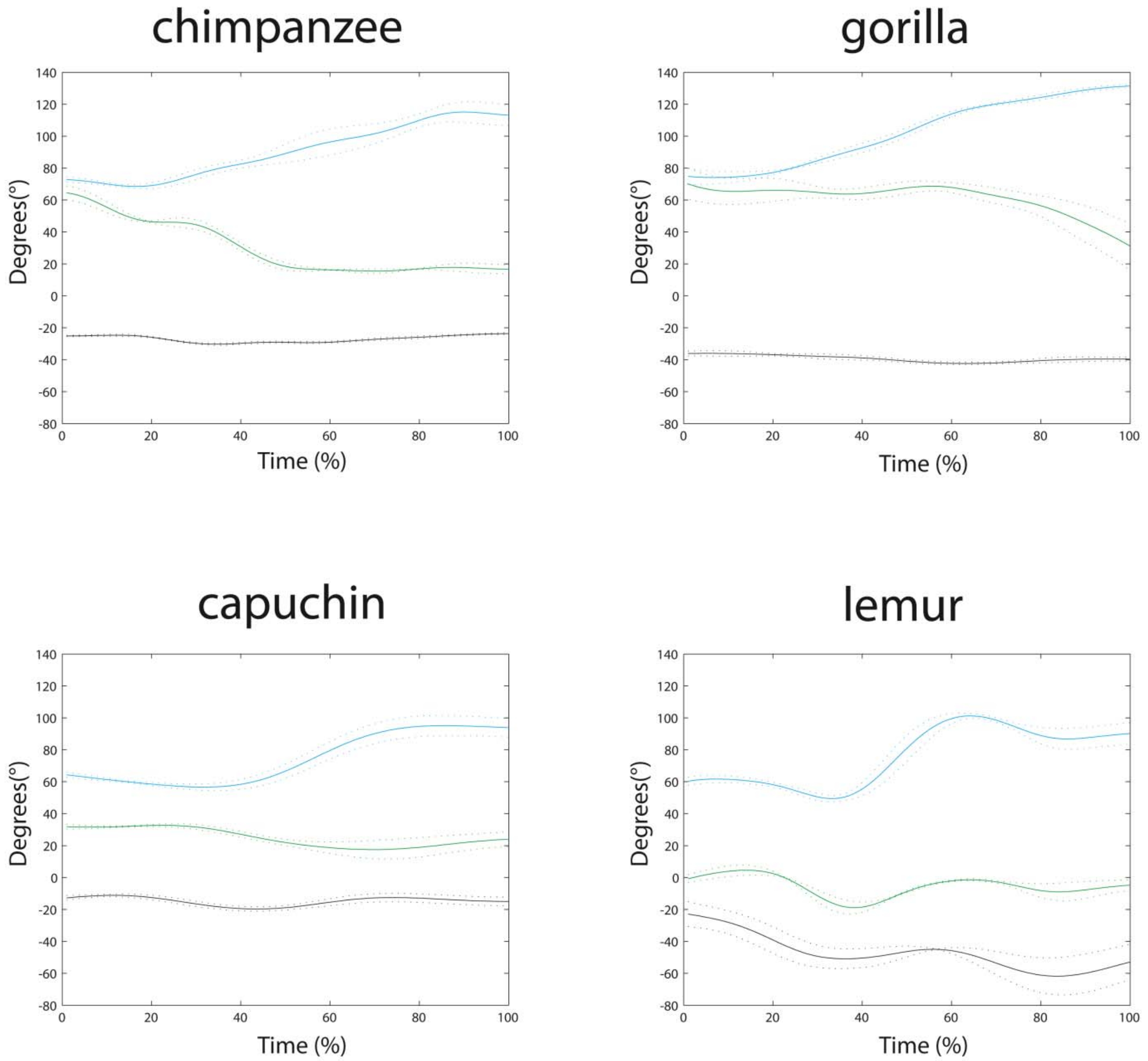
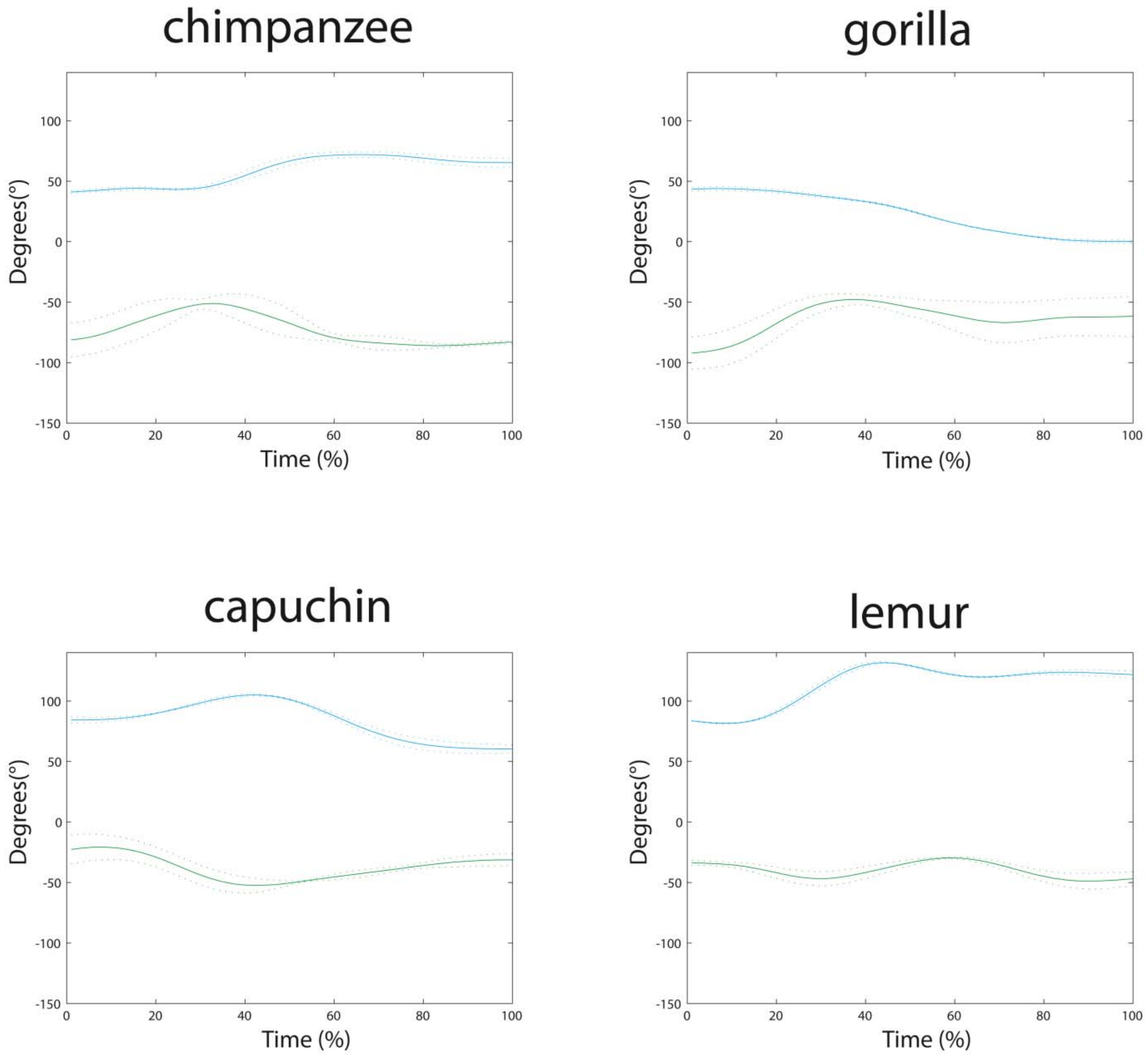


Figure B-3. Representation of the mean and standard deviation (dotted lines) of the **shoulder motion** for each non-human primate during prehension. In blue: flexion (+) and extension (-); in black: adduction (+) and abduction (-); in green: internal (+) and external (-) rotation.

ELBOW MOTION


chimpanzee

gorilla

capuchin

lemur

Figure B-4. Representation of the mean and standard deviation (dotted lines) of the **elbow motion** for each non-human primate during prehension. In blue: flexion (+) and extension (-); in green: internal (+) and external (-) rotation.

WRIST MOTION

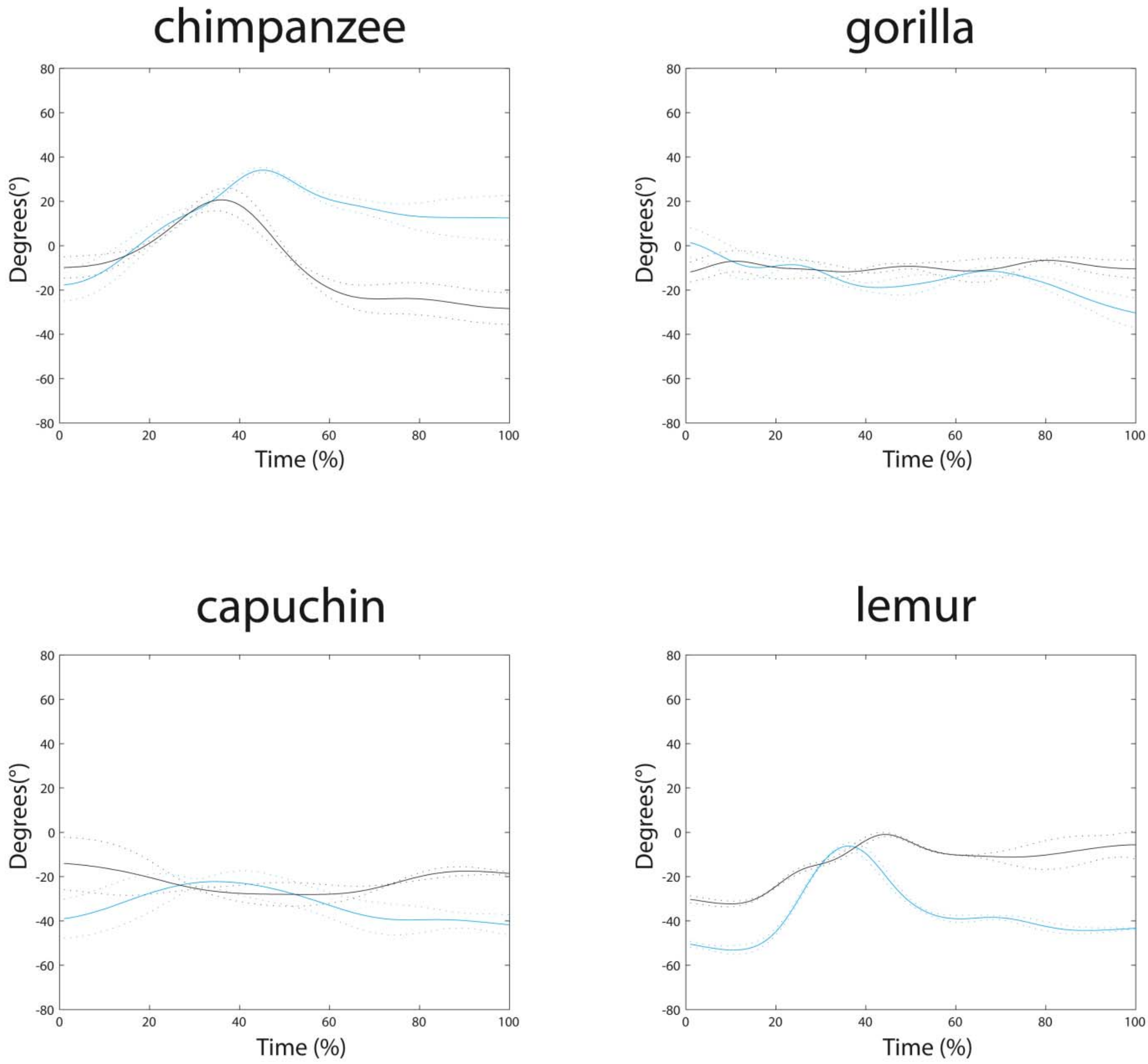


Figure B-5. Representation of the mean and standard deviation (dotted lines) of the **wrist motion** for each non-human primate during prehension. In blue: flexion (+) and extension (-); in black: adduction (+) and abduction (-) (respectively ulnar and radial deviation).

APPENDIX C

Methodological aspects pertaining to the cut off frequency used to filter kinematic data:

Several studies have used low-pass filters with a second order dual-pass Butterworth filter to filter raw displacement data in studies of the kinematics of prehension in both humans and macaques (*macaque*: Roy *et al.*, 2000, Roy *et al.*, 2002; Christel & Billard, 2002; Graham *et al.*, 2003; Masson *et al.*, 2004; Jindrich *et al.*, 2011; Nelson *et al.*, 2011; *human*: Jakobson & Goodale, 1991; Bootsma *et al.*, 1994; Paulignan *et al.*, 1997; Haggar & Wing, 1998; Masson & Bruin, 2009).

Moreover, several frequencies of video recording (50Hz, 100 Hz, 200 Hz, 300 Hz) are filtered with the same, or different, cut off frequency (6, 7,8 or 10 Hz) for both humans and macaques. For example, 6, 7, 8 Hz are used for video recordings at 60 and 100 Hz (Jakobson & Goddale, 1991; Haggar & Wing, 1998; Masson *et al.*, 2004; Jindrich *et al.*, 2011).

In order to determine the cut off frequencies to be applied on our data, we compared our kinematic variables of the wrist, and the movement duration from data filtered at 6 Hz and 10 Hz for both species and in both body postures. Next, we performed a t-test on the kinematic variables. For example, the direction of the wrist velocity peak does not differ between data filtered with a cut off frequency of 6 and 10 Hz. Moreover, the time (ms) when the peak occurred was not significantly different using both cut off frequencies (humans sitting: t = 0.9266, d.f. = 34, p-value = 0.3607; humans in a quadrupedal posture: t = 0.2685, df = 34, p-value = 0.7899; gorillas sitting: t = 1, df = 14, p-value = 0.3343; gorillas in a quadrupedal posture: t = 1, df = 14, p-value = 0.3343) (tables C-1, 2).

Finally, as the curves of both gorillas (fig. C-1) and humans (fig. C-2) were more smoothed at 6 Hz, we chose this widely used cut off frequency on the kinematics of prehension. Indeed, most of our data were not significantly different or exhibited acceptable differences for those which were significant when using both cut-off frequencies (tables C-1, 2).

Table C-1. Comparison between results obtained with cut off frequencies of 6 Hz and 10 Hz. Presented are the absolute values of wrist kinematic variables for gorillas in two body postures (significant differences appear in red).

	Kinematical variables	**Cut off at 6hz: mean values**	**Cut off at 10hz: mean values**	**Differences between the mean values of 6hz and 10hz**	**Differences between the SD values of 6hz and 10hz**	**t-test**
Gorillas in sitting posture	Mean of the wrist velocity (mm.-1s)	775.94±237.32	802.69±251.63	-26.75	-14.31	t=-4.6892, d.f.=14
	Amplitude of the wrist velocity peak (mm.-1s)	1819.12±675.14	1975.38±755.48	-156.26	-80.34	t=-5.6487, d.f. = 14
	Time to the wrist velocity peak (%)	231.11±55.94	255.56±55.59	-24.55	0.35	t=1, d.f. = 14
	Time to the wrist velocity peak (ms)	39.78±7.34	39.54±6.44	0.24	0.9	t=0.2384, d.f. = 14
	Duration of the deceleration phase (%)	347.78±66.63	342.22±64.2	5.56	2.43	t=1, d.f. = 14
	Duration of the deceleration phase (ms)	60.22±7.34	60.46±6.44	-0.24	0.9	t=-0.2384, d.f. = 14
	Movement duration (ms)	578.89±95.22	567.78±99.5	11.11	-4.28	t=3.1623, d.f. = 14
Gorillas in quadrupedal posture	Mean of the wrist velocity (mm.-1s)	1202.13±465.03	1232.54±467.68	-30.41	-2.65	t=-4.2618, d.f. = 14
	Amplitude of the wrist velocity peak (mm.-1s)	2414.89±915.96	2589±980.71	174.23	-64.75	t=-5.9906, d.f. = 14
	Time to the wrist velocity peak (%)	252.22±91.04	246.67±89.13	5.55	1.91	t=1, d.f. = 14
	Time to the wrist velocity peak (ms)	41.02±8.99	41.07±9.59	-0.05	-0.6	t=-0.0607, d.f. = 14
	Duration of the deceleration phase (%)	358.89±111.78	350±107.46	8.89	4.32	t=1.8353, d.f. = 14
	Duration of the deceleration phase (ms)	58.98±8.99	58.93±9.59	-0.05	-0.6	t=0.0607, d.f. = 14
	Movement duration (ms)	611.11±165.07	596.67±158.64	14.44	6.43	t=3.6665, d.f. = 14

Table C-2. Comparison between results obtained with cut off frequencies of 6 Hz and 10 Hz. Presented are the absolute values of wrist kinematic variables for humans in two body postures (significant differences appear in red).

	Kinematical variables	**Cut off at 6hz: mean values**	**Cut off at 10hz: mean values**	**Differences between the mean values of 6hz and 10hz**	**Differences between the sd values of 6hz and 10hz**	**t-test**
Humans in sitting posture	Mean of the wrist velocity (mm.-1s)	388.84±123.08	386.61±121.25	2.23	1.83	t=1.2526, d.f. = 34
	Amplitude of the wrist velocity peak (mm.-1s)	779.23±214.92	782.91±213.64	-3.68	1.28	t=-2.6057, d.f. = 34
	Time to the wrist velocity peak (ms)	413.71±96.1	412.29±98.7	1.42	-2.6	t =0.9266, d.f. = 34
	Time to the wrist velocity peak (%)	40.7±6.94	40.06±6.82	0.64	0.12	t=2.1073, d.f. = 34
	Duration of the deceleration phase (ms)	620.29±185.72	632.57±189.71	-12.28	-3.99	t=-1.7214, d.f. = 34
	Duration of the deceleration phase (%)	59.3±6.94	59.94±6.82	-0.64	0.12	t=-2.1073, d.f. = 34
	Movement duration (ms)	1034±242.85	1044.86±248.6	-10.86	-5.75	t=-1.496, d.f. = 34
Humans in quadrupedal posture	Mean of the wrist velocity (mm.-1s)	536.86±111.63	537.71±113.3	-0.85	-1.67	t=-0.8398, d.f. = 34
	Amplitude of the wrist velocity peak (mm.-1s)	1125.57±214.71	1126.46±214.96	-0.69	-0.25	t=-1.2595, d.f. = 34
	Time to the wrist velocity peak (ms)	342.86±75.72	342.29±79	0.57	-3.28	t=0.2685, d.f. = 34
	Time to the wrist velocity peak (%)	39.23±5.11	39.13±5.20	0.1	-0.09	t=0.4227, d.f. = 34
	Duration of the deceleration phase (ms)	537.14±132.81	537.14±130.8	0	2.01	t=0, d.f. = 34
	Duration of the deceleration phase (%)	60.77±5.11	60.87±5.2	-0.1	-0.09	t=-0.4227, d.f. = 34
	Movement duration (ms)	880±182.08	879.43±184.21	0.57	-2.13	t=0.3046, d.f. = 34

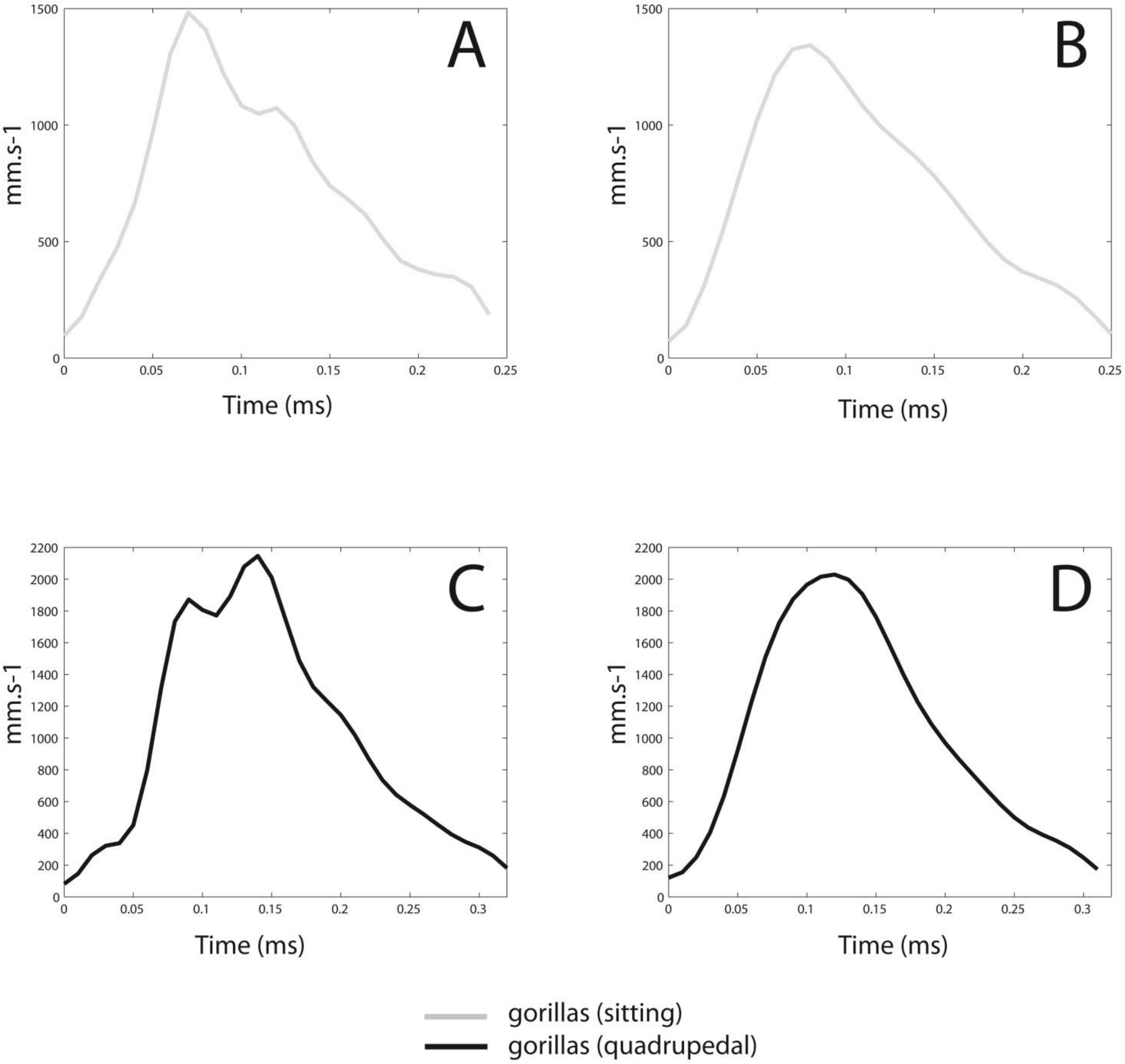


Figure C-1. Comparison of the effect of cut off frequencies of 6 Hz (B-D) and 10 Hz (A-C) on the wrist velocity of gorillas in sitting and quadrupedal postures during a typical prehension movement.

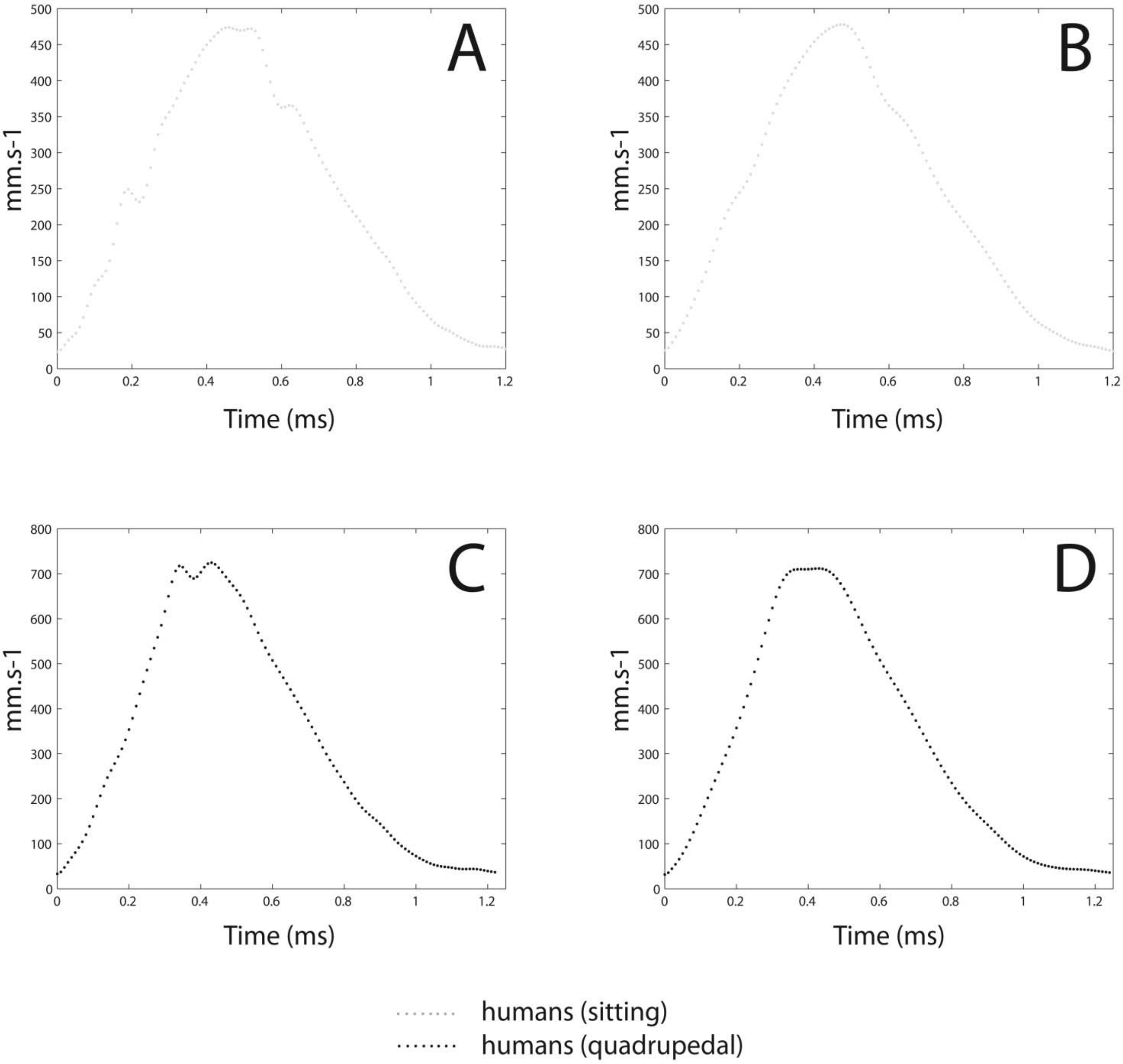


Figure C-2. Comparison of the effect of cut off frequencies of 6 Hz (B-D) and 10 Hz (A-C) on the wrist velocity of humans in sitting and quadrupedal postures during a typical prehension movement.

APPENDIX D

Methods of angular calculations based on the recommendation of the International Society of Biomechanics (ISB) (Wu *et al.*, 2005):

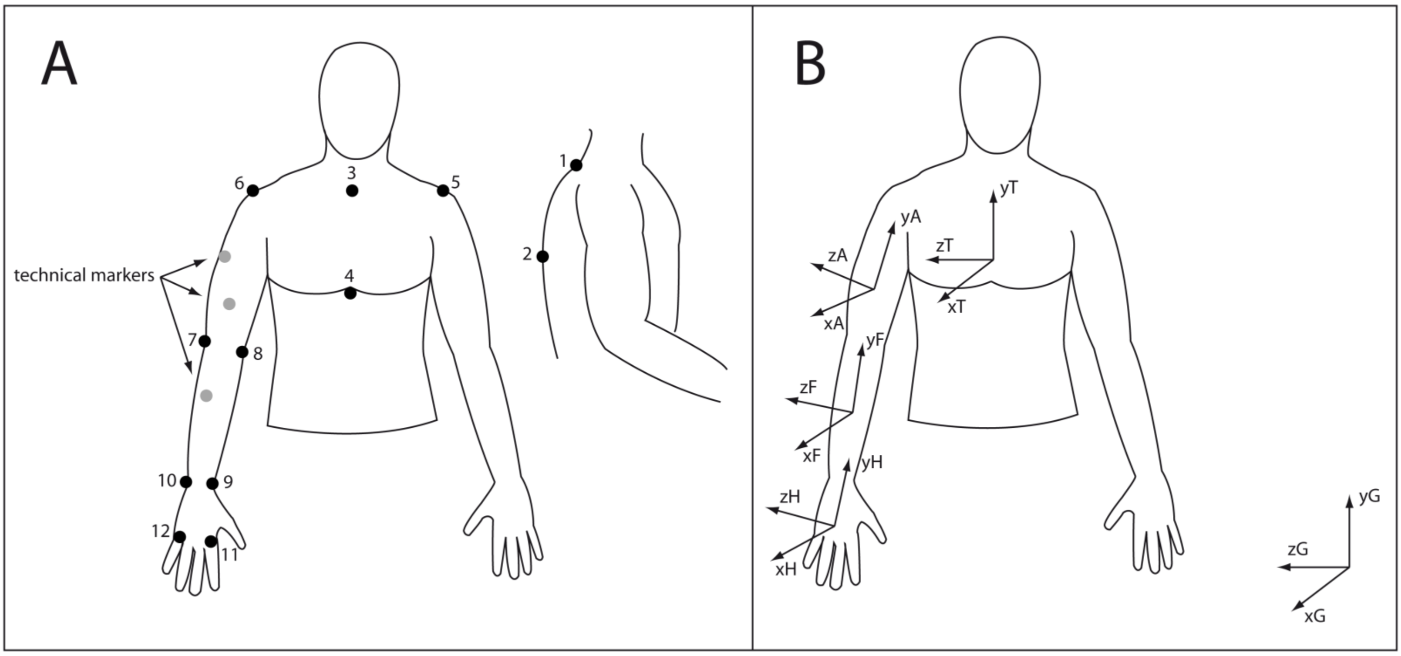


Figure D-1. Position of the landmarks (A) and the segment coordinate systems (B) on the forelimb. Two additional reflective markers, placed on the arm and on the forearm, helped to reconstruct the motion of the forelimb in humans.

Landmark legend (A): [1] processus spinosus of the 7th cervical vertebra, [2] 8th thoracic vertebra, [3] suprasternal notch, [4] xiphoid process, [5, 6] left and right dorsal point on the acromio-clavicular joint, [7, 8] medial and lateral epicondyles of humerus, [9, 10] radial and ulnar styloid processes, [11, 12] head of 2nd and 5th metacarpus.

Segment coordinate systems legend (B): G: Ground, T: Trunk, A: Arm, F: Forearm, H: Hand.

Methods:

● First, a segment coordinate system (SCS) was computed for each segment (trunk, arm, forearm, hand) using a minimum of three landmarks per segment (fig. D-1).

- In order to determine **the <u>SCS (G) of the ground</u>**, the position of landmarks [5] and [6] on the first frame were projected onto the ground. The first vector of the local axis system connecting the midpoint between these projected landmarks and the position of the digitized raisin placed on the ground, was described as $\overrightarrow{xG}$ and pointed forward. The second vector, described as $\overrightarrow{yG}$, corresponded to the vertical axis, perpendicular to the ground, pointing upward. Then the cross product of $\overrightarrow{xG} \wedge \overrightarrow{yG}$ gave the third vector $\overrightarrow{zG}$, pointing laterally. The three vectors were then normalised.

- In order to determine the **SCS (T) of the trunk segment**, the first vector connecting the landmarks [5] and [6] was named $\overrightarrow{zT}$, pointing laterally (toward the left forelimb when the left forelimb was used to grasp or toward the right forelimb when it was the right forelimb used to grasp). The second vector of the SCS was constructed using an intermediary vector connecting the landmarks [1] and [2] or [3] and [4] (depending on which of them were visible), and was named $\overrightarrow{T}$, pointing proximally. The cross product of $\overrightarrow{zT} \wedge \overrightarrow{\alpha T}$ gave the second vector $\overrightarrow{xT}$, pointing forward. Then, a second cross product $\overrightarrow{zT} \wedge \overrightarrow{xT}$ gave the third vector $\overrightarrow{yT}$ which was orthogonal to $\overrightarrow{zT}$ and $\overrightarrow{xT}$, pointing proximally. The three vectors were then normalised.

- In order to determine the **SCS (A) of the arm segment**, the first vector, connecting the landmark [5] or [6] (depending on the forelimb used to grasp, [5] for the left one or [6] for the right one) and the midpoint between landmarks [7] and [8] was named $\overrightarrow{yA}$, pointing proximally. The second vector was obtained by the cross product of $\overrightarrow{yA} \wedge \overrightarrow{yF}$ which gave the vector $\overrightarrow{zA}$, orthogonal to $\overrightarrow{yA}$ and $\overrightarrow{yF}$, pointing laterally. Then, a second cross product $\overrightarrow{yA} \wedge \overrightarrow{zA}$ gave the third vector $\overrightarrow{xA}$ which was orthogonal to $\overrightarrow{yA}$ and $\overrightarrow{zA}$, pointing forward. The three vectors were then normed.

- In order to determine the **SCS (F) of the forearm segment**, the first vector, connecting the midpoint between landmarks [7] and [8] and the midpoint between [9] and [10], was named $\overrightarrow{yF}$, pointing proximally. The second vector was constructed using an intermediary vector connecting the landmarks [9] and [10], named $\overrightarrow{\alpha F}$, pointing laterally (toward ulnar side). The cross product of $\overrightarrow{yF} \wedge \overrightarrow{\alpha F}$ gave the second vector $\overrightarrow{xF}$, which was orthogonal to $\overrightarrow{yF}$ and $\overrightarrow{\alpha F}$, pointing forward. Then, a second cross product $\overrightarrow{yF} \wedge \overrightarrow{xF}$ gave the third vector $\overrightarrow{zF}$ which was orthogonal to $\overrightarrow{yF}$ and $\overrightarrow{xF}$, pointing laterally. The three vectors were then normed.

- In order to determine the **SCS (H) of the hand segment**, the first vector, connecting the landmarks [11] and [12] was named $\overrightarrow{zH}$, pointing laterally (toward ulnar side). The second vector was constructed using an intermediary vector connecting the midpoint between landmarks [9] and [10] and the midpoint between [11] and [12], named $\overrightarrow{\alpha H}$, pointing proximally. The cross product of $\overrightarrow{zH} \wedge \overrightarrow{\alpha H}$ gave the vector $\overrightarrow{xH}$, which was orthogonal to $\overrightarrow{zH}$ and $\overrightarrow{\alpha H}$, pointing forward. Then, a second cross product $\overrightarrow{zH} \wedge \overrightarrow{xH}$ gave the third vector $\overrightarrow{yH}$, pointing proximally. The three vectors were then normed.

● Second, the orthogonal rotation matrix from the proximal SCS to the distal SCS was computed for each joint and was assumed to correspond to a ZXY mobile axes sequence to derive the three corresponding angles. In this way, the first rotation (flexion/extension) was around the Z axis embedded in the proximal SCS, the last rotation (internal/external rotation) was around the Y axis embedded in the distal SCS and the abduction/adduction took place around the X floating axis.

Trunk angles were obtained using ground and trunk SCS, shoulder angles using trunk and arm SCS, elbow angles using arm and forearm SCS and wrist angles using forearm and hand SCS.

Methods of the wrist velocity calculation:

The wrist velocity (also termed as wrist tangential velocity) is calculated from the filtered three dimensional Cartesian coordinates (x, y, z) of the mid-point of the two wrist landmarks [9] and [10] (the radial and the ulnar styloid processes) (fig. D-1) (Kudoh *et al.*, 1997). Then, the velocity is determined by the distance a given point travelled within 1 frame corresponding to 0.016 ms. as we filmed at 60 Hz (*i.e.* 60 frames per seconds). Thus the velocity was given by:

$$v=\frac{\sqrt{\Delta x^2+\Delta y^2+\Delta z^2}}{0.016}$$

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Influence of the Task on Hand Preference: Individual Differences among Gorillas *(Gorilla gorilla gorilla)*

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Key Words

Hand preference · Laterality · Gorilla · Grasping · Task complexity · Tool use · Extractive behaviour

Abstract

The degree of task complexity and bimanual complementarity have been proposed as factors affecting lateralization strength in humans. However, a large number of studies have demonstrated group-level lateral hand bias for different manual activities in numerous non-human primate species. However, no study has tested the effects that a variety of tasks may have in inducing differences in hand preference. Here, we aim to test if 3 adult gorillas exhibited a greater hand preference bias performing 4 tasks of varying complexity: grasping small versus large foods, proto-tool use task and tool use task involving greater visuospatial requirements. We found that (1) the complexity of the task does not necessarily induce a right-handed bias and (2) a subject can be right-handed for a complex task and left-handed for another one. These results, complemented by many publications on hand preference in non-human primates, reveal a great variability in hand preference, which makes it very difficult to deduce any details of hominin handedness with artefacts.

Introduction

The degree of task complexity and bimanual complementarity have been proposed as factors affecting lateralization strength [Uomini, 2009]. Right-handedness may have emerged in humans through the social transmission of tool-using activities. However, several studies have demonstrated population-level lateral hand bias

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for different manual activities in numerous non-human primate species including prosimians [Masataka, 1989; Ward et al., 1993], New World and Old World monkeys [Kimura, 1979; Fagot and Vauclair, 1991; Diamond and McGrew, 1994; Lacreuse and Fragaszy, 1996; Westergaard et al., 1997; Spinozzi et al., 1998], and great apes [Olson et al., 1990; Hopkins, 1993; Hopkins et al., 1993a, b; Hopkins and de Waal, 1995; Hopkins and Leavens, 1998; Corp and Byrne, 2004]. Very few data are available on hand preference in gorillas. Some authors have shown a significant right-hand preference on a mesh retrieval task [Olson et al., 1990]. Another study found a symmetrical distribution of subjects with right-hand, left-hand and no hand preference when simply reaching for food and a left-hand preference by gorillas tested on a spatial task requiring precise alignment of two openings [Fagot and Vauclair, 1988b]. A recent study found that there was no population-level manual bias for unimanual actions but, in contrast, that gorillas exhibited significant population-level right-handedness for bimanual actions [Meguerditchian et al., 2010].

These results challenge the assumption that laterality in hand use is a uniquely human characteristic [Warren, 1980; Corballis, 1991] and point out the need to take account of the level of task complexity in evaluating non-human primate manual laterality. In this context, several studies have tested the effect of a variety of tasks inducing different complexities in hand preference. Indeed, Trouillard and Blois-Heulin [2005] showed that strength of laterality in De Brazza's monkeys increased with task complexity. Chapelain et al. [2006] found increased individual lateralization for more complex experimental food-reaching tasks in Campbell's monkeys. For chimpanzees, hand preferences for termite fishing, a highly dexterous task, are very stable [Nishida and Hiraiwa, 1982]. Boesch [1991] reports stable individual hand use patterns for the most difficult or 'complex' tasks of nut cracking at Taï, whereas the same chimpanzees were ambidextrous for reaching and grooming. Sugiyama et al. [1993] and Biro et al. [2003] also found consistent individual hand preferences in wild chimpanzees at Bossou for nut cracking but not for picking food. Gorillas show a non-significant trend towards population right-handedness for the finest manipulations in processing edible plants [Byrne and Byrne, 1991; Byrne et al., 2001], while orang-utans are individually handed for feeding [Rogers and Kaplan, 1996], as are bonobos [Harrison and Nystrom, 2008; Chapelain and Hogervorst, 2009]. Some of these findings may be explained by the greater level of skill required for tasks involving tool use [O'Malley and McGrew, 2006], but strong hand preference is also found in tasks that do not involve direct tool manipulation. In addition, authors have different views on how to rank the tasks by complexity level, and there is no agreement as to what constitutes skilled or complex tasks [Sambrook and Whiten, 1997; Trouillard and Blois-Heulin, 2005]. Some relate complexity to the number of combined elements or multiple movements [MacNeilage et al., 1987; Boesch, 1991; Matsuzawa, 1991, 1996; Rugg, 2004, 2007; Hayashi, 2007]. Others consider precision grasping to be more complex motorically than palm grasping [Fagot and Vauclair, 1991; McGrew and Marchant, 1999; Harrison and Byrne, 2000], and indeed these precision tasks are more lateralized. Therefore, according to a scale of motor complexity, the simplest task of cracking coconuts with palm grasping should be the least lateralized. On the other hand, other authors use a different classification of object manipulations [Parker and Gibson, 1977]. They consider that simple prehension is less complex than proto-tool use (involving object-substrate manipulation) and than true-tool use (complex manipulation of an object in order to assess food or transform another object). Other authors consider that extracting embedded foods is important in the emergence of primate intelligence [Milton, 1981; King, 1986]. So, foods that are difficult to obtain have all been promoted as setting a selective premium on high intelligence [Parker and Gibson, 1977; Wrangham, 1977; Galdikas, 1978; Menzel, 1978; Parker, 1978; Clutton-Brock and Harvey, 1980; Milton, 1981, 1988; Menzel and Juno, 1985; Gibson, 1986]. A recent review by Chapelain and Hogervorst [2009] reflects heterogeneous approaches in a large number of studies and provides good evidence that it is crucial to find a task difficult enough to elucidate hand preferences of non-human primates. Finally, several authors have stressed the importance of considering the kind of task employed in the assessment of lateral preferences.

Here, we aim to quantify hand preference and to test if right-handedness in gorillas increases with the complexity of 4 tasks. Results are discussed within the framework of the emergence and evolution of manual laterality.

Methods

We examined hand preferences in 3 adult gorillas (*Gorilla gorilla gorilla;* 16.7 ± 3.2 years old), 2 females and 1 male, in 4 tasks (fig. 1). The first task was considered the least complex and the fourth the most complex. The first task involved the grasping of large food items in order to eat them (spherical fruits) and the second the grasping of small foods (spherical cereals) in order to eat them [Pouydebat et al., 2006, 2009]. The second task was considered to be more complex than the first. The third task involved a proto-tool use action consisting of cracking coconuts against a substrate in order to open them. The third task was considered more complex than the previous one. The fourth task, a tool-use one, required the use of a branch in order to extract crushed fruits hidden in a hole [Pouydebat at al., 2005]. This last task was considered to be the most complex. So, we consider that the grasping of large and small foods in order to eat them is less complex from a cognitive point of view than palm grasping in a proto-tool use task, which involves extraction of a hidden food [Parker and Gibson, 1977; Milton, 1981, 1988, 1993]. Concerning the proto-tool use task (coconut task) and the tool-using task (food extraction), subjects were not inexperienced as they had already accomplished these actions 5 times at least.

Each gorilla performed 30 trials of each task during several day sessions. One trial corresponded to a grasp (one grasp of small food, one grasp of large food, one grasp of a coconut and one grasp of a branch). Previous observations allowed us to record that there were no bimanual responses for these 4 tasks. All the tasks accomplished by gorillas were spontaneous. More than 95% of the tasks were accomplished in a tripod posture. The evaluation of the gorillas' hand preference was based on 2 measures. The first measure determined a binomial z-score for each subject, based on the total frequency of right- and left-hand task responses [Braccini et al., 2010]. We classified gorillas with z-scores higher than 1.96 or less than –1.96 as right- or left-handed, respectively ($p < 0.05$). We considered gorillas with a z-score between these values as ambipreferent. The second measure used was a directional handedness index (HI). For each subject, we calculated an HI using the formula (RH – LH)/(RH + LH), in which R and L were the total number of right- and left-hand responses, respectively [Spinozzi and Cacchiarelli, 2000; Lonsdorf and Hopkins, 2005]. This measure provides information on the direction of manual preference and varies from –1.0 (strong LH preference) to 1.0 (strong RH preference).

Results

Each of the tasks required different types of manual patterns. The first task involved a fine grasping posture with the distal phalanges of the thumb and the index finger, whereas the second, third and fourth tasks involved a whole-hand grasp-

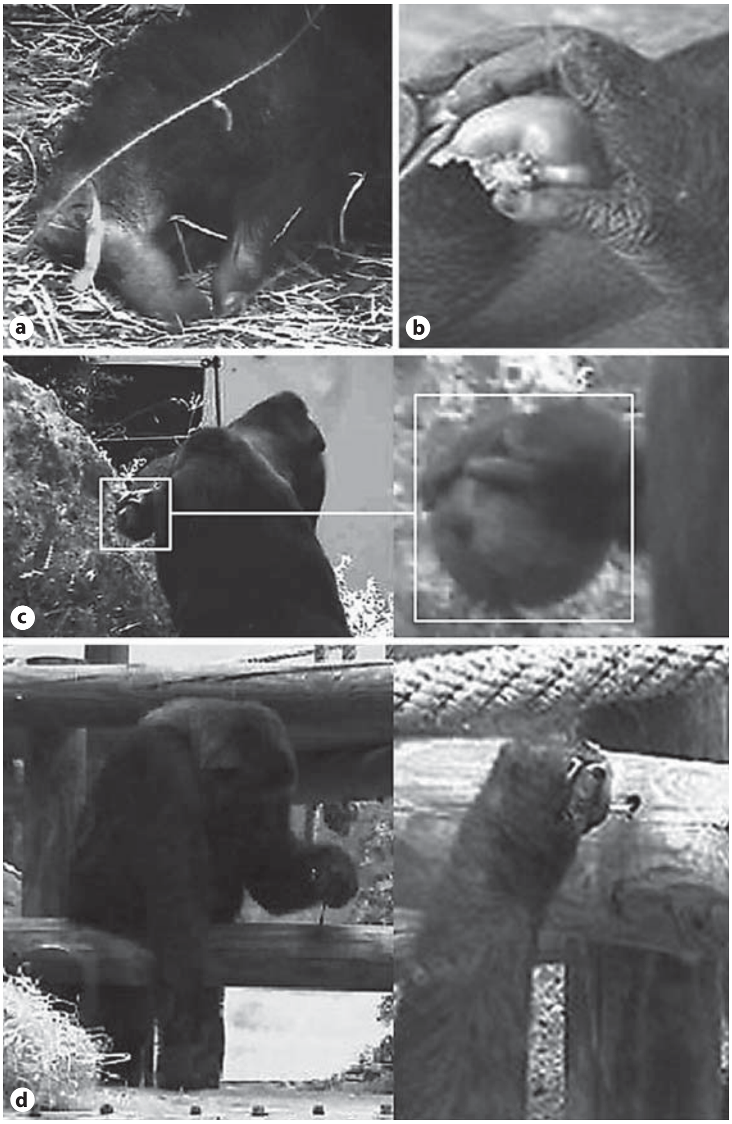

Fig. 1. Four tasks executed by gorillas. **a** Grasping small food. **b** Grasping large food. **c** Proto-tool use (cracking a coconut against a substrate). **d** Tool use (food extraction).

ing posture. The individual hand preferences shown by the 3 gorillas for each task showed (table 1, fig. 2) a significant individual-level right-hand preference for grasping small and large food, but not in the proto-tool use task for which only the male demonstrated an individual-level left-hand preference. In the grasping small food task, the mean HI score was 0.78. A significant right-hand bias occurred for all individuals ($p < 0.001$). In the grasping large food task, a significant right-hand bias oc-

Table 1. Individual hand preferences for each task

Subject	Grasping small food (1st/2nd digits grasping)			Grasping large food (palm grasping)			Proto-tool use (palm grasping)			Tool use (palm grasping)		
	HI	pref.	z-score	HI	pref.	z-score	HI	pref.	z-score	HI	pref.	z-score
Male	0.80	R*	4.20	0.93	R*	4.93	–0.33	n.p.	–1.64	–0.80	L*	–4.20
Female 1	0.73	R*	3.83	0.80	R*	4.20	–0.13	n.p.	–0.55	–0.67	L*	–3.47
Female 2	0.87	R*	4.56	0.87	R*	4.56	–0.20	n.p.	–0.91	–0.73	L*	–3.83

Pref. = Hand preference; L = left hand; R = right hand; n.p. = no preference; * $p < 0.001$; z-scores higher than 1.96 or less than –1.96 were classified as right- or left-handed, respectively.

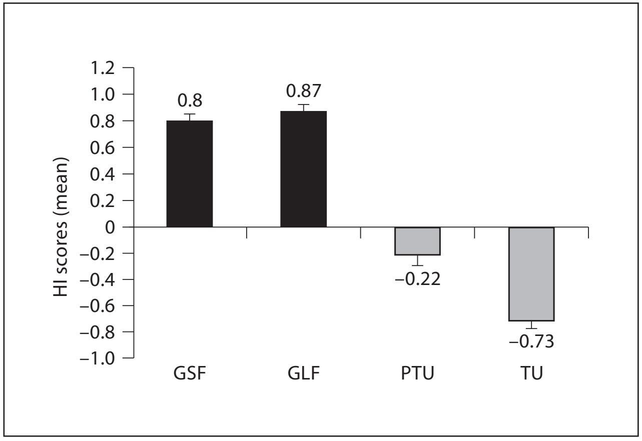

Fig. 2. Mean value of HI for each task. HI values range from –1 to 1 and correspond to the percentage of right-hand responses varying between 0 and 100. GSF = Grasping small food; GLF = grasping large food; PTU = proto-tool use; TU = tool use.

curred for all individuals ($p < 0.001$). In contrast, in the proto-tool use task, the 2 females did not deviate significantly from chance ($p > 0.10$) whereas the male showed a significant left bias ($p < 0.05$). Finally, in the tool-use task there was a significant left-hand bias ($p < 0.001$).

Discussion

The hypothesis suggested in this paper was that right-handedness increases with the complexity of the tasks. In order to test this assumption, we examined hand preferences in 3 adult gorillas performing 4 tasks of varying complexity.

Concerning grasping large food, we found a right-hand preference, which differs from results found in the literature. Indeed, other authors found no hand preference for unimanual tasks (grasping fruits and vegetables) but reported that ambipreference occurred [Meguerditchian et al., 2010]. On the contrary, our findings of a consistent bias for right-hand grasping of small food with a precision grip did not differ from those noted in gorillas by Byrne and Byrne [1991] and Byrne et al. [2001], in capuchins by Costello and Fragaszy [1988] and in bonobos by Christel [1994]. This leads us to ask questions about the right-handed bias at a population level that exists in some tasks and species. Furthermore, we found no laterality difference between grasping small food and large food. Does it mean that these two tasks are similar in complexity or that a more complex task does not necessarily induce a more lateralized behaviour?

In addition, there was no significant hand bias in the proto-tool use task except in the male, who demonstrated an individual-level left-hand preference. The null finding in the coconut task cannot be attributed to the fact that the animals were not experienced with this task (they had already accomplished it as often as they had the tool-using task), even if we can hypothesize that several day sessions would have induced the animals to develop a preference. So, this task, considered to be more complex than the first, involved a smaller lateral bias. These results raise questions about the postulate that the complexity of the task increases right-hand preference [MacNeilage et al., 1987; Uomini, 2009]. This result could also question the scale of motor complexity. Indeed, since both the large food and the proto-tool tasks involve palm grasping, the coconut task could be considered to be as simple as the task grasping large food.

A significant left-hand bias emerged for the tool-using action in the 3 gorillas, as is the case in wild chimpanzees for termite fishing in Gombe [Lonsdorf and Hopkins, 2005] and as noted by Fagot and Vauclair [1988a] for food extraction in baboons. In contrast, other researchers have demonstrated a consistent bias for right-hand reaching in the hole task in capuchins [Spinozzi and Truppa, 1999]. These results do not confirm that species-level right-handedness emerged through increasingly complex tool-using activities [Cashmore et al., 2008; Uomini, 2009]. It would now be necessary to test our assumption at a population level and to conduct the same experiment with other groups of gorillas. Finally, it would be interesting to compare actual primate tool users' artefacts to those of hominids in order to better infer hand preference among hominids.

Finally, we can wonder why there is inconsistent evidence on hand preferences in tasks that involve operations in hidden space. The double dissociation found between right-handedness for reaching and left-handedness for the branch test is important, even though it involved just 3 subjects. Why did this happen? For example, does the latter result have anything to do with a right-hemisphere spatial specialization being used for conceptualization of the hidden spaces?

Conclusion

First, we can conclude that (1) some lateral bias exists at a population level, (2) the complexity of the task does not necessarily induce a right-handed bias and (3) a subject can be right-handed for a complex task and left-handed for another one.

These results, complemented by many publications on hand preference in non-human primates, reveal a great variability, which makes it very difficult to infer hominin handedness with artefacts.

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Research report

Diversity of grip in adults and young humans and chimpanzees (*Pan troglodytes*)

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ABSTRACT

Grasping is essential for primates in numerous behaviors. A variety of different grasping techniques are used for obtaining food. Among humans, several studies have shown that the properties of the objects such as the size or the form influence grasp patterns. In addition, other works have tested the individual variability through grasping strategies and age and several studies have revealed some similarities between great apes and humans in grip types. Finally, results on hand preference are still equivocal and, for non-human primates, object parameters and age effect are rarely tested together, even though it is a methodological aspect important to consider. The study sought to determine whether grip type varied according to the age of the subject, the species (human versus chimpanzee), the size of the object and the hand used. Frame-by-frame analysis of hand contact strategies and statistical results indicated that (1) adults of both species used fewer contact strategies than juveniles and that there was a greater variability of contacts for small than for large objects (2) young juvenile chimpanzees and human children follow a similar grip types development, i.e. more frequent use of precision grips with age (3) juvenile chimpanzees used all five categories of grip and the adults used the "thumb-fingerpad(s)" more than the "precision grips" in addition to the "power grip" and (4) a right hand preference was greater for the grasping of small objects with "precision grips" in adults for both species. These results are discussed in relationship with neurology, morphology and grasping evolution.

1. Introduction

The hand of primates is used in several behavioral activities including locomotion, grooming, drinking, feeding, grasping of various objects and tool use [3,20,21]. Grasping objects involves various hand and digits' postures divided into different types ranged between two main grips: the former in which "the object may be pinched between the flexor aspects of the fingers and the opposing thumb" ("precision grips") and the latter in which "the object may be held in a clamp formed by the partly flexed fingers and the palm, counter pressure being applied by the thumb lying more or less in the plane of the palm" ("power grips") [41]. Several studies showed that the precision grip is available in the repertoire of great apes [8,9] and according to comparative works, capuchins are unique among the platyrrhine species for their ability to use functional precision grips [20].

Extensive kinematics and descriptive analyses of human hand posture relative to the properties of the grasped object have already been provided [5,15,17,49]. One study showed the effect of age and sex on digit contact strategy and posture during human precision grasp of spherical objects of different sizes [55]. Several woks deal with the role of brain organization and reveal variations in the pattern of hand preferences related to the grasping techniques [23,25,51]. Other researches concern the posture of the hand during grasping behavior among great apes [6] and New World monkeys (*Cebus apella*) [51], grasping behaviors for very small objects [6,8,23,25], grasping kinematics in primates [10,11] and diversity of grip in *Macaca mulata* [32]. Nevertheless, only few studies test the effect of the age on grip types used by chimpanzees [6,53]. Moreover, comparing humans and chimpanzees can be very valuable. First, chimpanzees are prolific tool-users and routinely manipulate small objects in the wild and in captivity, often to forage [3,21,56]. Second, the various grip types used by chimpanzees are highly comparable to those used by humans [4,8,13,39,53]. Indeed, both human and chimpanzee grip types fall into the grip categories identified by Napier [41]. Third, chimpanzees' neural anatomy supports independent movement of the digits [30], as humans. Finally, chimpanzees and humans share several features of the skeletal and muscular anatomy [31,45].

In this frame, research on the development of human manual grips has shown that children develop some forms of precision grip by the age of 3 years [18] and may be capable of simple precision grip forms as early as 1 year [34]. Manual skill increases with age [18,34] and children can perform all types of hand movements used

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by adults by around 7 [18] to 8 years old [34]. This developmental trend appears to be similar in chimpanzees and mountain gorillas [7,13]. Finally, individual differences exist in young chimpanzees hand preference. Handedness studies of chimpanzees indicated an equal proportion of right- and left-handed subjects with significantly more lateralized than no-preference subjects in reaching tasks [12,19,24,35,53]. MacNeilage et al. [33] noticed a left-hand preference for visually guided reaching, and a right-hand preference for fine manipulations among primates. By contrast, another study conducted on young chimpanzees revealed a great variability of grip types and that the left hand is more efficient than the right concerning imprecise grips of small objects, and the right hand is more efficient than the left for power grips of medium-sized objects [27]. Facing these results, we can wonder if (1) the variability of grip types could vary according to the age of the chimpanzee and if it is a human characteristic, (2) grip types, e.g. "precision grip" could change with age (3) the right hand would excel in fine manipulations and if its efficiency/accuracy would increase with age for both species.

In order to address these questions, the study sought to determine whether grip type varied as a function either of the age of the subject, the species, the size of the object and/or the hand used. First, an ethogram illustrating the repertoire of grip types for chimpanzees and humans was established. Second, hand preference in young and adult chimpanzees has been observed. It was expected that the variability of grip types is lower in human and with age for both species and that the precision grips could be more used by adults than by young subjects. Finally, we did not expect anything about hand preference as the previous results were very equivocal for chimpanzees.

2. Materials and methods

2.1. Subjects

The data represented in this study are based on institutional approval observations of 18 chimpanzees (*Pan troglodytes*) and on Institutional Review Board approved observations of 18 humans. Chimpanzees (Zoo de Beauval, France) were composed of nine adults (5 females, 4 males, age range 16–25 years, average 19 years, standard deviation 3.1) and nine juveniles (5 females, 4 males, age range 4–7 years, average 5.5 years, SD 1.5). The young juveniles were 5.5 years old (mean age), an age during which precision grip may be expected to be in the process of fine-tuning [14], which will allow us to expect to observe precision grip and compare the results with young humans. The human sample was composed of nine adults (5 females, 4 males, age range 23–59, mean age 38 years, SD 10.5) and nine children from 2 to 5 years old (5 females, 4 males, age range 2–5 years, mean age 3.5 years, SD 1.2). The young humans were 3.5 years old, an age during which manual skill appears to increase rapidly [18,34].

2.2. Procedure

For the human sample, 50 small objects and 20 large objects were scattered haphazardly on the floor, a flat and smooth surface, for each individual. The human subjects had to come into the room in a quadruped posture in order to grasp objects. Chimpanzees were observed three days per week during two months and the time of observations of each subject was standardized following the methods suggested in comparative ethology [1,29]. It was possible to identify individuals. The objects were scattered on the ground of the enclosure, a flat and smooth surface, when animals were locked away. The small objects involved spherical cereals and the large ones included small apples for human children and juvenile chimpanzees and large apples for human and adult chimpanzees. Subjects grasped the food and placed it in the mouth in order to eat it. The sizes of the objects were calibrated according to the length of the hand of the species. The length of the hand involved the distance between the proximal part of the third metacarpus and the distal part of the third ray (from the wrist, excluded, till the tip of the third digit). The diameters of the objects represented approximately 4% (3.80 ± 0.08) for small objects and 40% (38.10 ± 0.80) for large objects of the length of the animals hand.

During the experiments on chimpanzees and humans, the grips that could not be confidently identified were rejected and represented approximately 14 percent of the observations. The determination of the grip was made using a frame-by-frame analysis, with a Basler camera recording 250 images per second. A total of 2880 grasps were recorded for the two studied species and the two age classes (1260 grasps for human and 1620 for chimpanzees). For each grasp the surface of the hand in contact with the object was notes. The percentage of each grasping category was calculated on the basis of the total number of grasps observed in each species.

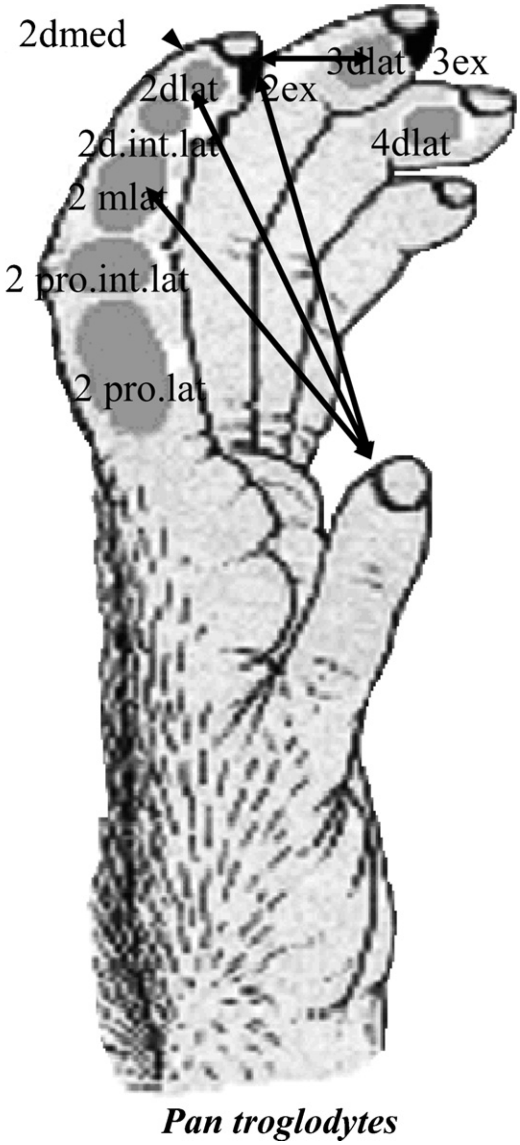

Fig. 1. Possible contacts between the fingers. Ex: extremity (tip); d: distal; lat: lateral; int.: interphalanx; pro.: proximal; m: middle.
Modified from Christel, 1993.

2.3. Ethogram and classification system

First, all the different contacts were defined (modified from [8]) following the anatomical terminology (Fig. 1) and quantified (Table 1). Second, from all these modes of grasping, five categories of grasping behavior have been determined (modified from [27]):

- *Category 1*: contact between the distal phalanges of the thumb and the index finger and the object, involving the pincer grip between the tips of the first and second finger in more than 80% of the cases. This category corresponds with the category called "precision grip" from Jones-Engel and Bard [27].
- *Category 2*: contact between the distal phalanx of the thumb and at least one distal part of another finger than the index. This category is called "thumb-to-fingerpad(s)" in Jones-Engel and Bard [27].
- *Category 3*: contact between the distal phalanx of the thumb, the lateral side of the middle, proximal phalanxes of the index finger and the object. This category included the same grip that Napier termed inefficient grip [42,43] and that Jones-Engel and Bard called "imprecise grip" [27].
- *Category 4*: contact between one or several fingers, except the thumb, and the object ("without thumb").

Table 1
Variability of the contacts between the fingers and the object used the species.

Category of grasping	Contacts	Human adult		Human children		Chimpanzee adult		Chimpanzee juveniles	
		S.O.	L.O.	S.O.	L.O.	S.O.	L.O.	S.O.	L.O.
Thumb-index grips	1p–2ex	X		X	X	X		X	
	1ex–2ex	X		X		X		X	X
	1ex–2dlat	X		X		X		X	X
	1ex–2p	X		X		X		X	
	1p–2dlat			X	X	X	X	X	X
	1p–2p	X		X	X		X	X	X
Thumb lateral	1p–2mlat					X		X	X
	1ex–2pr.lat					X		X	
	1ex–2d.int.lat					X		X	
	1ex–2mlat					X		X	X
	1p–2pr.lat					X		X	
Thumb distals	1p–2p–3p	X	X	X	X		X		X
	1p–2p–3p–4p		X		X		X		X
	1p–2p–3p–4p–5p		X		X		X		X
	1ex–3ex	X		X		X		X	
	1ex–2ex–3ex	X		X		X		X	
	1ex–2ex–3ex–4ex					X		X	
	1p–3p	X		X					
	1p–2ex–3ex	X		X	X	X		X	
Without thumb	2m.med–3m.lat					X		X	
	2d.med–3d.lat					X	X	X	X
Palm grips	1-2-3-4-5-palm		X	X	X	X	X	X	X
	1-2-3-palm		X		X	X	X	X	X
	2-3-4-5-palm			X		X	X	X	X
	1-2-palm				X	X	X	X	X

Ex: extremity (tip); p: pulp; d: distal; med.: medial; lat: lateral; int.: interphalanx; pro.: proximal; m: middle (see Fig. 3 for more explanation). S.O.: small objects; L.O.: large objects.

- *Category 5*: contact involving the palm, the thumb and one or several ventral part of other fingers and the object, involving the power grip of Napier [41] and Jones-Engel and Bard [27].

2.4. Statistical analysis

Statistical analyses were based on the five grip categories previously defined. We calculated the basic statistics (mean, SEM, coefficient of variation) for each grasping category per species. A two-way analysis of variance was performed to test the effects of grip type and of object size for each species and each age [50,58]. Species, age and the object size were treated as the fixed factors and the grip categories as a random effect. The effect of age within species was then tested over the residual [16]. The sequential Bonferroni test described by Rice [48] was used to limit the risk of mistakes in assessment of the experimental results ("overall experiment-wise error" [50]) and statistical significance was set at the 0.05 level. *F*-statistics for the fixed effects (species, age and the object size) were calculated by dividing the species and the squared size mean by the mean square for the random effect (category). Finally, a two principal-components analysis determined which of the grasping categories contributed most to the variation in the entire data set for both volumes of the objects. An analysis of variance (ANOVA) was performed on principal component 1 (PC1) and principal component 2 (PC2) to determine if there were significant differences among treatment means when all grasping categories were considered together. This approach was also used to control if some groups could emerge.

Concerning hand preference, for each task, we analyzed individual frequencies for the use of the left and the right hand using the two-tailed binomial test. We classified subjects with significant positive *z* scores ($z > 1.96$, $p < 0.05$) as right-handed and individuals with significant negative *z* scores ($z < -1.96$, $p < 0.05$) as left-handed. For each subject, we calculated a handedness index (HI) using the formula $(R - L)/(R + L)$, in which R and L were the total number of right- and left-hand responses, respectively. The resulting values, ranging from −1.0 to 1.0, differentiated each subject's hand preference on a continuum from strongly left-handed to strongly right-handed. Finally, we applied a one-sample *t*-test to the group data to evaluate whether, for each measure, the mean HI score per subject differs significantly from a chance distribution with a mean of 0.

3. Results

3.1. Variability of contacts

Chimpanzees used from 9 to 20 modes of contact in grasping small and large objects whereas humans used from 5 to 13 (Tables 1 and 2). For both human and chimpanzees, adults used fewer modes of contacts than juveniles and each subject used fewer modes of contacts to grasp large object than to grasp small objects (Fig. 1).

3.2. Grip type and object size

Statistical analyses were based on the five grip categories. Analysis of variance on the frequency data revealed significant main effects of grip type ($P < 0.001$) and of object size ($P < 0.001$), for both species and both ages. It also revealed a significant interaction between object size and grip type ($P < 0.001$) for both species and both ages. For example, in order to grasp small objects, chimpanzee adults used preferentially the "thumb-fingerpad(s)" category (category 2) and the lateral side of the index finger ("imprecise grip", category 3), whereas human adults never used this category and preferred the "precision grips" (category 1) almost exclusively ($P < 0.001$). Chimpanzee juveniles used most often the "imprecise grip" category and after the "precision grip" whereas human children used preferentially the "precision grip" and the "thumb-fingerpad(s)" category ($P < 0.001$) (Fig. 2).

In order to grasp large objects (Fig. 2), chimpanzee adults used "power grips" (category 5) preferentially, whereas human adults showed a clear tendency to use "thumb-fingerpad(s)" ($P < 0.001$). Chimpanzee juveniles used "power grips" preferentially whereas human children used "power grips" as often as

Table 2
Mean number (±standard deviation) of modes of contacts used by the six species of primates according to the volume of the object.

Species	Small objects	Large objects
Homo s. (adults)	10 ± 2.2	5 ± 1.6
Homo s. (children)	13 ± 3.2	10 ± 2
Pan troglodytes (adults)	21 ± 4	9 ± 2.5
Pan troglodytes (juveniles)	22 ± 4.3	14 ± 3.2

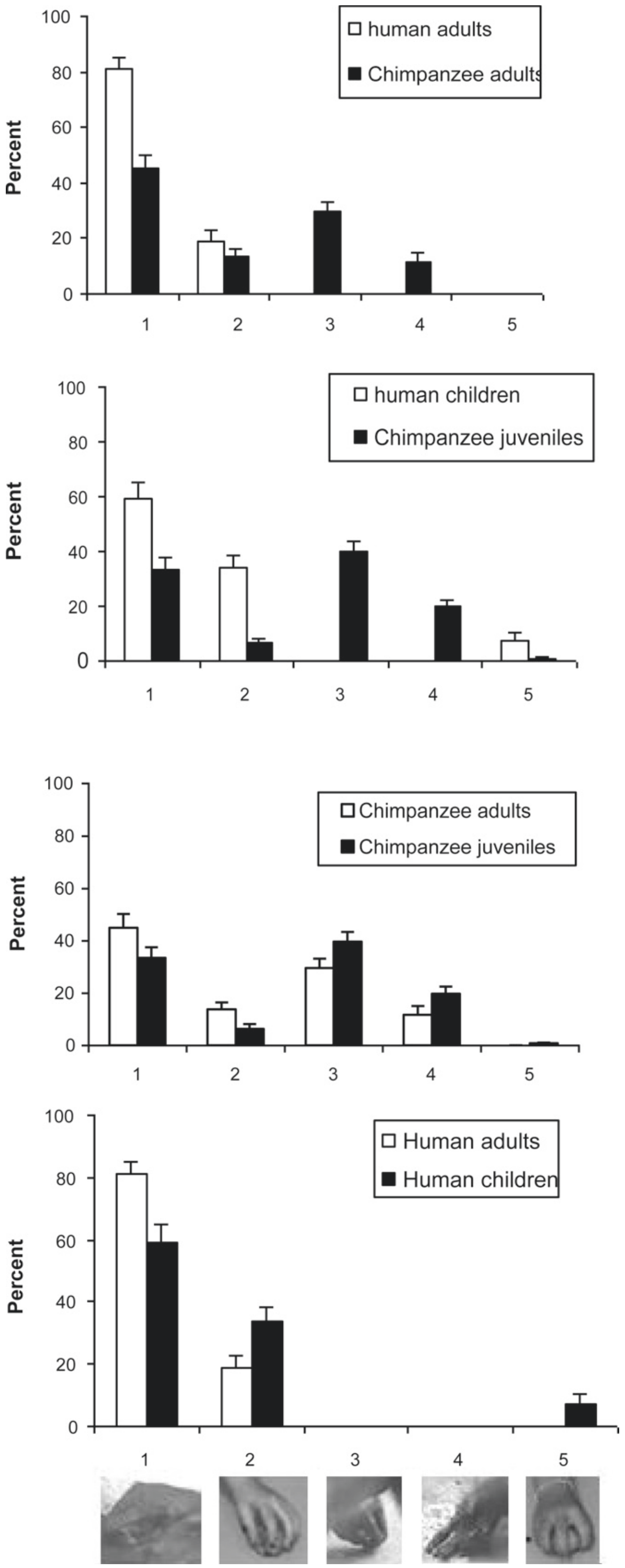

Fig. 2. Frequency of five different categories used to grasp small objects. 1. Thumb-index grips; 2. thumb-distal(s); 3. thumb-lateral; 4. without thumb; 5. palm grips.

“thumb-fingerpad(s)” grips ($P < 0.001$). Finally, human children are much closed to chimpanzee adults when they grasp large objects ($P > 0.05$) whereas they clearly differ when they grasp small objects ($P < 0.001$) (Fig. 3).

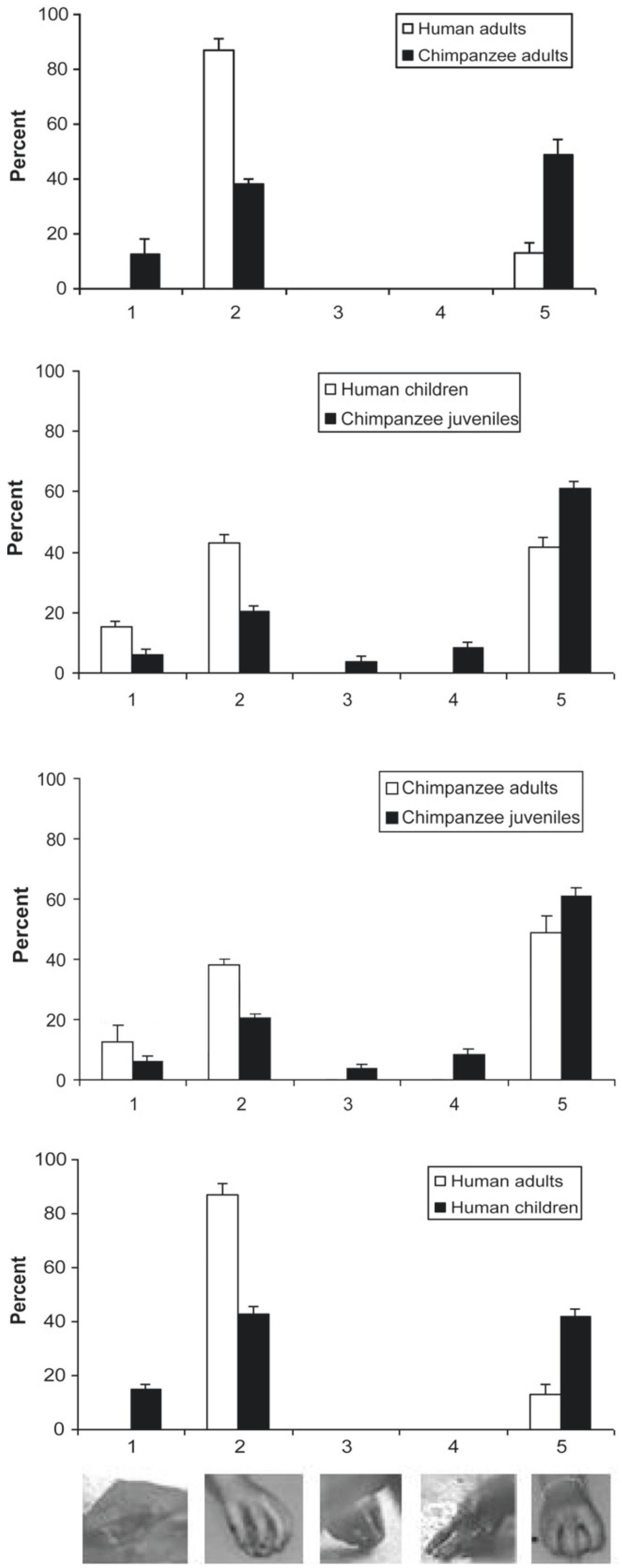

Fig. 3. Frequency of five different categories used to grasp large objects. 1. Thumb-index grips; 2. thumb-distal(s); 3. thumb-lateral; 4. without thumb; 5. palm grips.

3.3. Age effect in both species

One statistical question was whether grip types, i.e. “precision grip” could change with age. First, the age had an effect on the percentages of grasping categories used by humans and chim-

Table 3
Age effect in humans and in chimpanzees in the grasping of small objects.

Species	Variables	Species (1,8)	Individuals (8,36)	Species × individuals (8,36)
Humans (young and adults)	Thumb index grips	69,2*	1,7	95,4*
	Thumb-distals	54*	1,9	56,2*
	Thumb-lateral	–	–	–
	Without thumb	–	–	–
	Palm grips	35,4*	1,4	43,4*
Chimpanzees (juveniles and adults)	Thumb index grips	27,9*	1,8	64,5*
	Thumb-distals	63,9*	2,1	11,7*
	Thumb-lateral	35,2*	1,7	39,2*
	Without thumb	17,3*	1,4	51,2*
	Palm grips	5,8*	1,5	25,5*

F-values from two-way ANOVAs performed separately on the percentage of each grasping categories. The fixed effect of specie was crossed with the random effect of individuals.
– No data (percent of category = 0).
* $p < 0.05$.

panzees to grasp large objects ($P < 0.001$) and small objects ($P < 0.01$) (Tables 3 and 4). Indeed, whatever the volume of the object, *F* values were significant for each category of objects and both species. For example, concerning grip types used by human adults and children to grasp small objects, all the values were significant at the level $P < 0.05$, meaning that there is an effect of the age on all the grasping types used.

In addition, changes occurring with age presented some similarities, even if the categories of grasping are different (Fig. 2). To grasp small objects, human children use less often the "precision grips" and more often "thumb-fingerpad(s)" and "power grips" than adults ($P < 0.01$). To grasp large objects, human children use less often the "thumb-fingerpad(s)" and more often the "power grips" than adults ($P < 0.01$). To grasp small objects, compared to juvenile chimpanzees, chimpanzee adults more often use the "precision grip" and less often the "imprecise grip" ($P < 0.01$). To grasp large objects, chimpanzee adults used less often "power grips" category and more often "thumb-fingerpad(s)" category ($P < 0.05$). Finally, even if the categories used are different and their frequency too, the age had a similar effect on both species: an increase of the use of the "precision grip" and "thumb-fingerpad(s)" categories, a decline of the use of the "imprecise" and "power grips" categories.

Finally, age had an effect on hand preference (Figs. 4 and 5) both for human and chimpanzee ($P < 0.05$). In human, the use of right hand for grasping small objects with the category 1 ("precision grip") and for grasping large object with the category 5 ("power grip") increases with age. In chimpanzee, the use of right hand for grasping small objects with the category 1 ("precision grip") increase with age. Surprisingly, the left hand is used by young chimpanzee for grasping large objects with the category 5 ("power grip") whereas adults use the right hand.

3.4. *Principal component analysis*

The principal component analysis on the five categories used to grasp small objects (Fig. 5) showed that the variables most responsible for separation on PC1 were grips from the category 1 ("precision grips"), while the variables most responsible for separation on PC2 were grips from the category 5 ("power grips") and category 1 ("precision grips"). Performing an ANOVA on these scores indicated a highly significant difference among the means for PC1 ($F = 545.08$, $P < 0.05$) and for PC2 ($F = 142.43$, $P < 0.05$). Post hoc tests (Scheffe) for small objects indicated for PC1 that all species were different ($P < 0.05$, $N = 2$). For PC2, all species were different ($P < 0.05$, $N = 2$). The principal component analysis of the five categories used to grasp large objects showed that the variables most responsible for separation along PC1 was "palm" grasping, while the variables most responsible for separation along PC2 were thumb-lateral and without-thumb categories. The same topography of groups of species has been found. Performing an ANOVA on these scores indicated a highly significant difference among the treatment means for PC1 ($F = 420.32$, $P < 0.05$) and for PC2 ($F = 256.10$, $P < 0.05$). Post hoc tests (Scheffe) for large objects indicated for PC1 that all species were different ($P < 0.05$, $N = 2$). For PC2, all species were different ($P < 0.05$, $N = 2$).

3.5. *Hand preference*

We found a significant right-hand preference for grasping small food with the category 1 ("precision" grip) in all human ($P < 0.001$) and in all chimpanzee, specifically in adults ($P < 0.001$). By contrast, we found a significant left-hand preference for grasping large food with the category 5 ("power" grip) in most of young chim-

Table 4
Age effect in human and chimpanzees during grasping of large objects.

Species	Variables	Species (1,8)	Individuals (8,36)	Species × individuals (8,36)
Humans (young and adults)	Thumb index grips	570,9*	0,8	10,8*
	Thumb-distals	765,8*	1,8	34,3*
	Thumb-lateral	–	–	–
	Without thumb	–	–	–
	Palm grips	261*	1,2	43,5*
Chimpanzees (juveniles and adults)	Thumb index grips	11,1*	1,1	52,2*
	Thumb-distals	346,9*	1,4	12,3*
	Thumb-lateral	57,7*	1,6	10,6*
	Without thumb	149,9*	1,9	12,9*
	Palm grips	23,5*	0,9	84,1*

F-values from two-way ANOVAs performed separately on the percentage of each grasping categories. The fixed effect of specie was crossed with the random effect of individuals.
– No data (percent of category = 0).
* $p < 0.05$.

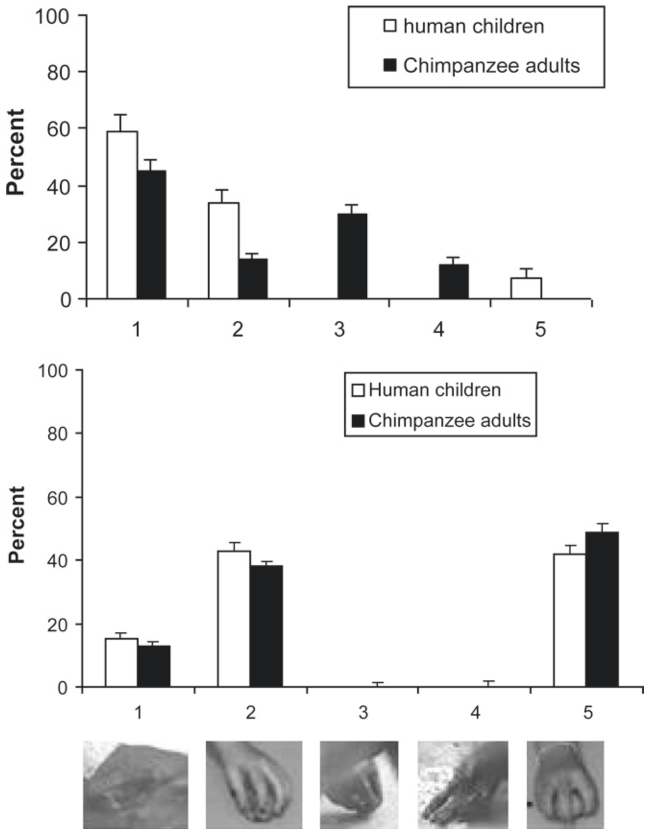

Fig. 4. Proximity between human children and chimpanzee adults to grasp small (a) and large (b) objects. 1. Thumb-index grips; 2. thumb-distal(s); 3. thumb-lateral; 4. without thumb; 5. palm grips.

panzee ($P < 0.01$) whereas adults use their right-hand preferentially ($P < 0.001$) for the same task. Concerning the grasping of small food with the category 3 (“imprecise grip”), the mean HI score for the chimpanzees, both young and adults, did not deviate significantly from chance ($P > 0.10$): four of them showed a left-hand preference and five showed a right-hand preference.

4. Discussion

Previous work examined the effects of the size and shape of objects in determining grasping patterns used by humans [15]. Here, by using objects of similar shape but with two different sizes, the contribution of digit contact strategies was examined. Adult subjects, both humans and chimpanzees, used more limited-digit contact strategies than, respectively, children and juveniles. Adults of both species were cognitively more familiar with grasping and their motor patterns may be more developed. In addition, humans grasped both small and large objects with “precision grips” whereas chimpanzees grasped small objects with “precision grips” and large one with “power grips”. As this result cannot be explained by different ratios of food size to hand size, we can suggest that human, when the object is not too heavy, prefers to grasp with the distal phalanges of their fingers than with the palm. This may allow human to have a better sensitive perception than the “power grips”. Finally, less inter-individual variability than reported by Wong and Whishaw [55] has been found concerning grip types. This may be due to the fact that our study monitored a larger range of grip types. To grasp large objects, when chimpanzee juveniles used “power grips”, adults opted more for “power grips” and also “precision grips”. Chimpanzee juveniles used all five categories of grip and the adults used the “thumb-fingerpad(s)” more than the “precision grips” in addition to the “power grips”. These results are quite different from those obtained by a previous study [6], which showed that older chimpanzees mostly used a pincer grip (included in the “precision grips”), on the smallest sizes of apple cubes and a “power grip” on the largest sizes. However, these contrasts may be due to the design of their study since the objects were presented to their subjects impaled on a stick. In addition, in all comparisons of grips of large objects across species and across age groups, “power grips” were more frequent than “thumb-fingerpad(s)” grips for the larger hands (chimpanzee vs. humans and adults vs. juveniles). As this result cannot be explained by different ratios of food size to hand size, we have to look for other explanations. Adult chimpanzees used more often the palm of their hand than human adults. This result could suggest that humans are looking for a better sensitive perception during the touch or that the learning of various manual activities requires more finger pads for humans than for chimpanzees. In addition, juveniles of both species used more often

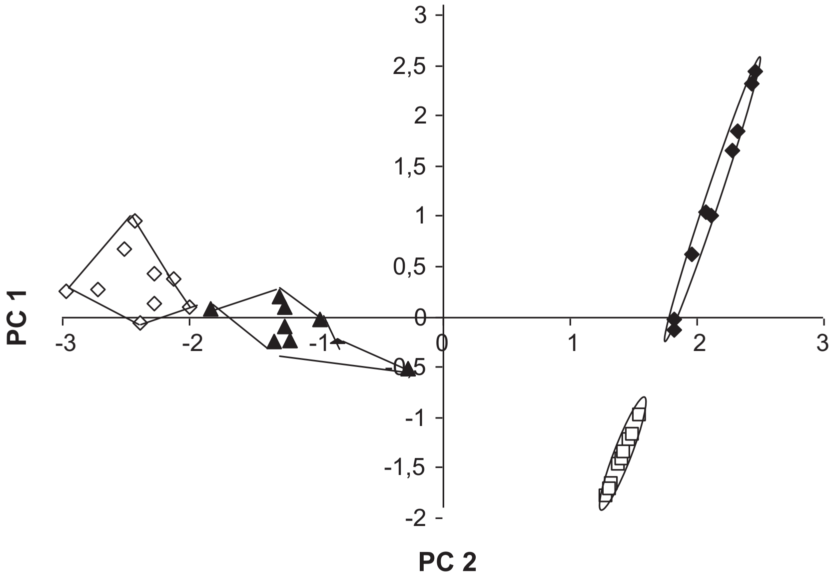

Fig. 5. Principal component analysis on the five categories of grasping used to grasp small objects (Principal component analysis on the five categories of grasping used to grasp large objects showed almost the same results). ◊ Chimpanzee juveniles; ▲ chimpanzee adults; □ human adults; ◆human children

the palm of their hand than adults. This could suggest that the influence of the learning and of the development of the touch sensation is involved in the choice made by adults to use more often the distal phalanges of their finger than the palm. Finally, the fact that human children seem to be like chimpanzee adults may be linked to the development of the nervous system.

Previous studies noticed that precision grips were not frequent before 8 years of age [6], which is not the case in our present experiment, where chimpanzee juveniles were 5.5 years old on average and often used pincer grips (1ex–2ex), involved in the "precision grips". Butterworth and Itakura showed that human children systematically selected precision grips to grasp small objects [6], contrary to the chimpanzees we studied. It is possible that they use less "precision grips" than humans as they have a relatively small thumb. However, previous studies [47] showed that it is possible to have a small thumb and to grasp with "precision grips" grip relatively frequently (e.g. gorillas). Our work showed that, in the same task, human children also selected the "power grips" for small objects, while chimpanzee juveniles used equally "precision grips" and "imprecise grips". If all these differences between experiments may be partly explained by methodological reasons (objects were not exactly the same for example), it may be that some individuals started to use "precision grips" very early, while others started later. Indeed, even among human children, the first application of a "precision grips" can happen between the age of 1 and 2 [18,34]. Furthermore, the development of the grasping behavior can be specific to one group and some non-human primates can early reproduce the behavior of adults who raised them. Finally, it seems that the juvenile chimpanzees and human children follow a similar development of these hand postures. At 5 years old, use the same precision grips used by human adults, though with less frequency and efficiency [18,34]. Similarly, 5-year-old chimpanzees possess the same ability to use precision grips. It will be useful in future studies to determine the age at which these movements first appear in young chimpanzees. In addition, differences between humans and chimpanzees may not be related only to ages but also to phylogenetic position, genetic heterogeneity, learning and morphological differences in hand structure. Indeed, while the saddle carpo–metacarpo joint of the thumb allows the thumb to oppose the other digits among chimpanzees [44], the extent of pad-to-pad surface area contact with the other digits is limited by the short thumb [37]. To add, the skeletal morphology of the carpals and metacarpals severely hinders the chimpanzee's ability to cup the palm [36] whereas in humans, cupping of the palm likely contributes to precision handling where fingertips are placed so that the object can be held with the help of the opposition of the thumb [28]. Moreover, the amount of force that the chimpanzee thumb can apply in a precision grip is lower than humans one [37,38]. Finally, various differences in thumb musculature [38] may explain the chimpanzee's difficulty with manipulating objects with the fingertips [28]. Those morphological differences explain why the chimpanzee "precision grip" is different from humans one and why they almost never use pad to pad grips (1p–2p in our study).

Another reason of the differences between chimpanzee and human grasping could be found in the anatomical structure of the nervous system. However, chimpanzees possess, as humans and gorillas, the neural anatomy that is involved with independent movement of the digits [7,22,26,30]. This result implies that the neural and muscular anatomy required for "precision grips" evolved at least from a common ancestor to humans, *Pan*, and *Gorilla*. Modern human hand morphology and neural control may have evolved as the use of precision grip expanded to more complex toolmaking. It will be very interesting to test this assumption in the future by working more particularly on capuchin monkeys, *Cebus apella*, which have already showed a high proximity with human in grasping and manipulative tasks [20,46].

To conclude, age is an important factor as already suggested for chimpanzee, prosimian, and human samples. Indeed, both strength and direction of lateral bias changes from the infancy/juvenile period to the adolescent/adult period [2,12,40,52–54,57]. Here, the variability of grip types vary according to the age both in human and chimpanzee, grip types change with age (i.e. "precision grip" increase) and the right hand excels in "precision grips" in the chimpanzee whatever their age. This last result agrees with those obtained by MacNeilage et al. [33] and by Hopkins et al. [23] who found that smaller food items elicited significantly more "precision grips" for the right hand. On the contrary, our result contrast with Jones-Engel and Bard [27] who did not find a right bias for precision grip and with Tonooka and Matsuzawa [53] who showed that the left hand was more frequently used for precision and imprecise grips with the juvenile and children subjects. Further studies on larger sample taking into account the body posture, the food position, the age and the task would be necessary to explain the diversity we quantified in terms of laterality. These results show, for another time, that it is almost impossible to deduce a model of laterality that could be used in the frame of the evolution and of neural organization. The inference of grasping behavior of earlier hominids with similar morphology is almost impossible if we consider the great variability of grip types and hand preferences. Finally, the genus *Pan* and *Homo* are close relatives but their grasp patterns and hand preference are more diverse than has been thought even if they share many similarities. Although it is difficult even impossible to infer the grip postures and hand preference of hominoid fossils, these results might imply that the common ancestor of apes was a primate that featured a great diversity of grasping patterns and a lateralized limb, with a hand preference probably varying according to the task and the body posture. A longitudinal study, on several years and on several representative species of the primate phylogeny, may help us to clarify all the controversies existing around this concept.

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Résumé

La préhension manuelle, impliquée dans l'acquisition de nourriture et la locomotion, est commune à tous les primates. Toutefois, les mécanismes de son émergence et de son évolution restent encore à élucider. Quels sont les facteurs 1) écologiques (propriétés de la nourriture et du substrat) conduisant à une plus grande utilisation de la main chez les premiers primates et 2) fonctionnels (posture corporelle, cinématique du membre supérieur) impliqués dans l'évolution de la préhension des primates?

Afin d'apporter des éléments de réponse, cette thèse a pour objectif de déterminer les stratégies comportementales et cinématiques de la préhension non contrainte d'espèces représentatives des grands groupes phylogénétiques primates (microcèbe, lémur catta, capucin, gorille, chimpanzé, humain).

Tout d'abord, les stratégies comportementales du microcèbe, présentant des convergences avec les premiers primates, suggèrent que l'arboricolie et l'omnivorie ont joué un rôle important dans l'émergence des capacités de préhension des primates. Ensuite, l'analyse de la préhension du gorille et de l'humain montre une influence limitée des postures corporelles sur les stratégies articulaires du membre supérieur. Enfin, la comparaison de toutes les espèces montre que certains invariants cinématiques de la préhension liés à la vitesse du poignet existent indépendamment des espèces et que d'autres semblent être lié au comportement des espèces. En outre, deux stratégies articulaires divisent les espèces favorisant les rotations (gorille et chimpanzé) de celles privilégiant les flexions-extensions (lémur, capucin, humain). Ces stratégies articulaires semblent avoir évolué indépendamment de leurs capacités préhensiles.

L'ensemble de ces résultats est discuté au regard des données comportementales et fonctionnelles connues et confronté aux théories actuelles sur l'origine et l'évolution de la préhension.

Mot clés : préhension, primates, comportement, cinématique, membre supérieur, évolution.

Abstract

Manual prehension, involved in food acquisition and locomotion, is common to all primates. However, the mechanisms of its emergence and evolution still remain to be elucidated. This prompts questions such as 1) what are the ecological factors (food and substrate properties) leading to an increase of the use of the hand in early primates, and 2) what functional factors (body posture, kinematics of the forelimb) are involved in the evolution of prehension in primates?

The thesis project aims to determine the behavioural and kinematic strategies of unconstrained prehension in representative species of the major lineages of primates (the mouse lemur, lemur catta, capuchin, gorilla, chimpanzee, human).

The behavioural strategies of the mouse lemur, convergent on early primates, suggest that arboreality and omnivory have played an important role in the origin of prehensile abilities in primates. The analysis of prehension in gorillas and humans shows a limited influence of body posture on the angular joint excursions and kinematic strategies. A comparison of all the species reveals that some kinematic invariants in the wrist velocity profile exist, independent of the species. Yet others appear to be related to the specific behaviour of the species. Moreover, two joint motion strategies divide the species, one favoring the rotations (gorillas and chimpanzees) and one involving more flexion-extension movements (lemurs, capuchins, humans). These joint motion strategies seem to have evolved independently of grasping ability.

The results are discussed in the context of current work and theories on the origin and the evolution of prehension in primates.

Keywords : prehension, primates, behaviour, kinematics, forelimb, evolution.