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THE SELF AND OTHERS:
A GLIMPSE INTO THE BONOBO MIND

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Titre:

"The self and others: a glimpse into the bonobo mind"

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General abstract

The question of how human intelligence evolved has been the focus of a vast amount of research. To investigate the evolutionary trail of our cognition and to better estimate when different cognitive capacities appeared through time, we must look to other species using the comparative approach. Theory of mind is one such cognitive capacity that has a fundamental role in the proper functioning of our social interactions. To possess a 'theory of mind' implies the ability to attribute mental states (goals, intentions, knowledge and beliefs) to one's self and to others. It is suggested that individuals in possession of this capacity can understand the reality of others, at least implicitly, even if that reality differs from one's own, and use mental states as a basis of interpreting and predicting the behaviour of others. Research efforts over the past 40 years have produced an increasingly complex picture of theory-of-mind related capacities in great apes, suggesting that a cognitive capacity previously thought to be unique to humans may be at least partially shared with animals.

My research aimed to investigate, through a variety of approaches, whether bonobos are able to maintain different perspectives of reality; their own and that of others. To address this, I attempted to shed light on three questions. First, how do bonobos perceive themselves in different kinds of self-images and how does experience modify such perception? Second, do bonobos socially learn from others in the context of feeding, even if they have contradictory knowledge about reality compared to what is being demonstrated to them by others? Third, are bonobos able to use previously acquired knowledge about others' behaviours to make pragmatic inferences when attending to their communication signals?

To answer the first question, I investigated how mirror-naïve bonobos reacted to a variety of contingent and non-contingent self-images in the form of video and mirror images, as well as footage of known and unknown conspecifics. I then investigated how the bonobos' perception of themselves in non-contingent video footage was influenced by prolonged mirror exposure. My findings provide evidence supporting the idea that bonobos do indeed have a sense of self but that this ability develops with experience.

To answer the second question, whether bonobos could learn from others through observation despite own contradictory experience, I designed an ecologically relevant social learning experiment that demonstrated that bonobos memorised others' food preferences and adhered to them, even if they knew viable alternatives. Importantly, socially acquired food preferences remained stable even after subjects became aware that both food types were palatable.

To answer my final question, I assessed whether bonobos could use previously acquired social knowledge about others' food preferences as premises for pragmatic inference when attending to their vocal behaviour. To do this, I ran a playback experiment that demonstrated that bonobos reacted differently to food calls of a demonstrator with a known food preference, compared to the food calls of a control individual with no known food preference. While subjects were not able to integrate all the information made available to them, they were able to integrate enough to draw inference from the two call providers' underlying difference in knowledge.

In sum, my findings provide ground to suggest that our last common ancestor was already in possession of a number of cognitive faculties that form the foundation of human intelligence. These findings, that range from perceiving one's own reality through a sense of self, to understanding the reality of others and incorporating their knowledge of reality, to finally using their knowledge of others' reality to make inferences of their communication signals, have provided, I hope, a further glimpse into the bonobo mind and, by extension, that of our common primate ancestors.

Keywords: ape, Bonobo, delayed self-recognition, food preference, foraging, language evolution, looking time, non-human primate, novel food, *Pan paniscus,* primate cognition, primate communication, self-awareness, social intelligence, social learning, Theory of mind.

Résumé general

La question de l'évolution de l'intelligence humaine a fait l'objet de nombreuses recherches. Pour étudier l’évolution de notre cognition et afin de mieux estimer l’apparition de nos différentes capacités cognitives dans le temps, nous devons nous tourner vers d'autres espèces en utilisant une approche comparative. La théorie de l'esprit est une de ces capacités cognitives qui joue un rôle fondamental dans le bon fonctionnement de nos interactions sociales. Posséder une «théorie de l'esprit» implique la capacité d'attribuer des états mentaux (objectifs, intentions, connaissances et croyances) à soi-même ainsi qu’aux autres. Certains suggèrent que les individus en possession de cette capacité peuvent, d’une part et de façon implicite du moins, comprendre la réalité des autres, même si cette réalité diffère de la leur, et d’autre part, qu’ils peuvent utiliser ces états mentaux comme base pour interpréter et prédire le comportement des autres. Les recherches au cours des 40 dernières années ont permis l’élaboration d’une image d’une complexité croissante des capacités liées à la théorie de l'esprit chez les grands singes, suggérant que cette capacité cognitive, considérée jusqu’à lors comme unique chez l’Homme est peut-être partagée au moins partiellement avec les animaux.

Mes recherches ont visé à étudier, par diverses approches, si les bonobos sont capables, ou non, de maintenir différentes perspectives de réalité; la leur ainsi que celle des autres. Dans ce but, j'ai souhaité répondre à trois questions. Premièrement, comment, les bonobos, se perçoivent-ils dans différents types d'images de soi et comment l'expérience modifie-t-elle cette perception? Deuxièmement, les bonobos apprennent-ils socialement des autres dans le contexte de l'alimentation, malgré le fait que leurs propres connaissances soient en contradiction avec ce qui leur est démontré par les autres? Troisièmement, les bonobos, peuvent-ils utiliser des connaissances déjà acquises sur les comportements d'autrui afin de faire des inférences pragmatiques lorsqu'ils perçoivent des signaux de communication de ces derniers?

Pour répondre à ma première question, j'ai mis en place une étude expérimentale afin d’évaluer comment des bonobos, naïfs, sans expérience préalable avec des miroirs, réagissaient à une variété d'images d’eux-mêmes et d’autrui. Plus précisément, des images de soi dans un miroir, des image de soi en vidéo directe ou non, ainsi que des images vidéo de congénères connus et inconnus. J'ai ensuite évalué comment la perception de leur propre image dans des séquences vidéos non-directes était influencée par l'exposition prolongée à leur reflet dans un miroir. Mes résultats soutiennent l'idée que les bonobos ont effectivement un sens de soi mais que cette capacité se développe avec l'expérience.

Pour répondre à la deuxième question qui visait à savoir si les bonobos pouvaient apprendre par l'observation des autres, malgré leur propre expérience contradictoire, j'ai conçu une expérience d'apprentissage social, écologiquement pertinente, qui a démontré que les bonobos mémorisaient et suivaient les préférences alimentaires des autres, même s'ils connaissaient des alternatives viables. De plus, ces préférences alimentaires acquises socialement sont restées stables même quand les sujets avaient pris conscience que les deux aliments proposés étaient appétissants.

Pour répondre à ma dernière question, j'ai évalué la capacité des bonobos à utiliser les connaissances sociales acquises précédemment relatifs aux préférences alimentaires des autres comme base d'information afin de faire des inférences pragmatiques lors de l'émission de vocalises de la part de ces derniers. Pour ce faire, j'ai mené une expérience en 'playback' qui a démontré que les bonobos réagissaient différemment aux vocalises alimentaires d'un démonstrateur ayant une préférence alimentaire connue, par comparaison avec les vocalises alimentaires d'un individu de contrôle sans préférence alimentaire connue. Bien que les sujets n'aient pas été en mesure d'intégrer toutes les informations mises à leur disposition, ils ont été en mesure d'en intégrer suffisamment et d'utiliser leurs connaissances au sujet des deux individus ayant émis les vocalises alimentaires pour faire des inférences basiques.

En somme, ces recherches fournissent un appui nous permettant de suggérer que notre dernier ancêtre commun était déjà en possession d'un certain nombre de facultés cognitives qui forment le fondement de l'intelligence humaine. Ces découvertes, qui vont de la perception de sa propre réalité à la compréhension de la réalité des autres donnent, je l'espère, un autre aperçu de l'esprit du bonobo et, par extension, de celui de notre ancêtre commun.

Mots-clés : aliments nouveaux, apprentissage social, Bonobo, cognition des primates, communication des primates, conscience de soi, durée d'attention, évolution du langage, grand singe, intelligence sociale, *Pan paniscus,* préférence alimentaire, primate non-humain, recherche alimentaire, reconnaissance de soi différée, Théorie de l'esprit.

1: General introduction

The human mind

Evolution of the human mind

The human mind is unique in the animal kingdom, doting us with a range of capacities that, at least at the level found in humans, are out of reach for any other species. Among these are our capacities for tool-making, imitation, self-awareness, language and theory of mind (Roth & Dicke, 2005). How, when and why humans evolved these capacities are questions that numerous research teams have been trying to elucidate for decades, with every finding bringing a little more clarity to the grand picture. While there is much to be learned about human evolution from the fossil record, much of the details linked to the evolution of our cognition leaves no trace at all (Hare & Yamamoto, 2017). In our effort to find answers, we must therefore turn to both our closer and more distant primate relatives in an attempt to find the evolutionary roots of the human mind and its associated cognitive processes. In adopting this comparative approach, we have found, time and again that not only are some of the faculties believed to be unique to humans, shared with our closer relatives, the great apes, but also, and more interestingly perhaps, so are the likely building blocks underlying these core capacities. By identifying the presence and absence of the evolutionary scaffold underlying the human mind we can shed light on the how, when and why of the emergence of these different capacities in the primate lineage.

This thesis offers a glimpse into the mind of one our closest extant relatives, the bonobo. More specifically, the research aims to focus on how bonobos perceive and form mental representations of themselves, and how they perceive and use the knowledge of others to shape their own behaviour through both social learning and as premises for inference during communicative acts. In doing so I hope to provide some new insight as to what the mind of our last common ancestor resembled over 7 million years ago (Endicott et al., 2010; Langergraber et al., 2012), that is, how they may have perceived reality, their own and that of others.

Pan and Homo: unveiling human evolution

In most research domains involving great apes, be it cognition, behaviour or ecology, the chimpanzee has been in the spotlight, leading to an extensive body of literature regarding the species. In comparison, the bonobo, closest relative to the chimpanzee, has been the focus of much less research. One reason for this disparity has been decade-long political turmoil in the Democratic Republic of the Congo, the country to which bonobos are endemic. Relative stability returning recently has led to an increase in the number of studies carried out on this species (Hare & Yamamoto, 2017). A second reason for the relative focus on the chimpanzee is the presumed similarities between the two *Pan* species (Stanford, 1998), leading many to believe that similar studies on the bonobo would simply be redundant. However, an increasing body of evidence is showing just how much the two species differ, with some arguing that in many ways, each of the two *Pan* species are more similar to humans than they are to one another (see Gruber & Clay, 2016; Hare & Yamamoto, 2017, p. 4, for a review). When trying to answer questions on human evolution, therefore, it has become increasingly clear that both *Pan* species need to be taken into consideration. Fortunately, the presently surging interest in the bonobo is taking us in the right direction (Hare & Yamamoto, 2017).

Human theory of mind

In the late 1970s, Premack and Woodruff (1978) defined 'Theory of mind' as one's ability to attribute mental states to oneself and to others. In their paper, the authors discussed the different states of mind that we, humans, are able to infer and attribute to others. Firstly and most widespread are assessments of the *purposes, goals* and *intentions* of others, but we also infer what others *believe*, *know*, *like* and so on and so forth. The ability to attribute mental states allows for much more efficient prediction and anticipation of others' behaviour and as such is a vital social tool (Baron-Cohen et al., 1985). Theory of mind is, as it turns out, paramount to many of the cognitive capacities that make us human and allow for our complex communication, cooperation and culture (Krupenye et al., 2016). While theory of mind requires experience, it is a natural human capacity that requires no teaching (Premack & Woodruff, 1978).

The paradigmatic test for the ability to attribute mental states, different from own, to others, has been to investigate the attribution of false beliefs. In the 1980s, research demonstrated that the capacity for explicit theory of mind (i.e., the attribution of false beliefs) is present in human children by age four. This was evidenced in a pioneer study by Wimmer and Perner (1983), in which children underwent a well-known paradigm generally referred to as the 'Location change task' (previously the 'Maxi-task' (Wimmer & Perner, 1983) or the 'Sally-

Ann task' (Baron-Cohen et al., 1985)). Since then, using nonverbal 'violation of expectation' paradigms, understanding of another's false beliefs has been evidenced in pre-linguistic infants as young as 15 months (Onishi, 2005) and understanding of false perceptions (Song & Baillargeon, 2008) and of what others see and don't see and therefore know and don't know (Surian et al., 2007) in infants as young as 13 months. The use of non-verbal testing paradigms has also opened new possibilities for testing nonhuman primates.

Theory of mind in great apes

Premack and Woodruff (1978) asked whether our close relative, the chimpanzee, had the capacity to form a theory of mind. Based on their findings that a chimpanzee, Sarah, was able to correctly understand the goals and intentions of humans struggling to carry out a number of different actions on video, they speculated that, indeed, chimpanzees might have a theory of mind not far different from our own. Since Premack and Woodruff's (1978) pioneer work, studies looking into theory of mind and mental state attribution in non-human animals have multiplied, revealing it as one of the most interesting cognitive capacities that can provide answers to a range of questions regarding the evolution of language, culture, teaching and more. However, most early attempts to find evidence for theory of mind in chimpanzees found only negative results (e.g. Povinelli & Eddy, 1996; Call & Tomasello, 1999). In the late 1990s positive results started to emerge, largely coinciding with improved methods (Call & Tomasello, 2008). Building on a comprehensive review by Call and Tomasello (2008), I review the literature that has led us to uncover the presence of a number of cognitive capacities indicative of theory of mind in great apes, more specifically, apes' ability to attribute mental states to others, namely their goals and intentions, their perception and knowledge, and even their false beliefs.

Goals and intentions

Inferring and attributing mental states to others allows one to better predict and anticipate the behaviour of others, which will enhance an individual's ability to compete and cooperate with others (Call & Tomasello, 2008). Reviewing the main findings in the 30 years since Premack and Woodruff's work, Call and Tomasello (2008, p. 189) came to the conclusion that chimpanzees were indeed able to "…understand the actions of others, not just in terms of surface behaviours but also in terms of the underlying goals, and possibly intentions, involved." Indeed, among the empirical research papers reviewed by Call & Tomasello

(2008) was evidence that chimpanzees could, for example, help a human actor access an out-of-reach object (Warneken & Tomasello, 2006) and discriminate between food providers who were ‘unwilling’ or ‘unable’ to supply food (Call et al., 2004).

The first direct test of the bonobo’s ability to understand another’s goal was carried out, to my knowledge, by Buttelmann and colleagues (2012) and yielded positive results. It was demonstrated that all species of great ape, including bonobos, understood which of two possible goals of a human experimenter had when carrying out identical actions. Depending on the context, which was presented to the subjects immediately before testing, the experimenter was either: i) trying to open a box to obtain a food reward within to give to the subject, or ii) simply playing with the box’s opening mechanism before taking a food reward from its pocket to give to the subject. Despite the identical actions, bonobos showed the ability to infer the experimenter’s goal based on the context in which the experimenter was operating.

A more recent study by Kano & Call (2015) demonstrated, with the use of eye-tracking technology, that bonobos, chimpanzees and orang-utans were able to successfully predict the goal-based action of a human actor reaching for a target object, demonstrating that they had an understanding of other individuals’ goals.

Perception and knowledge

Understanding another’s perception, what it sees and doesn’t see, or what is has seen or hasn’t seen, for instance, and therefore what it knows and doesn’t know can be tested in paradigms where the observer’s and actor’s visual perceptions differ (Call & Tomasello, 2008). Through a body of experiments chimpanzees have been found to be capable of gaze following (e.g. Tomasello et al., 1998) and of taking into account where signal receivers are looking during gestural communication (e.g. Kaminski et al., 2004; Liebal et al., 2004). Far stronger evidence is the finding that in competitive situations (usually for a food reward) subjects clearly know and take into consideration what competitors can and cannot see or hear and, therefore, what they can and cannot know (e.g. Hare et al., 2000, 2001; Melis et al., 2006; see Tomasello et al., 2003; and Call & Tomasello, 2008 for a comprehensive review).

One study on bonobos revealed that they were capable of inferring the target of another's attention (MacLean et al., 2012) based on what they knew the other had seen and therefore knew. That is, when an experimenter expressed surprise whilst looking in the general direction of an object that was either familiar or unfamiliar to him, bonobos and chimpanzees searched for an alternative target more often when the object was familiar than when it was not, indicating that subjects took into account what the experimenter had previously seen or not seen. Indeed, if the experimenter was already familiar with an object, then no surprise should have been expressed upon seeing it.

Another ability observed in all great apes is that of taking into account the attentional state of others in the case of gestural communication and modulating signals accordingly (e.g. Kaminski et al., 2004; Genty et al., 2009, 2015). For instance, Genty et al. (2015) demonstrated that bonobos use more audible than silent gestures when recipients were inattentive than when they were attentive, and vice-versa. While the ability to understand the goals, intentions, perceptions and knowledge of others is indicative of possessing a theory of mind, all these mental states relate to a perceived common reality. Calling for another level of cognition is the understanding that others may have false or different beliefs about reality, i.e., that realities between individuals may differ.

False beliefs

Amongst the higher levels of theory of mind, and until recently considered to be unique to humans, is the ability attribute 'false beliefs' to others. In this case, an actor's behaviour is predicted and explained, not by what an observer knows to be true, but by a judgement of what the actor believes to be true (e.g. an actor believes a reward is in a certain location while the observer knows that the reward's location has been changed). As previously mentioned, understanding others' false beliefs was first evidenced in 4-year-old children (Wimmer & Perner, 1983; Baron-Cohen et al., 1985) but it has since been claimed in infants as young as 15 months (Onishi, 2005). As mentioned, early attempts to demonstrate the ability to attribute false-beliefs in chimpanzees produced negative results (see Call & Tomasello, 2008 for a review), but a recent study by Krupenye et al. (2016) using eye-tracking technology, an anticipatory looking paradigm originally developed for use with young children (Southgate et al., 2007), and scenarios specifically crafted to capture the subject apes' attention (Kano et al., 2017) provided the first evidence that bonobos, chimpanzees and orang-utans are capable of anticipating the behaviour of an actor who holds a false belief. In Krupenye et al.'s (2016) experimental paradigm, the three species of great ape were subjected to two scenarios of the same experimental design. Two familiarisation trials were carried out during which a target object was hidden in two possible locations and subsequently 'retrieved' by an observing actor. In the test trials the target object was then moved from one location to the other, either in presence or absence of the actor, before being removed completely. The actor then returned and performed a central approach towards the hiding places. Subjects' performance was assessed based on whether they first looked at the location where the actor falsely believed the object to be (the target) or at the other location (distractor). Results showed that, despite having knowledge that the object is in neither of the two locations, subjects first looked at the target location where the actor would have believed the object to be, demonstrating an implicit understanding of others' false beliefs. Another recent study by Buttelmann et al. (2017) provided additional evidence that bonobos, chimpanzees and orang-utans are able to attribute false beliefs to others, anticipating the other's behaviour and acting upon this understanding in social situations where help was required.

Attributing mental states similar to our own to another individual is one thing, but the ability to attribute mental states different from our own is another, possibly a "…key marker of advanced social cognition" (Buttelmann et al., 2017, p. 1). Furthermore, and of particular interest, possessing this ability also implies recognising that others' actions are not based on reality, but on their 'version' of reality, on what they believe to be true, even if this is objectively false (Kano et al., 2017). This evidence of attribution of false belief in our closest relatives is highly important and further demonstrates the continuity between ape minds. In addition, it indicates that that the evolutionary emergence of theory of mind is much older than previously believed (Bugnyar, 2017). It is likely that theory of mind evolved to better allow individuals to predict and anticipate the behaviour of others in the complex societies of humans and other great apes (de Waal, 2016).

As mentioned previously, the vast majority of research into primates' theory of mind to date has been focused on the chimpanzee, and has been for the past 40 years. However, as also mentioned previously, more recent research focussed on bonobos, has brought to light their ability to understand others' goals (Buttelmann et al., 2012; Kano & Call, 2015), to infer the target of another's attention (MacLean & Hare, 2012), to attend to the attentional state of signal recipients during communicative interactions (e.g. Kaminski et al., 2004; Pika et al., 2005; Genty et al., 2015) and finally, to attribute false beliefs to others (Krupenye et al., 2016; Buttelmann et al., 2017). So far, results suggest that the bonobos' theory of mind much resembles that of the chimpanzees'. In fact, some findings (based on a battery of cognitive tasks) even suggest that bonobos may outperform chimpanzees in theory-of-mind tasks (Herrmann et al., 2010).

Theory of mind, and more particularly understanding false beliefs, requires that an individual be able to distinguish its own state of mind from those of others. This faculty requires a number of essential underlying building blocks and, at the very least, that individuals be capable of *distinguishing the self* as a separate and different entity from others and the surrounding environment.

Study 1: Understanding the self

Over 30 years ago, Gallup (1983) suggested that the ability for mirror self-recognition implied theory of mind. In the 1990s this view was questioned (e.g. Gergely, 1994) due to the fact that mirror self-recognition was known to emerge in infants as young as 15 months (Amsterdam, 1972; Lewis & Brooks-Gunn, 1979) while, at the time, empirical evidence showed that theory of mind was not fully present in children until the age of four (see Gopnik & Meltzoff, 1994 for a review) showing that the emergence of both cognitive capacities was not directly coupled. However, more recent work has pushed the age-limit to 15-month-old infants regarding false belief understanding (Onishi, 2005), suggesting a more direct link to the emergence of mirror self-recognition.

Self-recognition and self-awareness

Gallup (1998) suggested that self-recognition implied not only awareness, but also self-awareness, defined as an ability to become the object of one's own attention. He further suggested that being able to conceive of one's self is a prerequisite to being able to recognise one's self in a mirror. In addition, Gallup suggested that a self-aware individual was also in a position to infer equivalent states of awareness in others. By using information drawn from own experiences subjects could attribute various "…experiences, desires and knowledge" to others (Gallup, 1998, p. 241), an ability, key to complex social cognition as seen in humans. Self-awareness is, in Gallup's (1998) view, is nothing less than evidence for having a theory of mind capable of high level processes, such as attributing false beliefs.

The questions around self-recognition and self-awareness are heavily laden with controversy with a wide range of views on the subject. Those most conservative explain reactions in the mirror-mark test as being artefacts of manipulation during the experiments (e.g. Heyes, 1994, 1995, 1996). The more moderate views, for example, interpret mirror self-recognition as indicative of self-perception (i.e., recognising one's own appearance) (Nielsen et al., 2006) or of an understanding of 'body-concept' (i.e., that one's body is an entity on its own) permitting individuals to engage in kinaesthetic-visual matching using both the kinaesthetic sense they have of their own body and the visual feedback from the mirror (Mitchell, 1993, 1997). Finally, the richer interpretations more closely resemble Gallup's (1998) view that self-directed behaviour using one's mirror-image is indicative of self-awareness (e.g. Inoue-Nakamura, 1997; Swartz et al., 1999; Plotnik et al., 2006) or self-concept.

Mirror self-recognition

The recent finding that great apes have the ability for attribution of false beliefs, discussed above (Krupenye et al., 2016; Buttelmann et al., 2017), suggests that they can bear different perspectives of reality, their own as well as that of another. The fact that they have this ability further demonstrates that they must understand themselves as distinct, separate entities within the real world. Self-awareness is a complicated concept, and more difficult yet to test experimentally. However, one line of research to address this question has been to test for mirror self-recognition in a range of animals. Evidence for mirror self-recognition, though somewhat controversial (Anderson & Gallup, 2015; Gallup & Anderson, 2018), has also been found in non-primate species: bottlenose dolphins (Marten & Psarakos, 1994; Reiss & Marino, 2001), Asian elephants (Plotnik et al., 2006), manta rays (the biggest brained of all fish; Ari & D'Agostino, 2016), but also Eurasian magpies (Prior et al., 2008) and Clark's nutcrackers (Clary & Kelly, 2016). And while, to date, there is only evidence of mirror self-recognition in apes, but not other primates (e.g. Gallup, 1970; Lethmate & Dücker, 1973; Westergaard & Hyatt, 1994; Posada & Colell, 2007; see Swartz et al., 1999 for a review), this ability is usually not accessible to all individuals (e.g. Swartz & Evans, 1991; Povinelli et al., 1993; Walraven et al., 1995).

While mirror self-recognition has been evidenced in the bonobo through the observation of spontaneous self-directed behaviours (e.g. picking at the teeth or eyes) when presented with a mirror, in some cases from the first day of presentation (Westergaard & Hyatt, 1994;

Walraven et al., 1995), to the best of my knowledge, no controlled mirror/mark test has been carried out or at least reported for this species. In my research, I developed an alternative method to investigate aspects of self-recognition that was neither based on qualitative assessments of self-directed behaviours, nor on artificially inflicted paint marks. Instead, I argue that self-recognition should not be confined to the here and now, but should also reveal itself if subjects see footage of themselves that has been recorded in the past. Moreover, given the well documented individual differences in mirror self recognition in great apes, I further argue that self recognition is an acquired capacity that builds on key perceptual experience.

Rationale for study 1

In a first study, I sought to further our understanding of the bonobos' perception of the self and how that perception might be modified through prolonged mirror exposure. More specifically, I first investigated how mirror-naïve bonobos reacted to various forms of contingent and non-contingent self-images, in the form of video footage recorded before as well as real-time video and mirror feedback. I then compared subjects' responses to video images of others, either known or unknown conspecifics. Following this, I then investigated how prolonged mirror exposure influenced subjects' perception of themselves in non-contingent video footage. I theorised that prolonged mirror exposure would provide subjects with the key perceptual experience, that is, visual feedback of their own physical appearance, to allow them to develop a full visual self-image. In this case, a visual mental representation might be formed from exposure to one's mirror image and potentially stored in memory.

Study 2: Learning from others' knowledge

From the literature reviewed above, it appears that the bonobo has a theory of mind that is similar to the chimpanzee's (Krupenye et al., 2016; Buttelmann et al., 2017). Although these abilities have not been investigated in as much depth in bonobos it seems safe to assume that, like the chimpanzee, they understand the mental states of others, including others' states of knowledge, at least to some degree.

The transmission of behaviours can be achieved through a number of mechanisms. Some of these are quite simple and are due to mere social influence (e.g. contagion, social support), while others are more complex, such as social learning through stimulus enhancement, goal emulation, observational learning or imitation (Whiten & Ham, 1992).

For my research, I was only interested in the higher forms of social learning and, more importantly, in social learning processes that entail transmission of ecological behaviours (as opposed to behavioural techniques or object manipulations, as typically used in studies of social learning; e.g. Whiten et al., 1996; Horner & Whiten, 2005). In species possessing a theory of mind, such as the bonobo or chimpanzee, evidence of social learning of others' knowledge is also indicative that subjects attend to others' behaviour as reactions to reality, and modify their own behaviour in turn based on the others' knowledge.

In the wild, this can be achieved by observing how, for example, novel ways to interact with the environment spread through social groups (e.g. Hobaiter et al., 2014; Coelho et al., 2015). Experimentally, this can be achieved by first introducing states of knowledge to certain individuals (models or demonstrators), and checking whether others (subjects or observers) attend to these states of knowledge and make use of them to influence their own behaviour (e.g. Fryday & Greig-Smith, 1994; Dindo et al., 2008).

The benefits of social learning

Observation of group members, their actions and interactions, is key in gaining social knowledge, that is, how others relate to the environmental, social and contextual factors surrounding them, which can be key to survival (Galef & Laland, 2005). Indeed, social learning is a mechanism by which individuals can avoid risky trial-and-error learning, saving both time and energy (Hopper et al., 2011). Social learning has a great influence on the behaviour of an individual in a number of different domains: time spent foraging, food choice, motor patterns in foraging, mate choice and predator avoidance. These can all be influenced by what is observed in the behaviour of conspecifics (Galef & Giraldeau, 2001; Galef & Laland, 2005). For example, social learning of fear can be highly beneficial. Indeed, as Olsson and Phelps (2007, p. 1095) point out that "…exploiting aversive experiences of other individuals through social fear learning is less risky…" than experiencing aversive experiences directly. Whiten (2005) suggests that social learning acts as a "second inheritance system" adding to the already genetically coded behavioural traits.

Socially learned manipulations vs. socially learned knowledge

To date, the mechanisms of social learning have been investigated in a wide range of species, using observational and experimental techniques both in wild and captive populations (e.g. great apes: (Whiten et al., 2005; Dindo et al., 2011; Hobaiter et al., 2014; Clay & Tennie, 2017); monkeys: (Kawai, 1965; Dindo et al., 2008; van de Waal et al., 2013b); lemurs: (Stoinski et al., 2011); birds: (Aplin et al., 2014; Auersperg et al., 2014); see (Reader & Biro, 2010) for a non-exhaustive survey). A common approach has been to use either tool use (e.g. Call & Tomasello, 1994; Horner & Whiten, 2005) or manipulation of a 'puzzle box' or 'artificial fruit' (Whiten et al., 1996) in order to access a food reward. Such experiments have brought to light not only evidence of social learning (e.g. van de Waal et al., 2010, 2013b) but also of social diffusion (Dindo et al., 2008, 2011; Whiten & Mesoudi, 2008) and social conformity (e.g. Whiten et al., 2005; Dindo et al., 2009), findings with broad implications for theories of the evolution of culture (see Whiten & van de Waal, 2016a for a review). However, while most primates are capable of rich arrays of food manipulations, such as twisting, pulling, or peeling, in natural situations this rarely involves tool-use. Moreover, although some chimpanzee communities have well established tool traditions others do not (e.g. Gruber et al., ; Reynolds, 2005; Visalberghi et al., 2015) and, importantly, tool use is virtually absent in wild bonobos (Koops et al., 2015), raising questions about the extent to which such results are representative of social learning capacities more generally. Social learning, in other words, may be better investigated in relation to other, more ecologically relevant challenges.

Social learning in the context of feeding

The utility of social learning is particularly clear in young and naïve individuals where learning by observing individuals that have, essentially, survived to adulthood in a given environment can avoid great costs. By watching conspecifics and learning what, when, where and how to eat, individuals can reduce the risk of ingesting harmful foods and thus reduce the risk of intoxication (Addessi & Visalberghi, 2001; Galef & Laland, 2005; see Galef & Giraldeau, 2001 for review). For example, during weaning, young mammals must rapidly learn what foods must and must not be eaten in order to have a balanced diet and to avoid intoxication (Galef & Laland, 2005). Indeed, all young primates are attentive to adults during feeding, yet certain species within the order take social learning a step further: great apes and callitrichids are known to learn by imitation. In the former, social learning is "exclusively infant-initiated" whereas in the latter, adults "actively teach their young" (Rapaport & Brown, 2008).

Social learning with regards to foraging decisions has been demonstrated in a number of primate species whether by observation of naturally occurring behaviours in the field (see Rapaport & Brown, 2008 for a review) or experimentally in captivity (e.g. Dindo et al., 2008) and more recently experimentally in the field (e.g. van de Waal et al., 2013a). In their study, van de Waal et al. (2013a) demonstrated that in wild vervet monkeys, not only do weaning infants apply socially learned knowledge to conform to their groups foraging practices, but migrating adult males will even "…abandon personal foraging preferences in favour of group norms new to them" (2013a, p. 483). Social learning theory, it seems, can only benefit from focussing on more ecologically relevant contexts, such as acquiring knowledge about food palatability or foraging efficiency (van de Waal et al., 2013a, 2014).

Rationale for study 2

In a second study, I investigated whether or not bonobos were able to socially learn arbitrary food preferences of other group members through mere observation and whether they would adopt and maintain such a preference, even if this contradicted their own knowledge. In other words, bearing their own knowledge of reality, would subjects still be prepared to behaviourally adhere to another's knowledge of a contrasting reality? To achieve this, subjects were first exposed to two demonstrators systematically choosing one novel, artificially coloured food item over another. Second, I then tested whether subjects would preferentially choose the same coloured food as that eaten by the demonstrator. With an interest in the plasticity of social learning in mind, particularly how faithfully observers followed a demonstrator's lead, I first led one of the two demonstrators to prefer one colour (of a given food type) and then switched his preference to the other colour (with a another food type), such that the two demonstrators had opposing food colour preferences. This allowed me to investigate whether or not subjects would maintain the first food colour choice they had learnt or whether they preferred to choose as the last observed demonstrator had. In addition, this enabled me to control for any 'natural' colour bias that may have existed. Furthermore, I was interested in finding out whether subjects might maintain any choice for copying the demonstrators' opposing preferences and, importantly, despite their own better knowledge that both food colours were identical in palatability. This would demonstrate that the social learning had outcompeted the individual learning and that, in principle, they were able to maintain two realities, their own (i.e., all food is equally good) and that of the demonstrators (i.e., blue/pink food is good while the other is bad).

Study 3: Inference from social knowledge

Research into animal cognition often investigates capacities in isolated domains, such as self-recognition, social learning or communication. In my final chapter I aimed to integrate, across several domains, particularly how subjects draw inferences from others' vocal behaviour based on the knowledge acquired from their own experiences with different foods and from watching others interacting with different foods.

If one can understand another's knowledge and preferences, can this representation of another's reality be maintained and referred to as a source of information during communication? Research into the understanding of others' mental states is very rarely investigated in communication behaviour (see Crockford et al., 2012). Yet, once an understanding that others have different perspectives of reality is achieved, then this knowledge ought to be a source to refer to in order to draw inferences from others' communicative behaviours.

Inference in communication

The comprehension mechanism of language allows individuals to extract meaning from perceived signals. Upon hearing a vocalisation, primates seem to be able to form mental representation of other individuals, relationships and external events based on previously acquired knowledge (e.g. Cheney & Seyfarth, 1999; Zuberbühler et al., 1999; Seyfarth et al., 2005; Wittig et al., 2014). This cognitive skill is believed, by some, to be one of the necessary precursors to human language (Seyfarth et al., 2005). Some calls carry more specific meaning than others and a number of studies have revealed rudimentary meanings carried by certain primate calls or call sequences. These signals act in referential ways, as they transmit, to a receiver, information about external objects or events (Seyfarth et al., 2010) and allow, without any further visual or contextual cues, the receiver to make predictions about events in their environment (Clay et al., 2012). These 'functionally referential' calls in nonhuman primates have been studied particularly in alarm calling (Seyfarth et al., 1980; Zuberbühler, 2003, 2009; Arnold & Zuberbühler, 2006; Schel et al., 2010; Cäsar & Zuberbühler, 2012). In these studies, calls or call sequences were shown to contain sufficient meaning that an appropriate anti-predator response was observed in signal receivers.

Context-specificity is a pre-requisite for ‘functionally referential’ calls, and to successfully inform other group members about an external object or event (whether intentional or not) calls must be emitted within a given context. The combination of specific acoustic structure, and use in a specific context can thus elicit specific behavioural responses in signal recipients (Crockford & Boesch, 2003). While such evidence has been brought to light for a number of species of monkey, equivalent findings for great apes are relatively sparse. In fact, the vocal repertoire of bonobos, for instance, is described as being highly graded (de Waal, 1988; Bermejo & Omedes, 1999; Clay, 2010) with many possible call sequence variants, any one of which can be used in a number of different contexts (Bermejo & Omedes, 1999). Extracting meaning from such communicative signals as these, that have no single biological function, must therefore depend on more that the ‘explicit’ content of the call or call sequence.

In primate communication, evidence indicates that the capacities around comprehension are more cognitively complex than those relating to production and usage showing more flexibility, open-endedness, and assimilation to experience (Seyfarth & Cheney, 2017a, 2017b). And while in human language, comprehension of speech is far more complex, requiring that we integrate world knowledge, assumptions about shared cultural background, current context, or variables relating directly to the signaller (Seyfarth et al., 1980; Johnson & Smith, 1981), there is evidence that both call production and comprehension in primates can also be governed by additional variables (Smith, 1977). Indeed, evidence shows that primates use knowledge about their social, physical and contextual environment to determine a call’s meaning, beyond what is explicitly conveyed through the physical characteristics of a signal (e.g. Arnold & Zuberbühler, 2006; Slocombe et al., 2010; Cäsar et al., 2012). By making use of this pragmatic inference, a receiver can render a referentially broad signal into one with a highly specific meaning (Seyfarth & Cheney, 2017b), in difference to the notion of functional reference and more in line with how humans deploy referential processes. Studying the ability of primates to draw inference from vocalisations, gestures and even previously acquired social knowledge may provide valuable information regarding the origins of human inferential abilities.

If great apes have some sense of the self as being different from the others and that they also have an understanding and knowledge of the different mental states of others, which they can attend to and learn from, then it follows that they may be able to make inferences and predictions about others' behaviours and about their environment, from their communicative signals.

Rationale for study 3

In a third study, I investigated whether bonobos were able to take into account individually learned knowledge regarding foraging locations and socially learned knowledge of others when interpreting their communicative signals. That is, can bonobos use contextual cues and previously acquired knowledge regarding signal providers to infer meaning beyond that conveyed by the basic biological function of the perceived vocal signal? To achieve this, I provided subjects with two types of learning opportunity. First, individuals learned two food locations specifically associated to two different, artificially coloured foods. Following this, and in much the same way as in study 2, individuals were then given the opportunity to observe and to socially learn the idiosyncratic preferences of two demonstrators, each for one of the two coloured foods. I then ran a playback study using food calls from a demonstrator or from a control individual in order to simulate a feeding event with one of the two individuals. I predicted that the socially learned knowledge of the demonstrator's food colour preference and the individually learned association between the food colours and locations provided the premises for subjects to infer which food might be present upon hearing the food calls of the demonstrator individual.

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2: The study species - Bonobos (*Pan paniscus*)

A brief introduction

Demography

Bonobos are the last of the six species of hominids to have been discovered and described. They were previously believed to be a sub-species of chimpanzee and their status as a distinct species was only assigned in 1929 by Ernst Schwarz (de Waal & Lanting, 1997). Bonobos, along with chimpanzees, are the closest relatives of humans. We share a common ancestor dated back to approximately 7 million years ago (Endicott et al., 2010; Langergraber et al., 2012), whereas chimpanzees and bonobos shared a common ancestor that lived approximately 2.5 million years ago (Langergraber et al., 2012). The entire wild population is endemic to the Democratic Republic of the Congo (DRC) in central Africa where they inhabit lowland, mountain and swampy, tropical and subtropical rainforests. More recently, populations have been found in drier mosaic forests with savannah areas (Myers Thompson, 2002). At present, it is estimated that the species has a potential geographic range of approximately 500,000 km^2 within the Congo basin, however, a recent study estimates that only 28% of this range is suitable for bonobos (Hickey et al., 2012). Their distribution throughout this range is, therefore, patchy and discontinuous and even non-existent in some areas (Kano, 1984; Reinartz et al., 2006). The population trend of bonobos is ever decreasing and in 1996 the species' classification on the IUCN Red List of Threatened Species changed from vulnerable to endangered due to exploitation by humans and habitat loss (Fruth et al., 2016). It is generally accepted that the current wild population stands at 20,000 to 50,000 individuals (Reinartz et al., 2006). Recent evidence suggests that these numbers may be underestimates (Van Krunkelsven, 2001) while some estimates are lower still (Fruth et al., 2016).

Social structure

Bonobos live in large, multi-male, multi-female social groups. The fission-fusion groups of bonobos are usually comprised of 35-75 individuals, although communities with numbers as high as 120 have been recorded (Furuichi, 1989; Blount, 1990; de Waal & Lanting, 1997). Bonobos are a male-philopatric species (Furuichi, 1989) with female exogamy (de Waal, 1995). However, recent reported cases of males leaving their natal groups to join new communities suggest that the dispersal pattern of the species may not be as rigid as previously thought (Hohmann, 2001; Hashimoto et al., 2008). The hierarchy of bonobo social groups is still a topic of debate (Paoli et al., 2006). Commonly perceived as female-dominated (Parish, 1994; de Waal, 1995; de Waal & Lanting, 1997; Stanford, 1998; Vervaecke & Van Elsacker, 2000), it may be best described as egalitarian or non-exclusively female-dominated (Paoli et al., 2006; Stevens et al., 2007) and this is despite the fact that females are only 82.5% the size of their male counterparts (Parish, 1996). This non-exclusive dominance over the larger males is in fact enabled through the stable and collaborative alliances that females have evolved to form among themselves (Furuichi, 1997; Vervaecke & Van Elsacker, 2000; Paoli & Palagi, 2008). Bonobos are more socially tolerant than their close cousins, the chimpanzees, and this favours cooperation, food-sharing and a more peaceful co-existence (Hare et al., 2007; Clay, 2010; Hare & Kwetuenda, 2010).

Study site and subjects

La Vallée de Singes, France

"La Vallée de Singes" is a zoological park specialised uniquely in primates and home to the only group of bonobos in France and one of the largest group of zoo-held bonobos in the world. The group of 20 individuals is housed in a new infrastructure consisting of an indoor enclosure covering almost 400m^2 and an outdoor island covering approximately 1 hectare. At the beginning of my research, in 2014, the group was composed of 17 individuals, by the end of the study period, in 2016, there had been 3 births bringing that number up to 20 (N = 17, Age range: 0 - 46, see table 2.1).

Table 2.1. Composition of the study group at the “La Vallée des Singes” zoological park

Individual (♀)	**Sex**	**Code**	**Birth year**	**Age class**	**Study**
Daniela	F	DNL	1968	Adult	3
Lisala	F	LSL	1980	Adult	1
Ukela	F	UK	1985	Adult	3
Bondo $^{\mathrm{LSL}}$	M	BO	1991	Adult	--
Kirembo	M	KI	1992	Adult	1, 3
Ulindi	F	UL	1993	Adult	1, 2, 3
Diwani $^{\mathrm{DNL}}$	M	DW	1996	Adult	1, 2, 3
David $^{\mathrm{DNL}}$	M	DV	2001	Adult	1, 3
Khaya	F	KH	2001	Adult	1, 3
Lingala	F	LNG	2003	Sub-adult	1, 2, 3
Lucy	F	LY	2003	Sub-adult	2, 3
Kelele	M	KEL	2004	Sub-adult	1, 2, 3
Luebo $^{\mathrm{LSL}}$	M	LUE	2006	Sub-adult	--
Nakala $^{\mathrm{UK}}$	F	NK	2007	Juvenile	2, 3
Loto $^{\mathrm{UL}}$	M	LO	2009	Juvenile	2, 3
Moko $^{\mathrm{UK}}$	M	MO	2012	Infant	2
Khalessi $^{\mathrm{KH}}$	F	KLS	2012	Infant	2
Yuli $^{\mathrm{LY}}$	F	YU	2014	Infant	--
Swahili $^{\mathrm{LNG}}$	F	SWH	2014	Infant	--
Lokoro $^{\mathrm{UL}}$	M	LKR	2016	Infant	--

Note: Name, sex, identity code, year of birth, age-class and studies in which full participation was achieved; mothers of individuals are noted in superscript; age-class at the beginning of the study period and as defined by Kano (1984).

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3: Mirror experience modifies bonobos' perception of themselves

Manuscript under review at PeerJ

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Abstract

The question of whether animals have some sort of self-awareness is a topic of great interest and continued debate. A necessary precondition for self-awareness is the ability to visually discriminate the self from others, which has traditionally been investigated through mirror self-recognition. Although great apes generally pass mirror self recognition tasks, the interpretation of these results has remained controversial. The aim of this study was to investigate how bonobos (*Pan paniscus*) respond to different types of images of themselves and others. In the first part of the experiment, we presented mirror-naive subjects with three moving representations of themselves (contingent mirror image, contingent video footage, non-contingent video footage) and two representations of others (video footage of known and unknown conspecifics). We compared responses using a 'looking-time' paradigm, based on the finding that primates generally prefer to look at novel social stimuli. We found that subjects paid little attention to contingent images of themselves and, while interest in footage of known individuals was a little higher, subjects were most interested in non-contingent images of themselves and of unfamiliar individuals. In the second part of the experiment, we provided subjects with three months of *ad libitum* mirror access, after which subjects were retested with the same non-contingent video footage of themselves and of unknown conspecifics. We found that extensive experience with their own mirror-image significantly reduced interest in the non-contingent footage of self, but not in the footage of unknown individuals. We discuss possible interpretations of these findings, such as the formation of stable visual mental self-representations or response differences to familiarity, and their implications in relation to the on-going debate on self-recognition in animals.

Introduction

A fundamental question in comparative cognition is whether, or to what degree, non-human animals have something akin to human self-awareness, that is, whether they can recognise themselves as separate from others and the environment and whether they have some understanding of their own mental states. It is generally accepted that any form of self-awareness arguably presupposes visual self-recognition, which is empirically easier to address. Since the 1970s mirrors have been used as the main method of testing self-recognition in the visual domain, with two basic types of data collected. These studies have relied on describing spontaneous social, exploratory, contingent and self-directed behaviours (Swartz, Sarauw & Evans, 1999) or self-directed behaviour in response to inconspicuous marking of a body part, not visible without the aid of a mirror (the 'mirror-mark' test; Gallup, 1970).

Gallup's (1970) research on chimpanzees and macaques was pioneering, and has been followed by studies on a range of other primate species, including humans (Amsterdam, 1972), chimpanzees (Lethmate & Dücker, 1973; Suárez & Gallup, 1981; Calhoun & Thompson, 1988; Swartz & Evans, 1991; Lin, Bard & Anderson, 1992; Povinelli et al., 1993), bonobos (Hyatt & Hopkins, 1994; Westergaard & Hyatt, 1994; Walraven, Van Elsacker & Verheyen, 1995), gorillas (Suárez & Gallup, 1981; Ledbetter & Basen, 1982; Posada & Colell, 2007), orang-utans (Lethmate & Dücker, 1973; Suárez & Gallup, 1981), gibbons and siamangs (Lethmate & Dücker, 1973; Inoue-Nakamura, 1997; Suddendorf & Collier-Baker, 2009), monkeys (Lethmate & Dücker, 1973; Inoue-Nakamura, 1997), and prosimians (Inoue-Nakamura, 1997) (see Anderson, 1984 for review in primates).

Within the non-human primates, all great apes appear to be capable of mirror self-recognition (see Swartz, Sarauw & Evans, 1999 for review). In bonobos, for example, there is evidence of spontaneous self-recognition in mirrors (Hyatt & Hopkins, 1994; Westergaard & Hyatt, 1994; Walraven, Van Elsacker & Verheyen, 1995), due to mirror-guided self-directed behaviour (e.g. picking the teeth or eyes), in some instances from first exposure (Walraven, Van Elsacker & Verheyen, 1995), but we are not aware of any reports of studies using the 'mirror-mark' test on bonobos. In contrast monkeys (*Macaca silenus, Mandrillus sphinx, Papio hamadryas, Ateles sp, Cebus apella*) have consistently failed the 'mirror-mark' test while the evidence in gibbons and siamangs is contradictory (Lethmate & Dücker, 1973; Ujhelyi et al., 2000; Heschl & Fuchsbichler, 2009; Suddendorf & Collier-Baker, 2009). Regarding spontaneous self-directed behaviours, we are not aware of any evidence in monkeys (Inoue-Nakamura, 1997).

Mirror experiments have also been conducted with non-primate species with positive evidence in bottlenose dolphins (Marten & Psarakos, 1994; Reiss & Marino, 2001), Asian elephants (Plotnik, De Waal & Reiss, 2006), and even manta rays, the biggest brained of all fish (Ari & D'Agostino, 2016), suggesting that mirror self-recognition may have more to do with large brains in general, regardless of phylogenetic relatedness (but see Gallup & Anderson, 2018). Meanwhile, small-brained species, such as great tits, (Kraft et al., 2017) or cichlid fish (Hotta, Komiyama & Kohda, 2018), typically fail mirror self-recognition tasks, although there is some positive evidence from Clark's nutcrackers (Clary & Kelly, 2016) and Eurasian magpies (Prior, Schwarz & Güntürkün, 2008; but see Anderson & Gallup, 2015). However, the giant panda's failure of mirror self-recognition (Ma et al., 2015) suggests that absolute brain size alone is a poor predictor of mirror self-recognition, suggesting that the complexity of a species' social life may also play an important role (Gallup, 1998; Prior, Schwarz & Güntürkün, 2008).

In humans and great apes, the capacity to recognise one's self in a mirror emerges gradually and with appropriate experience. In western human cultures, the capacity to carry out self-directed behaviours in front of a mirror usually appears from 15-18 months of age and is fully expressed by 24 months (e.g. Amsterdam, 1972; Lewis & Brooks-Gunn, 1979; but see Keller et al., 2004, 2005; Kärtner et al., 2012 for evidence of delayed mirror self-recognition emergence in other cultures). In chimpanzees, early reactions to mirrors are similar in kind and latency to those observed in human children, but the behaviour does not emerge before 24 months (Lin, Bard & Anderson, 1992), and while not all individuals provide evidence of this capacity when tested (e.g. Swartz & Evans, 1991; Povinelli et al., 1993; Walraven, Van

Elsacker & Verheyen, 1995), in others, the behaviour is robustly present only from around 5 years of age (Swartz, Sarauw & Evans, 1999).

Behaviours typically observed by mirror-naïve animals are, first, social behaviours directed at the mirror (e.g. threatening or vocalising (Gallup, 1970)), followed by exploratory behaviours (e.g. reaching or looking behind the mirror), exploration of the contingency between the mirror-image and the subject's body, and, finally, exploration of body parts that are usually visually inaccessible, such as the teeth, eyes or genital regions (Swartz, Sarauw & Evans, 1999).

There is much controversy around how evidence of mirror self-recognition should be interpreted. On one end of the spectrum is the interpretation that positive evidence is an indicator of self awareness (Inoue-Nakamura, 1997; Gallup, 1998; Swartz, Sarauw & Evans, 1999; Plotnik, De Waal & Reiss, 2006) or even for a self-concept, defined by Gallup (1998, p. 240) as "…a sense of continuity, a sense of personal agency and a sense of identity". At the other end, reactions towards administered marks have been interpreted as mere artefacts of experimental manipulations (Heyes, 1994, 1995, 1996). More intermediate positions state that such behaviour qualifies as evidence for self-perception, that is, recognising one's own appearance (Nielsen, Suddendorf & Slaughter, 2006) or a basic understanding of one's own body as a separate entity from the surrounding world ('body concept'). The 'body-concept' hypothesis has been investigated in developing children, with the conclusion that objective self-awareness emerges in the second year of life, correlated with passing the 'mirror-mark' test, which suggests that the two capacities are linked (Moore et al., 2007). The notion of a 'body concept' is also key to an alternative hypothesis to self-recognition, which is that subjects simply engage in some form of kinaesthetic-visual matching as they identify the contingency between the kinaesthetic sense of their body and its movements and the objective visual image as provided by the mirror (Mitchell, 1993, 1997).

Several studies on children have tested the effect of contingency cues on self-recognition by presenting non-contingent images, usually delayed videos or simply photographs. One such study has shown that infants as young as 5 months are able to discriminate between video images of themselves and those of peers or objects. This finding has given rise to an important alternative explanation, which is that, at such a young age, infants do not recognise the self but at least respond to the self as being familiar (Legerstee, Anderson & Schaffer, 1998). Claims of self-recognition are easier to defend around the ages of 18-24 months when children start to show tell-tale spontaneous behaviours regardless of contingency cues (Lewis & Brooks-Gunn, 1979). Other studies, using a modified ‘mark-test’ further show a clear developmental trend between the ages of two and four for the emergence of self-recognition from non-contingent images, which appears to be more difficult than mirror self-recognition (Povinelli, Landau & Perilloux, 1996). In particular, younger children (i.e., 2-3 yrs.) had more difficulties to infer the presence of a sticker on their head from watching a 3-minute delayed video image of themselves than older children (i.e., 3-4 yrs.) suggesting that self-recognition from delayed videos requires an understanding that the self possesses a temporal continuity, a cognitive capacity that seemingly develops only by age 4. In a recent study, Hirata et al. (2017) used a similar variant of the ‘mark-test’ to test five subadult chimpanzees with extensive mirror experience (3 of 5 appeared to recognise themselves in mirrors). Here, subjects were tested with live video feedback, short-delayed video feedback (i.e., 1-4 seconds) and long-delayed video footage of self (one week). Among the control conditions, the authors used video footage of humans but not of conspecifics. The finding was that the three subjects capable of mirror self-recognition removed stickers placed on their heads more effectively and exhibited more self-directed behaviours than the other two individuals, when shown live and short-delayed video feedback but not when shown long-delayed video footage or other control conditions.

In sum, self-recognition from delayed, non-contingent self-images may thus be the most stringent test that an individual, human or non-human, possesses a visual mental representation of their own appearance, a sense of self, which appears to require sufficient exposure to mirrors.

Given their phylogenetic closeness to both humans and chimpanzees and based on their capacity for mirror self-recognition (Hyatt & Hopkins, 1994; Westergaard & Hyatt, 1994; Walraven, Van Elsacker & Verheyen, 1995) we investigated whether bonobos are capable of developing an understanding of their physical appearance if given extended experience with mirrors. The aim of this study was to address how bonobos respond to different visual images of self and others and to investigate how mirror exposure influenced perception of self-images when contingency cues are absent. To address this, we exposed subjects to different visual representations of themselves and of known and unknown conspecifics and considered subjects’ differing responses between conditions. We hypothesised that mirror-naïve individuals may not have an a-priori ability to recognise themselves, due to a lack of kinaesthetic-visual matching opportunities. To this end, we first exposed subjects to different depictions of the self and others. Two years later, following a 3-month period of *ad libitum* access to a mirror we exposed the same subjects again to key depictions of the self and others. We hypothesized that prolonged mirror-exposure would provide subjects with crucial perceptual experience regarding their own physical appearance, which subjects might use to develop a visual mental representation of self, enabling them at best, to recognise non-contingent representations of themselves, without the help of kinaesthetic feedback and at least to recognise them as being familiar.

We assessed interest in the different stimuli by comparing differences in looking times. This is based on the more general finding that both human and nonhuman primates generally spend more time looking at novel than familiar stimuli (e.g. patterns: (Fantz, 1964; Gunderson & Sackett, 1984; Gunderson & Swartz, 1985); objects: (Bachevalier, Brickson & Hagger, 1993; Pascalis & Bachevalier, 1998); conspecific faces: (Pascalis & Bachevalier, 1998; Gothard, Erickson & Amaral, 2004; Gothard, Brooks & Peterson, 2009)). We predicted that if bonobos show more interest in novel than familiar stimuli, then any footage of bonobos perceived as unfamiliar should cause longer looking times than footage perceived as familiar (similar to other primates: Gunderson & Sackett, 1984; Bachevalier, Brickson & Hagger, 1993; Pascalis & de Schonen, 1994).

Methods

Study site & subjects

The study was carried out at La Vallée des Singes Primate Park in Romagne (France) with a group of bonobos (2014: N=17; 2016: N=20; Table 3.1) housed in an indoor enclosure (400m^2) with access to two outdoor wooded islands (11,500m^2). Experiments were carried out from January to July 2014 and February to July 2016. Eight subjects (see Table 3.1) participated in all trials, which involved a 'looking-time' bias task with sequential stimulus presentation, a paradigm originally developed in the late 1950s for research with pre-verbal human infants (e.g. Fantz, 1963; Winters, Dubuc & Higham, 2015).

Table 3.1. Study subjects housed at La Vallée des Singes Primate Park, France

Individual	Code	Sex	Age-Class	Year of birth
Daniela	DNL	F	Adult	1968
Lisala	**LSL**	**F**	**Adult**	**1980**
Ukela	UK	F	Adult	1985
Bondo *	BO	M	Adult	1991
Kirembo	**KI**	**M**	**Adult**	**1992**
Ulindi	**UL**	**F**	**Adult**	**1993**
Diwani	**DW**	**M**	**Adult**	**1996**
David	**DV**	**M**	**Adult**	**2001**
Khaya	**KH**	**F**	**Adult**	**2001**
Lingala	**LNG**	**F**	**Sub-adult**	**2003**
Lucy *	LY	F	Sub-adult	2003
Kelele	**KEL**	**M**	**Sub-adult**	**2004**
Luebo *	LUE	M	Sub-adult	2006
Nakala *	NK	F	Juvenile	2007
Loto	LO	M	Juvenile	2009
Moko	MO	M	Infant	2012
Khalessi	KLS	F	Infant	2012

Note: Individuals having participated in all trials are indicated in bold (N=8). Individuals marked by an asterisk initially participated but were excluded for reasons detailed below. Age-class as defined by Kano (1984) at beginning of study.

Prior to testing, individuals were exposed to the equipment during one week to minimise any potential effects of novelty. Videos stimuli were then presented by means of an APPLE iPad (screen size approx. 15 cm x 20 cm) placed behind a transparent Acrylic panel (Fig. 3.1a) to which a PANASONIC HC-V100 full HD camera was fixed in order to record the subject's reaction face-on. The mirror stimulus was presented by means of a one-way mirror (25 x 30 cm) attached behind the same panel (Fig. 3.1b and c).

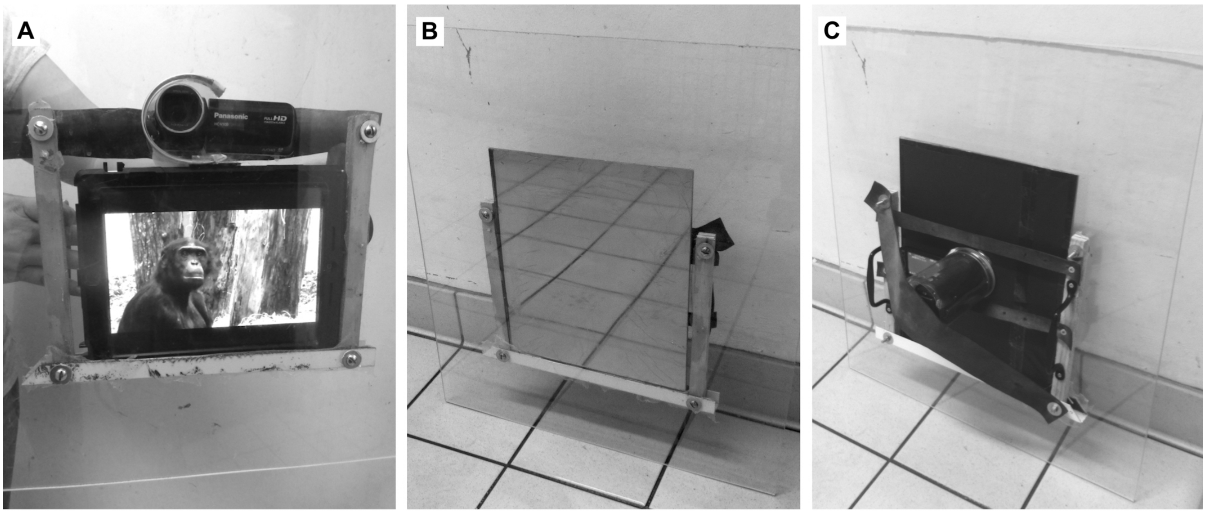

Figure 3.1. Portable acrylic panel for stimulus presentation. (a) Video camera and iPad displaying a non-contingent video stimulus. (b) Video camera and one-way mirror (front). (c) Video camera and one-way mirror (back). Photos by G.Shorland.

Part 1 - Before mirror exposure

The first part of the experiment was carried out in 2014 with N=8 subjects (4 males, 4 females, age range 9 – 34 years), none of whom had any known experience with mirrors. The experiment comprised five experimental conditions presented to all subjects in the following order: (1) contingent video footage of self (live feedback of self visible on an iPad: *C self*); (2) contingent mirror image of self (live depiction of self visible in a one-way mirror: *mirror*); (3) non-contingent video footage of self (previously recorded video footage of self visible on an iPad: *NC self*); (4) footage of known group member (previously recorded video footage of other group member visible on an iPad: *known*); (5) footage of unknown conspecific (previously recorded video footage of unfamiliar conspecific visible on an iPad: *unknown*) (see Appendix I: table A.I.1 and figure A.I.1). Footage for *'NC self'* and *'known'* were recorded during the *'mirror'* and *'C self'* conditions. Footage for *'unknown'* (N=2 males; N=1 female) were recorded at the 'Lola ya Bonobo' Sanctuary in the Democratic Republic of the Congo (see ESM 3.1 and 3.2 for sample footage). In both the *'known'* and *'unknown'* conditions, the footage showed generally inactive individuals glancing at the camera from time to time. Footage for stimulus presentation was selected at random, resulting in N=6 same-sex pairs and N=2 opposite-sex pairs for the *'known'* condition and N=4 same-sex and N=4 opposite-sex pairs for the *'unknown'* condition. An alternative design would have been to control for sex (i.e. to compare same-sex and different-sex footage). As this would have created sample size issues we opted for randomly assigning footage of *'known'* and *'unknown'* individuals to our eight subjects.

Each subject was presented with each of the five conditions once only and in the same sequential order over an eight-month period (see Appendix I: figure A.I.1). All video stimuli were presented very briefly, for total of 30 seconds, starting with the first glance from the subject towards the stimulus. A trial was terminated after 30s or as soon as a subject left. We are aware of the fact that fixed order stimulus presentation designs carry the disadvantage of potentially creating cross-condition dependencies. Any eventual differences in behavioural responses could therefore be explained in terms of behavioural habituation/sensitisation to some unknown aspects of the experiment rather than stimulus properties per se. Despite this well-known disadvantage, we opted for fixed order stimulus presentation because we were interested in eventual changes of attention due to prolonged exposure to a mirror. It was therefore essential that all subjects entered the experiment with the exact same stimulus history before and after mirror exposure. We consider it unlikely that this design could explain differences across conditions, mainly because stimulus exposure was very short (30s) and time lapse across presentations was generally very large (median = 38.5 days, range: 0-95).

Trials were carried out only when a subject was alone and inactive (i.e., resting or observing) in one of the indoor cages and at a suitable orientation and distance from the corridor (0.3-2.0 m). The subject was exposed to one of two portable devices, an iPad or a one-way mirror, each with a camera mounted to record looking responses (Fig. 3.1). We measured looking time during stimulus presentation as a proxy for interest, coded post-hoc from the video recordings. Coding was blind insofar as all videos were randomly labelled so that the rater (GS) was unable to infer the experimental condition. Videos were analysed frame-by-frame with MPEG Streamclip 1.9.2. Looking time was determined by measuring the duration between the first glance towards the stimulus and the beginning of gaze aversion. If multiple gazes occurred over the 30s stimulus presentation duration, we added them up. All clips were coded independently and blindly by a second rater (EG), which did not reveal any reliability issues (Pearson's correlation coefficient, $r = 0.93$, N=56).

Eight of 17 adult group members were tested and analysed in this study (see Table 3.1). Regarding the remaining individuals (N=9): One adult male (BO) participated in all experimental conditions but had to be excluded due to poor video quality, which prevented accurate coding. One adult female (LY) had to be excluded because she only participated in two conditions. Two individuals (NK and LUE) had to be excluded because they were too close to the camera, which prevented reliable coding of looking time. Finally, we were unable to test the remaining two adult females (DNL and UK) due to their lack of interest and participation. The dependent infants and juveniles (LO, MO and KLS) were not tested.

Part 2 - After mirror exposure

Fifteen months after the first part of the experiment, subjects were provided with prolonged access to a mirror to gain extended experience with mirror reflections of themselves. A mirror (45 x 115 cm) was placed in front of a resting platform of the indoor enclosure allowing *ad libitum* access over a period of three months (i.e., from Nov 2015 to Feb 2016). At this time of year, the group was kept inside due to cold weather conditions and the park was closed to the public. We did not quantify individual differences in the amount of time and qualitative differences by which subjects interacted with the mirror, but we are confident that over the three-month exposure (approx. 2 000 hours), all subjects had sufficient opportunities to familiarise themselves with their own mirror reflections.

In order to test the effect of mirror experience on the subjects' perception of their own non-contingent image, all individuals that had participated in part 1 (N=8) were retested with two critical conditions (identical to those in part 1), non-contingent video footage of self (*NC self*) and video footage of unknown conspecifics (*unknown*). Stimulus presentation began 10 - 20 days after removal of the mirror. All aspects of presentation were identical to part 1. The time lapse between the first and second stimulus presentation for a given subject and condition was held constant for each subject averaging at approximately 22 months (see Appendix I: figure A.I.1).

Statistical analyses

In a first analysis, prior to the 3-month mirror exposure, we modelled looking time with a linear mixed model (LMM), with looking time as the response variable and experimental condition as the main predictor variable. We included subject ID as random intercept. We added age as control predictor to account for the possibility that younger individuals might show more interest than older individuals (Westergaard & Hyatt, 1994; Walraven, Van Elsacker & Verheyen, 1995). Looking time and age were square root transformed to achieve homogenous and approximately normally distributed residuals. We tested this full model against an informed null model (Forstmeier & Schielzeth, 2011). The null model included only age as predictor and subject ID as random intercept. We tested the difference between the full and null model with a likelihood ratio test (LRT, Dobson, 2002). Note that this comparison is equivalent to more traditional p-value significance testing of 'experimental condition' (models with vs. without experimental condition).

Post hoc diagnostics were implemented in order to test the stability of the model. This entailed running the full model eight times, each time removing data of one of the eight individuals. This permitted us to verify whether one of the individuals was influential with respect to the interpretation of our model results. Results of this procedure indicated stable model results, such that exclusion of any one individual did not change the conclusions of our analysis.

In a second analysis, we tested how looking time was affected by the interaction between stimulus type (self vs. unknown, i.e., self Y/N) and prolonged mirror exposure (non-exposed vs. exposed, i.e., exposed Y/N) using a LMM. Once again, we controlled for age, which was included in the respective null model, and we implemented post-hoc diagnostics, testing the stability of the model. Again, diagnostics results indicated stable model results.

Statistical analyses were carried out with R v. 3.1.2 and lme4 v. 1.1-11 (R Core Team, 2014; Bates et al., 2015). The data that support the findings of this study are available in appendix I (Table A.I.2).

Compliance with ethical standards

Ethical approval: All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. This experimental study was authorised and given ethical approval by the "La Vallée des Singes" scientific coordinator and zoological director. Trials were carried out opportunistically when and where subjects felt so inclined. The study was inline with the ARRIVE guidelines and recommendations from the EAZA and the AFdPZ code of ethics.

Results

The first part of the experiment consisted of exposing all subjects to different motion images of themselves, of other group members, or of unfamiliar conspecifics (see Appendix I: figure

A.I.1). The results of the model indicate that looking time was affected by experimental condition (LRT, $\chi^2 = 25.87$, d.f. = 4, P<0.001; Fig. 3.2; Table 3.2).

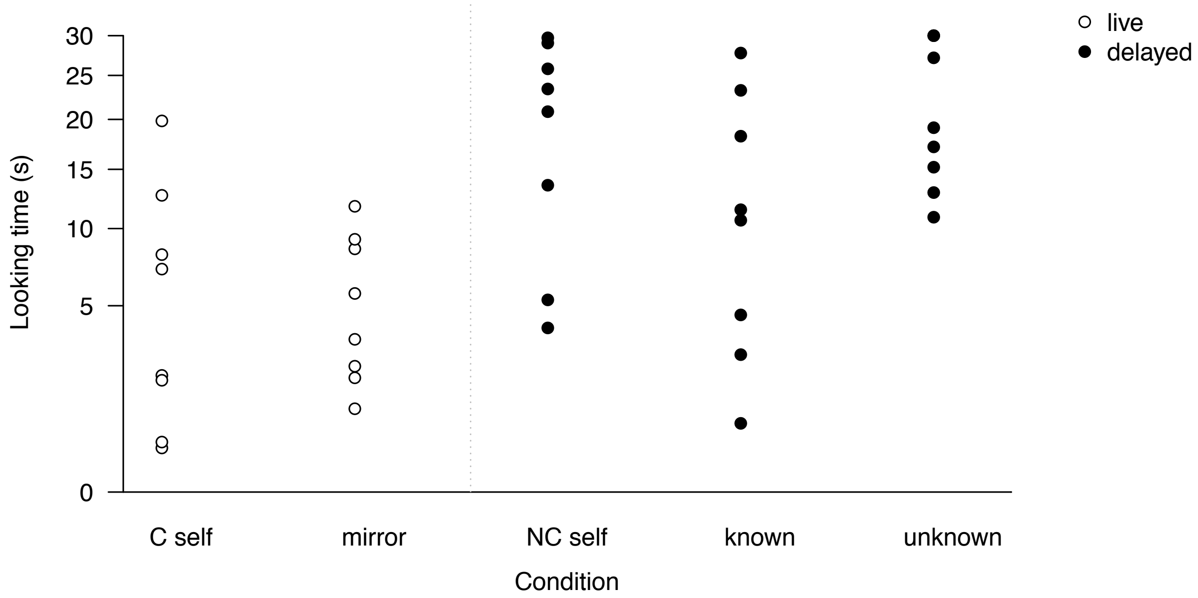

Figure 3.2. Subject looking time (circles) and model prediction (squares) for the five test conditions; note that looking time was square root transformed for modelling but for presentation we back-transformed it along the y axis. Conditions are presented chronologically from left to right.

Table 3.2. Result of the LMM testing the effect of condition on looking time.

	Estimate	Standard error	*t*
Intercept	3.18	0.44	7.18
Condition (*C self*)			
- *Mirror*	0.01	0.49	0.02
- *NC Self*	1.98	0.49	4.03
- *Known*	1.03	0.49	2.08
- *Unknown*	2.26	0.49	4.58
Age	-0.12	0.03	-3.75

The model predictions for looking time in both '*C self*' and '*mirror*' conditions were relatively low, just under five seconds (4.7s and 4.8s, respectively, model predictions, Fig. 3.2, see Table 3.3 for descriptive results calculated from the raw data), whereas for the '*NC self*' and '*unknown*' conditions predicted looking times were at least 10 seconds longer (17.3s and 19.7s, respectively). Predicted looking time for the '*known*' condition, however, lay in between (10.3s).

In sum, subjects showed more interest in non-contingent images of themselves than contingent images of themselves (both on the iPad and the mirror) and also more interest in unfamiliar than familiar conspecifics.

Table 3.3. Descriptive results: experimental condition, mirror exposure, median looking-time and quartiles calculated from raw data.

Condition	Mirror exposure	Median looking time	Quartiles
C self	non-exposed	4.6	1.4 - 9.3
mirror	non-exposed	4.5	2.2 - 8.7
NC self	non-exposed	22.1	11.5 - 26.6
known	non-exposed	11.1	4.1 - 19.5
unknown	non-exposed	18.1	14.6 - 27.9
NC self	exposed	7.4	4.4 - 10.2
Unknown	exposed	18.5	11.5 - 29.7

In a second part, we provided subjects with three months of *ad libitum* mirror access to test whether prolonged mirror experience with the opportunity to interact freely with their mirror-image would influence the way they perceived the delayed video footage of themselves. Following this treatment and almost two years after the previous trials, subjects were retested with non-contingent footage of themselves (*NC self*) and of an unknown conspecific (*unknown*), the two conditions that elicited most interest (Fig. 3.2). The full model was significantly different from the null model (LRT, χ^2=18.06, d.f.=3, P<0.001; Fig. 3.3, Table 3.4), indicating that looking time differed as a function of mirror-exposure, stimulus identity, and their interaction. The interaction effect was close to significance (LRT, χ^2=3.61, df=1, P=0.057), indicating that interest, as measured by looking time, was substantially lower in the '*NC self*' condition after the three-month mirror-exposure than before (model predictions: 17.3s vs. 7.2s, respectively), which was not the case for the '*unknown*' condition (model predictions: 19.7s vs. 16.3s, respectively).

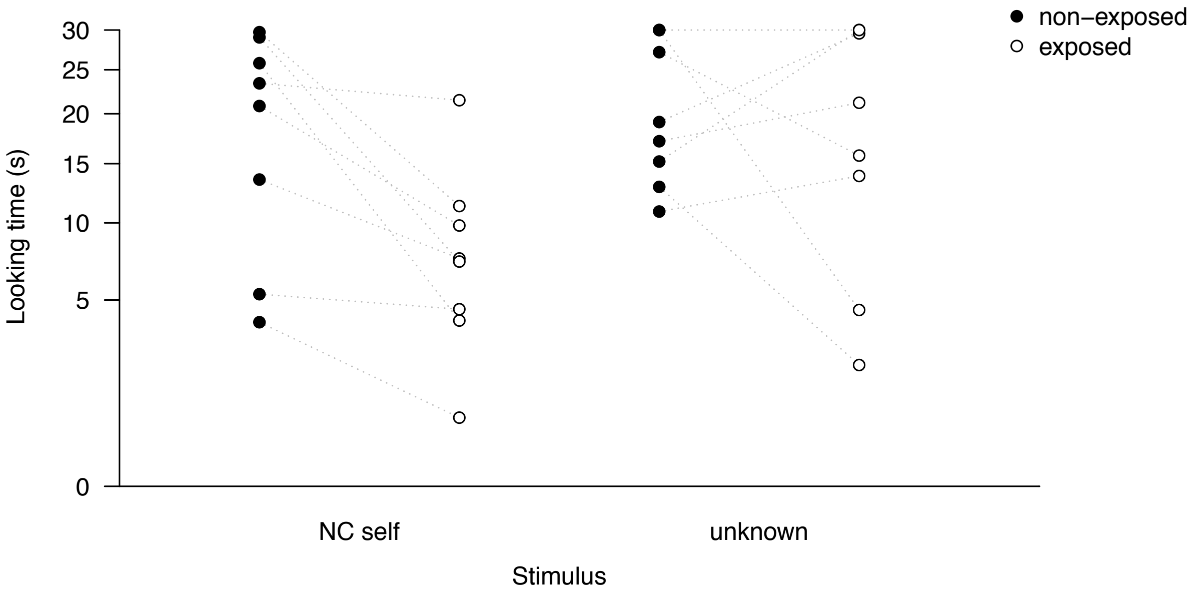

Figure 3.3. Subject looking time (circles) and model predictions (squares) before and after three-months *ad libitum* mirror exposure; note that looking time was square root transformed for modelling but for presentation we back-transformed it along the y axis.

Table 3.4. Result of the LMM, testing the effects of stimulus identity (self vs. unknown) and mirror-exposure (non-exposed vs. exposed) on looking time.

	Estimate	Standard error	*t*
Intercept	5.85	0.35	16.63
Mirror-exposure (non-exposed)			
- exposed	-0.40	0.39	-1.04
Stimulus identity (non-self)			
- self	-0.27	0.39	-0.71
Mirror exposure : Stimulus identity	-1.07	0.55	-1.96
Age	-0.17	0.03	-6.41

These results suggest that the prolonged mirror exposure decreased subject interest in their non-contingent self-images but not their interest in the images of unfamiliar individuals.

Discussion

In this study we were interested in how mirror-naive bonobos responded to different contingent live and non-contingent delayed images of themselves, as well as of known and unknown individuals, and how prolonged mirror-exposure influenced the response to non-contingent video footage of self. To address this, we carried out a two-part experiment during which subjects watched motion images depicting either themselves or another individual. In the first part of the experiment, subject response to three types of self-images (mirror reflection, contingent video feedback and non-contingent video footage) was compared with response to video footage of familiar and unfamiliar conspecifics. Results revealed low interest (as assessed by looking time) in the mirror condition and in contingent footage of the self. In contrast, interest was high in both non-contingent footage of self and footage of unfamiliar individuals while interest for footage of known individuals lay in between.

We draw the following tentative conclusions from these patterns. First, given that our subjects were mirror-naïve and that human and nonhuman primates generally show more interest in novel than familiar stimuli, including faces (Pascalis & de Schonen, 1994; Pascalis & Bachevalier, 1998; Gothard, Erickson & Amaral, 2004; Dufour, Pascalis & Petit, 2006; Gothard, Brooks & Peterson, 2009) we predicted high interest in all but the '*known*' condition. However, subjects showed surprisingly little interest in the '*contingent self*' and '*mirror*' conditions while, as predicted, they showed high interest in the '*non-contingent self*' and '*unknown*' conditions.

We can think of several interpretations of these contrasting findings. First, high interest for the '*non-contingent self*' could indicate that subjects did not recognise this footage as a representation of self, but as an unfamiliar individual, similar to the '*unknown'* condition, which elicited a similar amount of interest. More difficult to explain is the low interest elicited by the two contingent self-images (*contingent self* and *mirror*).

One possible explanation here is that given that stimulus exposure was very short (30s), subjects were effectively prevented from engaging in tell-tale behaviours of self-recognition, such as exploration of visually inaccessible body parts and contingency testing, but only responded with gaze. As a result, the two contingent stimuli (*contingent self* and *mirror*) contained less movement than the non-contingent stimuli, which may account for differences in interest. However, the 'movement' hypothesis is not supported by the fact that '*known*' conspecifics caused less interest than '*unknown*' conspecifics (Fig. 3.2), suggesting that 'familiarity' was, at least partially, responsible for the documented differences in interest.

An alternative and more parsimonious explanation therefore is that non-contingent movement is generally more interesting than contingent movement. Taken to the extreme, this ‘movement’ hypothesis suggests that bonobos have no self-concept but simply show interest in independently moving conspecifics. However, this interpretation is at odds with the fact that the ‘*known*’ condition caused less interest than ‘*non-contingent self*’ and ‘*unknown*’ conditions, all of which moved in asynchronous ways. It is also at odds with the current literature, which suggests that great apes, including bonobos, are capable of self-recognition, so we consider this a less likely interpretation.

Another explanation might be that subjects were already familiar with the contingency of their own reflection from experience with windows and water surfaces or from watching their own shadows. However, although such experiences are likely to familiarise subjects with contingent movements, they do not provide elaborate visual feedback and will not permit subjects to observe and learn much about their own physical features for self-recognition.

In the second part of the experiment, we provided subjects with extended experience of self-reflections by giving them uninterrupted access to a mirror for three consecutive months. Although we did not test each subject specifically for mirror self-recognition, we predicted that, if bonobos are capable of self-recognition, as previously proposed (Hyatt & Hopkins, 1994; Westergaard & Hyatt, 1994; Walraven, Van Elsacker & Verheyen, 1995), then the mirror experience provided should enable subjects to form a mental representation of their own appearance, paving the way to generalised self-recognition regardless of stimulus type. Following the mirror exposure phase, we therefore retested subjects with the two critical stimuli, non-contingent footage of self (*NC self*) and footage of an unknown individual (*unknown*), between 10-20 days after the mirror was removed. Results showed that after prolonged mirror exposure, subject interest in the non-contingent footage of self decreased, while interest levels for the footage of an unknown individual remained. We are confident that the decrease of interest for the ‘*non-contingent self*’ condition cannot simply be explained in terms of habituation given the fact that the stimulus was presented once for 30s, 22 months prior to the second 30s presentation and given the fact that no change was observed in the ‘*unknown*’ condition.

Again, these results are consistent with the interpretation that the prolonged mirror exposure allowed subjects to form a visual mental representation of their own reflection, which then affected their future interest in non-contingent footage of themselves. Whether or not subjects correctly identified their mirror-image as a depiction of the self remains a matter for interpretation. Indeed, a more parsimonious explanation is that response patterns in the second part of the experiment were not due to recognising the self but a by-product of differences in perceived familiarity (e.g. Legerstee, Anderson & Schaffer, 1998). The three-month mirror exposure having allowed for familiarisation with all visual details of themselves, the observed drop in interest might simply be explained as subjects having perceiving the '*non-contingent self*' footage as "familiar" following the mirror exposure, while the '*unknown*' footage remained novel and of high interest. Furthermore, these results are at odds with the previously mentioned 'movement' hypothesis. If subjects were simply interested in watching independently moving conspecifics, then the loss of interest in '*non-contingent self*' footage remains unexplained.

Finally, it is always possible to craft arguments based on combinations of the above interpretations, such as an interactions between familiarity and movement, to explain the observed response patterns. In the end, however, 'self' is a mental construct, accessible only to its owner, which makes it inherently difficult for one experiment to provide compelling supporting evidence. In this sense, we see our study as providing converging evidence and elaboration of how one of our closest living relatives acquires and processes visual representations of itself.

Reflections on the experimental design

First, regarding the fixed sequence design, we find it unlikely that this had an effect on subject interest mainly because stimulus presentation was of short duration (30 s) and because trials were spaced out over time. Furthermore, if fixed sequence presentation had an effect we would have expected a steady decrease in interest as trials progressed but this was not the case. We acknowledge that a completely randomised design would have been preferable but opted against it, due to the low number of subjects available for testing.

Second, using looking-time as a proxy for interest is a dependent variable that has often been criticised as being unreliable or uninformative. Nevertheless, we opted to base our study on it, mainly because, as a general pattern, in tasks relating to face recognition of conspecifics, all species tested show a visual bias for novelty (Pascalis & de Schonen, 1994; Pascalis & Bachevalier, 1998; Gothard, Erickson & Amaral, 2004; Gothard, Brooks & Peterson, 2009; but see Winters, Dubuc & Higham, 2015 for an overview of issues and controversy concerning the looking-time paradigm), while a visual bias for familiar stimuli has only been observed in studies comparing conspecific vs. (novel) hetero-specific faces (Fujita, 1987; Demaria & Thierry, 1988). Familiar stimuli were also preferred in a reaching paradigm for familiar vs. novel hidden objects (Shinskey & Munakata, 2005). Furthermore, during visual processing and formation of mental representations in human infants a bias for a familiar stimulus precedes an inevitable and consistent bias for a novel stimulus (Roder, Bushnell & Sasseville, 2000). Overall, we therefore think that our looking-time paradigm was an adequate way to assess perceived familiarity of conspecific faces in bonobos.

Third, we consider the possibility that the differential loss of interest in the second part of the experiment was caused by the different background features in the video clips. Eye-tracking data would help to resolve this issue. However, we do not think this is a likely explanation because if subjects were mainly interested in the background, then the observed difference of interest in contingent and non-contingent conditions in the first part of the experiment remains unexplained.

Fourth, one of our lines of argument is that the prolonged mirror experience enabled subjects to familiarise themselves with their physical appearance. It would have been desirable, in hindsight, to collect systematic data on how subjects behaved in front of the mirror, both quantitatively and qualitatively. In this way we could have confirmed each subject's ability for mirror self-recognition, based on self-directed behaviours, such as using the mirror to inspect body parts that are normally visually inaccessible.

Finally, and again in hindsight, an interesting point of comparison in the second part of the experiment would have been a second presentation of the '*known*' condition. However, based on the fact that the subjects have extensive opportunities to observe their conspecifics daily and were thus extremely familiar with their physical appearance, we find it unlikely that subject interest in this condition would have been any different after the mirror-exposure. Therefore, if we conclude from our results that the low interest in '*non-contingent self*' in the second part of the experiment is due to familiarisation with the bonobo depicted in the mirror-reflection, then interest should be similar to what has been observed in the '*known*' condition, albeit in the first part of the experiment. Our data support this interpretation (see Table 3.3).

Conclusion

We suggest that, given sufficient mirror exposure, bonobos acquire the ability to use mirror-reflection of themselves to learn about and familiarise themselves with their own physical appearance. This, in turn, modifies their perception of self depictions, even if detached from the here and now. Whether or not this is evidence of self-recognition cannot be concluded with confidence, due the alternative interpretations outlined above. Yet, our study is in line with the current literature that demonstrates that bonobos are capable of mirror self-recognition (Hyatt & Hopkins, 1994; Westergaard & Hyatt, 1994; Walraven, Van Elsacker & Verheyen, 1995) and further adds to the hypothesis that self recognition has to be acquired. Much remains to be elucidated regarding the mechanisms and the implications of the great apes' capacity for the development of self-recognition, such as the amount of mirror exposure minimally necessary or the stability of self-recognition over time. Regarding this last point, findings are contradictory, while Calhoun & Thompson (1988) found that young chimpanzees were still capable of mirror self-recognition, even after one year with no mirror-exposure, de Veer et al. (2003) found that the capacity declined with age.

Regardless of how compelling our data are, a philosophically and empirically interesting problem concerns the implications of self-recognition for questions about self-awareness and awareness of others. As mentioned, mirror self-recognition has also been demonstrated in other species, particularly dolphins, and elephants, which has led to claims about their cognitive capacities, such as having "…complex social understanding and empathic behaviour" (Prior, Schwarz & Güntürkün, 2008, p.1642). Mirror self-recognition, in other words, may just be one part of a package of cognitive capacities obtained from convergent evolution (Plotnik, de Waal & Reiss, 2006; but see Mitchell, 2012). Whether or not there are such intrinsic links, such as suggested by Gallup (1982) in terms of connection between self-recognition and empathy, or even theory of mind (e.g. Gallup, 1991; Gergely, 1994; Suddendorf & Collier-Baker, 2009; Anderson & Gallup, 2015; Dale & Plotnik, 2017), needs to be addressed with further research.

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4: Social learning of arbitrary food preferences in bonobos

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Abstract

A particularly fruitful approach to investigate social learning in animals is based on paradigms involving the manipulation of artefacts. However, tool use and elaborate object manipulations are rare in animals living in natural conditions, including most primates, suggesting that social learning evolved in other contexts where fitness consequences are higher, such as discriminating palatable from noxious foods, recognising predators or understanding social hierarchies. Here, we focussed on one such context by investigating whether bonobos socially learned others' arbitrary food preferences through mere observation. To this end, we trained two demonstrators to prefer (or avoid) distinctly coloured food items, treated with either a sweet or bitter agent. The demonstrators then displayed their newly acquired preferences in front of naïve subjects. In subsequent choice tests, subjects generally matched their choices to the demonstrators' preferred food colours, despite the fact that subjects had already tasted the equally palatable colour alternative. Moreover, social learning was instant insofar as six of seven subjects preferred the demonstrated food colour from the first trial. We discuss these findings in light of the current debate on the evolution of social learning and cultural norms in animals.

Introduction

Over the past decades, social learning (i.e., learning from others) has become a major topic in the field of comparative cognition. Social learning can be highly adaptive as it allows individuals to avoid costly trial-and-error learning, saving both time and energy and avoiding dangerous mistakes (Hopper et al., 2011). Social learning can also favour the rapid spread of advantageous behavioural innovations and, as such, it acts as a 'second inheritance system' in addition to phylogenetically acquired behavioural traits (Whiten, 2005). Social learning is likely to be adaptive in many domains, including foraging, mate choice or predator avoidance (Galef and Giraldeau, 2001; Galef and Laland, 2005) and can even take place between species (Avarguès-Weber et al., 2013). This is particularly relevant for young and naïve individuals, who can avoid costly or maladaptive behaviour by observing and learning from more experienced and older individuals that have, essentially, survived to adulthood in a given environment (Galef and Laland, 2005).

Over the years, substantial efforts have been made to investigate the mechanisms of social learning across different groups of animals, using both observational and experimental techniques in wild and captive populations (e.g. apes: Clay and Tennie, 2017; Dindo et al., 2011; Hobaiter et al., 2014; Whiten et al., 2005; monkeys: Dindo et al., 2008; Kawai, 1965; van de Waal et al., 2013b; lemurs: Stoinski et al., 2011; birds: Aplin et al., 2014; Auersperg et al., 2014; see Reader and Biro, 2010 for a non-exhaustive survey). A common approach to study social learning has been to use paradigms that require manipulation of a container ('puzzle box') to extract an edible reward. A particularly successful variant is the ("artificial fruit"; Whiten et al., 1996), which can be opened through various means (e.g. lifting or sliding a door) to obtain a reward within. Such experiments have brought to light not only evidence of social learning (e.g. van de Waal et al., 2010, 2013b) and social diffusion (e.g. Dindo et al., 2008, 2011; Whiten and Mesoudi, 2008) but they have also contributed to the current debate (see van Leeuwen and Haun, 2013; van Leeuwen et al., 2015 for a critical view; and Aplin et al., 2015; Whiten and van de Waal, 2016a for responses) on social conformity in animals (e.g. Dindo et al., 2009; Whiten et al., 2005). Overall, these findings have broad implications for theories of the evolution of culture (see Whiten and van de Waal, 2016b for a review) as they begin the unravel the basic building blocks for the human capacity for culture, many of which are shared with non-human primates.

Another particularly common experimental paradigm in the laboratory is to expose subjects to inaccessible food rewards that can only be accessed using a tool (e.g. Call and Tomasello, 1994; Horner and Whiten, 2005). However, while tool use is taxonomically widespread, it is generally rare in most primate and non-primate species (Hunt et al., 2013), raising questions on the extent to which experimental paradigms based on tool use are adequate to investigate social learning capacities in such species. Most primates are capable of rich arrays of manipulations, such as twisting, pulling, or peeling, but these manipulations tend to be structurally simple (but see Byrne et al., 2001) and rarely involve tool-use. Moreover, although some chimpanzee communities have well established tool traditions (Visalberghi et al., 2015) others only rarely use tools (Lamon et al., 2017; Lamon and Zuberbühler, 2015; Reynolds, 2005), and tool use is curiously absent in wild bonobos (Koops et al., 2015) and many other primate species. Equally important, although social learning may give naïve observers an advantage in some types of problem solving such as moss-sponging in chimpanzees (Hobaiter et al., 2014) and nut-cracking in tufted capuchins (Coelho et al., 2015) and chimpanzees (Marshall-Pescini and Whiten, 2008), it is difficult to see how this could translate into fitness consequences, in terms of increased survival or reproductive success. Is it possible that social learning has evolved in response to other challenges that animals face in the wild?

Social learning, in other words, may be better investigated in relation to more ecologically relevant challenges, such as learning how to interact with socially powerful group members or neighbouring groups or learning how to identify animal species that can pose a predatory threat. A relevant study here has been that chimpanzees learn rapidly from each other how to react to humans, a major predator of chimpanzees (Samuni et al., 2014). Another ecologically relevant domain for social learning to discriminate edible from noxious plants (van de Waal et al., 2014, 2013a). Although neophobia is clearly adaptive when encountering novel foods (Addessi et al., 2005), it exposes individuals to starvation when environmental conditions become unstable. A more adaptive strategy may be to follow a ‘copy-when-uncertain’ strategy when relying on individual learning alone is risky (Laland, 2004). Evidence of social learning of food choice has been brought to light in several bird species (e.g. house sparrows: Fryday and Greig-Smith, 1994; red-winged blackbirds: Mason and Reidinger, 1981). In primates, food-related social learning is influenced by a number of factors, including sex, rank, age and association (Coussi-Korbel and Fragaszy, 1995) and in some species ingestion of novel foods is facilitated by the mere presence of conspecifics, regardless of what they eat (e.g. tufted capuchin: Addessi and Visalberghi, 2001; chimpanzee: Finestone et al., 2014), while in other species, individuals appear to learn something about the palatability of foods from observing others (e.g. cotton-top tamarin: Snowdon and Boe, 2003; vervet monkey: van de Waal et al., 2013a).

Another important factor in primate social learning of foraging behaviour is the attention that young and naïve individuals pay to adult behaviour (Rapaport and Brown, 2008). Immature individuals often wait for more experienced individuals to begin foraging before following suit with the same food (e.g. Tarnaud, 2004; Whitehead, 1986; reviewed by Rapaport and Brown, 2008). In apes, adult chimpanzees show more caution and close observation of conspecific food-handling when presented with novel foods than familiar ones (Gustafsson et al., 2014). Infant apes are very attentive to their mothers during foraging and show high rates of co-feeding (Jaeggi et al., 2010; Rapaport and Brown, 2008; Ueno and Matsuzawa, 2005). Food sharing and co-feeding between mother and offspring seem to provide infants with direct learning opportunities and has been observed in lowland gorillas, orang-utans, chimpanzees and bonobos (see Rapaport and Brown, 2008 for review). Interestingly, this effect can be so strong that in orang-utans, for example, the diet differences between mothers is larger than between mothers and their offspring (Jaeggi et al., 2010). Despite these considerations, individual learning remains an important mechanism for acquiring food aversion (e.g. pigtail macaques, spider monkeys, Fairbanks, 1975; tufted capuchins, Visalberghi and Addessi, 2000) or complex forms of food processing (e.g. nettle feeding in gorillas, Tennie et al., 2008). Some feeding behaviours are even thought to be part of species-specific behavioural repertoires (e.g. rough-leaf swallowing in chimpanzees and bonobos, Menzel et al., 2013) although social influences likely aid the spread of such behaviours (Huffman and Hirata, 2004).

Another general finding in empirical work on social learning is the importance of the seeding demonstrator's identity. Chimpanzees, for example, show a clear bias for copying older, higher-ranking and more knowledgeable individuals (Biro et al., 2003; Kendal et al., 2015). However, low ranking individuals may be just as effective in seeding novel behaviours when there is no 'model competition' (i.e., when there are no older or higher ranking individuals acting as demonstrator) (Watson et al., 2017). Yet, in a recent field study with chimpanzees, a novel behaviour, 'moss-sponging' invented by the alpha male, was shown to spread through the community via two transmission patterns. Initial spreading was within a spatio-temporal, proximity-based cohort but then mainly through the matrilines (Lamon et al., 2017), a pattern not previously reported in captive groups. The study thus indicated considerable flexibility of behaviour transmission patterns in chimpanzees. Another theory suggests a link between the patterns of social learning of young and low-ranking individuals and their alleged urge to socially ‘conform’ to the behaviour of older and higher-ranking individuals, as predicted by de Waal’s (2001) bonding- and identification-based observational learning model (BIOL). De Waal’s BIOL model further predicts that social learning is determined by the quality of the social bonds between demonstrators and subjects, with socially close individuals more likely to learn from each other (e.g. Zuberbühler et al., 1996). Conformity can be defined as changing one’s behaviour to match that of a group majority, sometimes going against one’s own knowledge to do so (Asch, 1956). This idea has inspired much research on social conformity (e.g. Dindo et al., 2009; Hopper et al., 2011; Vale et al., 2017; van de Waal et al., 2013a; Whiten et al., 2005), but the results are still controversial, and interpretations of conformity made by some (Aplin et al., 2014; van de Waal et al., 2013a) are claimed, by others, to lack supporting evidence and draw premature conclusions (see van Leeuwen and Haun, 2013; van Leeuwen et al., 2015 for a critical view; and Aplin et al., 2015; Whiten and van de Waal, 2016a for responses). For example, in one such experiment, migrating male vervet monkeys abandoned their personal food preferences to adopt an opposite preference shown by their new group, which has been interpreted as social conformity and potent social learning (van de Waal et al., 2013a; Whiten and van de Waal, 2016a; but see van Leeuwen et al., 2015).

In the present study, we were interested in testing whether bonobos are able to socially learn arbitrary food preferences of other group members through mere observation and whether they would adopt and maintain such preference regardless of own knowledge that both options were equally palatable. To achieve this we ran a social learning experiment comprising of a series of testing blocks in which subjects observed two demonstrators consistently choosing food items of one novel colour over another. Subjects were then tested to find out whether they preferred to choose food of the same colour as the demonstrator. We predicted that, if subjects observed demonstrators exhibiting a clear choice bias for one novel food colour over another, they would match this bias above chance level in subsequent choice tests. As subjects had no prior experience with these foods, we predicted social learning to be particularly strong during the first testing block when subjects were still naïve relative to these foods. We were also interested in whether subjects were prepared to maintain such socially learned food preferences, even after having experienced the respective colour alternatives.

Methods

Ethical statement

The study was authorised and ethically approved by the management of “La Vallée des Singes”. Although two individuals were regularly isolated for short periods of time (<30 min) during this study, they were specifically selected based on their propensity to choose isolation from the group on occasion thus avoiding stress for both the isolated individuals and the group as a whole. The keeper isolated the individuals using methods regularly used on the group when encouraging individuals to pass from one cage to another. When stress was detected within the group, testing was postponed. The study was in line with recommendations in the ARRIVE guidelines, and Animal Behaviour (1992) as well as the EAZA and the AFdPZ code of ethics.

Study Site and Subjects

Testing took place between February and November 2014 at La Vallée des Singes primate park, Romagne (France). Subjects were selected from a large group of captive-born bonobos (N = 17, 8 males and 9 females, age range: 14 months - 45 years, mean = 15.2 years, see table 4.1) housed in a large indoor enclosure (400m^2) with access to two outdoor wooded islands covering 11,500m^2 total.

Table 4.1. Study subjects housed at La Vallée des Singes and role in the experiment

Individual	Sex	Birth year	Age-class	Role
Diwani (DW)	M	1996	Adult	Demonstrator
Kelele (KEL)*	M	2004	Adult	Demonstrator
Ulindi (UL)	F	1993	Adult	Observer
Lingala (LNG)	F	2003	Sub-adult	Observer
Lucy (LY)	F	2003	Sub-adult	Observer
Nakala (NK)*	F	2007	Juvenile	Observer
Loto (LO)	M	2009	Juvenile	Observer
Moko (MO)	M	2012	Infant	Observer
Khalessi (KLS)	F	2012	Infant	Observer

Note: Individuals marked by an asterisk had the same father; age-class as defined by Kano (1984)

Two adult males, one intermediately ranking (DW) and one low ranking (KEL), were selected as demonstrators based on the ease with which they could be isolated without apparent signs of stress to anyone. The experiment consisted of six testing blocks, three for each condition (details are specified below). Testing was dependent on the personal motivation of each individual to, first, observe the preference demonstrations, and, second, participate in the food choice tests. Therefore, only 7 of 17 individuals (two males and five females, age range: 14 months to 20 years, mean = 7.4 years) participated in the experiment (see table 4.1). One individual (LNG) participated in only three of six testing blocks, again, due motivational reasons. The remaining six individuals completed all six testing blocks.

Food Preparation and Presentation

Two food types, raw courgettes and cooked egg whites (hereafter 'egg'), were used throughout the experiment. Individuals were familiar with the natural taste of these foods. Courgette is a lesser-valued food; egg is highly valued, but only familiar as hard-boiled and in the shell. For the first two phases of a testing block (Demonstrator Training and Preference Demonstration), the two food types were altered in taste and colour to obtain (a) sweet pink courgette, (b) bitter blue courgette, (c) sweet blue egg and (d) bitter pink egg. We alternated the colour associated with the palatable food to control for any eventual colour preference by the demonstrators. The courgette was sliced and quartered before being soaked overnight in either pink food colouring and a sweet additive (liquid sugarcane), or blue food colouring and a bitter additive (Bitrex® aqueous solution 2.5%, 0.2ml per 5cl of water: 100ppm). For the egg, either blue food colouring and a sweet additive or pink food colouring and a bitter additive were added before cooking the mixture in a microwave oven and cutting it into small pieces (approximately 2 x 2 x 0.5 cm). For the third and final phase of a testing block (Observer Testing) the two food types were altered in taste and colour to obtain only sweet pink and blue foods and no bitter foods. Pink and blue food colouring where chosen as few to no foods of these colours are included in the group's regular diet.

To determine food preferences, items were offered manually. To this end, the experimenter (GS) placed a cube of each colour of a given food type on two identical white plastic trays (20 x 20 cm), which were placed, side by side, against the bars of the cages allowing the individual to reach for the food using either the fingers or lips (Fig. 4.1a). The position (left or right) of the different coloured food items was balanced and pseudo-randomised, insofar as given colour was presented on the same side for no more than three consecutive trials.

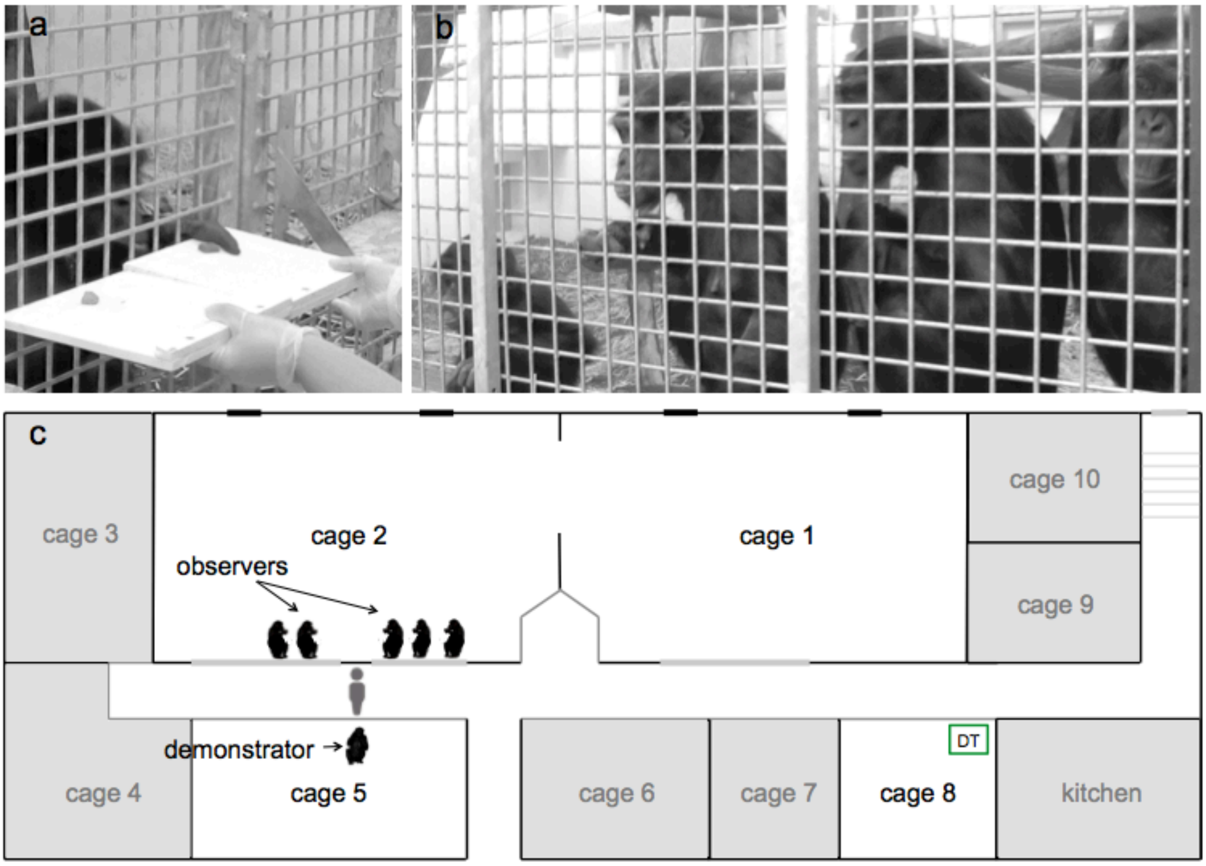


Figure 4.1. Experimental setup for social learning experiment – a) Manual food presentation using 20 x 20 cm white plastic trays and demonstrator choice; b) observers watching a Preference Demonstration, c) The Preference Demonstration Phase is illustrated showing the demonstrator in cage 5 and the observers across the corridor in cage 2. DT marks the location used in cage 8 for the Demonstrator Training Phase.

Experimental Design

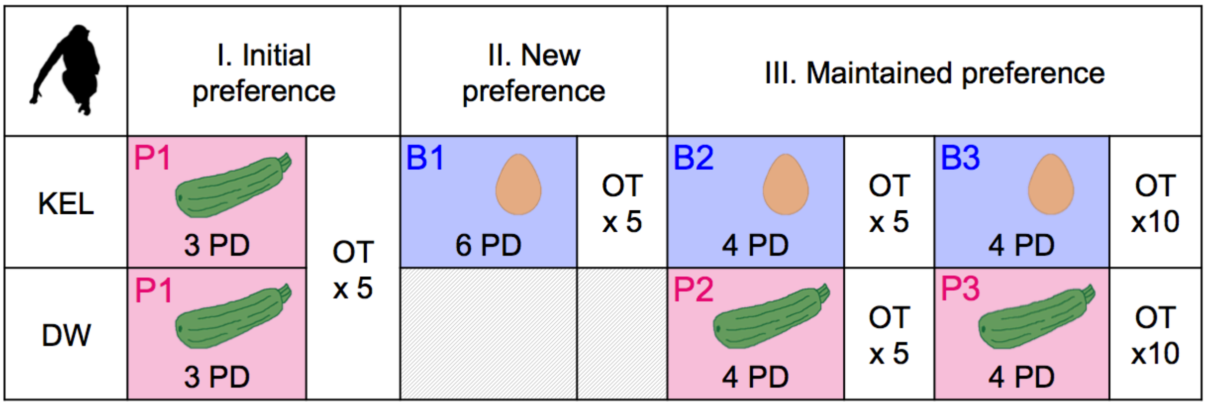
The experiment was carried out in six testing blocks (P1, B1, B2, B3, P2 and P3, see fig. 4.2). Each testing block consisted of three distinct phases: (1) Demonstrator Training Phase (demonstrators were given the choice between two artificially coloured foods (pink or blue) one of which was rendered unpalatable); (2) Preference Demonstration Phase (subjects observed demonstrators choosing their preferred food colours; (3) Observer Testing Phase (subjects were given the choice between pink or blue food (courgette or egg, see fig 4.2). For detailed explanations see below. In three testing blocks (P1, P2 and P3) demonstrator(s) were presented with pink and blue courgette, and demonstrator preference was for the pink and in the three remaining testing blocks (B1, B2 and B3) the demonstrator was presented with pink and blue egg and demonstrator preference was for blue egg.

Demonstrator Training Phase

In the initial training phase the two demonstrators, DW and KEL, learned that pink courgette was palatable (artificially sweetened), whereas blue courgette was unpalatable (artificially made bitter). In subsequent testing blocks KEL then learned the reverse colour pattern, albeit with a different food type: blue egg was palatable, while pink egg was unpalatable. To this end, both individuals were offered the choice between the pink and blue food (courgette or egg, depending on the testing block, see fig. 4.2 for details), one sweet, one bitter, in private (Fig. 4.1c – cage 8, location marked DT). Food presentation lasted 10 seconds after a first choice had been made. Both individuals were given the choice 10 times, although we found that the colour-taste association was learned after just one experience with the bitter food. From the next trial onwards, both individuals consistently chose the sweet colour first and either ignored or only cautiously tasted and discarded the bitter colour second. Demonstrator Training was recorded using a PANASONIC HC-V727 full HD camera equipped with a SENNHEISER MKE 400 external microphone.

Preference Demonstration Phase

Following the Demonstrator Training Phase, a demonstrator was isolated and given the choice between the pink and blue food, while the rest of the group observed his choices from the opposite cage (Fig. 4.1b and 1c - cages 5 and 2). Demonstrators were allowed to choose 10 times. Food presentation lasted 10 seconds after a first choice had been made, so that observers could see more clearly which food had been chosen and which had been rejected. Preference Demonstrations were carried out once a day over several consecutive days (see fig. 4.2 for details).



	I. Initial preference		II. New preference		III. Maintained preference			
KEL	P1 3 PD	OT x 5	B1 6 PD	OT x 5	B2 4 PD	OT x 5	B3 4 PD	OT x10
DW	P1 3 PD		▨	▨	P2 4 PD	OT x 5	P3 4 PD	OT x10

Figure 4.2. Experimental design - Testing block order, demonstrator(s) identity, number of Preference Demonstrations (PD), food used and preferred colour as well as number of Observer Tests (OT) following each Preference Demonstration Phase. Testing period for each testing block in chronological order: P1: Feb, B1: Jul, B2: Aug, B3: Sep, P2: Nov, P3: Nov.

We first ran testing block P1, in which both DW and KEL were demonstrators and both showed a clear preference for the pink courgette. We chose to start with both demonstrators showing the same preference to highlight the salience and strength of the demonstrated preference to the observers. Once established, we proceeded to testing block B1 in which KEL was sole demonstrator and his colour preference was switched, albeit with a novel food type, so that his preference was for blue egg. We then proceeded to testing blocks B2 and B3, again with KEL demonstrating his preference for blue egg, followed by testing blocks P2 and P3, with DW demonstrating his maintained preference for the pink courgette (see fig. 4.2). The number of demonstration days varied among testing blocks (i.e. three consecutive demonstration days for each demonstrator in P1, six consecutive days for the sole demonstrator in B1 and four consecutive demonstration days for the sole demonstrator in B2, B3, P2 and P3 resulting in N=170 observable food choices for KEL and N=110 observable food choices for DW in total).

During the Preference Demonstration Phase both the demonstrators and the observers where filmed in order to record both the choices of the demonstrators and the number of trials attended to by each observer (demonstrator: PANASONIC HC-V727 full HD camera equipped with a SENNHEISER MKE 400 external microphone; observers: PANASONIC HC-V100 full HD and PANASONIC HC-V727 full HD cameras). Subject attention to demonstrator food choice (i.e., looking towards the demonstrator and observing his choice) was coded post-hoc by GS from the video footage and from oral commentaries recorded during the demonstrations. Subject attention for a given trial was coded conservatively as either '1' or '0' (i.e., 1 = observing, 0 = not observing). Individuals observing from outside the camera range were recorded with help from a trained animal keeper.

Observer Testing Phase

Following the Preference Demonstration Phase for each testing block, observers underwent individual preference testing in which sweetened pink and blue foods (courgette or egg) were presented to them simultaneously. During the Observer Testing Phase, both food types were prepared in the same way, but liquid sugarcane was used for all food types to rule out any possibility of odour cue-based choices by the observers. Food presentation ended as soon as a choice had been made and was carried out opportunistically on all participating observers (N=7) in all of the indoor cages and the outdoor enclosure.

Observers were tested five times each in P1, P2, B1 and B2, and 10 times each in P3 and B3. Testing was opportunistic but no two consecutive tests were carried out on a given individual unless the individual had resumed another activity before being retested. Whenever possible, testing was carried out in private in order to avoid feeding competition with other members of the group. Testing was carried out over two or three consecutive days following the Preference Demonstration Phase and was filmed using a PANASONIC HC-V100 full HD camera in order to record the colour chosen as well as the side of the chosen food item. As choices were always unambiguous and clear, we did not carry out any inter-observer reliability tests.

Statistical Analyses

Statistical analyses were carried out using R 3.1.2., GUI 1.65 and SPSS version 22. Datasets are available in the supplementary materials (ESM 4.1). Wilcoxon exact sign rank tests were used to test comparisons between: 1) Subject attention to the two demonstrators (i.e., the percentage of DW and KEL preference demonstration trials observed by each subject); 2) Performance in the first choice test, (i.e. number of matched and non-matched choices made in the first test following each preference demonstration). For the overall performance (i.e., the number of matched and non-matched choices made by each subject overall), we ran a Generalised linear model with a quasi-binomial error structure. We modeled the probability of making matched choice across all trials per individual as a function of age and proportion of observed demonstration trials.

Results

Preference Demonstration Phase

Demonstrator performance

KEL and DW's performance during Preference Demonstrations was close to perfect. They chose the correct colour first in 97% and 99% of trials and ate the correct colour exclusively in 95% and 96% of trials, respectively (i.e. pink courgette in P1, P2 and P3 and blue egg in B1, B2 and B3; KEL N=170 and DW N=110, see Preference Demonstration Phase in methods for details).

Attention to demonstrators

Observers paid more attention to preference demonstrations by DW than by KEL, but not significantly so (mean percentage of demonstrations watched by the subjects (N=7): DW 35.4%, KEL 29.8%, Wilcoxon exact test, Z = -1.014, V = 8, exact *P* = 0.38, two-tailed).

Observer Testing Phase

First choice performance

For the first trial of the first testing block (P1) all observers were naïve having had no personal experience with the artificially altered foods. Nevertheless, six of seven subjects chose the colour chosen by the demonstrator. When analysing first choices across all testing blocks, individuals chose the matched colour significantly more often than the non-matched colour (Z = -2.64, V = 21, *P* = 0.031, two-tailed, Wilcoxon exact test; Fig. 4.3). Of the seven subjects, six chose mostly the matched colour as their first choice for each testing block, and only one chose the matched and non-matched colour equally, suggesting that, as per our predictions, individuals immediately experienced a significant bias towards the foods chosen by the demonstrators, a clear demonstration of rapid social learning.

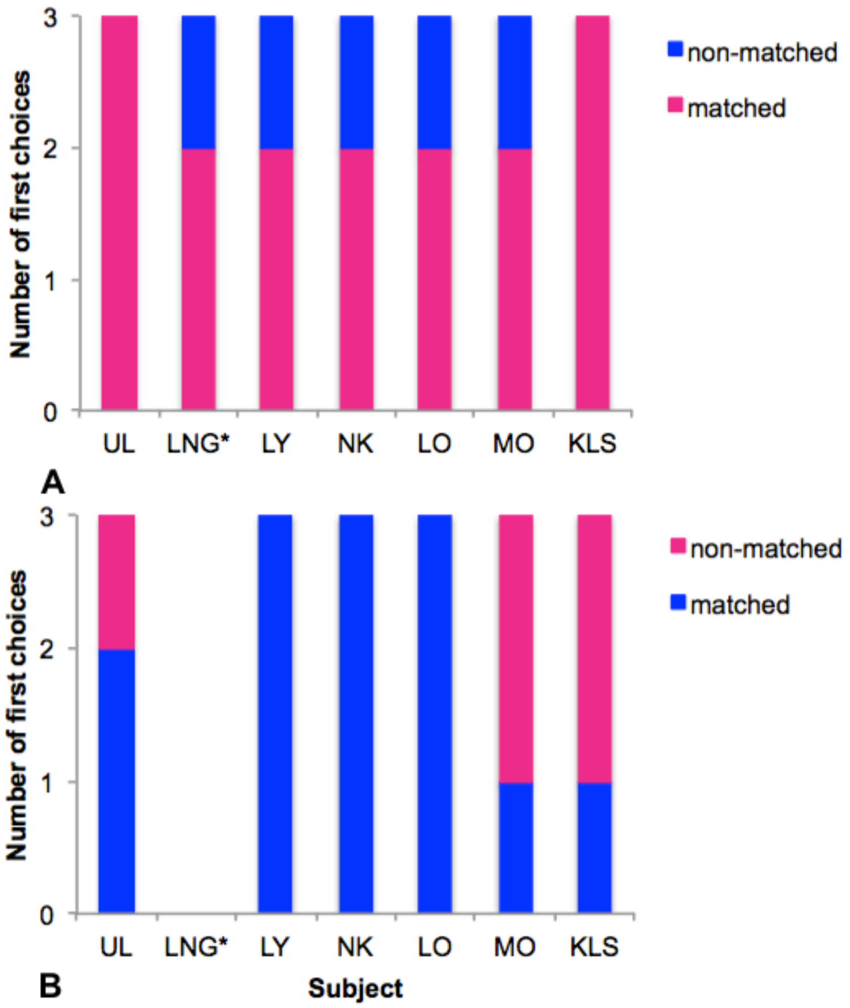


Figure 4.3. Number of matched and non-matched colour choices for each subject in the first choice test (Observer Testing Phase): A) pink testing blocks (P1, P2, P3), B) blue testing blocks (B1, B2, B3), subjects classed by decreasing age from left to right.

Overall performance

Taking into account the observers' overall performance in choosing the matched colour, results show that the food preference of the demonstrators continued to have an influence on observer colour choice. Indeed, the model demonstrated that subjects matched their choices to those of the demonstrators significantly above chance levels (see table 4.2 and figure 4.4 for raw data).

Table 4.2. Results of the logistic regression modelling the proportion of successful trials (N = 7).

	Estimate	Standard error	Z value	P
Intercept	0.64	0.09	6.85	0.002 ***
Age	7.33	1.60	4.59	0.010 *
Proportion of trials observed	1.65	0.50	3.32	0.029 *

Note: Estimates are on a logit scale

This is important because, over the course of the experiment, all observers occasionally tasted the alternative colour choice (i.e., unmatched choice), which was identical in taste and palatability to the matched choice (both treated with liquid sugarcane). Nonetheless, they chose the food colour preferred by the demonstrators above chance.

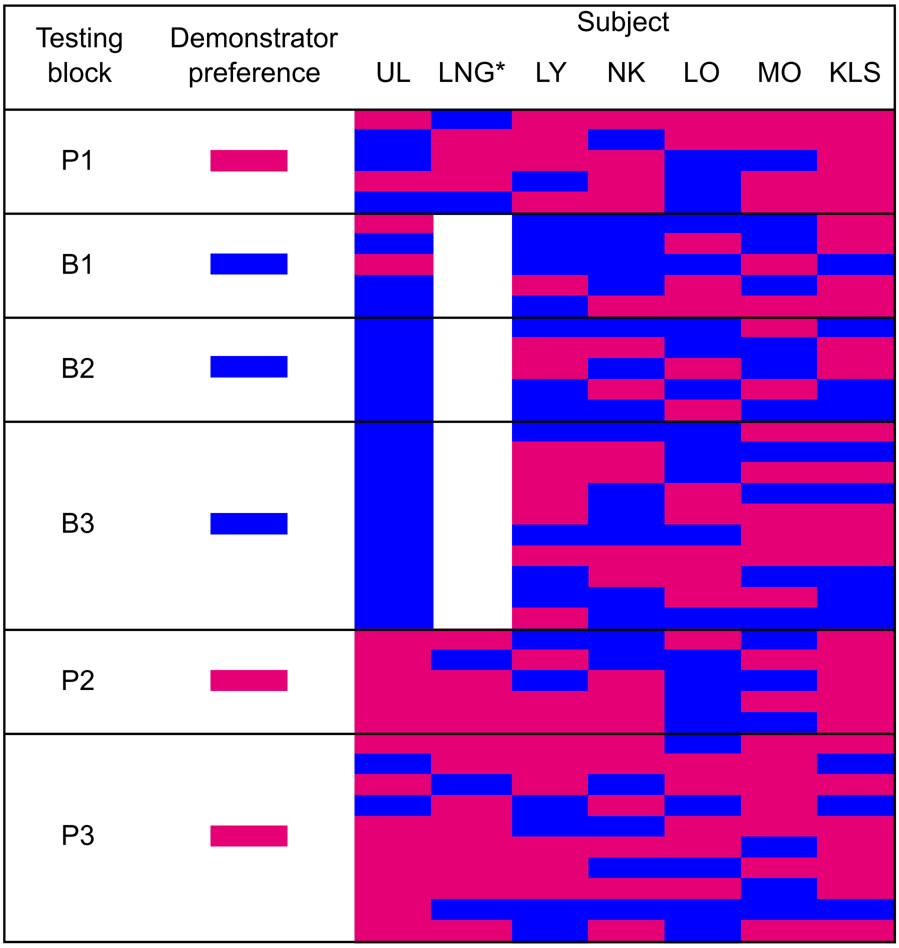


Figure 4.4. Testing block, demonstrator preference and all subject choices during the Observer Testing Phase for all six testing blocks (shown in chronological order).

Furthermore, both age and proportion of trials observed had a significant positive effect on the proportion of successes. (Table 4.2, Figs. 4.5 and 4.6).

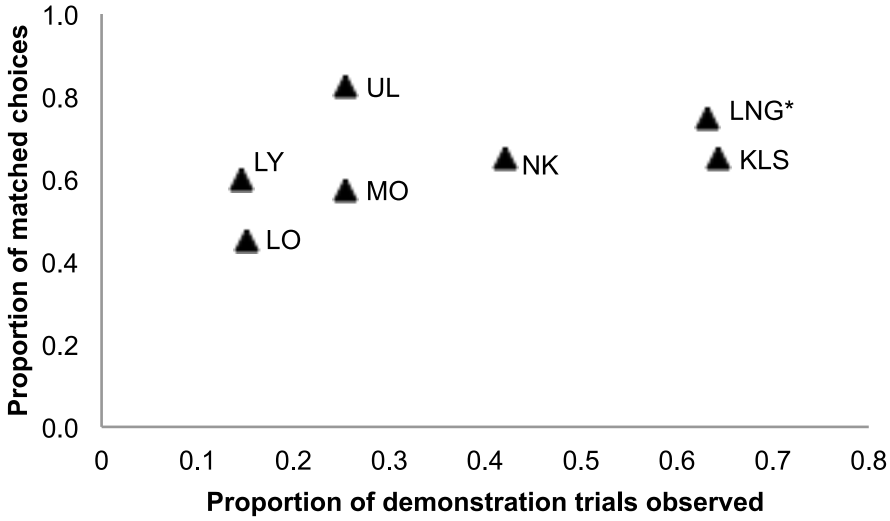


Figure 4.5. Proportion of matched choices made during Observer Testing Phase and proportion of Preference Demonstration trials observed by each subject. LNG, marked by an asterisk, participated in only P1, P2 & P3.

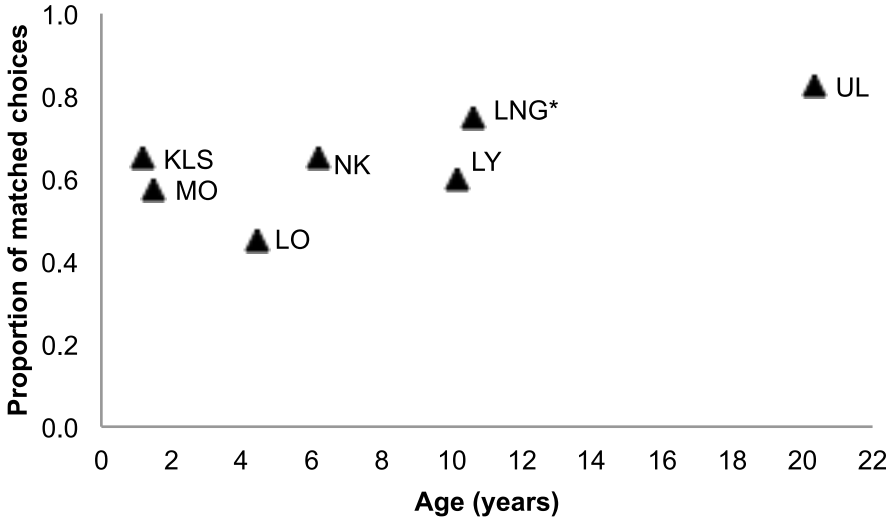


Figure 4.6. Proportion of matched choices made during the Observer Testing and subject age in months. LNG, marked by an asterisk, participated in only P1, P2 & P3.

When considering individual performance (i.e. proportion of matched choices during the Observer Testing Phase), it can be noted that there is considerable inter-individual variability (Table 4.3). Indeed, six of seven subjects chose the matched coloured food more often than the non-matched coloured food.

Table 4.3. Individual performance over all six testing blocks

Subject	*N*	Proportion of demonstration trials observed	Food colour choice matched : unmatched	Performance (%)
UL	40	0.25	33:7	82.5
LNG	20	0.63	15:5	75.0
LY	40	0.14	24:16	60.0
NK	40	0.42	26:14	65.0
LO	40	0.15	18:22	45.0
MO	40	0.25	23:17	57.5
KLS	40	0.64	26:14	65.0

Note: Proportion of demonstration trials observed, number of matched and unmatched choices and percentage of matched choices made by subjects. One individual (LNG) participated in the Observer Testing Phase for only three of the six testing blocks: P1, P2 & P3.

Discussion

In this study we sought to investigate whether bonobos are capable of acquiring and retaining information relating to arbitrary food preferences of fellow group members through mere observation. In other words, can bonobos socially learn the different food preferences of other group members and do they abide to these even if doing so goes against their own experience and knowledge (i.e., despite knowing that both colour alternatives are equally palatable)? In our experiment, both demonstrators were exposed to trial-and-error learning to install an arbitrary preference for visually novel food items, which led immediately to a clear bias for the palatable food. Subjects were then provided with the opportunity to observe both demonstrators and we found that they developed an immediate preference for the food item chosen by the demonstrator, demonstrating rapid and reliable social learning. Furthermore, and importantly, this effect occurred despite subjects being exposed to a complex demonstration pattern during which one demonstrator demonstrated opposing colour preferences for different foods (see fig. 4.2). We noted considerable inter-individual differences during the crucial Observer Testing Phase, which was not sufficiently explained by subject age nor exposure to demonstrations (see fig. 4.5 and 4.6); individuals that observed only a few demonstrations were just as likely to succeed in the Observer Testing Phase as individuals that observed many demonstrations, suggesting that even minimal exposure is sufficient for social learning.

Our second finding relates to the fact that subjects' performance continued to be biased towards the demonstrated preference, as indicated in the subjects' overall performance, even after individuals had opportunities to taste the alternatively coloured foods (i.e., when both coloured foods were known to be equally palatable). This propensity to adhere to the demonstrator preference might be expected of naïve subjects, in line with a 'copy-when-uncertain' strategy, suggesting that subjects perceived uncertainty during testing which increased their willingness to rely on social information (Galef et al., 2008; Kendal et al., 2015). In some studies with apes and human children subjects have been found to follow the demonstrator's strategy even if this meant going against their own personal preference (e.g. human children, Gergely et al., 2002; chimpanzees, Hopper et al., 2011) while in other studies this was not the case (Vale et al., 2017). Vale and colleagues (2017), for instance, demonstrated that chimpanzees preferred to rely on their personal experience with unpalatable foods rather than to conform to group norms. Observation of group members eating the previously "unpalatable" food did, however, promote the re-exploration of that food through social learning. In other studies, animal species relied more on their own experience, ignoring any cues from conspecifics as to food palatability (e.g., house sparrows: Fryday and Greig-Smith, 1994).

In our study, following their initial choice, not only were subjects rapidly exposed to the alternative colour choice, but in choosing the alternative colour they were immediately rewarded, just as they were when copying the demonstrator. And yet in our study, subjects generally adhered to preference shown by the demonstrator. One potential explanation for subjects adhering to demonstrator preference, despite possessing the knowledge that both foods were equally palatable, might come from some sort of desire to conform (as predicted by de Waal's (2001) BIOL model, although the author predicted a desire to confirm specifically to higher ranking and older individuals), perhaps for the sake of social cohesion (Hopper et al., 2011). In humans, this effect is particularly strong if a novel behaviour is shown by several or a majority of group members. Conformity predicts that individuals will change their own behaviour and adopt the majority behaviour in order to comply with what they perceive as 'social norms' (van Leeuwen and Haun, 2014). Whether or not such social influence really requires a majority (e.g. Asch, 1956) or comes into play even when the behaviour has initially been demonstrated by a minority, is often unclear (Hopper et al., 2011; but see Cialdini and Trost, 1984 for a review). In our study we did not test specifically for conformity, although we demonstrated that several group members adopted the same preference (non-exclusively) as that expressed by the two demonstrators, and this was despite having knowledge that both foods were equally palatable. Another explanation is that subjects were following a sensible survival strategy: if a demonstrator systematically refuses to eat a certain food, then it may be reasonable to assume that he does so for a good reason. In the present case, following the demonstrator's choice and following a 'better-safe-than-sorry' strategy was cost free. In our study, the two demonstrators were a middle- and a low-ranking male, but nevertheless social learning took place, as shown, for example, by the results obtained for UL, a high-ranking adult female, who was most strongly influenced by these males (i.e., UL made the highest number of matched choices of all subjects, see table 4.3). Perhaps, similarly to chimpanzees, in the absence of 'demonstrator-competition' (i.e., the presence of the usually more favoured, older and higher-ranking demonstrators), low-ranking individuals can successfully seed a behaviour (Watson et al., 2017). This finding is thus at odds with one of de Waal's (2001) bonding- and identification-based observational learning model predictions, which is that, for social learning to take place, demonstrators ought to be high ranking individuals, a pattern that has been found in both captive (Horner et al., 2010) and wild chimpanzees (Hobaiter et al., 2014) although kin-based learning may be more important in establishing long-term behavioural traditions (Lamon et al., 2017)The underlying drivers of such behaviour open questions for future research.

Conclusion

We conclude that, even in the absence of olfactory and taste cues, bonobos are able to acquire and memorise others' food preferences and are prepared to adhere to them, if they lack prior knowledge, even when the demonstrator is low ranking. Bonobos, similar to humans, are susceptible to acquiring information from watching the behaviour of others even if demonstrators are socially unimportant and even adhere to these learned behaviours despite personal knowledge that there is no additional reward in doing so. This finding is thus at odds with one of de Waal's (2001) bonding- and identification-based observational learning model predictions, which is that, for social learning to take place, demonstrators ought to be high ranking individuals, a pattern that has been found in both captive (Horner et al., 2010) and wild chimpanzees (Hobaiter et al., 2014) although kin-based learning may be more important in establishing long-term behavioural traditions (Lamon et al., 2017). Furthermore, while this study does not allow us to draw conclusions regarding the social learning mechanism(s) at work, the results, even if due to simple stimulus enhancement, demonstrate that subjects matched their choices to those of the demonstrators regardless of the colour, food type and demonstrator identity. We believe this supports the fact that learning from others in the context of food acquisition is of paramount importance.

Finally, it is important to point out that our findings were made in the context of an ecologically important situation, i.e. learning about novel foods, which highlights the fact that social learning theory is likely to benefit from paradigms that focus on ecologically relevant problems.

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5: Early signs of pragmatic inference in bonobos (*Pan paniscus*)

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Abstract

In human language, links between utterances and meaning are often indirect and mediated by pragmatic inferences, a process by which linguistic content is integrated with non-linguistic information, such as physical and social context, shared knowledge or prior interaction history. To understand the evolutionary origin of this ability we tested experimentally whether bonobos (*Pan paniscus*) can make inferences about food potentially available to them, from hearing food calls of other group members with known, but different food preferences. To this end, we trained two demonstrators to prefer either blue or pink chow, and selected a third individual as untrained control. Subjects observed the trained demonstrators displaying their preferences and learned that the novel foods were available to them in two specific locations, though never simultaneously. In subsequent playback experiments, we then broadcast the food calls of a demonstrator and control individual to assess subjects' foraging decisions. Only one of 10 subjects performed in line with predictions of the hypothesis that human-like pragmatic inference is within the bonobo's cognitive reach. However, post-hoc analyses showed that, after hearing demonstrator calls, all subjects exhibited individual biases for either one of the two food locations, a significant

difference to their responses to calls from the control individual. These findings suggest that subjects remembered that the demonstrator, but not the control individual, possessed an idiosyncratic food preference, but not necessarily which one, thus demonstrating a basic level of pragmatic inference.

Introduction

There is general agreement that the evolution of language is best studied as a collection of capacities, sometimes with independent evolutionary histories, some relating to production and use and others to comprehension (Darwin, 1871; Seyfarth & Cheney, 2010). As cognitive capacities do not leave direct traces in the fossil record, an indirect way of studying their evolution is by comparing mental processes and communication capacities across primates, such as attribution of meaning (e.g. Seyfarth et al., 1980; Zuberbühler et al., 1999; Arnold & Zuberbühler, 2006; Cäsar et al., 2012), grammar-like combinations (e.g. Clarke et al., 2006; Ouattara et al., 2009; Schel et al., 2010; Clay & Zuberbühler, 2011), intentionality (e.g. Crockford et al., 2012; Schel et al., 2013b; Genty & Zuberbühler, 2014; Townsend et al., 2017) or social awareness (e.g. Tomasello & Zuberbühler, 2002; Slocombe & Zuberbühler, 2007; Clay & Zuberbühler, 2012). The logical foundation of this approach, dating back to Darwin, is that more closely related species should be more similar in terms of their cognitive capacities than more distantly related ones (Darwin, 1871).

In primates, capacities related to signal comprehension appear to be cognitively more complex than those relating to production, with evidence for flexibility, open-endedness, and assimilation to experience (Seyfarth & Cheney, 2017a, 2017b). Comprehension concerns the process of drawing inference from perceived signals (Clark, 1977; Johnson & Smith, 1981; Seyfarth & Cheney, 2017b) and complexity arises if recipients integrate across different sources of information, beyond simple event-signal associations. In human language, this involves multiple processes that go far beyond adhering to the literal meaning of speech utterances and can include world knowledge, assumptions about shared cultural background, current context, or variables relating directly to the signaller (Seyfarth et al., 1980; Johnson & Smith, 1981). According to an influential theory by Grice (1975), meaning in language emerges from juxtaposing linguistic content onto four maxims of conversation: quality, quantity, relevance and order of information conveyed by communicative partners.

Animal communication is usually seen as free from such complexities. The classic case is the alarm call system of vervet monkeys, with different predator alarm call types closely tied to corresponding predator encounters, which allows recipients to directly respond to the calls (Seyfarth et al., 1980), but this may be similar to what has been observed in classical Pavlovian learning paradigms. The fact that vervet monkeys show relatively distinct responses to different alarm calls has been taken as a way to define the meaning of these calls (Seyfarth & Cheney, 2010; but see Zuberbühler et al., 1999). Essentially the same model of call-referent relation has also been used to interpret other types of calling behaviour, such as those in relation to food (e.g. Di Bitetti, 2003; Gros-Louis, 2004; Schel et al., 2013a), food quantity or quality (e.g. Gros-Louis, 2004; Clay & Zuberbühler, 2009, 2011; Clay et al., 2012), different predator types (e.g. Zuberbuhler et al., 1997; Cäsar et al., 2012) or the nature and directionality of aggressive interactions (e.g. Slocombe & Zuberbühler, 2005a; Slocombe et al., 2010).

More recently, however, this basic notion of meaning in animal calls has become a topic of debate (Wheeler & Fischer, 2012). In particular, there is evidence that both call production and comprehension can be governed by additional variables (Smith, 1977), such as a subject's knowledge about their social, physical and contextual environment, which will determine a call's meaning, beyond what is explicitly conveyed through the physical characteristics of a signal (e.g. Arnold & Zuberbühler, 2006; Slocombe et al., 2010; Cäsar et al., 2012). Animal communication, in this view, almost always takes place within a context shared by signaller and receiver and this appears to affect the emergence of meaning (Loukusa & Moilanen, 2009; Seyfarth & Cheney, 2017b). Chimpanzees, for example, use social knowledge to infer the nature of out-of-sight aggressive interactions from listening to the exchange of referentially unspecific social calls (Slocombe et al., 2010). Such pragmatic inference on part of a receiver can render a referentially broad signal into one with a highly specific meaning (Seyfarth & Cheney, 2017b), which is at odds with the notion of functional reference but more in line with how humans deploy referential processes.

The aim of this study was to probe more deeply into the nature and flexibility of pragmatic inference in great ape communication. To this end, we investigated whether our close relatives, bonobos, were able to interpret calls beyond their basic biological function (e.g. food calls have a basic function of advertising the presence of food) by taking into account social knowledge about others' communicative idiosyncrasies. Our experimental design took advantage of the fact that bonobos show individual vocal recognition (Keenan et al., 2016) and typically vocalise when encountering food, sometimes in relation to food quality (Clay & Zuberbühler, 2009, 2011). We artificially established individual differences in food preferences in two members of a large captive group to test whether listeners could mentally represent such differences and base their foraging decisions on such knowledge. To this end, we played back the food calls of two individuals, one with a known preference for blue food and dislike of pink food, the other with no preference for one food over the other. We predicted that subjects would show more foraging effort for blue food than for pink food when hearing calls of the first individual, but that no such difference would be observed when hearing calls of the second.

Methods

Study site and subjects

Research was carried out between February 2015 and October 2016 on a group of bonobos at 'La Vallée des Singes' primate park, Romagne, France. The group of 20 individuals (9 males and 11 females, 0 - 46 years, see Appendix II: Table A.II.1) lived in an indoor enclosure (400m^2) composed of 10 interconnected cages with access to two outdoor wooded islands covering 11,500m^2. Three individuals, a mother and her two adult and subadult sons, were separated from the group in the December of 2015 in preparation for departure to a different zoo.

Experimental design

The experiment sought to simulate a situation in which a subject could make inferences about the location of food, based on who provided the information. To this end, we trained two individuals to prefer either blue or pink chow (see Appendix II: text A.II.1 for methods), while a third individual served as a control, with no trained preference for either food colour. In the first phase, subjects were exposed to demonstrators selecting their preferred foods (pink or blue). Second, and in parallel with the first training experience, subjects learned that two adjacent food troughs contained either blue or pink food chow. After these two training sets, we carried out a playback experiment, which consisted of subjects hearing recorded food calls from a demonstrator or control individual to test whether they adjusted their foraging decisions based on whose calls they heard (Appendix II: fig. A.II.1). A more detailed description of the training regime and experimental procedure is available in the supplemental material (Appendix II).

Food preparation & presentation

Monkey chow, a food highly valued by bonobos, was presented in its natural, unaltered form to obtain food calls from the three call providers for subsequent playback experiments. For the experiments, we then presented monkey chow in either with its natural or modified taste (bitter) and modified colour (pink/blue), depending on the experimental phase (phase 1: observational learning; phase 2: foraging training; phase 3: playback experiment; see below). The taste and colour were modified using a bitter additive (Bitrex®) and artificial food colouring. Taste modification was only implemented on the food destined for the demonstrators (for details of food preparation and presentation see Appendix II: text A.II.2, fig. A.II.2).

Call recordings & stimuli

We obtained recordings of food calls given to monkey chow from two demonstrator individuals (KEL and DW) and one control individual (LNG) by providing monkey chow in their unaltered state (i.e. 1 x 3 cm, natural tasting, light brown chow; see Appendix II: text A.II.3 for details of call recordings and stimuli preparation). To this end, chow was given in a scatter feed throughout eight small cages of the indoor enclosure. For KEL we carried out 10 recording sessions from which 10 call sequences were obtained; DW: nine recordings, 10 sequences obtained; LNG: 12 recordings, six sequences obtained (see Appendix II: fig. A.II.3 for a spectrogram of a call sequence and ESM 5.1 for the corresponding sound file).

Phase 1: Observational learning

In a related study (Chapter 4) we established that bonobos could learn individually distinct, arbitrary food preferences of other group members through mere observation. We used two individuals (KEL, DW) as demonstrators. Both had been trained to prefer either blue (KEL) or pink (DW) chow, as part of the previous experiment (Chapter 4). During preference demonstrations, artificially dyed blue or pink chow was offered to the demonstrators manually and in full view of the subjects (fig. 5.1). Both demonstrators showed a very clear preference for their assigned colour (first choices: KEL – blue 99.6%, DW – pink 100%), providing subjects with an unambiguous learning opportunity. Preference demonstrations consisted of the experimenter (GS) placing two chow pellets of each colour (i.e. four total) on two identical white plastic trays (20 x 20 cm), placed side by side against the bars of the cage, allowing the demonstrator to select them using either his fingers or lips (Appendix II: fig. A.II.4). The position (left or right) of blue or pink food items was counter-balanced and randomly determined, with the restriction that a given colour could not be presented on the same side for more than three consecutive trials (for supplementary information see Appendix II: text A.II.4).

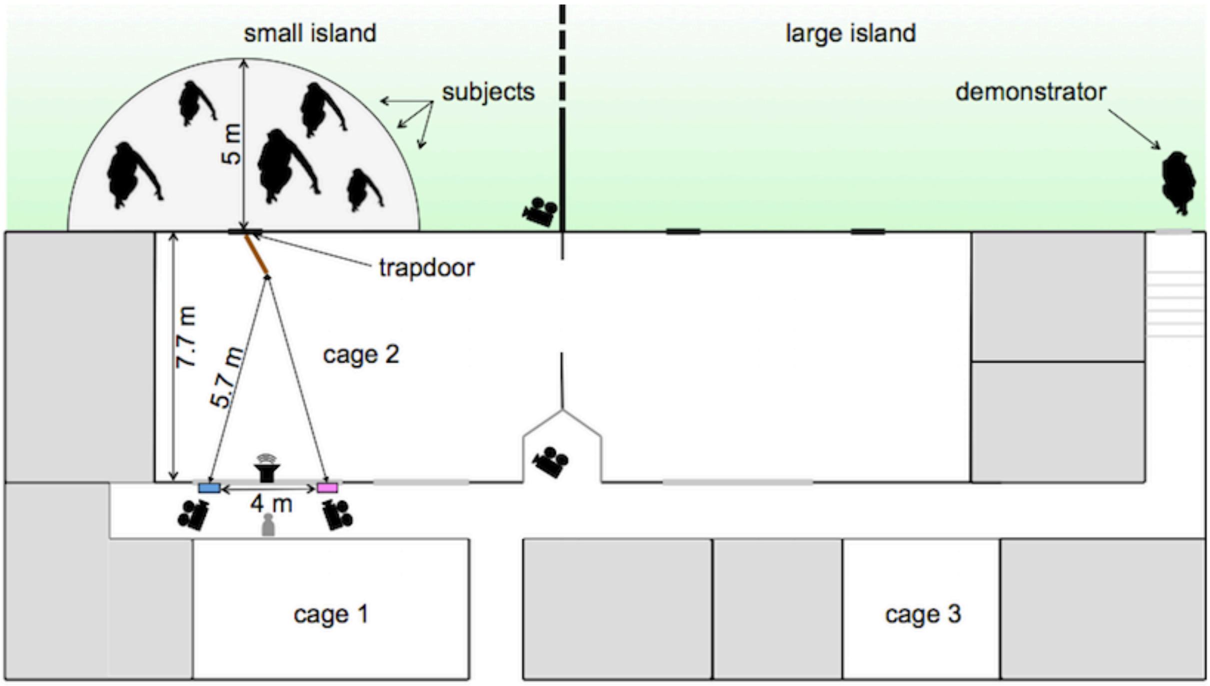

Figure 5.1. Layout of indoor and outdoor enclosures for the three experimental phases: *Phase 1 – observational learning*: demonstrators (KEL, DW) were held individually in cage 1 (demonstration room) and given a choice of pink and blue chow. Subjects were able to observe this process from across the corridor in cage 2 (observation room). *Phase 2 – foraging training*: blue or pink chow was provided to the subjects in one of two adjacent food troughs, 4 metres apart and equidistant from the point of entry (trapdoor). *Phase 3 – playback experiment:* a loudspeaker was placed at midpoint between the two food troughs. The demonstrator whose calls were to be played back was lured away to the large island so as to be out of earshot, while subjects were required to be on the small island within 5 metres of the trapdoor. During each trial, the experimenter (GS) positioned herself at midpoint between the two food troughs to document the subjects' foraging behaviour.

Phase 2: Foraging training

Two white, plastic feeding troughs (51x10x8cm) were fixed to the bars of cage 2 at two points, 4 metres apart and equidistant from the entrance from the small island (fig. 5.1). Blue chow was always supplied in the left trough, pink chow always in the right one, this rule was randomly assigned. The content of the troughs was visible to subjects only when standing right next to and peering into them (Appendix II: fig. A.II.5). Two training periods were put in place in order to allow subjects to learn the food colour - food trough association (March-April and June-July 2015). During training only one food trough was baited on a given day and chow was supplied continually in that food trough throughout the day in order to allow a maximum of individuals to feed at that location (for supplementary information and baiting regime data see ESM 5.2). Demonstrators were also permitted to feed at the food trough during this phase in order to increase the plausibility of the feeding event for the subsequent playback, albeit only for their preferred food colour (e.g. blue for KEL). Subjects' food choices were documented using a PANASONIC HC-V100 full HD camera. A second inactive PANASONIC HC-V727 full HD camera was set up in front of the non-baited trough to create identical conditions as for the playback experiment.

Phase 3: Playback experiment

Despite considerable efforts, we did not manage to lure DW away from the group, which unfortunately ruled him out as call provider in the experiments. Given the amount of time and effort necessary to implant a food preference and demonstrate this preference to others, we were unable to select another individual to replace DW as 'pink demonstrator'. In the final playback phase, we therefore used recordings of food calls from only one of the demonstrators (KEL, blue preference) and the control individual (LNG, no preference) as playback stimuli. Calls were broadcast from a speaker positioned between the two feeding troughs in cage 2 (fig. 5.1); neither trough was baited during playback trials. Before each trial, the respective call provider was lured away from the experimental site onto the large island, using a small quantity of a high quality food so as to be out of earshot from the playback stimuli and hearing his or her own calls (fig. 5.1). This was an essential precondition to set up a plausible scenario for subjects (Slocombe et al., 2009).

Another condition for a playback trial was that at least one subject had to be positioned on the small island within a five-metre radius from the open trapdoor leading into cage 2 (fig. 5.1). The likelihood of this being the case was increased by baiting the area with a small quantity of grain at irregular intervals. To monitor the identity of individuals present, the small island was surveyed with an AQUILA VIZION Smartvizion FIX' HD 720P IP camera, positioned on the roof of the building, above cage 2, overlooking the area in front of the trapdoor (fig.

5.1). The camera was linked via Ethernet to a LINKSYS WRT54G Wireless-G router from which the image was transmitted to an iPad via Wi-Fi (Appendix II: fig. A.II.6 for example of image), allowing the experimenter inside to decide when the trial could be initiated. A further condition was that no individual was inside the indoor enclosure.

Once all these conditions were in place, a playback trial was initiated, which consisted of subjects hearing a sequence of four food calls originally emitted by either KEL or LNG whilst feeding on chow in its natural (i.e. uncoloured and unchanged in taste) state. Following each playback trial, the subjects' reactions were recorded over a period of 1 hour. This allowed us to observe and record the behaviour of a maximum number of individuals upon entering cage 2, despite considerable variation in latency between stimulus broadcast and subsequent visits to the food troughs. We used three cameras, two positioned in the corridor, in front of each trough, and a third one with an overall view of cage 2 (see fig. 5.1 for camera disposition; two PANASONIC HC-V727 full HD cameras and one PANASONIC HC-V100 full HD camera; for supplementary information on criterion for subject participation see Appendix II: text A.II.5).

N=12 playback trials were carried out between September 2015 and October 2016; N=6 in the test condition (KEL: blue preference) and N=6 in the control condition (LNG: no preference). Due to the difficulty of simultaneously meeting all conditions for a playback trial, the choice between test and control conditions was opportunistic and dependent on which individuals had been successfully drawn onto the large island and out of ear-shot while the subjects were in the 5m zone and the indoor enclosure was empty (for a timeline of events throughout the experiment see ESM 5.3). N=10 subjects (3 males; 7 females, age range: 5 – 46 years; Appendix II: table A.II.1) participated in the experiment (test condition 1: N=10, control condition N=9). Two infants (MO, KLS) also took part in the experiment, but we did not include their data, as they were still dependent on their mothers. The average number of subjects per trial was 4.5 (median = 4.5, range = 1-8, N=12 trials).

Our prediction was that, if subjects could relate the calls to a demonstrator's personal food preference, as witnessed during their training, then they should forage for (a) blue chow after hearing KEL's calls, and (b) indiscriminately, i.e., blue or pink chow, after hearing LNG's food calls.

Coding and analyses

Data coding was carried out by the GS on an APPLE MacBook Pro using Squared 5 software MPEG Streamclip 1.9.2©. Although the most salient subject response to the playback stimuli was approaching the troughs and expressing foraging behaviour, it was still obvious to them that it was the experimenter who ultimately provided the food. As mentioned, no food was provided during the playback trials, to the effect that subjects encountered empty troughs after responding to the playback. We were therefore also interested in whether subjects expected the experimenter to refill the trough that, assumingly, had been previously emptied by the call provider. We therefore analysed two response variables at the blue and pink feeding troughs: (1) 'Expectation', measured as the proportion of total time present spent looking at the experimenter while sitting within one of the two designated zones (a behaviour often observed during foraging training; see Appendix II: fig. A.II.7) and (2) 'Exploration' (a) peering into a feeding trough (y/n) and/or (b) probing using the fingers (y/n). (ESM 5.4 and 5.5 for video examples of exploration and expectation behaviour).

We ran two analyses, one for expectation and one for exploration (i.e., peer & probe). First, we modelled expectation as the response variable with a generalised linear mixed model (GLMM) with binomial error structure. The response variable was the proportion of time spent looking at the experimenter out of the total time a subject spent in that colour zone. The interaction between test condition (call provider with preference versus call provider without) and trough (blue versus pink) was the main predictor variable. We also included a binary control predictor, which indicated whether the subject had attended (or not) to the last demonstration event prior to a given playback trial ('demonstration exposure'). Subject identity and playback trial were included as random intercepts. We tested the full model against the null model (which included the demonstration exposure main effect, subject identity and playback trial as random intercepts) with a likelihood ratio test (LRT (Dobson, 2002)).

Second, we modelled exploration using a GLMM with binomial error structure, i.e. whether or not the subject explored the correct trough. As before, the interaction between test condition and trough was the main predictor variable. Demonstration exposure was included as a control predictor, subject identity and playback trial were included as random intercepts, and included total time spent in the colour zone as offset term. We tested the full model against a null model (which included the demonstration exposure main effect, and subject identity and playback trial as random intercepts) with a likelihood ratio test (LRT (Dobson, 2002)).

Finally, we considered the individual mean frequencies of the two exploratory behaviours, peer and probe, separately. The sample size for probing was too low for any statistical analyses. For peering, however, we ran a non-parametric Wilcoxon signed rank test to compare each individual's Δ (mean frequency of peering at the pink food trough minus mean frequency of peering at the blue food trough = delta) between the test and control conditions.

Statistical analyses were carried out using R v. 3.4.3 and lme4 v. 1.1-15.

Compliance with ethical standards

This experimental study was inline with recommendations in the ARRIVE guidelines as well as the EAZA and AFdPZ code of ethics. This experimental study was authorised and given ethical approval by the "La Vallée des Singes" scientific coordinator and zoological director. Although two individuals were regularly isolated for short periods of time (<30 min) during this study, they were specifically selected based on their propensity to choose isolation from the group on occasion thus avoiding stress for both the isolated individuals and the group as a whole. When stress was detected within the group, testing was postponed. Furthermore, the individual selected as control caller was also selected for a natural propensity to spend time away from the group.

Results

For expectation, we found that subjects generally spent little time looking towards the experimenter following playback trials, regardless of experimental condition. The full model was not significantly different from the null model (Generalized linear mixed model, likelihood ratio test (LRT): $\chi^2 = 4.20$, d.f. = 3, P = 0.2409, Appendix II: fig. A.II.8, table A.II.2), suggesting that the playback stimuli did not trigger obvious expectation towards the experimenter.

For exploration, when comparing the full and null models, we found the predicted effect, but slightly beyond the conventional significance level (LRT: $\chi^2 = 6.97$, d.f. = 3, P = 0.0728, fig. 5.2, Appendix II: table A.II.3). More importantly, this effect was largely driven by one individual (NK), casting doubt on whether other group members understood the contingency.

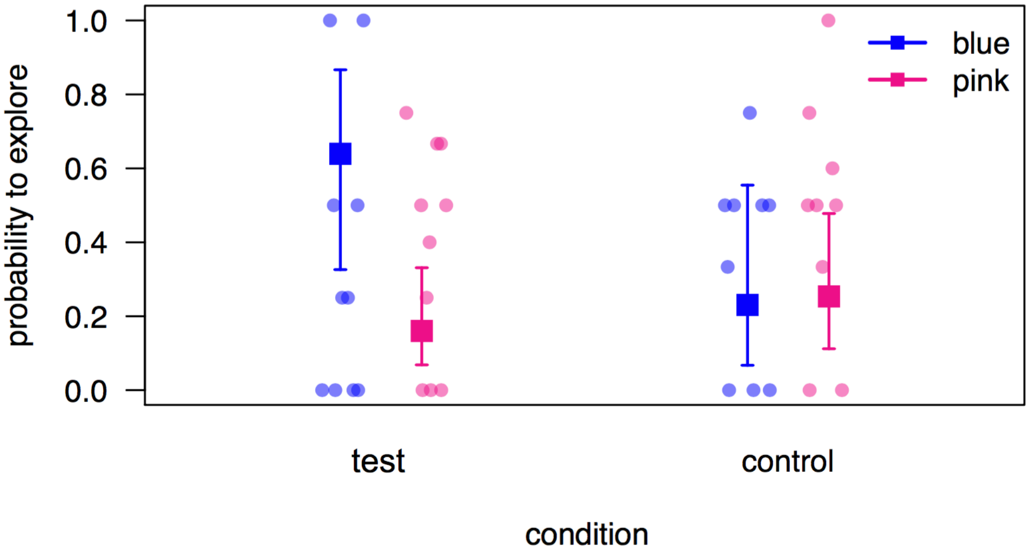

Figure 5.2. Probability of subjects exploring the blue or pink food troughs in test and control conditions. Circles represent the average probability to explore for each subject (10 subjects participated in the 6 test trials and 9 subjects participated in the 6 control trials). Squares with bars represent model estimates with 95% confidence intervals.

We then analysed the frequencies of subjects' exploration behaviour at the two food troughs separately. 'Probing' was generally rare and only N=5 subjects exhibited the behaviour (see ESM 5.6 for figures). For 'peering', we found similar median responses of subjects to test and control conditions (fig. 5.3; see ESM 5.6 for figures). In particular, as predicted, subjects were indifferent following LNG's food calls (control) and did not peer preferentially in one of the two food troughs. For KEL's food calls, we found the same pattern at the group level, that is, subjects did not preferentially peer into the blue food trough following KEL's food calls. However, when analysing the data at the individual level, we found a significantly higher *overall trough bias* in the test (KEL calls) than the control condition (LNG calls), although (in breach with our prediction) the bias was not specifically directed to the blue food trough (fig. 5.3).

We followed up on this unexpected finding and calculated the absolute differences (Δ) in peering behaviour (fig. 5.3) at to the two troughs for both test and control conditions. LNG was excluded from the analysis as she participated in only the test condition. Seven of nine subjects showed a trough bias for peering in the test condition (blue: N=3, pink: N=4, see Appendix II: fig. A.II.9) while only three of nine subjects showed a bias in the control condition (blue: N=1, pink: N=2, see Appendix II: fig. A.II.9), a significant difference (Wilcoxon signed rank test, pink-blue Δ, test vs. control condition, N=6 (2 ties), V=21, P=0.036, two-tailed).

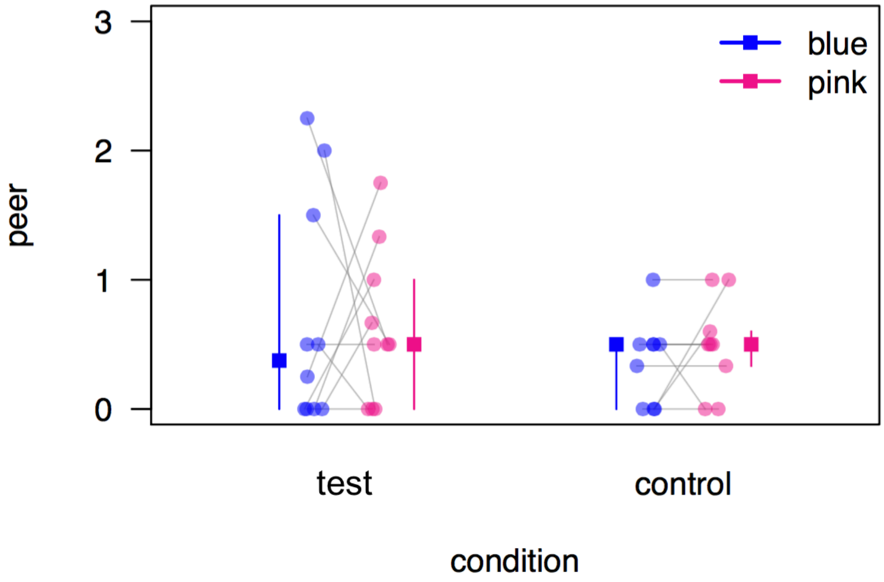

Figure 5.3. Mean frequencies of peering across individuals at the blue and pink food troughs in test and control trials. Circles represent mean frequencies of peering across individuals. 10 subjects participated in the 6 test trials and 9 subjects participated in the 6 control trials. Squares with bars represent medians with 25% and 75 % quartiles. Subjects in the test condition show higher bias for one of the two troughs than subjects in the control condition.

We encourage the reader to further explore our raw data (ESM 5.7) and analyses with an interactive tool (ESM 5.6).

Discussion

The aim of this study was to investigate whether bonobos are able to draw inferences from previously acquired knowledge about other individuals' food preferences. The design was based on the bonobos' capacity for individual vocal recognition (Keenan et al., 2016) and their documented propensity to vocally communicate about food quality when encountering food (Clay & Zuberbühler, 2009, 2011). We predicted that if subjects were able to draw inference upon hearing another's food calls, then their foraging choices should be influenced by this knowledge. Specifically, in the test condition, we expected them to preferentially explore the food trough associated with the caller's preferred food, whereas in the control condition we did not predict any biased responses. To address this, we provided subjects with the opportunity to learn two opposing demonstrator preferences (KEL: blue; DW: pink) through observational learning. We then trained subjects to find blue food in one food trough and pink food in another, though never simultaneously. Once established, we deployed a playback paradigm to simulate a feeding event either by one of the demonstrators (KEL; blue preference) or by a control individual (LNG, no preference). We then measured subjects' foraging responses to the playback stimuli to investigate whether they took into account the food preference shown by the demonstrator, and lack thereof for the control individual, when exploring the food troughs after entering cage 2. For pragmatic inference to take place in our experiment, the subject first has to associate the identity of a demonstrator (*A*) to his preferred food colour (*B*), an association that can be formed during the preference demonstrations. Secondly, the subject then has to associate the two coloured foods (*B*) to two different trough locations (*C*), an association that can be formed during the foraging training. If subjects successfully learned that *A* was associated to *B* and that *B* was associated to *C* then upon hearing a food-associated call from caller *A*, subjects had the premises to infer that food was present at location *C*.

Although we did not specifically test whether subjects had formed (*A*-*B*) and (*B*-*C*) associations, there is other evidence (Clay & Zuberbühler, 2011) suggesting that this was within the subjects' capabilities. However, in comparison to other similar playback studies (Slocombe & Zuberbühler, 2005b; Clay & Zuberbühler, 2011) the present design was more complex, insofar as subjects were expected to learn the preferences and trough locations associated to two colours of the same food rather than to two different foods. Furthermore, demonstrators were observed to eat the coloured foods in one room (cage 1, fig. 5.1) but these same foods were available to subjects in another room and only at two specific locations (cage 2, fig. 5.1).

To assess cognitive performance, we analysed two composite measures, exploration and expectation, and found that the full models were not significantly different from the null models. However, the model prediction for exploratory behaviour revealed an effect in the predicted direction (fig. 5.2), although this was largely driven by one individual (NK), who performed exactly as predicted under the pragmatic inference hypothesis. This individually biased outcome is in line with previous research on apes showing inter-individual differences in cognitive capacities (Herrmann & Call, 2012), although there may have been other reasons. When further analysing the two exploratory behaviours (peering and probing) separately, we found that probing behaviour was rare and shown only by a minority of subjects. For peering, however, we found a significantly higher trough bias in the test than in the control condition, suggesting that subjects presumed a trough bias, but disagreed about the direction (fig. 5.3).

Clearly, the task in this playback experiment was complex, requiring subjects to form various associations about food preferences of other group members, knowledge about where and when pink and blue chow was available, and recognising others' food calls individually. The ability of making pragmatic inferences requires command and integration of all these sources of knowledge. Subjects were provided with extensive opportunities to learn these associations but our data suggest that (1) not all animals were able to form these associations and/or to recall them during the playback experiments or that (2) subjects were pursuing different foraging strategies.

For example, it is possible that, rather than associating KEL to *blue* chow, and *blue* chow to the *left* trough, some subjects formed a less sophisticated representation, such as an association between KEL to *coloured* chow, and/or *coloured* chow to *either* one of the two troughs.

Another aspect to consider is that KEL may simply have been a more pertinent food-call provider than LNG and his calls may have been more motivating due to the fact that he had served as demonstrator for this and a prior study (Shorland et al. *submitted*) showing at the very least a clear link to the food supplied during demonstrations. Equally possible is a scenario in which subjects remembered that KEL had a food preference (in contrast to LNG), but could not recall whether this was for pink or blue chow. Even if this were the case, our results are still in line with the hypothesis that bonobos are able to draw at least basic inferences about other individuals' food preferences, although there may be individual differences in how many contingencies subjects were able to recall during the playback experiment.

Second, another way to explain the opposing patterns for trough peering, reported in fig. 5.3, is that individuals did understand the complex nature of the task but chose to respond in different ways. For example, following playback of KEL's food calls (indicating presence of blue food) a reasonable foraging decision might have been to explore the pink rather than the blue trough (based on the assumption that KEL had already exploited the blue trough. Other individuals may have followed a scrounger strategy, by exploring the blue trough for leftover chow after KEL's feeding. However, during foraging training, we consistently only baited one of the troughs on any given day, so subjects had no reason to believe that pink chow would be available on the same day as blue chow.

Conclusions

In conclusion, while we acknowledge that the task posed to subjects was complex on many levels our data suggest that at least one individual performed in line with the hypothesis that bonobos are capable of pragmatic inference. Other subjects also differentiated between a call providers with a known food preference and that with none, suggesting that they are, at a vary basic level, able to take others' knowledge into account, although our study does not reveal much about the content of this knowledge. Overall, we consider these results important for current theories of language evolution as they suggest that the ability to make inferences based on social knowledge emerged somewhere during the speciation period some 6-10 million years ago, when the common ancestor of bonobos and humans split into separate lines.

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6: General discussion

Comparative cognition and human evolution

The question of human evolution has elicited a huge amount of interest for several centuries (Linnaeus, 1758; Darwin, 1859) and, while there is much to learn from all that can be found in the fossil record, there is a huge amount of what defines us as humans that has left no physical trace. This is particularly true with regards to cognition. In order to find the evolutionary trail of such a defining characteristic of our species, we are obliged to look to non-human animals that show more or less phylogenetic proximity with our own species. Here lies the fundamental basis behind the whole research approach termed 'comparative cognition'. By identifying similarities and differences in species with differing phylogenetic closeness and complementary to information gained from the fossil records, we can better estimate when certain traits, capacities and precursors appeared. This is as true for aspects of our communication system and the evolution of language as it is for all aspects of cognition, especially those capacities that have long been thought to be unique to humans, such as theory of mind.

Theory of mind involves the attribution of mental states to one's self and to others (Premack & Woodruff, 1978), including goals, intentions, knowledge and beliefs (Call & Tomasello, 2008). As such, possession of such a capacity suggests that individuals can understand, at least implicitly, the reality of others, even if, as demonstrated in recent 'false belief' tasks, that reality differs from one's own. This capacity is key in our everyday social interactions and as such had triggered much interest from the research community. Of primary interest was the emergence of theory of mind during child development but this was closely followed by empirical research into the presence of theory of mind in non-human species, particularly in our closest relatives, the great apes. The field of primate cognition is a vast one with countless different facets in both the physical and social worlds. In seeking to find the answers to questions throughout this vast field we can, as a scientific community, contribute to drawing the bigger picture, and provide answers to our on-going interrogations on the evolution of human cognition.

***Pan* diversity**

Despite the phylogenetic closeness of the two *Pan* species to humans, there has long been a broad chasm between the interest and investment of research into the chimpanzee's behaviour, ecology and cognition and that of bonobos. While the first long-term studies of wild bonobos began in the 1970s (Kano, 1982), it is only since the mid 1980s and increasingly in the past 10 years that this chasm has begun to close (Hare & Yamamoto, 2017). As mentioned earlier, this discrepancy can be explained in part by the long lasting political unrest and conflict in the DRC, rendering access to wild bonobos almost impossible, along with the low number of captive specimens, but also, the fact that for a long time the two species were thought to be one, and even after discovery that they were in fact two distinct species in 1929 (de Waal & Lanting, 1997) bonobos were considered to be too similar to chimpanzees to warrant much interest (Hare & Yamamoto, 2017). However, empirical findings over recent years and the comparisons drawn between chimpanzees, bonobos and humans highlight just how important a role the bonobo plays in allowing us to test ideas linked to human evolution (Gruber & Clay, 2016).

Findings relating to how much of our cognition we share, and with which of the two *Pan* species, allow us to make inferences about the evolutionary pathway of human cognition (Krupenye et al., 2017). In fact, in a number of aspects, humans show more similarity to one of the two *Pan* species than the two sister taxa show to each other, demonstrating that by looking at only one of the two species we are in the impossibility of getting the full picture and that the study of bonobos is by no means redundant (Prüfer et al., 2012; Gruber & Clay, 2016; Hare & Yamamoto, 2017). The two species are, indeed, very closely related and show many similarities. For example, both live in large, mixed-sex, fission-fusion social groups with male philopatry and female migration as well as prolonged infant dependency and absence of paternal care (see Gruber & Clay, 2016 for a recent review of the similarities and differences between the two species). There are nonetheless many differences between the two species and the most important of these lie in their social organization. For instance, while chimpanzees show very strong bonds among the philopatric and related males (Nishida, 2012), bonobo males show surprisingly weak bonds among themselves, favouring long term bonds with their mothers and other females (Furuichi, 1997; Surbeck et al., 2011). Conversely, unrelated female bonobos form strong bonds and alliances (Parish, 1994), which allow them to dominate over the males (Furuichi, 1997; Vervaecke & Van Elsacker, 2000;

Paoli & Palagi, 2008), in stark contrast to the male-dominated chimpanzee groups. These differences in social organization, it would seem, have resulted in differences in cognitive abilities between the two species. Indeed, compared to chimpanzees, bonobos present a more cooperative social organisation. They are more prosocial, more tolerant, and show more positive responses towards strangers than do chimpanzees (Hare et al., 2007; Tan et al., 2017).

It has been suggested that in the short period of time since the two *Pan* species split, estimated at approximately 2 mya (Langergraber et al., 2012), differences in ecological and socio-ecological pressures have shaped differences between the cognitive abilities of the two species. This increased tolerance for others observed in bonobos might in fact allow them to perform better in tasks that involve cooperation and coordination of actions with others (e.g. Hare et al., 2007; Pika & Zuberbühler, 2008) and tasks involving theory of mind (Herrmann et al., 2010). Thus, the study of bonobos seems vital to the understanding of human evolution and how environmental and social differences contribute to differences in cognition.

Research summary

Recent research efforts have provided new and exciting insight into the theory of mind of great apes, including bonobos (e.g. Krupenye et al., 2016; Buttelmann et al., 2017). Despite these recent findings, the gaps that remain in our knowledge of the bonobo's capacities for theory of mind make it impossible to correctly infer the cognitive capacities that must have been present in our last common ancestor (Krupenye et al., 2017). The main goal of this research was to investigate, through a variety of approaches, whether bonobos are able to maintain different perspectives of reality, their own and that of others. Through this research, I attempted to shed light on three questions from quite diverse domains in the field of primate cognition. How do bonobos perceive themselves in different kinds of self-image and how might mirror experience modify such perception? Do bonobos socially learn from others in the context of feeding and how does such knowledge shape their feeding behaviour? Are bonobos able to use previously acquired knowledge relating to group members and the environment to successfully implement pragmatic inference and thus add meaning to perceived communicative signals?

Self-perception

The first study related to the bonobo's ability for self-recognition and the probable sense of self as separate from others and the world. In particular, I sought to further our understanding of how bonobos perceive themselves and how prolonged experience with a mirror might modify that perception. To achieve this, I first investigated how mirror-naïve bonobos reacted to a variety of contingent and non-contingent self-images, in the form of video or mirror feedback, as well as video images of known and unknown conspecifics. I then investigated whether the bonobos' perception of themselves in non-contingent video footage was influenced by prolonged mirror exposure. I predicted that such experience provided subjects with extensive visual feedback of their own physical appearance and allow them to develop a full mental representation of their self-image. This representation, if stored in memory, could potentially modify the manner in which an individual perceives its self-image, regardless of the presence or absence of contingency cues.

My findings suggested that prolonged mirror experience modified bonobos' perception of themselves in delayed, non-contingent video images of themselves. It would seem that the bonobos were able to learn a visual mental representation of their morphological self and retrieve this representation when later presented with self-images that provided no contingency cues to aid with self-recognition. Indeed, subjects seemed to recognise the familiarity of the self-image.

While this study does not demonstrate conclusively that subjects demonstrated self-recognition, previous studies have shown that this is within the bonobos' cognitive capacities (Hyatt & Hopkins, 1994; Westergaard & Hyatt, 1994; Walraven et al., 1995). These findings indicate that bonobos can recognise non-contingent self-images as representative of reality, making some sort of link between what they have learned from interactions with a mirror and the moving image portrayed on the tablet screen. If the subjects attained mirror self-recognition during their extensive mirror experience, the fact that they were able to treat their non-contingent image as familiar indicates that they were able to attribute some sense of continuity to the mental representation of themselves. The findings thus indicate a possible sense of continuity of the self, argued to be a key element of 'self-concept' by Gallup (1998). Indeed, by recognising the self in a self-image that is not from the 'here and now' one must have some understanding that the self has continuity through time.

The implications of possessing a sense of self are still a topic of high controversy. Does self-recognition indicate self-awareness? Are there intrinsic links between self-recognition, empathy and theory of mind, as has been suggested by several authors (e.g. Gallup, 1982, 1991; Gergely, 1994; Suddendorf & Collier-Baker, 2009; Anderson & Gallup, 2015; Dale & Plotnik, 2017)? Although each of these abilities have been individually demonstrated in bonobos (e.g. self-recognition: Westergaard & Hyatt, 1994; empathy: Clay & de Waal, 2013; theory of mind: Krupenye et al., 2016) the possible links between the different abilities have not been systematically addressed and bringing to light the differences between chimpanzees, bonobos and humans in this regard is necessary to better understand the evolution of human cognition. Finally, my results are encouraging in terms of the technological approach, validating tablet computers as a useful tool to assess perception and allowing for interesting future experimental designs.

Social learning

In the second study, I aimed to assess whether bonobos could learn something about others' food preferences through mere observation and whether they use this knowledge to shape their feeding choices. I carried out a social learning experiment within an ecologically relevant context, pertaining to food preferences and choices. Social learning is a broad and heavily researched domain of animal social cognition that provides answers regarding how behaviours spread through populations and even how cultural traits emerge. We might consider, however, that in a species known to possess theory of mind, social learning opportunities provide individuals not only with information about the physical, social or contextual environment, but also with insight into another individual's perceived reality. While social learning increases an individual's chance of survival by allowing it to learn how to behave and operate in its environment, theory of mind, facilitates life in social groups by permitting an individual to predict and anticipate the behaviour of other individuals, which in itself can increase one's ability to compete or to cooperate with others (Call & Tomasello, 2008). With this in mind, I investigated whether or not bonobos were able to socially learn the arbitrary food preferences of others through mere observation. Furthermore, I questioned whether they might adopt and maintain such preference regardless of their own knowledge that both proposed foods were identical in quality and taste. This approach differs from most social learning studies and investigates, not the acquisition of a novel manipulation or technique, but the assessment of another’s knowledge and the decision-making based on that knowledge.

Through six testing blocks, I exposed subjects to the food choices made by two different demonstrators who had been trained to systematically choose one novel coloured food item over another. I then provided subjects with repeated choice tests to find out whether or not they preferred to choose the same food colour as that eaten by the last observed demonstrator. The experimental paradigm was somewhat complex insofar as one demonstrator first preferred one colour with a given food type and then switched his preference to the other colour with a second food type, resulting in the two demonstrators having opposing colour preferences, albeit with two different food types. I was further interested to find out whether subjects might maintain any choice for copying the demonstrators’ opposing preferences despite having the knowledge that both food colours were equally palatable. I predicted that social learning would be particularly strong during the first testing block, when subjects were still naïve relative to these foods, but that the effect might wane with increased experience with the foods.

An important factor to consider in this study is that subjects did not remain naïve to the alternative choice for very long. Not only were subjects rapidly exposed to the alternative choice, but in choosing the alternative they were immediately rewarded, just as when copying the demonstrator. And yet I found that subjects continued to generally adhere to the demonstrators’ preferences despite knowledge that either choice carried the same reward. The motivations behind such choices are not the focus of the study here but might be explained by a desired towards group conformity. Another explanation is that following the demonstrator is a sensible survival strategy: if someone systematically refuses to eat a certain food type, then it may be reasonably assumed that he/she has a good reason to do so. In my experiment, following the demonstrator’s choice was cost free, possibly a manifestation of a ‘better-safe-than-sorry’ strategy.

The findings from the second study demonstrated that, even in the absence of olfactory and taste cues, bonobos are able to acquire and memorise others’ food preferences and are prepared to adhere to them. In concordance with my predictions, this was particularly true when they had no prior knowledge regarding the foods, but while I predicted that the tendency to copy demonstrator food choice might wane, I observed that this tendency was relatively stable despite increased own experience with the foods and knowledge that both food types were palatable. This pattern suggests that there may have been some social factors influencing subject food choice.

Interestingly, the experiment demonstrated successful social learning from two low- and medium-ranking males in a species that is renowned for its (non-exclusive) female-dominated society (Stevens et al., 2007). In many social learning experiments, the importance of demonstrator identity has been highlighted, suggesting that high-ranking and older individuals make for better demonstrators from which more successful social learning can be achieved (e.g. Biro et al., 2003; Kendal et al., 2015). However, my findings perhaps reflect those found in recent research, which indicated that, in the absence of 'demonstrator competition', even low-ranking individuals can be successful demonstrators (Watson et al., 2017).

Social learning is often considered and discussed in terms of the transmission of adaptive behaviours from one individual to another, which increases the fitness of individuals, allowing them to avoid the costs and risks associated to individual learning (Galef & Laland, 2005; Hopper et al., 2011). Social learning is also considered a mechanism through which 'cultures' can emerge and spread through social groups (e.g. Hobaiter et al., 2014; Gruber et al., 2015). As such, the ability for social learning has been termed a 'secondary inheritance system' complementing traits that are transmitted genetically (Whiten, 2005). One little discussed implication of social learning, on the cognitive level, is how successful social learning is related to a subject's understanding of another's mental states. In the case of a species known to have a theory of mind, at least on some level, if individual *A* can take into account individual *B*'s behaviour (behaviour which is based on *B*'s knowledge) and *A* modifies its behaviour based on those observations of *B* then, surely, successful social learning might indicate that the learner, *A*, has at least some implicit understanding of the *B*'s mental state in terms of knowledge, goals or desires. This is more disputable for species that allegedly do not possess theory of mind where other mechanisms must inevitably be responsible for adaptive social learning. If we consider these findings under this light then my results suggest that not only can bonobos learn from the knowledge of others but that, given their capacity for theory of mind, this learning potentially demonstrates their awareness of others' mental states, their knowledge and their preferences.

Pragmatic inference

The third and final study aimed to assess whether bonobos could use previously acquired social knowledge about another's food preferences and knowledge of the environment as premises for pragmatic inference when perceiving a communicative signal. With socially learned knowledge of others' idiosyncratic behaviours in hand, signal recipients are in a position to potentially use this knowledge, along with knowledge of their environment (physical, social or contextual) to infer meaning beyond that which is explicitly conveyed by a signal. In this instance, keeping track of another's assessment of food quality (i.e., its food preference) might allow a listener to infer additional meaning when perceiving a food call, using not only its knowledge regarding the call provider but also regarding the environment. This pragmatic inference, thus, integrates information from both communicative signals and contextual cues to enrich the recipients understanding of a signal.

In this final study, I questioned whether or not bonobos were able to take into account, on the one hand, individually learned knowledge regarding foraging locations and, on the other hand, socially learned knowledge regarding behavioural idiosyncrasies of others when interpreting perceived communicative signals. More specifically, could they use contextual cues and previously acquired knowledge relative to signal providers to infer meaning beyond that explicitly conveyed by a vocal signal? To address this question I first provided subjects with two types of learning opportunities. Subjects individually learned two food locations specifically associated to two different, artificially coloured foods, and simultaneously, subjects had the opportunity to socially learn the idiosyncratic food colour preferences of two demonstrators through observation, similarly to the second study. Following this training period, I ran a playback study using food calls from a demonstrator or from a control individual in order to simulate a feeding event involving one or the other. I predicted that the socially learned knowledge of the demonstrator's food colour preference and the individually learned association between the food colours and locations provided the subjects with the premises for pragmatic inference. Thus, subjects might infer which food was being supplied when they heard the food calls of the demonstrator individual, while no such inference could be drawn from the control individual's food calls.

My findings demonstrated that bonobos reacted somewhat differently to the food calls of a demonstrator individual known to have a specific preference for a novel coloured food, than they did to the food calls of a control individual with no known association to the novel foods. While the observed difference was not as I had predicted (i.e., subjects were not able to correctly predict which food colour might be supplied when they heard the broadcast food calls), subjects did show a significantly higher bias for one of the two locations (although not necessarily the one corresponding to the demonstrators preferred food) in the experimental than in the control condition. I interpreted this as an indication that, while subjects were not able to integrate all the knowledge that was available to them to draw the correct inference (i.e., learned food location, only one food available on a given day, learned food preference, food calls indicative of a feeding event, etc.), they were able to integrate enough to bias their foraging behaviour to one food location, as opposed to randomly foraging in both locations. I believe that, while subjects clearly struggled with this complex task, this may have been the product of a capacity for pragmatic inference.

This finding has some implications for the on-going debate about the evolution of the human language faculty. Through the investigation of communication and its underlying cognitive mechanisms in primates, and by identifying traits that can be categorized as precursors to language, we can estimate how far different elements of our language-relevant cognitive capacities go back in the lineage. The importance of the comparative approach has been highlighted by many (e.g. Hauser et al., 2002; Fitch, 2005; Zuberbühler, 2005; Arbib et al., 2008; Fedurek & Slocombe, 2011; Genty et al., 2014). And yet the study of pragmatics, as a means to provide insight into the evolution of human language, has been the centre of little research focus (Scott-Phillips, 2015), despite the fact that one of the subcomponent of the language faculty is, arguably, the ability to attribute mental states to others (e.g. intention, knowledge). In both animal and human communication, contextual cues are used in addition to perceived signals to infer further meaning (Fischer & Price, 2017). The evidence provided here demonstrates that, in bonobos, pragmatic inference can be based on previously acquired knowledge, relating not only to the signal emitter but also to the environment, which suggests that this inferential ability, or at least the scaffold to this ability, was likely already present in our last known common ancestor. More in depth and finely tuned research into the inferential abilities of our closest relatives are required to follow up on this hypothesis.

Limitations and future perspectives

Experimental studies with animals are fraught with limitations and constraints. One limitation, present in all three studies presented here, is sample size. Indeed, despite the fact that I carried out my research on one of the largest zoo-held populations of bonobos in the world (i.e., N=17-20), subject participation was relatively low (i.e., study 1, N=8; study 2, N=7; study 3, N=7), caused by motivation difficulties in individuals and the fact that isolation of subjects for the purpose of testing was not feasible.

In the first of my three studies, the reduced sample size led me to design the experimental protocol with a fixed sequence for stimulus presentation for different conditions, a decision that remains controversial. However, my choice enabled all subjects to have the exact same experience with the stimuli as the experiment progressed, hereby reducing some additional noise in the data, which facilitated comparisons across the key conditions. I believe that fixed-order stimulus presentation was a justifiable compromise, given the short stimulus exposure time (i.e., 30s) and the fact that stimuli were generally presented over a long period minimising the chance of habituation occurring. Furthermore, and supporting my decision, the results indicate no pattern of habituation.

In hindsight, the results for the second part of the experiment would have been reinforced with the presentation of an additional control condition, such as a repetition of the '*known'* condition. In addition, with a larger sample size, ideally the subjects could have been split into two groups, one group gaining prolonged mirror experience while the other would have been exposed to an adequate control experience, such as a transparent screen of the same size. Certainly, such a protocol would benefit from a larger sample size with pseudo-randomised presentation order. Finally, and given that, to the best of my knowledge, a mirror-mark test has not yet been reported for this species, investigating this ability for self-recognition might have been a means to complement and enrich the results presented here. Additional factors that would ideally have been controlled for are 1) the time each subject spent engaging with the mirror and 2) how subjects might have reacted to the *unknown* condition had they been exposed to the videos of that unknown individual over an extended period of time. This would eliminate the possibility that my findings reflect only familiarisation with a seemingly 'unknown individual' seen many times (*non-contingent self*) and the maintained novelty of an 'unknown individual' seen once (*unknown*).

The research protocol for my second study was relatively straightforward. The principal limitation observed involves the number of choice tests that subjects underwent in each testing block following observation of the preference demonstrations. Following the first two testing blocks for each colour (i.e., P1, P2, B1 and B2) subjects underwent only 5 choice tests, while, following the final testing block for each colour (i.e., P3 and B3) subjects underwent 10 choice tests. This design required that the data be pooled across testing blocks for statistical analyses. Ideally, subjects would have been subjected to 10 choice tests following each testing block.

In addition to this limitation, and given the importance of the model's identity observed in other research (e.g. Biro et al., 2003; Kendal et al., 2015; Lamon et al., 2017; Watson et al., 2017) this study would certainly have benefited from the simultaneous collection of observational data in order to define the dyadic bonds between the demonstrators and the subjects. Such information, along with a higher number of choice tests, would have provided further insight enabling me to interpret the results on another level, taking into consideration the possible social factors influencing not only the bonobos ability for social learning but also their propensity to maintain the copying behaviour despite better knowledge. In addition, an experimental protocol enabling me to confirm that the subjects had learned to associate the demonstrator identity to the preferred food would have been extremely useful in allowing me to discard the possibility that the subjects were simply copying the last behaviour observed.

The last of my three studies was the most complex, both in terms of experimental design and in terms of the task set for the subjects. While in this study subjects demonstrated their ability for pragmatic inference on a basic level, this may be a valuable a starting point from which investigation of this ability can be furthered. First and foremost, the task may have been too difficult, as subjects had to learn several different associations in order to possess the premises for pragmatic inference. On the one hand, the association between demonstrator identity (*A*) and the preferred food colour (*B*) and on the other hand, the association between the food colour (*B*) and its specific food location (*C*). Clear results following my initial predictions would have validated the fact that these two associations had been correctly acquired, however, my results did not provide such clear results.

Unfortunately, I was not able to verify that both these associations had been correctly learned. While the social learning study indicates that subjects can learn that *A* is associated to *B*, there is perhaps an alternative explanation. Indeed, testing that subjects had, in fact, associated a demonstrator's identity to the preferred food colour would be necessary to exclude the possibility that the social learning was influenced by a simple recency effect. Similarly, I was not able to test specifically whether the food colours had been associated to the two food locations. In light of previous studies (e.g. Slocombe & Zuberbühler, 2005b; Clay & Zuberbühler, 2011), however, I believe that it is safe to assume that this was well within the bonobos capacities, particularly given their extensive training.

One factor that might have further encumbered these learned associations is the fact that while subjects observed demonstrator preferences in one room, their own experience with the two foods was in another room. In addition to these associations, for which I actively provided learning opportunities, there are other associations linked to the context that may or may not have been learned. For example, when I was standing between the two feeding locations to carry out a trial this could have been indicative to subjects that food might be supplied in one of the food locations on that day; but also, if food was supplied in one food location on a given day, then only that location would be baited on that day; and when food calls were perceived from the general direction of the food locations, it could indicate that one of the food locations was being bated; finally, when food calls were perceived, the identity of that out-of-sight caller had to be inferred from vocal recognition (Keenan et al., 2016). All of these contextual cues provided knowledge, which had to be integrated in order to provide an appropriate response to the playback stimulus.

It is important to consider that the experiment was designed with the intention of using both demonstrators, trained in study 2 (KEL and DW), as call providers for the playback. As such, preference demonstrations provided information to the subjects on the opposing food preferences of the two demonstrators throughout the experiment and with playback trials carried out for both, each call provider would have served as control for the other. However, although I was easily able to isolate DW from the rest of the group for the preference demonstrations, I failed to draw him away from the group in order to run even a single playback trial using his calls. Given the circumstances, the preference demonstrations involving DW were superfluous, providing unnecessary information to the subjects, which may have added confusion to an already complex task.

Conclusions

In this research, I addressed the overall question of whether bonobos are able to understand and maintain different perspectives of reality, their own and that of another. Considering the past literature and present findings, I conclude that bonobos are able to understand themselves as distinct entities, separate from others and the surrounding world. I further conclude that bonobos cannot only observe and understand how others relate to reality, but that they also learn from it and can modify their behaviour accordingly. Finally, I investigated whether bonobos are able to understand that, when others communicate, they do so from the communicators' perspective, which may be different from their own. Here, I can only provide mixed evidence in support. In particular, I observed a pattern that suggests that pragmatic inference is within the cognitive realm of bonobos, though at a more basic level, integrating fewer elements from their knowledge and the contextual information available than perhaps they might have.

While empirical evidence points to the fact that our closest non-human relatives do indeed have the capacity, at least to a certain extent, for theory of mind, there remains, no doubt, a chasm between their capacities and ours. It is possible that the fully-fledged theory of mind possessed by humans has evolved as a result of living in complex societies in which individuals depend more and more on one another for their survival. As a result of this interdependency, humans have become more and more concerned about others' wellbeing, showing altruistic behaviour, empathy and capacities for the understanding of the mental states of others from a very young age (e.g. Zahn-Waxler et al., 1985; Onishi, 2005; Warneken & Tomasello, 2009). While most of these abilities have not been evidenced in non-human species, to the extent in which they are present in humans, evidence of precursors, building blocks or rudimentary elements of these abilities has been slowly emerging, particularly with regard to our closer relatives (e.g. Warneken & Tomasello, 2006; Clay & de Waal, 2013; Krupenye et al., 2016).

My research adds to the growing body of data on bonobo cognition (Hare & Yamamoto, 2017) and encourages more research into this species, which seems to differ in many ways from its better-researched cousin, the chimpanzee, on which most research on human evolution is based. The bonobo could potentially tell us a different story when it comes to human evolution and our last common ancestor.

Taken together, and compared to the extensive knowledge that we have of chimpanzee social cognition, it seems safe to suggest that our last common ancestor was already in possession of the faculties investigated in this research. From perceiving one's own reality through a sense of self, to understanding the reality of others and learning from their knowledge of that reality and finally using that knowledge of others' reality in combination with contextual cues to disambiguate communicative signals.

And, finally, we now know a little more than we did before about the social cognition of the enigmatic bonobo.

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Appendices

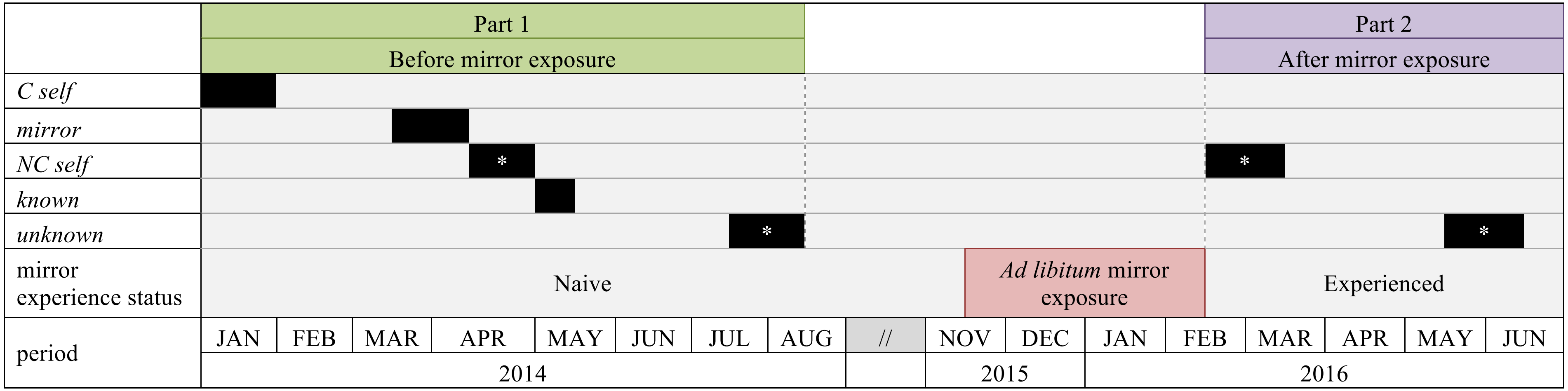
Appendix I.

Supplementary information for Chapter three: Mirror experience modifies bonobos' perception of themselves.

Table A.I.1. Experimental conditions, definition and device used for each experiment.

Condition	Stimulus description	Device	Part
C self	Contingent video image of self with no direct eye contact	iPad	1
Mirror	Contingent image of self with direct eye contact	Mirror	1
NC self	Non-contingent video footage of self	iPad	1 & 2
Known	Video footage of known group member	iPad	1
Unknown	Video footage of unknown conspecific	iPad	1 & 2

Figure A.I.1. Experimental timeline - Condition presentation sequence, before (part 1) and after (part 2) prolonged mirror exposure.



* For each subject the time-lapse between '*NC self*' presentation before and after mirror exposure is identical to that between '*unknown*' before and after.

Table A.I.2. Raw dataset - Identity, age and looking time (sec) for the five conditions in part 1 and for the two repeated conditions in part 2 of the experiment.

		Total looking time (sec)						
		Mirror-naïve					**Mirror-experienced**	
INDIVIDUAL	**AGE (Mo.)**	***C self***	***mirror***	***NC self***	***known***	***unknown***	***NC self***	***unknown***
Lisala	405	1.96	5.68	3.88	10.64	12.92	0.68	2.12
Kirembo	253	0.28	1	5.32	4.52	10.88	4.52	13.88
Ulindi	243	1.8	8.52	13.56	0.68	15.2	7.48	30
Diwani	209	7.16	2.28	20.84	18.24	30	9.8	4.48
David	150	19.84	1.88	25.8	11.48	27.16	3.96	15.76
Khaya	147	0.36	3.36	29.04	27.76	17.16	7.28	21.2
Lingala	126	12.68	9.2	29.72	2.72	19.12	11.32	29.56
Kelele	114	8.12	11.76	23.4	23.24	30	21.48	30

Appendix II.

Supplementary information for Chapter five: Pragmatic inference in bonobos.

Table A.II.1. Group composition at La Vallée des Singes, Romagne, France, and role of different group members in the present study

Name	Code	Sex	Birth year	Age-class	Role
Diwani	DW	M	1996	Adult	Demonstrator
Kelele	KEL	M	2004	Subadult	Demonstrator
Daniela	DNL	F	1968	Adult	Test subject
Lisala	LSL	F	1980	Adult	*
Ukela	UK	F	1985	Adult	Test subject
Bondo	BO	M	1991	Adult	*
Kirembo	KI	M	1992	Adult	Test subject
Ulindi	UL	F	1993	Adult	Test subject
David	DV	M	2001	Adult	Test subject
Khaya	KH	F	2001	Adult	Test subject
Lingala	LNG	F	2003	Subadult	Test subject & Control
Lucy	LY	F	2003	Subadult	Test subject
Luebo	LUE	M	2006	Subadult	*
Nakala	NK	F	2007	Subadult	Test subject
Loto	LO	M	2009	Juvenile	Test subject
Moko	MO	M	2012	Infant	
Khalessi	KLS	F	2012	Infant	
Yuli	YU	F	2014	Infant	
Swahili	SWH	F	2014	Infant	
Lokoro	LKR	M	2016	Infant	

Note: Demonstrators (N=2), control (N=1), test subjects (N=10). * Individuals separated from main group (N=3). Age-class, as defined by Kano (1984), at the start of the study.

Text A.II.1. *Demonstrator preference reinforcement*

We trained one demonstrator (KEL, a low-ranking adult male) to prefer artificially coloured blue chow over alternatively coloured pink chow. We trained another demonstrator (DW, a medium-ranking adult male) with the inversed preference (pink over blue chow). This training, along with the subsequent preference demonstrations, required frequent isolation from the group, which both KEL and DW, probably due to their lower social standing, endured without apparent signs of stress and without causing obvious tension in the group. Both KEL and DW had been trained for these specific food colour preferences in a prior experiment (Chapter 4). Both demonstrators successfully completed their training in which they were each isolated on two consecutive days and presented with the choice of blue or pink chow. This process was carried out twice, once as initial training and again immediately before beginning the preference demonstrations in view of the subjects. Finally, we identified a control individual (LNG, a low-ranking subadult female), who did not undergo any preference training.

In a previous experiment (Chapter 4), both demonstrators, DW and KEL, had gained experience with artificially coloured foods and their associated tastes. Nonetheless, a learning period with the chow was necessary in order to introduce the new coloured food type and reinforce their manipulated colour preference. On two consecutive days, the demonstrators were isolated one after another in a cage with **no vis-à-vis** (see cage 3, fig. 5.1) and were presented with the food ten times, food presentation lasted 10 seconds after a first choice had been made. DW was presented with natural tasting pink and bitter blue chow (see text A.II.2 for details about food preparation) and KEL was presented with natural tasting blue and bitter pink chow. Both individuals used their previous knowledge regarding the colour-taste associations and immediately chose the palatable colour first. This process was carried out once for an initial learning phase and again as a reminder previous to the Preference demonstration phase. Demonstrator preference reinforcement was recorded using a PANASONIC HC-V727 full HD camera equipped with a SENNHEISER MKE 400 external microphone.

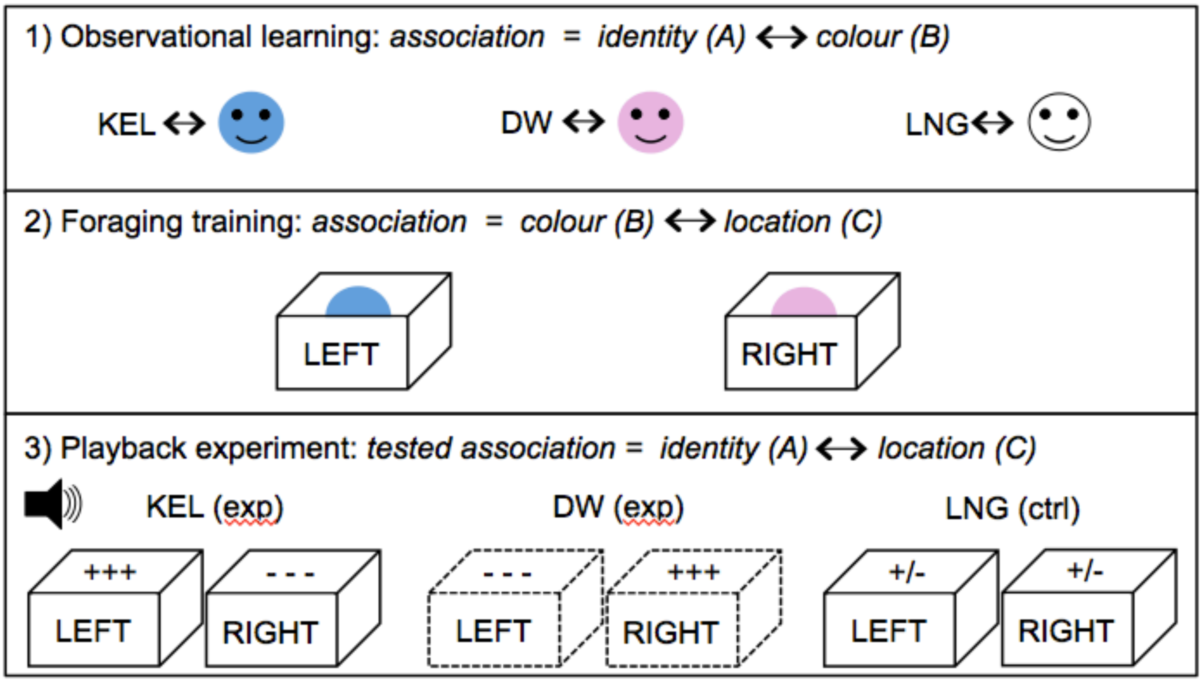


Figure A.II.1. Three phases of the experiment: 1) Observational learning: Subjects were provided with the opportunity to learn by observation the association between a demonstrator (KEL, DW) and its preferred food colour (*A*-*B*); 2) Foraging training: Subjects were provided with the opportunity to learn by individual experience and observation the association between food colour and a specific food trough (*B*-*C*); 3) Playback experiment: Tested whether subjects were able to associate the identity of a call provider (KEL, LNG) to a food trough (A-C). Phases 1 & 2 were carried out simultaneously and continued in between playback trials of phase 3.

Text A.II.2. *Food preparation and presentation*

Monkey chow (SDS® Old World Monkey Chunks, henceforth, chow) was used throughout the experiment. This food was familiar and highly valued for all group members and part of their daily mixed scatter feeds. To instil individually distinct, colour-driven food preferences in the two demonstrators (KEL, DW), the chow pellets were altered in size, taste and coloration. KEL was trained to prefer blue and reject pink chow by repeated exposure to $1cm^3$ pieces of naturally tasting blue and bitter tasting pink chow. DW was trained in the opposite way, that is, by repeated exposure to $1cm^3$ pieces of naturally tasting pink and bitter tasting blue chow. When provided to the test subjects during foraging training the chow pellets were altered in size and colour only (i.e. $1cm^3$, pink or blue, see fig. A.II.2). Colouration was obtained by soaking the chow in a mixture of water and blue or red artificial food colouring followed by air- or low temperature oven drying. Bitter taste was obtained by soaking the chow in a solution of water and a bitter additive (Bitrex® aqueous solution 2.5%, 0.35ml per 5cl of water: 175ppm). Pink and blue foods are rarely or never part of the group's regular diet.

Figure A.II.2. Pink and blue monkey chow for use in foraging training and preference demonstrations.

Text A.II.3. *Call recordings & stimuli*

A library of calls produced by KEL and DW for use as stimuli was built up in March, April and June 2015, calls from LNG were recorded in April and May of 2016. Food-associated call sequences produced by the demonstrator (KEL) and the control caller (LNG) were recorded during morning scatter feeds of chow (in its natural state) that were supplied to the group as a whole in their indoor enclosure following the first morning feed. Calls were recorded using a MARANTZ PMD660 solid-state recorder and a SENNHEISER MKH416T directional microphone. The caller was recorded from a distance ranging between 1m and 8m. In order to identify calls produced by KEL or LNG, the experimenter (GS) focused on only one individual at a time and marked each call with a click that could later be visualized on a spectrogram. Call recordings were transferred onto an APPLE MacBook Pro and visualized in spectrogram format using the software Raven Pro 1.4 with a spectrogram window size of 512. Call sequences produced by KEL and LNG were identified, isolated, cleaned of click markings and background noise and saved as WAV audio files with a sampling rate of 44.1kHz with 16-bit accuracy before being imported into iTunes. Stimuli were played from iTunes on an APPLE MacBook Pro using a BOSE SoundLink Mini Bluetooth Speaker. Volume settings varied with each stimulus track and were defined by ear with help of the animal keeper by placing the speaker at a short distance and adjusting the volume setting so as to achieve the most realistic call amplitude for a bonobo at that distance. Call sequences were excluded when there was overlap with other calls or background noise.

When possible, the stimuli were composed of the first four calls from a call sequence, a sequence being defined as a series of calls with call intervals shorter than one second (see fig. A.II.3 for an example of a stimulus). When no such sequences were obtained from call recordings, four consecutive calls (max. call interval 36 sec.) were selected and call intervals were modified to replicate natural call intervals from existing call sequences. All stimuli were thus composed of four consecutive calls and lasted no longer than 4 seconds from the start of the 1st call to the end of the last call.

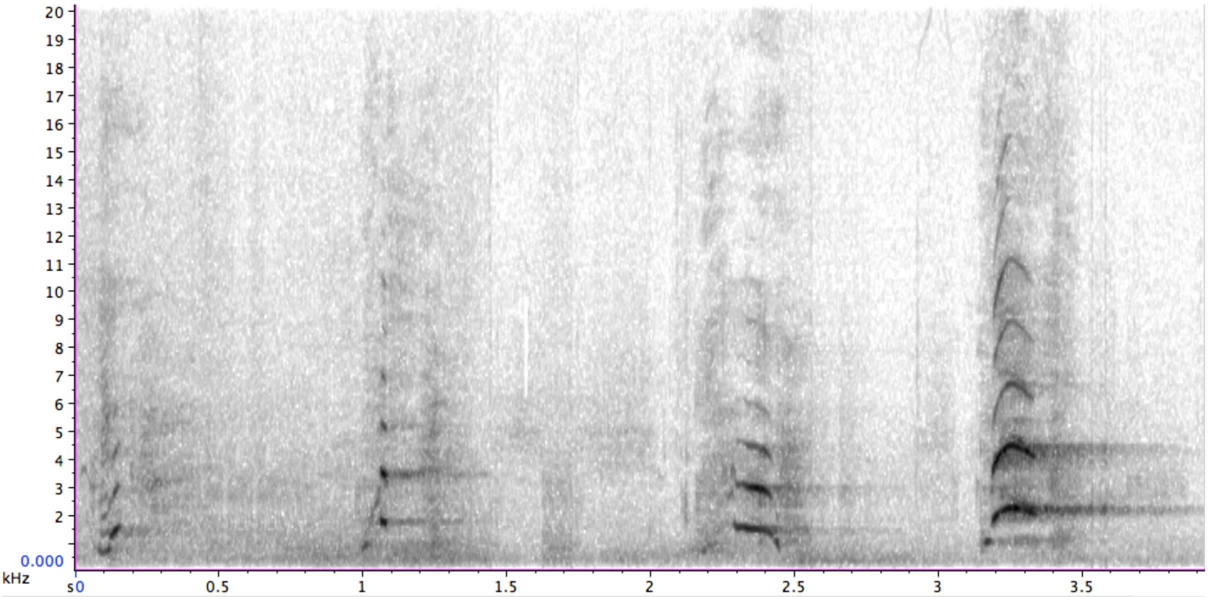


Figure A.II.3. Example of a stimulus from KEL used for the playback experiment. Clicks used to mark calls from focal individual have been removed and natural call intervals preserved.

Figure A.II.4. Presentation of pink and blue chow to KEL during a preference demonstration in full view of the subjects, using 20 x 20cm white plastic trays.

Text A.II.4. *Phase 1: Observational learning*

A demonstrator, either KEL or DW, was isolated and given the choice between two pellets of pink and two pellets of blue chow ten times, while the rest of the group observed from the opposite cage (cages 1 and 2, fig. 5.1). Food presentation lasted five seconds after a first choice had been made. Maintaining food presentation for 5 seconds allowed observers to witness the rejection of the second food item. An initial demonstration phase consisting of three demonstration days per demonstrator was carried out early April 2015 and a reminder period of four demonstration days per demonstrator was carried out early June 2015. After this, refresher demonstrations took place at intervals of approximately 3-4 weeks. Subjects did not attend and observe all demonstrations. In a previous study (Chapter 4), Shorland *et al*., found that subject exposure to food preference demonstrations was positively correlated to successful social learning of those food preferences, we therefore controlled for the exposure to demonstrations statistically. During winter months, playback experiments were not possible as the group as a whole was kept indoors, nonetheless a reminder period of two demonstration days per demonstrator was carried out in January 2016 and yet another, of four demonstration days per demonstrator in May 2016 before resuming playback experiments. After each playback trial, reminder demonstrations took place at intervals of approximately 4 weeks. Demonstrators KEL and DW chose their preferred colour first in 99.6% and 100% of trials (N=240 for each demonstrator). All subjects attended to at least one preference demonstration during the initial demonstration phases in April and June 2015. On average, the 10 subjects attended to 30.2% of KEL's preference demonstrations (value is the mean percentage of feeding events observed).

Figure A.II.5. Pink, baited, feeding trough (dimensions 51x10x8 cm)

Figure A.II.6. Example of the view from the rooftop IP camera surveying the 5-metre radius and surrounding areas in front of the trapdoor on the small island.

Text A.II.5. *Criterion for subject participation*

The criterion for subject participation in the playback experiment was met when an individual, present in the 5m zone in front of the trapdoor during call playback, came to at least one of the two feeding troughs within the one-hour period. During a one-hour period following stimulus playback, the experimenter (GS), remained immobile, standing at equal distance from the two feeding troughs, facing cage 2 (fig 5.1) and gazing forward. Verbal observations were made for audio recording.

Figure A.II.7. Experimental set-up (wide-angle view) showing the designated blue and pink zones and respective feeding troughs where subject behaviour was coded. The loudspeaker is located at the centre point.

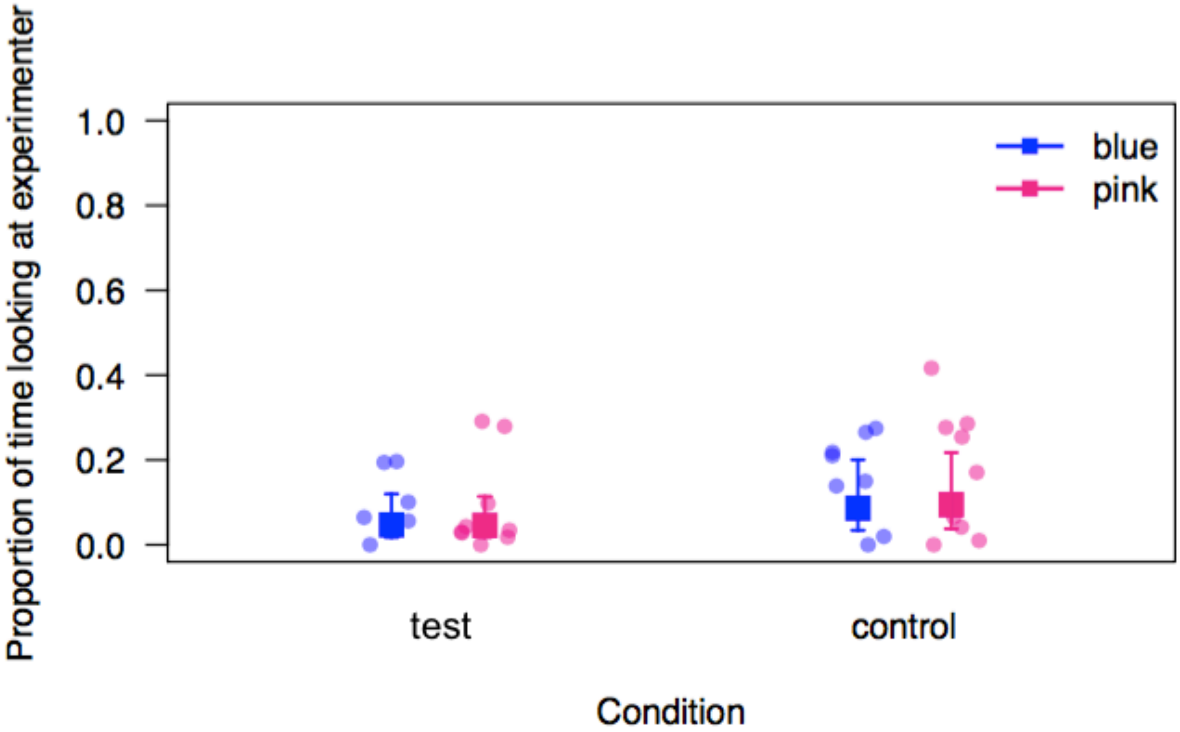


Figure A.II.8. Proportion of time spent looking at the experimenter (i.e. expectation) at the blue or pink feeding troughs. Circles represent the average proportion of time spent looking at the experimenter (expectation) for each subject (10 subjects participated in the six test trials and 9 subjects participated in the six control trials). Squares with bars represent model estimates with 95% confidence intervals.

Table A.II.2. Result of the GLMM testing for differences in expectation behaviour

	Estimate	Standard error	*Z*
Intercept	-2.89	0.51	-5.69
Demonstration exposure (no versus yes)	1.04	0.15	6.81
Condition (control versus test)	-0.65	0.47	-1.39
Location (blue versus pink)	0.10	0.07	1.37
Interaction (condition*location)	-0.13	0.21	-0.64

Note: Terms in parentheses indicate the two levels for each factor.

Table A.II.3. Result of the GLMM testing for differences in exploration behaviour.

	Estimate	Standard error	*Z*
Intercept	-4.62	0.79	-5.82
Demonstration exposure (no versus yes)	0.94	0.62	1.51
Condition (control versus test)	1.78	0.93	1.91
Location (blue versus pink)	0.13	0.83	0.15
Interaction: condition*location	-2.36	1.14	-2.07

Note: Terms in parentheses indicate the two levels for each factor.

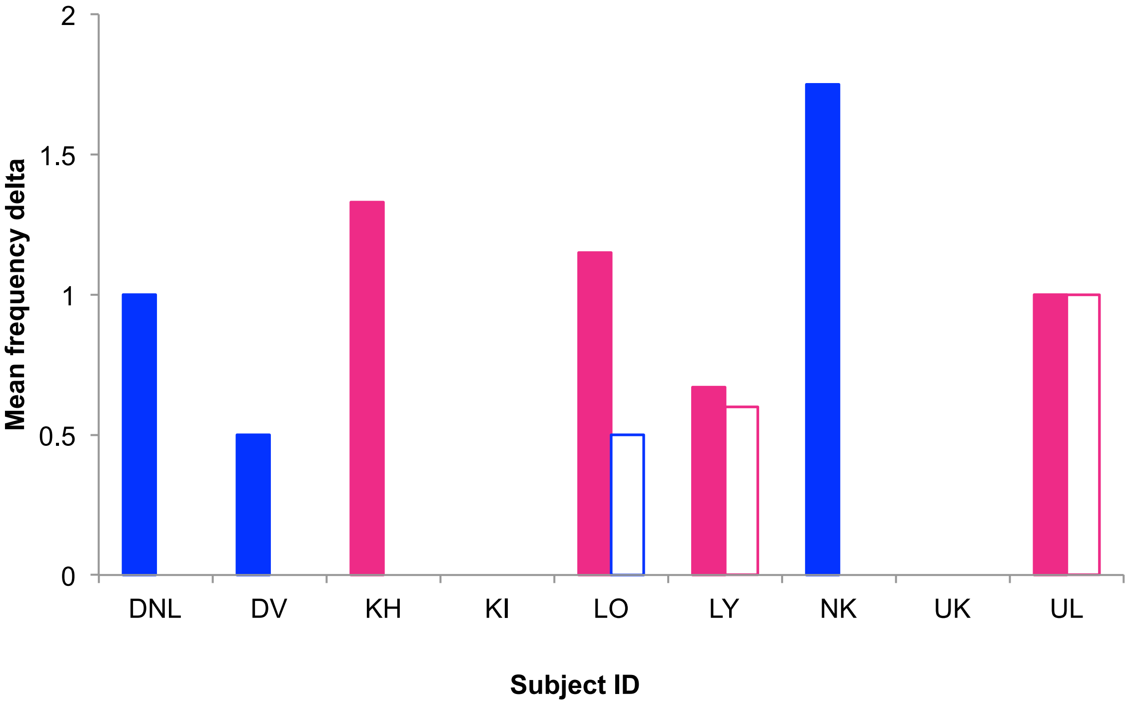


Figure A.II.9. Peer - Mean frequency delta (i.e., absolute difference : mean frequency of peering at pink minus mean frequency of peering at blue = Δ) between the two food locations in test (full bars) and control (empty bars) conditions. Colours indicate the direction of the trough bias. (10 subjects participated in the six test trials and 9 subjects participated in the six control trials). Two of the ten subjects were excluded from this analysis: UK, as she expressed peering behaviour not once and LNG, as she did not participated only in the test conditio

List of Tables

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List of Electronic Supplementary Materials

Chapter 3 ESM https://figshare.com/s/652f82e4e9ad5cb6025b

ESM 3.1. Example footage from La Vallée des Singes, France. (video)

ESM 3.2. Example footage from Lola ya Bonobo, DRC. (video)

Chapter 4 ESM https://figshare.com/s/a8170ec71b7d8ae3bec9

ESM 4.1 Research data. (Excel file)

Chapter 5 ESM https://figshare.com/s/18b19105c7a296e4b221

ESM 5.1. Example playback stimulus - KEL call sequence. (sound file)

ESM 5.2. Foraging training regime and supplementary information. (Excel file)

ESM 5.3. Experimental timeline. (Excel file)

ESM 5.4. Example of exploration by NK. (video)

ESM 5.5. Example of exploration and expectation by NK. (video)

ESM 5.6. Interactive results manual and package installation file. (PDF and .tar.gz file)

ESM 5.7. Raw data. (csv file)