



Research article

Ape recognition of familiar human faces changed by time and COVID-19 face masks

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ABSTRACT

Reports of primates being able to recognise familiar humans are rare in the literature and tend to be regarded as anecdotal. The COVID-19 pandemic created two unique conditions facilitating the observation of spontaneous face recognition in zoo apes: i) lengthy gaps in contact with human visitors due to lockdowns and zoo closures, and ii) the wearing of face masks obscuring at least half the face of familiar individuals. Here, I report on the historical context of the familiarity between a primatologist and individual apes of two species, how those apes consistently showed recognition of this particular human over a time span of up to thirty years, how facial recognition was extended to family members, and how recognition persisted even when a significant portion of the face was obscured by a mask. This constitutes, to my knowledge, the first documented cases of recognition of familiar human faces changed by time and COVID-19 face masks in two great ape species. Although based on just two individuals, the documentation of this ability is important because it arose in a more naturalistic and spontaneous context compared to typical face processing research in which primates are tested with experimental stimuli in a laboratory setting. Implications for face processing theory and applications for the therapeutic utility of faces are discussed. These observations provide insight into the evolutionary origins of face recognition and, sitting at the interface of science and society, are of interest to a wide audience.

1. Introduction

Faces display unique individual configurations of features. They can also express aspects of emotion and personality [1]. Face recognition is a complex skill that is an important indicator of the cognitive abilities of nonhuman species [2]. In humans, being able to recognise familiar faces is a crucial skill for establishing and maintaining social interactions and relationships. Humans can recognise familiar faces with little effort but struggle considerably to recognise unfamiliar faces. This is because the brain processes familiar and unfamiliar faces differently. The 'stability from variation' theory of face processing [3] suggests that the human brain is very good at stabilising how the face appears by building 'average' representations. Specifically, it dilutes diagnostic features which vary *within* the same person in different contexts whilst enhancing those that vary *between* people. This ability has also been found in chimpanzees (*Pan troglodytes*), who can, like humans, create an average exemplar of a multitude of different facial expressions from the same individual exhibited over different times and contexts [4]. In turn, this ability may facilitate the mirror self-recognition capabilities evidenced in some chimpanzees [5]. Rhesus monkeys (*Macaca mulatta*), who do not show self-recognition [6], are also unable to create such an average facial template [4].

Some other social species are also able to recognise the faces of familiar conspecifics (e.g. from chimpanzees [7], through cattle (*Bos*

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taurus) [8], to pigeons (*Columba livia*) [9]), although the evidence from monkeys is mixed, with success at least taking longer to achieve despite their being the most popular models for face processing research [10,11]. Species demonstrating the ability to recognise familiar humans range from other primates including rhesus macaques [12], through dolphins (*Tursiops truncatus*) [13], sheep (*Ovis aries*) [14] to mockingbirds (*Mimus polyglottos* [15]). Dogs (*Canis lupus familiaris*) can also discriminate emotion in human facial expressions [16], likely reflecting the domestication hypothesis [17].

These are complex skills involving holistic face recognition and image processing which can be learned through repetition [18]. Studies have found that humans can struggle when identifying familiar faces they have learned when presented under different conditions; for example, a change of angle [19]. Sheep can also identify familiar faces presented at angles and similarly share this dip in performance [14]. This is likely due to neural systems shared by both species with the temporal lobe specialising in this important task, and a right hemispheric bias also implicated [20]. While chimpanzees likely also show this bias [21], monkeys, by contrast, lack such neural specialisation [11]. Sheep have been found to remember fifty individual sheep faces over a two-year period and to show recognition of both conspecific and human faces following separations of 8–12 months [22].

Zoo primates are good candidates for the investigation of cross-species facial recognition, as has been suggested for domesticated species with whom humans work closely [14], as their enhanced exposure to human visitors and keepers may make them experts in human faces. Both monkeys and chimpanzees have been found to be better at distinguishing human faces than those of conspecifics when their exposure to humans is higher [12,23–25]. However, while we know a great deal about how visitors affect the behaviour of zoo animals including primates [26], our understanding of whether and how those primates may recognise familiar humans is poorly understood. Reports of primates remembering and recognising familiar humans fail to appear in the scientific literature due to their anecdotal nature. However, examples of this recognition sometimes appear in media reports; for example, the recent emotive reunion of primatologist Jan van Hooff with the 59 year-old dying chimpanzee, Mama, with whom he had worked for many years and had not seen for several months (<https://www.youtube.com/watch?v=INa-oOAexno>). Therefore, these kinds of reports are important as they have implications for human-nonhuman animal relationships, especially in captive settings. They suggest that it can really matter who the person is, not just that they are a person.

The wearing of masks is unusual and previously only reported in the literature in terms of being part of the personal protective equipment (PPE) worn by the caretakers at some Primate Research Centres; notably, chimpanzees exposed to these masked faces were reported as having lost some of their ‘human face expertise’ [24]. A recent study, however, did include masked faces in its investigation of how familiarity with human caretakers versus zoo visitors affected the attention of apes [27]. Using a dot-probe paradigm and static photographs [27] chimpanzees and gorillas were found to show an attentional bias for unfamiliar over familiar faces, when the expression was neutral and including when wearing a mask, likely due to a novelty effect, reflecting curiosity or threat detection [28]. This study also showed that valence (a surprised expression) obliterated any distinction based on familiarity.

During my initial research as a primatologist, and continuing since then, I have observed how some individual animals show explicit recognition of me. This brief report presents two case studies of individual apes of different species who showed the strongest evidence of recognition. They have consistently shown recognition over a time span of thirty years, have also displayed recognition of family members, and, most recently, evidenced continued recognition while I was wearing a face mask as part of the COVID-19 pandemic protective measures. Since the face mask obscures so much of the face, it is suggested that the eyes may have particular importance in the long-term recognition of individual faces for these apes. These observations are important to document for the literature as too often they are dismissed as mere anecdotes. Arguably, such findings are more authentic as they emerge from real-world situations rather than from more typical data based on two-dimensional photographs presented in laboratory settings.

2. Methods

2.1. Case studies and background

2.1.1. Boris

Boris is an adult male chimpanzee (*Pan troglodytes*) residing in Chester Zoo, UK. He has an interesting life history as he was originally caught in the wild in 1966 as an infant, likely meaning that his family group would have been killed, and was then bought from a New York pet shop by a lady who raised him in her apartment for three years. When he outgrew this housing and became too boisterous, his owner looked at multiple zoos around the world and decided to send him to Chester Zoo to join an existing group. Boris did exceptionally well at learning to display species-specific behaviour, so much so that he rose to the top of the dominance hierarchy and became alpha male in a multi-male group. This group contained males and females ranging from infants to adults of up to 50 years of age, being predominantly parent-reared and having continuous full contact. Boris was the alpha male of the group when I first met him in 1992 while conducting PhD observations.

The group had an outdoor grass island surrounded by a water moat, which contained climbing trees and ropes, bushes and tunnels for shade and cover and onto which scatter feeds were thrown from an adjacent roof. The group also had an indoor enclosure containing a multi-level platform structure with ropes and hammocks and an indoor water moat. Enrichment feeding holes were available on the wall of the enclosure and the chimpanzees were provided with sticks to fish for yogurt. Scatter feeds were also given through the rooftop.

Having experienced a traumatic start in life and then a period of hand-rearing and human enculturation, Boris retains an interest in people and also displays certain mannerisms less typical of chimpanzees as a whole; for example, blowing raspberries and clapping. He was looked after by a senior keeper for all of his time at Chester Zoo until 2019 when this keeper, to whom he also showed clear recognition, retired. A series of additional keepers have arrived and left over the years.

2.1.2. Asante

Asante is now an adult female western lowland gorilla (*Gorilla gorilla gorilla*) residing in Twycross Zoo, UK; however, when I first met her in 1992 while conducting PhD observations, she was a juvenile, having been born in 1985. At that time, Asante was housed with just one other gorilla, a younger male called Ti. The two youngsters had continuous full contact and spent most time in an indoor enclosure with platforms, rocks and ropes, alternating access to a large grass outdoor enclosure also used by a neighbouring primate group. Water and food were freely available. Asante was born at Twycross Zoo where she received some hand-rearing. She then had a team of keepers looking after her, some whose tenure was long and others who left after shorter durations.

2.2. Procedure

I recorded how the apes responded to me when I approached the glass front of their enclosures following a long-term absence; for Asante, this was ten years, for Boris, this happened repeatedly on occasions following separations of one year, four years, and then varying periods ranging from days to months at a time. Observations were recorded *ad libitum* and sometimes supplemented by photography and video recording. In terms of recognition of family members, the apes' building of recognition was facilitated by association because I was with the family members. However, this changed when the children were older and able to visit apart from me. It may be expected that familial resemblance of facial features could act as cues for the apes to recognise my children, but in the case of my husband, there would be no such cues. With respect to recognising me with a face mask, this was at a time when all visitors and zoo staff were wearing masks such that the apes would have become somewhat used to this initially strange feature that was consistently worn by every human near them. I again recorded how the apes responded to me when I approached the glass front of their enclosures, wearing a face mask, following a long-term absence; for Boris, of seven months, for Asante, three years.

3. Results

3.1. Initial recognition

I first met Boris in 1992 while studying his group as part of my PhD into African ape personality at the University of Cambridge. Having spent so much time with the chimpanzee group day after day (over a thousand hours during the entire study period), Boris and three of the other adults (Heidi, Mandy and Nicky) showed clear recognition of me. They would 'greet' me when I arrived each day, Boris by approaching me, gazing at my eyes, nodding, sometimes reaching his hand out with palm upward, and making the pout face which was always more humanised than in other chimpanzees and was described anthropomorphically by zoo visitors and keepers as

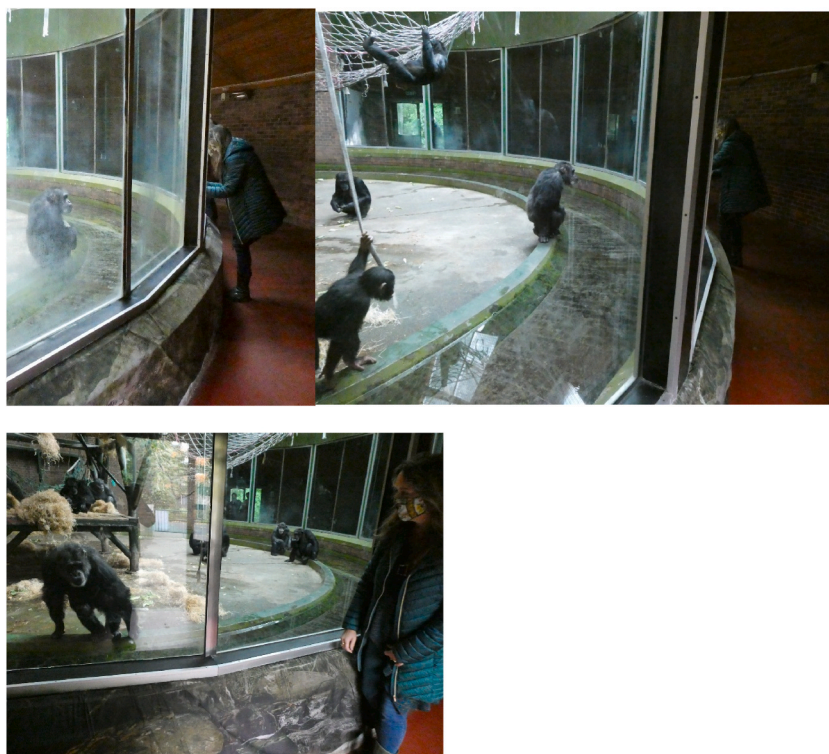


Fig. 1. Chimpanzee Boris at Chester Zoo approaches the author at the front of the enclosure and a game of chase ensues

'blowing kisses'. Heidi, Mandy and Nicky would stare at me and nod their heads. They sometimes approached but rarely interacted further. Sometimes Boris' levels of arousal led to him first initiating a charge and jumping on the glass, before he would sit with arms crossed over his knees, gazing at my face, sometimes rolling his tongue around his mouth and pouting, and sometimes then initiating a game of chase, whereby each of us ran around the enclosure perimeter to touch a wall before the other one, and then returning to the starting point and resuming. I estimate that this recognition pattern formed after two weeks of daily observation, evolving from ignoring me, through to watching, then approaching, then interacting with me.

Like Boris, Asante and her companion, Ti, showed clear recognition of me and would show this by approaching when I arrived each day. Asante would sit quietly gazing at my face, looking at my eyes, tapping her teeth, and then make the pout face resembling 'blowing kisses'.

3.2. Recognition over time

After my initial intensive study period, I was only able to visit the chimpanzee group every two years or so, although I carried out some further observations for a week in each of 1993 and 1996. After relocating to Chester in 1997, I was then able to visit regularly, alone, with my family, or with groups of students on field visits. Each time, regardless of the interval length between visits, Boris reacted in the same way whenever he saw me. When I entered the enclosure, he saw me, immediately rose from his position on the platform or floor, and approached me at the glass to gaze and then make the pout face, with a game of chase often following (Fig. 1; SI Video 1).

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Similarly, I was only able to visit the gorillas a handful of times after completing my observations. As soon as I went into Asante's new enclosure, where she was now housed in a group with a silverback male, other adult females and youngsters, she approached me, sat looking at my eyes and made the pout face just as she had done previously (Fig. 2).

3.3. Recognition of family members

Over the years from 2000 onwards, I introduced to Boris each of my three children and he has also shown signs of recognition (approaching and face-gazing) towards each of them as well as my husband, including when I am not present. To them, Boris will gaze and sometimes approach and do the pout face. This, in itself, is remarkable because obviously these little humans change rapidly and dramatically in appearance over time due to maturation. They, like myself, also change their physical appearance by the use of accessories such as hoods and spectacles, and change their hair styles, facial hair and sometimes colour (Fig. 3). I estimate that I would have visited Boris on average once a month during the period 2000 to 2011 when the children were young. These visits would mostly have been with one or more of the three children and only a few would have included my husband. From 2012 onwards, visits were less frequent and I would estimate occurred every three to four months, again with the same family composition.

Fig. 4 shows Boris having approached the glass when I visited with my eldest son. Videos in the SI (2 and 3) show family interactions. Video 2 shows Boris clearly gazing toward my daughter and me, proceeding to look away but with glances back to check our presence. When I walk away, Boris then does the pout 'kiss' to my daughter. Video 3 shows Boris following me, with my husband, son and daughter, round the corner of the island, where he then sits watching. When I move off, he follows, blowing raspberries. In both of these videos, another visitor shouting out Boris's name can be heard but Boris's attention was maintained on our family.

I also visited the group with non-family members on an infrequent basis and with student groups at least once a year. Each time, Boris showed the same recognition and interactions with me.

Visits to Asante were less frequent and therefore recognition of family members was not examined.



Fig. 2. First visit to gorilla Asante in ten years



Fig. 3. The author (top row), and two family members (elder son, middle row; younger son, bottom row), illustrating appearances changing due to maturation and accessorization



Fig. 4. The author (left) and son (right) with Boris at the front of the enclosure

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3.4. Recognition of masked face

During the COVID-19 pandemic lockdowns in 2020 and 2021, zoos were closed and I was not able to visit Boris and his group for seven months. When I did visit again after this gap, I had to wear a protective mask and I wondered whether this would affect Boris' ability to recognise me. It did not; as soon as I entered the indoor house, Boris rose from his resting position on one of the elevated platforms and made his way down and across the enclosure to sit on the moat edge in front of the glass. He acted in exactly the same way as he usually did, gazing and, within 10 s, making the pout face (Fig. 5).

When I visited Asante after a period of three years, at the start of 2022, I had to wear the protective mask due to the ongoing COVID-19 pandemic. As was the case with Boris, the mask did not prevent Asante recognising me, and she immediately approached me at the glass, behaving in the same way as she usually did, gazing and, within 10 s, making the pout face (Fig. 5; SI Video 4).

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Fig. 5. First visits with COVID-19 face mask to (left) chimpanzee Boris, seven months since previous visit, and to (right) gorilla Asante, three years since previous visit

4. Discussion

Both Boris and Asante showed signs that they recognised me as a familiar human, both over time and when much of the face was obscured by a mask, thus lending some support to the suggestion that the eyes play an important role in inter-species face recognition. According to the stability from variation theory of face processing [3], Boris and Asante have shown that they were able to recognise the familiar face because they had formed a robust representation of it; this would have involved concentrating on aspects of appearance that are essential for identification, providing stable diagnostic information, while disregarding non-essential and therefore non-diagnostic aspects.

As both a chimpanzee and a gorilla succeeded in showing recognition of a familiar face, the evolutionary and comparative implications are not so straightforward. One might expect chimpanzees to be more similar to humans in this ability because of the expectation that their cognitive and neural mechanisms are likely also shared, but gorillas are less closely related to both humans and chimpanzees. Gorillas also show more limited evidence of self-recognition when compared to chimpanzees [29]. However, the fact that sheep have also been found to be skilled at recognising human faces [14] suggests that this capacity may be a product of convergent evolution and is as yet undiscovered in other mammalian species. It may be that the neural or cognitive requirements necessary for facial recognition are ancestral, but that the recognition behaviour is not always expressed without a good deal of priming in the form of regular human exposure.

This report is based on just two individuals who may not necessarily be representative of all individuals of those species; however, the documentation of this ability is important because it arose in a more naturalistic and spontaneous context compared to typical face processing research in which primates are tested with experimental stimuli in a laboratory setting, often with two-dimensional photographs [27]. The chimpanzees and gorillas were living in groups and, not subject to testing, they could choose how to behave and whether and how to engage with humans. The recognition and interactions observed attest to the importance of the relationship developed between the primatologist and the apes, and these kinds of findings have important implications for human-nonhuman relationships both in captivity and the wild. Building on the evidence that chimpanzees encode individual faces in a similar way to humans [4], this report provides initial evidence that gorillas may also share this ability. It is also important to note that it is valuable for reports such as this current one to be accepted into the scientific literature, even if not typical of the current and increasing emphasis on replicability.

Both Boris and Asante experienced hand-rearing [30] and this early close experience with humans may be an important factor predisposing these particular individuals to be more attentive to human faces, and consequently to be more likely to remember and recognise them in the future [31]. However, there were other apes in both of these groups who had also experienced some hand-rearing and yet their responses were different. Likely due to his background, Boris often manifested characteristics that were different from other chimpanzees, some of which were shared by other individuals who had also experienced hand-rearing. One of these characteristics was his interest in humans, particularly those he came to know well, with whom he would often interact.

That the ability of these two apes to recognise a familiar human was not hindered by the wearing of a mask covering half the face is interesting because it reveals finer details that may point towards the importance of the eyes in the facial recognition process, representing an avenue worthy of further investigation. Chimpanzees have shown some preference for direct rather than averted human gazes [32] and for the top part of human faces when discriminating between pictures [33]. Further testing for a possible preference for the eyes or for the upper section of the face (portrayed in the upper visual field) would add to evidence showing that chimpanzees [21], like humans [34], have a left visual field bias for facial features, potentially reflecting neural lateralisation in the brain [35]. The observations reported here do not support the findings that chimpanzees cared for by staff wearing PPE were less able to process faces, although these humans were not just wearing face masks, but also face shields and hair nets [24]. It could also be argued that recognition is not solely based at the facial level, but instead likely involves a more holistic feature integration process that takes in the whole body, including muscular structure and also hairline, which has been found to be important for human face recognition [36]. This may be supported by the ability of Boris to have repeatedly recognised the family members whose physical appearance changed substantially over time, not just in terms of facial features such as hair style and colour, facial hair, the wearing of glasses, hoods and

hats, etc., but also whole-body differences in stature. However, whereas dolphins have been found to use body features more than facial features when recognising their human trainers [13], great apes, including humans, favour the face and in particular the eyes [37].

Considering that the mouth in particular is obscured by the wearing of a mask and that this is one of the key features of a face to which gaze is directed in humans [38], likely because of its role in verbal communication, the continued ability of these apes to recognise individuals is interesting. Further research building on this initial documentation of recognition over time, with different decorations, and with face masks, is recommended. Similarly, building on work with both chimpanzees [39] and gorillas [37], use of eye-trackers would permit more detailed analysis of exactly where the apes' attention is focused when gazing at the human face.

The spontaneous and naturalistic responses reported in this paper differ markedly from face stimuli used in typical experimental testing paradigms and, as such, have greater ecological validity. A fundamental question in the literature revolves around whether animals showing recognition of faces in pictures are demonstrating their ability to process information from two-dimensional images rather than necessarily showing that they possess a representation of a specific individual per se [40]. The responses reported here go some way to supporting the view that these apes were demonstrating that they have an encoded representation of familiar individuals which facilitates the recognition of particular humans in real life, over considerable periods of time, and when substantially masked. These responses were different to the apes' behaviour in front of typical zoo visitors. This highlights the importance of long-term relationships that can exist between primates and those with whom they are familiar. I acknowledge my positionality and potential for observer bias in the processes I describe in this report; however, I took measures to wait for the apes to respond to me without interacting first and only then did I respond to them. Further study, preferably with video data, is recommended to continue to explore these important aspects of interspecies communication.

There are important applications of this work in terms of helping primates – and other animals – in conservation and captive settings. Faces are comforting, and stimulation from showing conspecific and familiar human faces has been found to reduce stress and fear at the behavioural, autonomic and endocrine level [41]. Pictures of faces could therefore have some therapeutic utility in a variety of contexts, including during unavoidable isolations and separations, translocations, and veterinary interventions.

Ethical approval

Ethical permission for the original observational studies was given by the University of Cambridge Ethics Committee.

Funding

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Availability of data and materials

Photographic illustrations are provided here in the article; further details are available from the author by request. No preregistration of this study was made.

Public significance statement

This brief report reviews the ability of nonhuman animals to recognise familiar human faces, then focuses on the historical context of the familiarity between a primatologist and individual apes of two species, how those apes consistently showed recognition of this particular human over a time span of up to thirty years, how facial recognition was extended to family members, and how recognition persisted even when a significant portion of the face was obscured by a mask. This constitutes the first documented cases of recognition of familiar human faces changed by time and COVID-19 face masks in two great ape species. It addresses the competencies of ape cognition in terms of the 'stability of variability' theory of face processing in humans and provides initial evidence that gorillas may share this system of processing with humans and chimpanzees. Applications for the therapeutic utility of faces are discussed.

CRedit authorship contribution statement

Lindsay Murray: Writing – review & editing, Writing – original draft, Methodology, Formal analysis, Data curation, Conceptualization.

Declaration of competing interest

There are no competing interests.

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