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Social learning of arbitrary food preferences in bonobos

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ABSTRACT

A 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 natural conditions, 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. 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. 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 having already tasted the equally palatable colour alternative. Both age and exposure to demonstrator preference had a significant positive effect on the proportion of matched choices. Moreover, in a context where errors can be costly, social learning was instant insofar as six of seven subjects used socially learned information to influence their very first food choice. We discuss these findings in light of the current debate on the evolution of social learning in animals.

1. Introduction

Over the past decades, social learning has become a major topic in the field of comparative cognition (Whiten and van de Waal, 2018). Social learning, or more specifically "learning that is influenced by observation of, or interaction with, another animal (typically a conspecific) or its products" (Heyes, 1994) 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). Furthermore, social learning can favour the rapid spread of advantageous behavioural innovations and, as such, 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. Indeed, within a given ecological niche, different species are likely to be faced with the same requirements and constraints, as such, information acquired from heterospecifics can be just as valuable as that acquired from conspecifics (Avarguès-Weber et al., 2013). For example, the existing literature documents cases of interspecific social learning of food source location in insects (Dawson and Chittka, 2012) and fish (Coolen et al., 2003), of predator recognition and avoidance in mammals (Kitchen et al., 2010; Zuberbühler, 2000) and reptiles (Vitousek et al., 2007) and of nesting site preference in birds (Seppänen and Forsman, 2007). The importance of social learning 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 underlying social learning across different groups of animals, using both observational and experimental techniques in the wild (e.g. apes: Hobaiter et al., 2014; monkeys: Kawai, 1965; birds: Aplin et al., 2014) and in captivity (e.g. apes: Clay and Tennie, 2018; Dindo et al., 2011; Whiten et al., 2005; monkeys: Dindo et al., 2008; van de Waal et al., 2013b; lemurs: Stoinski et al., 2011; birds: Auersperg et al., 2014; see Reader and Biro, 2010 for a non-exhaustive survey). A common approach to study social learning processes has been to use paradigms that require manipulation of a container ('puzzle box') to extract an edible reward. A particularly successful variant is the

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'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 also of 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, 2016a for a review) as they begin to 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. However, 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), and although this capacity for tool use may translate into fitness consequences in certain contexts, for example, by providing highly nutritional foods when usual food resources are scarce (Yamakoshi, 1998), tool use may not be as significant for survival as general foraging strategies.

Social learning, in other words, may be better investigated in relation to more universally 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. Indeed, a recent study has revealed that chimpanzees learn rapidly from each other how to react to humans, a major predator of chimpanzees (Samuni et al., 2014). Regarding more ecologically relevant generalised foraging strategies, one of the key domains for social learning is to discriminate edible from noxious foods (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) but also in primates, where food-related social learning is influenced by a number of factors. These include sex, rank, age and association (Coussi-Korbel and Fragaszy, 1995) and while 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), in others, individuals appear to learn something about the palatability of foods by observing others (e.g. cotton-top tamarin: Snowdon and Boe, 2003; vervet monkey: van de Waal et al., 2013a). Acquisition of such social information may be permitted by simple social learning processes such as stimulus or local enhancement (Whiten and van de Waal, 2018).

One 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, orangutans, chimpanzees and bonobos (see Rapaport and Brown, 2008 for review). Interestingly, this effect can be so strong that in orangutans, 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). Following an initial phase in which young primates preferentially learn from their mothers, their pool of accessible information broadens as their social learning strategies evolve and they begin to learn from other group members (Whiten and van de Waal, 2018).

When these strategies lead to learning from other group members, then selectiveness for specific models can become apparent. In a recent review, Whiten and van de Waal (2018) presented four selective learning biases evidenced in primates when they learn from other group members. Namely, bias for 'knowledgeable' or 'expert' models; for older models, for models of a specific sex or for conformity (i.e., copying a behaviour expressed by a majority of one's group). Indeed, a general finding in empirical work on social learning in primates highlights 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. Indeed, in recent years, evidence for the flexible use of social learning strategies (i.e., what, when and whom to copy) has been found in several species spanning across taxa, from fish and birds to rats and primates (see Kendal et al., 2018; and Rendell et al., 2011 for reviews). This flexible use of social learning strategies is reflected in changes linked to ontogeny, experience, state and context (Kendal et al., 2018) and is likely an important factor as individuals enter the third phase of social learning proposed by Whiten and van de Waal (2018), which occurs when individuals migrate to new groups and are confronted with new locations and populations. For example, in an experiment in the wild, migrating male vervet monkeys abandoned their personal food preferences to adopt an opposite preference shown by their new group, which has been interpreted as potent social learning with a conformist bias (van de Waal et al., 2013a; Whiten and van de Waal, 2016b).

In the midst of these potential strategies for social learning, we were interested in experimentally assessing social learning in bonobos, in a universally ecologically relevant situation, i.e., food choice. In the present study we tested whether bonobos are able to socially learn the arbitrary food preferences of a group member acting as demonstrator through mere observation and whether they would adopt and maintain such preference regardless of their own knowledge that both options

were equally palatable. To achieve this we ran a social learning experiment comprising of a series of experimental 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 artificially coloured foods, we predicted social learning to be particularly strong during the first experimental 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.

2. Methods

2.1. Ethical note

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.

2.2. Study site and subjects

The experiment took place between February and November 2014 at La Vallée des Singes primate park, Romagne (France). Study 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 1), housed in a large indoor enclosure (400 m^2) with access to two outdoor wooded islands covering 11,500 m^2 in total.

Two adult males, DW and KEL, were selected as demonstrators based on the ease with which they could be isolated without apparent signs of stress to any of the group members. Six experimental blocks were carried out, each consisting of a *Demonstrator Training phase* (DT) for the demonstrators, followed by a *Preference Demonstration phase* (PD) in front of the subjects and finally an *Observer Testing phase* (OT) in which subjects underwent repeated choice tests. Three of the six experimental blocks were in the pink condition (i.e., demonstrator preference was for pink courgette) and three in the blue condition (i.e., demonstrator preference was for blue egg, further details are specified below). Testing was dependent on the personal motivation of each individual to, first, observe the Preference Demonstrations (PD), and, second, participate in the food choice tests of the Observer Testing phase (OT). Therefore, only 7 individuals of the 17 group members (two males and five females, age range: 14 months to 20 years, mean = 7.4 years) participated in the experiment (see Table 1). One individual (LNG) participated only in the three experimental blocks of the pink condition, again, due motivational reasons. The remaining six individuals completed all six experimental blocks.

Table 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

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

2.3. Experimental design

We carried out six consecutive experimental blocks, three for the pink condition (P1, P2, P3) and three for the blue condition (B1, B2, B3) (Fig. 1). Each experimental block consisted of three distinct phases: (1) Demonstrator Training phase (DT): demonstrators were given the choice between two artificially coloured foods (pink or blue) one of which was rendered unpalatable; (2) Preference Demonstration phase (PD): subjects observed demonstrators choosing their preferred food colours from a distance ranging from approximately 180 cm, across the corridor, to 500 cm on nearby structures or tunnels; (3) Observer Testing phase (OT) : subjects were given the choice between palatable pink or blue food (courgette or egg, see Fig. 1). For detailed explanations see below. In the pink condition (blocks P1, P2 and P3) demonstrator(s) were presented with pink and blue courgette, and demonstrator preference was for pink courgette. In the blue condition (blocks B1, B2 and B3) the demonstrator was presented with pink and blue egg and demonstrator preference was for blue egg.

2.3.1. Demonstrator training phase (DT)

In the initial Demonstrator Training phase (DT) for the first experimental block (P1), the two demonstrators, DW and KEL, learned that pink courgette was palatable (artificially sweetened), whereas blue courgette was unpalatable (artificially made bitter). In the three following experimental blocks (B1, B2, B3), KEL then learned the reverse colour pattern, albeit with a different food type (i.e., egg). Training for this new preference was achieved by presenting palatable blue egg, and unpalatable pink egg. Finally, in the last two experimental blocks (P2, P3) DW was provided with refresher training for a maintained preference for pink over blue courgette. In total, DW underwent 30 trials of food preference training with the pink courgette, while KEL underwent 10 with the pink courgette and 30 with the blue egg. To this end, at the start of each experimental block, the demonstrators were visually isolated from the rest of the group (Fig. 2a – cage 8, location marked DT) and were offered the choice between the pink and blue food (courgette or egg depending on the experimental block, see Fig. 1 for details), one sweet, one bitter. Food presentation lasted 10 s after a first choice had been made. The first choice was defined as the first food touched, although in all cases this was also the first food item eaten. 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 (DT) was recorded using a PANASONIC HC-V727 full HD camera equipped with a SENNHEISER MKE 400 external microphone.

2.3.2. Preference demonstration phase (PD)

Following the Demonstrator Training phase (DT), a demonstrator was isolated and given the choice between the pink and blue food (Fig. 2b), while the rest of the group observed his choices from the opposite cage (Fig. 2 a - cages 5 and 2 and Fig. 2c). Demonstrators were allowed to choose 10 times. Food presentation lasted 10 s 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 (PD) were carried out once a day over several consecutive days (see Fig. 1 for details).

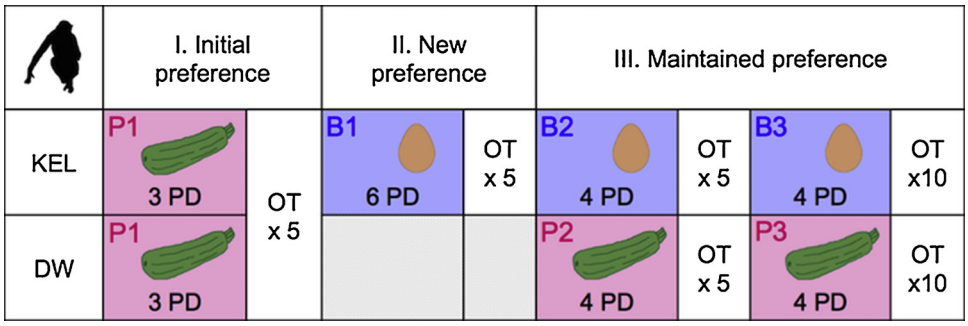

Fig. 1. Experimental design - Experimental block order, demonstrator(s) identity, number of Preference Demonstration (PD) days, food used and preferred colour as well as number of Observer Test trials (OT) following each Preference Demonstration phase (PD). Each experimental block began with a Demonstrator Training phase (DT) consisting of 10 food presentations each, not represented on this figure. Testing period for each experimental block in chronological order: P1: Feb, B1: Jul, B2: Aug, B3: Sep, P2: Nov, P3: Nov.

We first ran experimental 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 increase the salience and strength of the demonstrated preference for the observers. Once established, we proceeded to experimental 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 continued in the blue condition with experimental blocks B2 and B3, again with KEL demonstrating his preference for blue egg. Finally, we carried out experimental blocks P2 and P3, with DW demonstrating his maintained preference for the pink courgette (see Fig. 1). The number of demonstration days varied among experimental 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, see Fig. 1).

During the Preference Demonstration phase (PD) both the demonstrators and the observers where filmed in order to record both demonstrator colour choice 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., defined as the subject's head and eyes oriented towards the demonstrator whilst the choice was made, regardless of posture) 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.

2.3.3. Observer testing phase (OT)

Following the Preference Demonstration phase (PD) for each experimental block, observers underwent individual preference testing in which sweetened pink and blue foods (courgette or egg) were presented to them simultaneously. For the Observer Testing phase (OT), both food types were prepared in the same way, but liquid sugarcane was used for all food 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 blocks P1, P2, B1 and B2, and 10 times each in blocks 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. In order to avoid feeding competition with other group members, the default protocol was to test subjects in the absence of other group members. It was, however, unavoidable that some subjects (5 of 7) witnessed at least one choice test of another subject. In terms of their overall exposure, this was an insignificantly small proportion with far less influence than the Preference Demonstrations (PD) observed (see

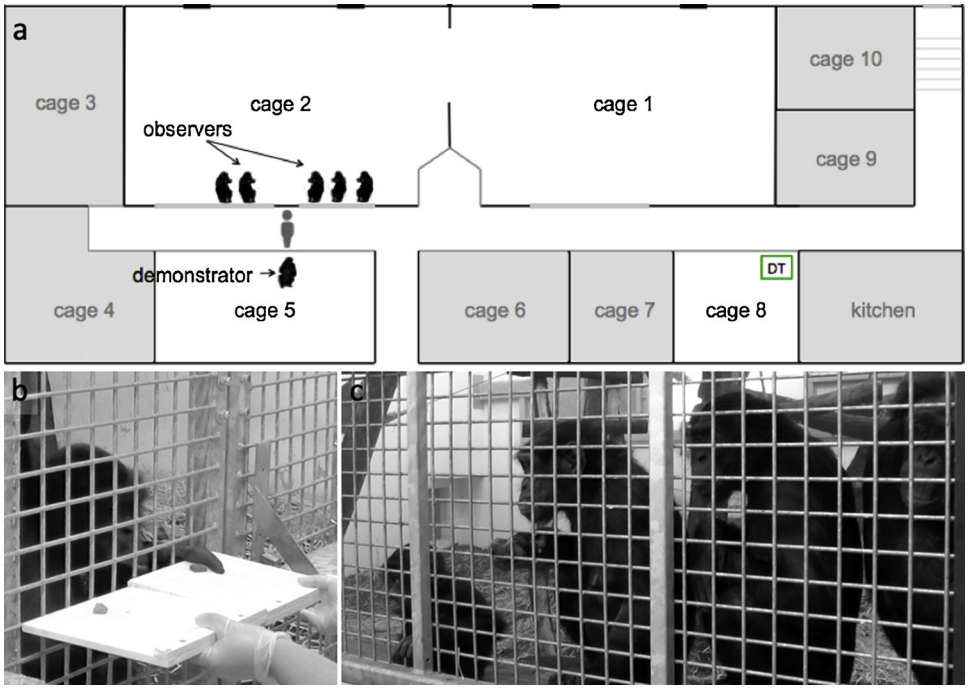

Fig. 2. Experimental setup for social learning experiment – a) The Preference Demonstration phase (PD) is illustrated showing the demonstrator in cage 5 and the observers across the corridor in cage 2. DT marks the location used in cage 8 for the Demonstrator Training phase; b) Demonstrator choice, manual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

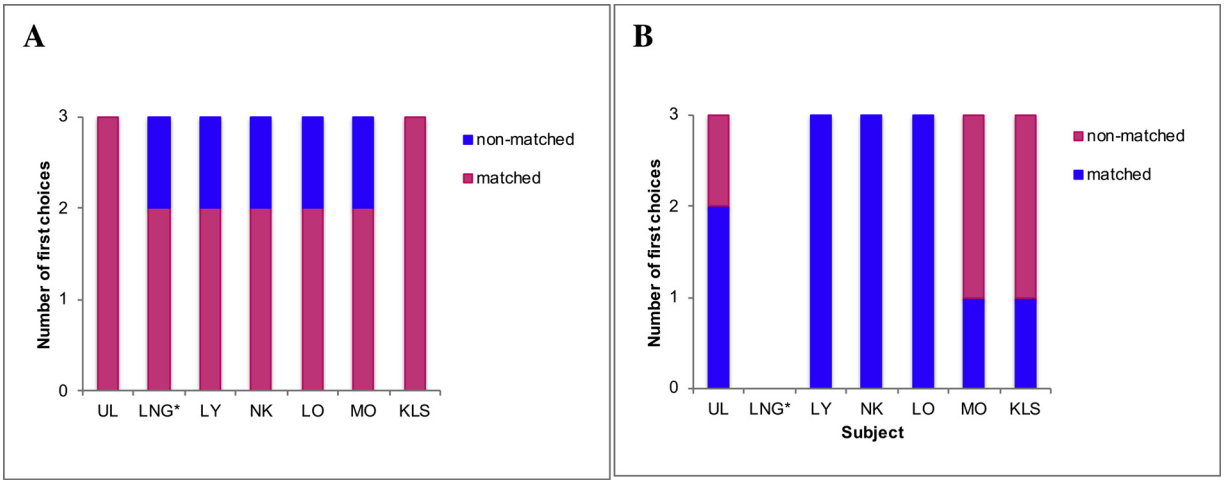

Fig. 3. Number of matched and non-matched colour choices for each subject in the first choice test of the Observer Testing phase (OT): A) pink experimental blocks (P1, P2, P3), B) blue experimental blocks (B1, B2, B3), subjects classed by decreasing age from left to right.

supplementary material, table S1). Testing was carried out over two or three consecutive days following the Preference Demonstration phase (PD) and was filmed using a PANASONIC HC-V100 full HD camera in order to record the colour chosen. As choices were always unambiguous and clear, we did not carry out any inter-observer reliability tests.

2.4. 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. For all members of the group, 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 given experimental block (i.e., Demonstrator Training (DT) and Preference Demonstration (PD)), the two food types were altered in taste and colour to obtain sweet pink courgette and bitter blue courgette for the pink condition, and sweet blue egg and bitter pink egg for the blue condition. We alternated the colour associated with the palatable food to control for any natural colour bias. The courgette was sliced and quartered (size approximately $2 \times 2 \times 0.5$ cm) 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%, 0.2 ml per 5 cl of water: 100 ppm). 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 $2 \times 2 \times 0.5$ cm). For the Observer Testing phase (OT) 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 selected as few to no foods of these colours are included in the group's regular diet. We chose not to carry out a control for a natural colour bias as doing so would have provided the subjects with unwanted experience with the two food colours.

To determine preferred food choice, 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. 2b). The position (left or right) of the different coloured food items was balanced and pseudo-randomised, insofar as no given colour was presented on the same side for no more than three consecutive trials.

2.5. Statistical analyses

Statistical analyses were carried out using R 3.1.2., GUI 1.65 and SPSS version 22. Datasets are available online [https://doi.org/10.17632/tczyxb9wvh.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 (PD) 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 (PD)). 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 modelled the probability of making matched choice across all trials per individual as a function of age and proportion of observed Preference Demonstration (PD) trials.

3. Results

3.1. Preference demonstration phase (PD)

3.1.1. Demonstrator performance

KEL and DW's performance during Preference Demonstrations (PD) 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 (PD) in methods for details).

3.1.2. Attention to demonstrators

While observers paid more attention to Preference Demonstrations (PD) by DW than to those by KEL, the difference was not statistically significant (mean percentage of demonstrations watched by the subjects: DW 35.4%, KEL 29.8%, Wilcoxon exact test, $Z = -1.014$, $N = 7$, exact $P = 0.38$, two-tailed).

3.2. Observer testing phase (OT)

3.2.1. First choice performance

For the first trial of the first experimental 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 in this first trial. When analysing first choices across all experimental blocks, individuals chose the matched colour significantly more often than the non-matched colour ($Z = -2.64$, $N = 6$, $P = 0.031$, two-tailed, Wilcoxon exact test; Fig. 3; one subject, LNG, could not be included in this analysis as she partook in only 3 of the 6 experimental blocks). Of the seven subjects, six chose mostly the matched colour as their first choice for each experimental block, and

Table 2
Results of the logistic regression modelling the proportion of matched 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*

Estimates are on a logit scale. *p < 0.05; **p < 0.01.

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 by observation.

3.2.2. 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 supported the fact that subjects matched their choices to those of the demonstrators significantly above chance levels (see Table 2 and Fig. 4 for raw data).

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 more than the alternative.

Furthermore, both age and proportion of trials observed had a significant positive effect on the proportion of matched choices (Table 2, Figs. 5 and 6).

When considering individual performance (i.e. percentage of matched choices during the Observer Testing phase (OT)), it can be noted that there is considerable inter-individual variability (Table 3), variability which can be explained in part by the age of subjects and their attention to Preference Demonstrations (PD) (as shown in the model).

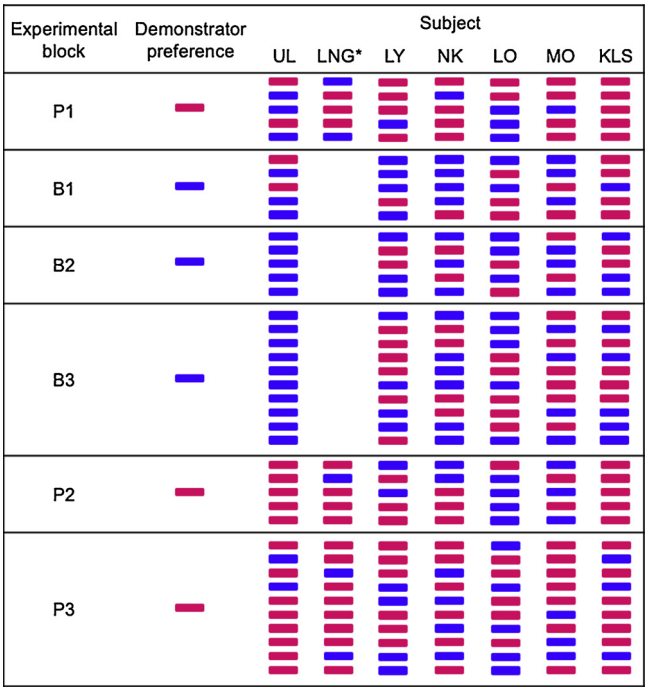

Fig. 4. Experimental block, demonstrator preference and all subject choices during the Observer Testing phase (OT) for all six experimental blocks (both subject choice trials and experimental blocks are shown in chronological order).

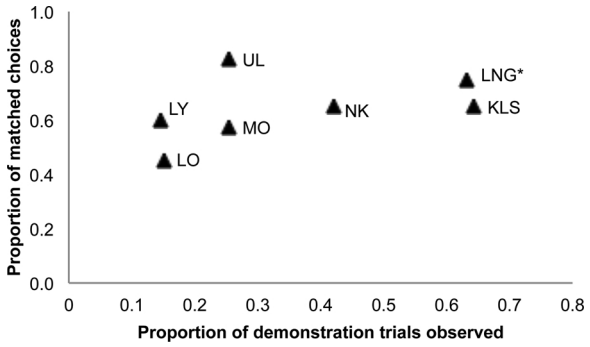

Fig. 5. Proportion of matched choices made during Observer Testing phase (OT) and proportion of Preference Demonstration (PD) trials observed by each subject. LNG, marked by an asterisk, participated in only P1, P2 & P3.

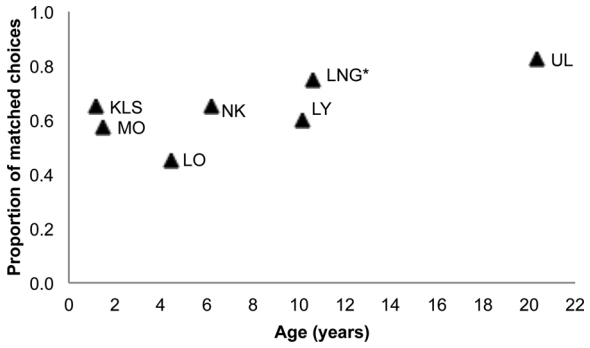

Fig. 6. Proportion of matched choices made during the Observer Testing phase (OT) and subject age in years. LNG, marked by an asterisk, participated in only P1, P2 & P3.

Table 3
Individual performance over all six experimental blocks.

Subject	*N*	Proportion of demonstration trials observed	Food colour choice matched : unmatched	Performance (% matched)
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

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 (OT) for only three of the six experimental blocks: P1, P2 & P3.

Nonetheless, six of seven subjects chose the matched food colour more often than the unmatched food colour.

4. 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. In a series of six

experimental blocks, subjects were then provided with the opportunity to observe demonstrator preferences before being presented with the choice of two colour alternatives of an otherwise identical food item. The results, as demonstrated by the number of matched choices made by the subjects in the first choice of each experimental block, showed that the subjects had 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 (KEL) demonstrated opposing colour preferences for different foods (see Fig. 1). In this paradigm which confronted the subjects with the question of "what to eat?" it is likely that the mechanism at work is simple stimulus enhancement as is often the case with this and other everyday behavioural questions such as "where to sleep?" or "who and what to beware of?" (Whiten and van de Waal, 2018).

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, see Fig. 4 for frequencies of alternative colour choice throughout the experiment). We noted considerable inter-individual differences in performance during the crucial Observer Testing phase (OT), which was at least partially explained by subject age and exposure to Preference Demonstrations (PD) (see Figs. 5 and 6); indeed, younger individuals and those that observed only a few demonstrations were less likely to match their choices to those of the demonstrators in the Observer Testing phase (OT) than older individuals or those that observed many demonstrations. It seems quite intuitive that performance should improve with increased exposure to demonstrator preference, however, the result observed in relation to subject age is in contradiction with the general finding that suggests that juvenile primates are more prone to use social information than are adults (e.g. Coelho et al., 2015; Matsuzawa, 1994). In the present study we found that older subjects were those most likely to match their choices to those of the demonstrators.

When considering the possible explanations for subjects generally adhering to demonstrator preferences we must consider the recent findings which have revealed that rather than being set rules, social learning strategies are used flexibly at the individual, group and population level (see Kendal et al., 2018 for a non-exhaustive review of theoretical and empirical support for a broad range of social learning strategies), in fact a recent study in the wild has demonstrated that this flexibility can even be at the species level (Bono et al., 2018). In their review, Kendal et al. (2018) present a variety of strategies as to when, whom and what to copy. 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 the preference shown by the demonstrator. This propensity to adhere to demonstrator preference might be in line with a 'when' learning strategy more expected of naïve subjects: 'copy-when-uncertain'. This would suggest that subjects perceived uncertainty during testing which increased their willingness to rely on social information (Galef et al., 2008; Kendal et al., 2015) rather than their own experience. 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. This pattern of relying more on one's own experience than on social information from conspecifics has also been observed in other animal species. For example, Fryday and Greig-Smith (1994), demonstrated that the amount of food consumed by house sparrows was influenced not by demonstrator consumption, but by their own previous experience with the food (i.e., palatable untreated food or unpalatable quinine-treated food).

Regarding a possible "who" strategy, there is much empirical work to support model-based biases, for instance the propensity to learn from older and higher ranking group members (e.g. Biro et al., 2003; Kendal et al., 2015). In our study, the two demonstrators were not the highest ranking male in the group, nor were they the oldest, and neither one was directly related to any of the subjects, 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 3 and Fig. 4). This result may be indicative of a 'who' bias for 'knowledgeable' or 'expert' models (Whiten and van de Waal, 2018) or 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 are able to 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).

Kendal et al. further present a set of frequency-dependant biases. Indeed, 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 conform 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, since subjects did not have to adhere to the behaviour of a majority, instead 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. The underlying drivers of such behaviour open questions for future research.

5. 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, even when the demonstrator is not a high ranking individual. 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. Furthermore, while this study does not allow

us to draw conclusions regarding the exact social learning mechanism (s) at work, the results, even if due to simple stimulus enhancement, as has been suggested for social learning of many of the day-to-day behaviours (Whiten and van de Waal, 2018), demonstrate that subjects matched their choices to those of the demonstrators regardless of the colour, food type and demonstrator identity. We believe this supports not only the fact that learning from others in the context of food acquisition is of paramount importance but also provides further support to the ongoing discussion around the flexible use of social learning strategies.

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 more universal ecologically relevant problems.

Declaration of Competing Interest

None

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.beproc.2019.103912.

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