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Social Contagion Beyond Humans: an investigation on contagious yawning, exploring visual, auditory and tactile perception of a non-biological agent (an android) in primates and humans with intact vision and blind.

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ABSTRACT

The main function of yawning remains disputed. Contagious yawning has been demonstrated within species (e.g. humans; chimpanzees), across species (e.g. humans and dogs) and has been primarily linked to empathy. These communicative signals transferred through body language or facial expressions constitute the basis of social cognition. The current work investigates the nature of contagious yawning in a series of four studies (two with chimpanzees, two with humans - full sighted and blind individuals). The first study used a live presentation to chimpanzees of familiar and unfamiliar humans, portraying a closed mouth, gape and yawn condition. Chimpanzees were more likely to catch yawns from an unknown, rather than familiar human. Yawning triggered soporific behaviour, laying down, gathering leaves, making their beds, only when exposed to visual and auditory yawn stimuli, denoting a form of contagion different from mimicking or imitation behaviour, and here termed Experiential Contagion. The second study explored if the contagious behaviour extended to a non-biological unfamiliar object (an android) portraying the same experimental conditions. Chimpanzees caught yawns from the android and displayed the same form of Experiential Contagion. The third study measured (within humans) the implicit contagious response to perception of yawning (observed in videos) using facial electrophysiology and eye tracking. The fourth study (across agents) explored, for the first time, yawn contagion through tactile perception. It found that blind individuals yawned contagiously when touching an inanimate object, the android, that was tactually perceived as yawning. Collectively, findings show contagion can be triggered by visual, auditory and tactile perception, regardless of the biological nature of the perceived stimuli. Robotics and Artificial Intelligence can provide neuroscience with novel opportunities to explore other social interaction behaviours, and warrants future developments of the auditory and tactile biofeedback system, developed during this work, as a tool for blind individuals’ facial recognition and self-portrayal.

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DECLARATION

This thesis is submitted to City, University of London in support of my application for the degree of Doctor of Philosophy. It has been composed by myself and has not been submitted in any previous application for any degree.
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TABLE OF CONTENTS

TABLE OF FIGURES

TABLE OF TABLES

1 GENERAL INTRODUCTION & STATE OF THE ART

An effective form of communication is essential for all social beings. Natural spoken language is one of the great outcomes of the human evolutionary process. In addition to spoken language, social primates, both humans and non-humans, communicate through physical gestures, body language and facial actions, some of which are not part of the most common linguistic communication. At the centre of this thesis stands yawning, a widespread facial action, which also happens to be contagious (Provine, 1986).

Starting with a historical overview, cognitive and behavioural mechanisms that were previously thought to underlie yawning in humans and non-human primates are elaborated upon. This will be followed by a summary of contemporary theories and a description of controversial issues, such as the functions of yawning and the similarities and differences in humans and non-human animals.

1.1 A brief introduction to yawning

We may all yawn, possibly several times every day. We tend to yawn when we have just woken up, when we need to go to sleep, when we are bored, and in between all those stages. Thus, we have both anecdotal and empirical evidence of a possible relationship between spontaneous yawning and sleep (Depute, 1994). Many authors (Guggisberg et al., 2007; Sato-Suzuki et al., 1998; Kita et al., 2000) have taken these assumptions, as well as some research findings, as proof that there should be some common physiological and biochemical bases. In other words, structures and substances that are implicated in the transition between rest and arousal, waking and sleep (and vice versa) are also thought to be, at least partially, involved in the action of yawning (Provine et al., 1987).

Most evidence seems to suggest that the major triggers of yawning are centred around the hypothalamus and paraventricular nucleus. The bulbus and the area surrounding the pons which also connect with frontal regions seem involved in the action of yawning and whole sleep/wake rhythm, rest and arousal level modulation.

According to Giganti, et al., (2010), “Serotonin could be involved in the time preceding sleep onset, as we know it increases progressively before sleep” (Jouvet, M., 1995). Furthermore, various neuropeptides and neurotransmitters are thought to be associated with yawning control (Agiolas, A. & Melis M., 1998). “Adrenocorticotropin, α-melanocyte-stimulating hormone, acetylcholine, dopamine, nitric oxide, excitatory amino acids and oxytocin have a facilitatory effect, while serotonin and noradrenaline have different effects (facilitatory or inhibitory) according to the receptor involved; GABA and opioid peptides have an inhibitory effect. It is well known that many of these substances are involved in sleep-wake regulation” (Giganti, et al., (2010)).

A yawn is often a repetitive, highly stereotyped motor behaviour, mostly characterised by a wide opening of the mouth, accompanied by a long inspiration, followed by a brief acme and a short expiration. In humans, the process might be accompanied by an audible sound at the time of exhalation, during which, for cultural and social reasons, both the opening of the mouth and the associated sound, are often covered or disguised. Although these are the most commonly known features, a yawn is not merely an act of simply widely opening the mouth, but rather an intricate, highly coordinated set of movements. Together this results in a flexion, followed by an extension of the neck and a wide dilation of the laryngopharynx, with robust stretching of the diaphragm and many anti-gravity, facial and extremity muscles. The behaviour is considered as highly stereotypical (Provine et al. 1987), partly because the predominant and unmodified characteristics are observed in all cultures and most animals (Walusinski, 2010) but also because there have been no reports of any environmental input that has changed any component of the behaviour, including the sequence of movements.

1.2 Historical background and perspectives of yawning

The “father of Medicine”, Hippocrates, attempted to develop theories about the possible causes, purpose and consequences of yawning as far back as c. 460-370 BC (Coxe, 1846), while Descartes (Hall, 1972), Diderot (1937), Boissier de Sauvages (Dulieu, 1969), and many others, attempted to explain the physiological bases of yawning. Over the past centuries, scholars such as J. M. Charcot (1825-1893), observed and categorised the pathological aspects of yawning. For many centuries, yawning was considered a respiratory symptom. However, behaviours involving abnormal movements and disorders, such as convulsions, later attributed to hysteria (Gilles de la Tourette, 1890), were noted to be accompanied by bursts of yawning. Although the underpinnings of the neurobiology of yawning are still debated today, recent work seems to suggest that we are getting closer to a potential explanation of its intimate and elusive purpose. Some of the theories offered about the origin and functions of yawning will be presented here.

The English physician David Hartley (1705–1757), was heavily influenced by Isaac Newton's discoveries and attempted to explain aspects of human physiology using physical laws based on the actual laws of gravity. Like Hippocrates, who transposed Aristotle's knowledge of nature into 4 'humors', Hartley proposed that perceived sensations and voluntary acts were dependent on the vibration of particles that composed human tissue and were invisible to the eye. These "vibrations" travelled the length of the nerves and thereby gave substance to the 'animal spirits' of Descartes. He therefore prefigured the concept of molecules described by Webb in his 1989 work on Hartley:

"Depending on the circumstances, yawning and stretching may be considered part of the five classes of vibratory movements. When yawning occurs during attacks of fever and other diseases, it appears caused by sudden, strong contractions in the membranes of the mouth, throat, trachea and oesophagus, whereas stretching appears caused by skin contractions". (Hartley, 1755)

Pierre Brisseau associated yawning and epilepsy for the first time in his Traité des mouvements simpatiques ('Treatise on Sympathetic Movements') in 1692. He stated:

"The signs of an imminent attack of epilepsy are a disturbance of the soul and the senses, heaviness and pain in the head, vertigo, irritating insomnia, weariness in the joints, trembling of the limbs, ringing in the ears, yawning, heart palpitation, difficulty breathing, nausea, cardialgia, etc. All of these signs are more or less present in epileptics. […] Because blood circulates with difficulty around the lungs, yawning is easy to deduce in those about to be struck by a fit of epilepsy." (Brisseau, 1692)

He attributed the transmission of information from one body part to another to a fluid circulating in the nerves, which he called ‘sympathies’:

“Such is the admirable constitution of man and animal, that those parts with seemingly different functions are however intertwined such that they all more or less influence one another […] But aside from this general harmony, there are different parts that have a more direct connection, that are linked by different means, such that the state of one has a pronounced influence on the state of another, or is at least altered by the changes that it experiences; this is due to the Greek sympathia and the Latin consensus; and sometimes the effect is much more pronounced on the part in sympathy than on the part originally affected. […] Since specific sympathies depend on nerves that have closer connections, weak causes can set them into motion; stronger causes are needed to bring about the well pronounced effects of general sympathy. All men are not equally subject to sympathies, because the nervous nature is not equally sensitive in all; hence, the same cause that brings about the most pronounced sympathies in one person, causes none in another; the corresponding action is limited to its centre, because the nerves of that person are less sensitive. It is strictly to the general consensus that we must attribute this imitative force that obliged Monro to repeat all that he saw being done. M. Whytt attributes yawning and involuntary vomiting to it; but I nonetheless do not know whether simple physical consensus is capable of generating these phenomena by itself.” (Brisseau, 1692)

Surprisingly, very few authors described yawning in animals or children. Charles Porée (1685–1770) spoke about yawning during a public session of the Académie des Belles-Lettres de Caen in 1756 where he observed:

“Birds yawn, just as man and several other animals do, but their yawning is different from ours. The lower part of the bird’s beak is stable, whereas the upper part is mobile through a hinge connecting the bones of the bird’s head to its beak. Our upper jaw is fixed, the lower jaw is mobile and moves with the temporal bones. When man yawns, the lower part of the mouth opens; while the mechanism differs, nature’s intention is the same and reaches the same objective. The rest of this observation has mere curiosity value. We yawn when we are born; the first infant to be born set the example. This movement cannot be attributed to worry, as the infant knows the society he enters. Hunger and sleepiness are not the immediate cause; food

will be administered through a new channel. So, at first yawning has to be related to the change the infant experiences as he begins to breathe and thereafter, to the new course the blood works its way through. It can also be seen as a sign of weariness caused by the fatigue of birth and the new oscillation of the humors. All these changes are admirable and show a providence worthy of our deepest esteem. Nonetheless, one could complain that birth as well as death are difficult, and life is often less tiresome." (Porée, 1756)

In 1831, in a dissertation on the development of intellectual faculties amongst wild and domesticated animals in the Annales de Sciences Naturelles by Adolphe Dureau de la Malle (1777–1851), the author reported having such close ties to his dog that the latter started yawning when he saw his master yawn! It took 177 years for contemporary authors to publish a study, in which the phenomenon was empirically tested, and from which the same conclusions were drawn (Joly-Mascheroni, Shepherd, & Senju, 2008).

Contrary to the general assumptions at the time, François Broussais (1772–1838) broke away entirely from his contemporaries and predecessors in his Traité de physiologie appliqué à la pathologie ('Treatise on Physiology Applied to Pathology'), published in 1834:

"If we wish to study the mechanism of yawning, which can be considered as the first sign and main phenomenon of boredom, either moral or physical, we will encounter serious problems. Yawning has been related to the need to breathe, or considered a means to renew the air stagnating in the lungs after respiration has slowed for some time. This is an error – one must only be a practitioner to know with certainty that dyspnea alone never produces yawning. […] The lungs seem to be much less influenced by yawning than the stomach … [If] the need for air is not the principal cause of this deep aspiration, then what can its purpose be? Could it be to swallow air, and to cure an ill stomach?" (Broussais, 1834)

Robert Whytt (1714–1766), a Scottish medical professor from Edinburgh, was well known for having described tubercular meningitis. His explanation of 'sensations' (sensitivity) in involuntary movements makes him a forerunner in the area of reflexes, just as his interest in the effect of emotions during diseases makes him the father of psychosomatic pathology. Pearce, J.M. (1997) quoted a whole section of Whytt's (1777) description:

"The different parts of our body receive from nerves not only the power to feel and move, but also a very specific sympathy that is either general and spreads out over the entire animal system, or particular, meaning that it is mainly exerted between certain parts. Whether we want to or not, we close both our eyelids every time there is a threat to one of our eyes. A sudden bright light striking our eyes sometimes causes blindness. Hippocrates observed that the sudden sight of a snake can make the face go pale. When a hungry person sees food he likes, he experiences a more abundant secretion of saliva than before having seen the object. Yawning and vomiting often occur by the simple sight or sound of someone yawning or vomiting. In this work on nervous disorders, I will mainly examine those that have the effect of a weak, delicate and unusual nervous constitution; and in this category I place the majority of symptoms that physicians have commonly described as windy, spastic, hypochondriacal, hysterical and vaporous […] Those that can suddenly be felt in the entire body or that travel through it; shivers, a feeling of coldness in certain parts as if water were being poured on them; at other times, an unusual feeling of fire […] Heart palpitations, rapidly changing pulse, most often natural, sometimes unusually slow, and other times quick or frequent, more often faint that strong, and in certain cases irregular or intermittent […] A dry cough with breathing troubles, or a convulsion or tightening of the bronchi, an accident that may come back periodically, yawning, hiccups, frequent sighing, a feeling of suffocation or constriction that seems to be caused by a lump or large object lodged in the throat, fits of crying and convulsive laughter".

The Scottish physician John Abercrombie (1780–1844), published a book entitled: Pathological and Practical Researches on the Diseases of the Brain and Spinal Cord, in which he described the strange phenomenon encountered in certain hemiplegics, where the paralysed arm moves up towards the mouth simultaneous to yawning. This occurrence disappeared as soon as the paralysis subsided (Abercrombie, 1828).

The Genevan physician and child psychologist Edouard Claparède (1873–1940), in his journal for teachers entitled L'Educateur, published an article in 1924 that drew on the work of the German Valentin Dumpert in 1921. The author was the first to propose that a large contraction of the diaphragm was what resulted in a yawn but importantly that this was part of pandiculation, rather than being associated to breathing as it was previously thought. This advancement resulted in the first proposal to pioneer today's neuromuscular theory, in which yawning originates in the diencephalon:

"Yawning is only incomprehensible when considered alone. On the contrary, it becomes clearer if we see it as part of a more general reflex, the reflex of stretching. It is well known that yawning hardly ever occurs without general stretching of the body. This is striking in certain animals, such as dogs or cats. It is also evident in small infants, and very often in adults" (Edouard Claparède (1924).

In the book entitled La contagion mentale ('Mental Contagion', 1905), André Vigouroux and Paul Juquelier wrote that as they saw yawning as a reflex, by nature it would be contagious, and they used this notion to develop a hypothesis that became successful under the term *'théorie de l'esprit'* (mind theory). Their proposal stated that "by involuntarily mimicking the gestures, actions and emotions of others, we acquire the ability to decode the feelings of the person observed" (Walusinski, O. 2010). Interest in this theory was renewed with the discovery of mirror neurons at the end of the 20th century: "The sight of coordinated, rhythmic actions that have become reflexes for those who perform them, provokes in onlookers motor reactions that are perfectly involuntary but also rhythmic and that represent a rough reproduction of the perceived acts" (Rizzolatti, Fogassi, & Gallese, 2001).

1.3 Yawning in humans

In humans, yawning is generally associated with boredom (Bell, 1980), tiredness (Suganami, 1977), fatigue and sleepiness (Provine & Hamernik, 1986). As summarised above, over the past centuries there have been diverse hypotheses postulated about the occurrence and possible causal role of yawning: Psychological (Imitation (Provine, 1986), Separation (Fogel, 1980)); Hormonal (Adenocorticotropic hormone (ACTH) (Donovan, 1978); Neurological (Coma and vegetative state (Braunwald et al., 1987)). There is empirical evidence to support some of the many pathological and symptomatologic links with other behaviours and conditions, such as brain hypoxia (Karasawa et al., 1982) and Pontine tumours or lesions (Bauer et al., 1980; Geschwend, 1977). Paradoxically, yawning may also occur in circumstances of high mental activity and demand. Charles Darwin observed this paradox, stating that: "Under slight fear there is a strong tendency to yawn" (Darwin, 1872). This apparent conflict between two paradoxically opposed approaches in attempts to define yawning, and the possible meaning of the behaviour, is still strongly evidenced today. One may conclude that yawning can take different functional roles. Part of these paradoxical views relating to yawning could refer to the previous association that "The torments of boredom are associated with an upsurge of arousal" (Berlyne, 1960). Furthermore, the view of yawning as a way of enhancing arousal levels (Baenninger et al., 1996; Birnholz et al., 1981) has come after evidence of an increase in motility (Baenninger et al., 1996) and brain activation (Karasawa et al., 1982; Kasuya et al., 2005) after yawning. However, many authors disagree with this argument as they could not find an arousing effect on the brain, whether measured by electroencephalogram recordings (EEG) or the autonomic nervous system, measured by heart rate variability (Guggisberg et al., 2007; Walusinski, 2010).

There is a popular belief that yawning is a response to elevated CO2 or depressed O2 levels in the blood. However, Provine, Tate & Geldmacher (1987) found no evidence to support this hypothesis. Foetal yawning in amniotic fluid shows evidence against any association between oxygenation capacity and yawning (Prechtl et al., 1990). Taking the evidence mentioned above, the seemingly obvious relationship between spontaneous yawning (i.e. non-related to external events) and sleep, as Giganti et al., (2016) stated, is not so obvious anymore. However, the time proximity between these common events, boredom or sleepiness and yawning, is so often seen in humans that it is difficult not to assume that there should be a common physiological, even biochemical, basis.

Yawning can be observed in all vertebrates (Depute 1974), warm and cold-blooded animals, reptiles and even fish (Walusinski, 2010), which are known to possess a much more archaic brain to that of primates. Studies exploring yawning ethology, pathology or any of the behavioural mechanisms of yawning, some of which were thought to accelerate blood flow to improve oxygenation of the brain, have not managed to reliably associate yawning as a response to cerebral anaemia, as

Johan de Gorter (1755) originally described. During the 20th century, however, consistent referencing of this much debated notion is still in evidence today. Guggisberg and collaborators reviewed the evidence for the origin and function of yawning and concluded that theories describing a physiological role lack support (Guggisberg et al., 2010). The same year, Giganti and Salzarulo (2010) stated that although yawning is a behaviour performed throughout the life span, they were able to show it originated during foetal life in the womb (Walusinski, 2006). This is important because any foetal movement is studied very carefully as it is considered to reflect the normal development of the whole nervous system.

Through technical advances in diagnostic sonography, foetal motility is thought to involve functional and maturational properties of the foetal hemodynamic and muscular systems (Giganti, Ficca, Cioni & Salzarulo, 2006). This is partly why yawning recognised from the 14th week through ultrasound techniques, together with the oromandibular motion, swallowing and even arm stretching, are considered good signals of functional maturation of the brainstem, basal ganglia and other brain structures. Furthermore, the importance of foetal yawning has been attributed to represent an important marker for an early diagnosis of disharmonious brainstem maturation (Walusinski, 2010), see Figure 1.1 below.

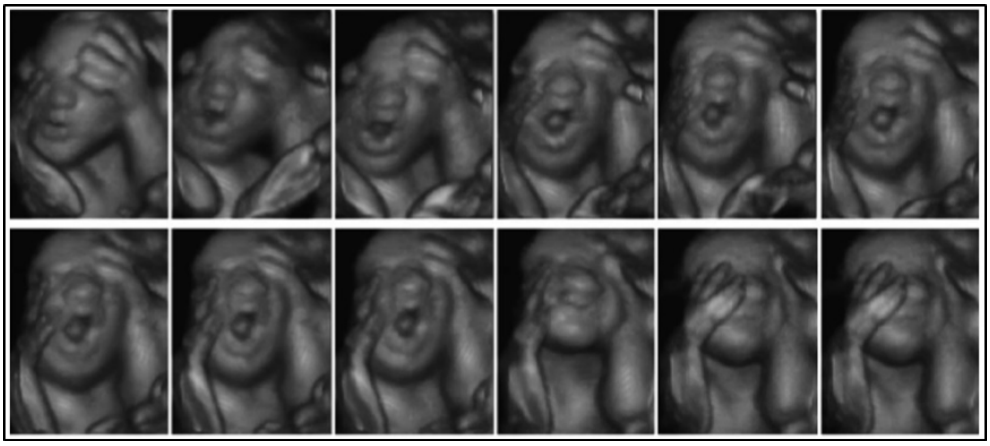


Figure 1.1 3D US serial imaging showing an ample, slow, and very deep inspiration, with the mouth wide open in foetal yawning during the second to third trimester. Note the generalized stretching of muscles in the face and neck (With permission from Wolfgang Moroder (Photographer) in The Ultrasound Review of Obstetrics & Gynecology, 2005) (Travail personnel) [CC-BY-SA-3.0 http://creativecommons.org/licenses/by-sa/3.0)

Human existence is reliant on a balance of sleeping, awakening, loving, feeding, and more sleeping. Although, as mentioned before, there seems to be an obvious relationship between a spontaneous yawn and drowsiness or sleepiness, such a basic physiological need state is also linked to hunger and thirst. This relationship has been attributed to a common functional basis, both physiological and biochemical, between rest, arousal and yawning. Some authors highlight a contrast between morning and evening yawning (Giganti et al., 2010).

A review by Guggisberg et al. (2009) looked into behavioural studies and electroencephalographic recordings of brain activity measured before and after episodes of pandiculation. In this work the assessed evidence demonstrated that a yawn tends to occur while the agent is in a state of low vigilance. If yawning occurs more frequently than the general perception of normal, it is considered excessive or abnormal. Yawning can also be considered abnormal when it is thought to have been triggered by other stimuli that are not fatigue, boredom or contagion. Up to now, there is no general consensus as to the exact frequency of yawning that would be considered abnormal. The threshold of abnormality found in literature ranges from 2 yawns/10 min (Singer et al., 2007) to 30 yawns/10 min (Cattaneo et al., 2006). Abnormal frequency of yawning appears to be an underexplored neurobiological phenomenon. Although the cause of abnormal frequency of yawning in humans is unknown, it has been found in a wide range of conditions (e.g. Thompson, 2010). Paradoxically, yawning provoked by a normal physiological event is considered a ubiquitous behavioural occurrence. Krestel et al. (2015) report that patients who experienced abnormal yawning often have supratentorial cerebral or brainstem infarctions (Singer et al., 2007; Cattaneo et al., 2006; Chang et al., 2008; Krasnianski et al., 2003; Walusinski et al., 2010). Cattaneo postulated a ‘‘denervation hypersensitivity’’ mechanism as cause of abnormal pathological yawning as a sign of brain stem ischaemia (Cattaneo et al., 2006). In principle, the “denervation hypersensitivity” would disconnect the reputed to be yawning centre in the brainstem from (inhibitory) control of other cranial nerves and structures, and this is in line with postulated hypotheses regarding excessive yawning in amyotrophic lateral sclerosis (ALS) patients (Williams, 2000) or the appearance of long lasting hiccups often occurring after medullary infarction (Park et al., 2005). Singer, Humpich, Lanfermann & Neumann-Haefelin (2007) reported the occurrence of abnormal yawning during anterior circulation stroke. However, explorations on the supposed lesion topography and extension is still needed (Krestel et al., 2015). Since yawning can be observed under so many and such varied circumstances, up to now, it is not possible to account for a general function.

1.4 Yawning in non-human animals

In non-human animals, many different kinds of yawning have been observed. For instance, Charles Darwin considered a certain form of yawning to be a deliberate act of threat:

“Baboons often show their passion and threaten their enemies in a very odd manner, namely by opening their mouths widely as in the act of yawning. Mr. Bartlett has often seen two baboons, when first placed in the same compartment, sitting opposite to each other and thus alternately opening their mouth; and this action seems frequently to end in a real yawn” (Charles Darwin 1873).

Darwin probably may have used the words ‘as in the act of yawning’ because the baboons only perform the gaping mouth component of true yawning. Thus, Darwin distinguished between the ‘threat yawn’ and the ‘true yawn’, i.e. the physiological yawn’ (Seuntjens, 2005). It appears that the reason why Bartlett and Darwin considered the ‘threat yawn’ as threatening, is because they deduced that “both animals wish to show to each other that they are provided with a formidable set of teeth” (Darwin, 1873).One hundred years later, Milner-Brown made a similar observation:

“This [yawn] is no idle action but a form of communication. It is an invitation for every other baboon to look at those huge canine teeth – weapons of offence and defence that develop in males at puberty to much greater size than in females. A yawn is a threat gesture, and may precede a sudden attack in the ritual of establishing and maintaining dominance. The yawned-at baboon needs to respond at once, showing either a bigger yawn or a clear and customary signal of submission”. (Milner-Brown, et al., 1973).

Bolwig’s account on the behavioural repertoire of the chacma baboon (Papio ursinus) did not subscribe fully to the above view of the ‘threat yawn’ (Bolwig, 1959).

In contrast, Bolwig held this type of yawning behaviour to be a primary displacement activity expressing anxiety, comparable with human yawning out of nervousness. This type has been called the ‘tension yawn’. Another distinction can be made between the directed and the undirected yawn. In the directed yawn, the monkey’s gaze is directed towards the source of tension, whereas in the undirected yawn the monkey does not gaze but rather stares away. According to the British ethologist Kenneth R. L. Hall, this undirected yawn “would appear to be simply a tension or arousal indicator” (Hall, 1967). See examples in figure below.

Figure.1.2 Baboon yawning with eyes closed (left: Photo Roz Joseph) and with eyes open (right: Photo Der Siegel)

The baboon’s directed mouth-gaping or yawning was considered by Altmann (1967) to be a powerful threat. In contrast to earlier accounts, Altmann regarded the undirected yawns of little or no communicative significance.

In mandrills (Papio shinx) Baenninger (1987) found what he thought constituted two different types of yawning. In the first type, the animal raises its head and opens its mouth so widely that its teeth are exposed, particularly the large canines that are characteristic of males. This response lasts 4 to 5 seconds and is never seen in females. In the second type of yawn, the head is raised only slightly and the mouth does not open widely enough to expose the teeth, which remain covered by the lips. This second type of yawning lasts 1-2 seconds and is shown in both sexes (Baenninger, 1987).

The different types of yawning behaviour in baboons can be distinguished with relative ease, each of which may be comparable with yawns in the human behavioural repertoire. The interpretations of different yawns in macaques are comparable with the interpretations of yawns in baboons (Deputte, 1994). They all seem to have a communicative nature but with potential polarised ends of the scale with regard to what type of message is intended. There are (A) the ‘physiological yawns’ that are associated with periods of inactivity and with falling asleep and waking up, and (B) the ‘affective yawns’. Within the category of affective yawning is what may sometimes be called the “indistinctive tension yawn”. Redican, quoting earlier researchers, stated:

“Yawning often occurs in situations of mild stress in the rhesus (Macaca mulatta) and bonnet macaque. Pigtailed and bonnet macaques, especially males, are said to yawn when the group or individual is threatened but when the physical manifestation of dominance relationships is inhibited, such as when a human observer enters a group area” (Redican, 1975).

“The second type of affective yawning is sometimes called the ‘threat yawn’. This one is characterised by bared teeth, especially the canines, being directed towards an opponent” (Baulu, 1973).

Various lines of evidence have been proposed to link the frequency of yawning in adult males to dominance rank in sexually dysmorphic, polygynous species, as stated by Redican (1975) and Bertrand (1969). The various interpretations of different types of yawns in macaques and other primates are provided here because they are comparable with chimpanzees and, most importantly, humans. The highest order of primates, for example, the group of animals conformed by lemurs, tarsiers, monkeys, but also apes and humans and, even Old-World monkeys (Cercopithecoidea) are the closest to Homo sapiens from the rest of the animal kingdom, and thus, putative assumptions and theories about their yawning-related behaviours would apply relevantly to the human ones.

In all the primates, and therefore in all the Old-World monkeys and apes, yawning is present in their behavioural set. (See table 1 below).

Table 1 Old World monkeys and apes in which yawning is present in their behavioural set adapted from Deputte & Fontanelle (1980).

Type of Primate	Research Studies
BABOONS GENUS: PAPIO	Chacma baboon [Papio ursinus] (Bolwig 1959) [Papio cynocephalus Anubis] (Hall & DeVore 1965) Mandrill [Papio sphinx] (Benninger 1987) [Papio hamadryas] (MacDonald 1965: 150; Kummer 1968)
MACAQUES GENUS: MACACA	Rhesus monkey [Macaca mulatta] (Hinde 1962); (Baulu 1973) Cynomolgus monkey [Macaca fascicularis] (Deputte & Fontanelle 1980) Celebes macaque cynomolgus monkey [Macaca fascicularis] (Deputte & Fontanelle 1980) [Macaca radiata (Nolte 1955: 81) Celebes macaque [Macaca nigra] (Hadidian 1980) Macaca silenus (Bertrand 1969) Stump-tailed macaque [Macaca arctoidus] (Bertrand 1969) Olive baboon [Macaca anubis] (Packer 1979: 42) Tonkean macaque [Macaca Tonkeana] (Anderson and Wunderlich 1988) Pigtail monkey [Macaca nemestrina] (Louboungou & Anderson 1987) Macaca fuscata (Troisi et al., 1990)
GREAT APES PONGIDAE:	Chimpanzee (Schneider 1950; Goodall 1968; Nishida 1979) Gorilla (Schaller 1963) Orangutan (Rijksen 1978) Bonobo (Blount 1990; de Waal, 1997)

1.5 Social interaction and yawning

The stance of some authors such as Guggisberg et al. (2010) on the origin of spontaneous yawning as a social signal has been criticised by many, including Gallup (2010), stating that any social or communicative value of yawning among humans and non-human primates, is likely to be a derived feature, while the underlying primitive function, is physiological. These authors, and indeed the rest of this section, deal with the subject of spontaneous yawning, as opposed to its contagious aspect, which will be fully addressed later. Given the universality of the yawning behaviour being found across most vertebrates, and the frequency of its incidence in a number of various physiological conditions and social contexts, it is likely that, instead of serving one purpose, yawning is multifunctional across a number of species (Gallup, 2010).

One of the debates found in the literature relies on an evolutionary perspective. Even though some authors argue that the social/communication hypothesis is sufficient to explain selection for yawning among all vertebrate species (Guggisberg et al., 2010), some ignore the fact that the first jawed vertebrates were fishes, and therefore presumably they might have been the first to yawn (Baenninger, 1987). However, it is still unknown how social some of these animals are, or indeed whether there are any communicative aspects to their behaviours. Therefore, in some cases, no social role of yawning would neatly apply, at least not as simple as that described by the social/communication hypothesis. There is a possibility that part of the controversy is caused by the fact that the advocates of the communication hypothesis postulate their theory on the basis of the social aspect being the precise and only origin of yawning, and this contradicts their own assumption of yawning being multifunctional. One question that needs to be asked, though, is whether one of the functional roles of spontaneous yawning, is simply forming part of an information-processing mechanism. An attempt to answer this question will be presented in the chapters to follow.

It should be noted from the start, that most of the evidence provided here, is of the observational kind. A clear distinction should be made between (a) descriptions, (b) contexts of occurrence, and (c) valid speculations about the potential function within a communicative perspective. With regard to (a) and (b), there are no problems. However, speculations about the function, or multiple functions that seem to have been advocated, become problematic, partly because the theories are not only reliant on the communicational factor attributed to the behaviour per se. As mentioned above, there is evidence of an information processing system at work, when someone (animal or human) behaves in a manner that is in turn perceived, either seen or heard, by others, as in the case of a wide-open yawn. Therefore, there would be a system whereby information is transferred across, intended or not, which is communicated, whoever the sender or receiver. This “signal” is transferred, across species and, as the work presented in this thesis will show later, this “signal” is transferred across agents and through sensory modalities we were not aware of. What remains as unconvincing evidence to support the social communication hypotheses (Guggisberg et al., 2010) seems to be the attribution of the communicative aspect of yawning as being the solely social evolutionary purpose of the behaviour per se. There is a possibility that the behaviour became communicative, and perhaps this result is what occurred through evolutionary processes. Although most biologists and ethologists agree that nearly all vertebrates yawn, it remains undecided whether yawning is morphologically similar in primates, mammals, birds, reptiles and amphibians, let alone in fish and in humans.

One commonly known fact, used as supportive evidence towards a social and communicative aspect of yawning in humans, is the puzzling phenomenon of yawning being contagious (Provine 1986, 1989a, 1989b; Platek et al., 2003). In the next sections, the principal findings of those investigations will be presented in more detail.

1.6 Controversial issues related to yawning

1.6.1 The relation between emotion and empathy and yawning

The efficiency and communicative success of non-spoken forms of communication rely on many factors, beginning with the ability to perceive them, (intact sensory perception, i.e. vision) and a clear understanding of the significance of all possible gestures, facial actions and expressions. A large amount of studies on facial perception have focused, understandably, on exploring the intricate processes involved in emotion expression and emotion perception, starting from Darwin in the 1800s through to, amongst many others, Bradley et al., (1997) Whalen et al., (2001), de Gelder et al (2012) and more recently pioneering studies performed by Jiahui, Yang & Duchaine (2018). Even though the ability to accurately express emotions and to infer emotional states of others is crucial for social interaction, not all facial gestures involve emotions. With respect to yawning, the assumption here is that not all facial actions and gestures necessarily carry an emotional component. They can, nevertheless, be commonly relatable and instrumental to non-verbal communication.

In the first two studies of this thesis, the behaviours presented to the animals are behaviours that do not relate to any emotion and actions which the animals perform themselves, i.e. yawning, whether it is presented live by a human (experiment 1) or whether it is presented by an inanimate agent (experiment 2). In the case of experiment 3, the participants have intact vision and are therefore able to perceive the behaviour presented in video format, and have had experience of performing the action themselves, i.e. yawning. Again, the experimental conditions remain constant and there is no emotion expressed. In the case of blind individuals (experiment 4), the participants are able to perceive the action through tactile modality. Human blind individuals develop the capacity to interpret other people's facial expressions through auditory perception and via other means, such as interpreting instances of silence, intonation and relying on their previous experience. In the case of yawning, this is a behaviour they perform themselves, therefore they have experience of how it feels to yawn. The contagion process is explored here through tactile perception for the first time, and as a non-emotional facial expression. Observational research on animal behaviour does not provide sufficient evidence of all the possible processes that might underlie the particular behaviour being explored. No specific cognitive or particular mental processes, are assumed, either on the part of the animals, or on the part of the humans in this thesis. When exploring animal behaviour, it is sometimes difficult not to approach the subject from an all-or-none point of view but an attempt has been made here. Sometimes it is also not possible to work within the common notion of cognition in general without taking into consideration evolutionary or simply individual differences in cognitive processes across the species. In the recent past, "researchers approached the study of cognition tentatively, with the ghost of Behaviourism looming large" (Vonk, 2016). The observational evidence in the animal studies presented here are demonstrated by the behaviour displayed which denotes a response to their exposure to the stimuli. It is possible to interpret the results of animal behaviour exploration studies by interpreting the data within the "associative learning" model without considering that the formation and generalization of associations between stimuli or between behaviours and their respective resulting responses would occur in a complete absence of cognition.

Therefore, the intention here is that of reporting the behaviours displayed without going deeper into the possible cognitive processes that may be underlying such behaviour.

Behavioural and physiological evidence from humans is not taken as suggestive of any particular cognitive process here, either. Leaving the potential emotional factors aside, one can state more neutrally, that by investigating the behaviours animals display immediately after being exposed to specific actions of others, (importantly, actions the perceiving animal performs too), one can take their responses as potential evidence of an association between what is being perceived with an event that had already been experienced by the animal or human before. In this thesis, this re-enacting of the behaviours of others, which do not necessarily involve emotion, will be referred to here as ‘experiential contagion’.

1.6.2 A brief introduction to the concept of Empathy

Another controversial issue in the perception of yawning concerns the potential role of empathy. The most common understanding of the definition of empathy is the sharing of experiences, which are implicated in the many aspects of social cognition and regulation of emotions. These may also include aggressive, moral and prosocial behaviours, while empathy-related responses include caring and sympathetic concern. According to Eisenberg et al. (2009), empathy-related responses can even pave the way to moral reasoning.

While some authors state that the capacity for two individuals to resonate with each other affectively (i.e. feel in common with each other, internally feel or experience the same affective state than the other), prior to any cognitive understanding, is the basis for developing shared emotional meaning, they also point out that this is not enough for mature, empathic understanding (Decety et al., 2010). Such understanding requires the formation of an explicit representation of the feelings of another person as an intentional agent, which necessitates additional computational mechanisms beyond the affect sharing level (Decety et al., 2008). Most scholars agree that empathy includes both cognitive and affective components (Decety and Jackson, 2004; Eisenberg and Eggum, 2009) that have different developmental trajectories. Based on various approaches, combined with empirical evidence from affective neuroscience and developmental psychology, a model was proposed that included bottom-up processing of affective sharing and top-down processing in which the perceiver's motivation, intentions and attitudes influence the extent of an empathic experience, and the likelihood of prosocial behaviour (Decety, 2005; Decety & Meyer, 2008). In their proposal, a number of distinct and interacting neurocognitive components may contribute to the experience of empathy: (1) affective arousal, which is considered a bottom-up process in which the amygdala, hypothalamus and orbitofrontal cortex (OFC) underlie a series of rapid and prioritised processing of emotional signals; (2) emotion comprehension and, which depends on both self-awareness and other-awareness, including the medial prefrontal cortex (mPFC), ventromedial (vmPFC) and temporoparietal junction (TPJ). It also encompasses (3) the regulation of emotion, which in turn relies on executive functions initiated in the intrinsic corticocortical connections of the OFC, mPFC and dorsolateral (dl) PFC, and in networks connected to subcortical limbic structures involved in processing information with an emotional component attached to it. “These networks operate as top-down mediators, which are crucial in regulating emotions and thereby enhance flexible and appropriate responses” (Decety, 2010). Practically all the models that describe empathic mechanisms make strong references to emotion as one of the most important bases of the processes involved (Norscia, 2011; O’Hara, 2011; Demuru, 2012; Palagi, 2009). However, evidence to support the argument that emotion is involved in these processes is debatable and therefore, the involvement empathy may have in these issues is an open question and will be addressed here.

There is, though, “ample behavioural evidence demonstrating that the affective component of empathy is developed earlier than the cognitive components” (Decety, 2010). Prior. Before to the onset of language, the primary method by which children can communicate is by reading faces (Leppanen and Nelson, 2009). Regarding the affective component of a response, it is already known that this is involuntary. However, authors regard aspects of the affective components to be reliant on mimicry and somatosensory resonance between other and self (Decety, 2010). Plenty of studies have already looked at and confirmed both positive and negative emotion-related scenarios (Leppanen and Nelson, 2009; Decety, 2010). For instance, new-borns and infants become vigorously distressed shortly after another infant begins to cry (Dondi et al., 1999). Discrete facial expressions of emotion have been identified in new-borns, including joy, interest, disgust and distress (Izard, 1982), suggesting that subcomponents of emotional experience and expression are present at birth. However, these potential subcomponents have not been explored extensively enough. Since the theories presented here are not investigated from a developmental perspective, one can argue that because the stimuli employed have been experienced by all the subjects involved, and that all participants (humans or animals) are adults, both interpretations are left open, namely that these processes are either hard-wired in the brain or could have been learned through development. Haviland and colleagues stated that human new-borns are capable of imitating expressions of fear, sadness, and surprise by 10 weeks of age (Haviland & Lewica, 1987), preparing the individual for later empathic connections through affective interaction with others. Many go as far as claiming to have found in children a lack of remorse or guilt, both of which, in relation to the present study in adulthood, are regarded as risk factors in developing hostile, aggressive or violent behaviour (de Wied et al., 2006).

The general consensus seems to be that empathy is the ability to identify other people’s thoughts, intentions, desires and feelings. Most authors also seem to agree with the idea that empathy involves the ability to respond to the mental states of others in an appropriate manner and with the right emotion (Warrier et al., 2004). However, major differences in several factions of empathy have been documented in various psychiatric and developmental conditions, including autism (Baron Cohen et al., 2004), bipolar disorder (Derntl et al., 2012), and major depressive disorder (Bora et al., 2008). Some authors claim that children suffering from certain developmental disorders are considered to possess limited empathic capacities and diminished concern for the wellbeing or feelings of others (Decety, 2010).

The two major components of empathy described above are factions comprising affective empathy, which relates to the actual drive to respond to others’ mental states with the appropriate level of emotion, as well as factions relating to cognitive empathy, which is the ability to recognise another’s mental state or feeling. Although psychiatric conditions, such as schizophrenia, are regarded within the group of diminished empathic responses, there are also specific individual differences within this psychiatric disorder group, which relate to their likelihood to report higher personal distress and emotional contagion (Lehmann et al., 2014). Conversely, individuals within the autistic spectrum are more likely to display difficulties with their cognitive, but not the affective empathy capacity (Baron Cohen et al., 2004; Baron Cohen, 2009). These differences within groups are important aspects of empathic behavioural responses and guide us towards finding alternative, multifaceted theories on how the empathic process works, not to mention the multifactorial structure of empathy (Davis, 1980; Decety & Jackson, 2004).

A multifactorial structure refers to stages constituting the end behaviour, considering the potential individual contribution towards the end result. Some argue that empathy relies upon, but is also distinct from, the ability to identify the emotional state of the target (Happé, Cook, & Bird 2017). Authors suggest that this important distinction between empathy and emotion identification abilities are constructs of which the failure to attend to, and consequently take into consideration, could result in an interference with the correct interpretation and measurement of differences in empathic responses. These are generally associated with experimental manipulations or clinical conditions (Coll, Michel-Pierre et al., 2017), but are also relevant for the general population. Many suggest that the definition of empathy should be refined. If this is the case, there would be a possibility that the new definition would include a clear delineation of exactly at which level these individual stages are particularly affected. This new interpretation would probably entail devising a quantitative measurement of empathy. Speculating further, considering different levels, measuring sizes, or extent of empathic responses, may have potentially diverse consequences. Acknowledging these levels and stages of specific aspects of the perceived behaviour may serve to illuminate the exact component of the structural character of another's multifactorial behaviour, which is bound to have an impact on the empathic response itself, or lack thereof.

Summarising, empathy has been measured in relation to types of responses to facial expressions, which is still one of the most powerful ways to communicate emotions (Frith, 2009). Central to the recognition of facially expressed emotions is the attention to the eyes (Batty & Taylor, 2003). Even though the studies presented here do not give rise to a major influence of emotion, there will be explorations of the impact that eye gaze and fixation patterns may have, when looking at another individual’s face, while also investigating whether this constitutes an empathic response.

Thereby, the generally assumed potential affective and cognitive components of empathy-related behaviours will not be ignored here. Rather, the emphasis in the present work is on finding other potential components that may be associated with yawning behaviour, such as contagion. In doing so, this presents an opportunity to question the generally indiscriminate use of the terms mimicry, imitation and contagion.

1.6.3 Contagion

Contagion, in its most general sense, is the spreading of an entity or influence between individuals in a population via direct or indirect contact (Dodds et al., 2017). Contagion processes, therefore, arise broadly in the social and biological sciences, manifested by, for example, the spread of infectious diseases and computer viruses, the diffusion of innovations (Rogers, 1995), political upheavals (Lohmann, 1998), and the spreading of religious dogma (Stark, 1996). Current mathematical models of contagion, fall into one of only two broad categories, where the critical distinction between them can be explained in terms of the dependence on consecutive contact with the agent; that is to say, the level to which the resulting outcome of the exposure to a contagious agent is regulated by the existence or absence of an earlier exposures.

There are standard assumptions about the types of contagion that have been explored so far, and, in general, they form part of mathematical models of infectious disease-spreading, for example, the classic SIR of model Murray (2002) and Kermack et al. (1927), and in some models of social contagion (Goffman, et al., 1964). One problem with these models is that there is no interdependency between contacts; rather, the infection probability is assumed to be independent and identical across successive contacts. All such models, therefore, fall into a category that authors call independent interaction models. By contrast, what are called “threshold models” claim that an agent would only be infected if a particular amount of exposures was exceeded. At that instance infection would be most likely.

Social contagion is generally described by these threshold models (e.g. the spreading of false information or what would nowadays be called ‘fake news’). When the individual approaches the thresholds, it is normally due to the strong nature of the effect, whereas other interdependencies are thought to have no repercussion that would ordinarily be the cause for contagion. As Schelling, et al., (1973) describes, where individuals either deterministically or stochastically (Bikhchandani et al., 1992) “decide” whether or not to adopt a certain behaviour based either partially, or completely, on the preceded choices of others. Based on such models, one can describe contagious yawning by developing a new model that covers the physiological and pre-motoric consequences of the perception of a potentially infectious behaviour, in a live scenario, without references to diseases or even behavioural, economic consequences. Instead, an alternative way to think about the interdependence of single or successive events is necessary. This may or may not need to be explored in terms of memory capacity or memory dependence: independent interaction models assume (although implicitly) the presence of memory and so do (also implicitly) the threshold models. However, another implicit assumption by the independent interaction models, is that they regard the infection process that is not reliant on memory.

The effect of memory in the immune system is regarded inherent in responses such as an allergic reaction. Hence, as is going to be shown here, just a minimal parting from a full independence is necessary to modify the collective dynamics. It is therefore hoped that this model may also shed light on the spread of actual infectious diseases, or indeed other types of contagious behaviours, such as laughter or crying. The new models may explain complex disorders characterised by repetitive, sudden, constant, typically involuntary movements or motoric activations, such as tics and other sudden movements or sound productions. Not only can these not be controlled, but they are also highly prominent in the symptomatology described for Tourette’s Syndrome, Williams syndrome and other developmental disorders, such as autism. Furthermore, they are also, many of these repetitive behaviours or movements are puzzlingly present in congenitally blind children and adults. Neither of these models, however, explains the subtleties of contagious processes in the way that they are going to be explored here.

The contagious processes of concern in this work would fall within psychological, physiological and, ultimately, social contexts with regards to the communicative nature of the behaviour, which seem to possess an intermediate level of interdependency. Furthermore, no variable has been explored in this manner before, but the behaviour may still exert an impact on others, which could, for example, be traced back to the models that establish a possible basis on memory and a recollection of behaviours of others or self, which would have obviously been experienced previously. Moreover, the relationship between threshold models, interdependent interaction models, and any likely intermediate approach is still not clear, and therefore deserves further investigation.

In summary, although there has been a wide range of research undertaken in the area of, for example, imitation, much of the limited knowledge we possess about contagion remains contentious and debatable. The principles behind contagion, such as conceivable origins of the action, clues for evolutionary pathways and the human and animal consequences of the type of behavioural contagion explored here, are, as mentioned before, still a source of debate (Platek, 2010; Gallup, 2008; Gallup, 2009). Furthermore, the different sensory modalities through which contagion can occur have not been fully explored. This will be addressed here. Importantly, there is a need to establish to what extent these potential principles behind contagion may influence physical, psychological, physiological, behavioural and cognitive events in the self and others. Future explorations may very well lead us to pursue a different route to explain this particular phenomenon of contagion. If this was the case, and consequently, an extended definition of contagion becomes necessary in order to fit the particular case of behaviours such as yawning, then so be it. As it stands, there is no clear theoretical difference between concepts such as imitation, copying, emulation, or mimicking and the differential characteristics or parameters by which they would be considered applicable, or not, to yawning.

1.6.4 Contagion versus mimicry and imitation

An extensive body of research shows that most humans have a strong tendency to respond with a congruent facial expression when observing an emotional face (Dimberg, 1982; Dimberg and Thunberg, 1998). It is well established that most research investigating responses to emotional expressions regards this social interaction, based on facial gestures, as reliant on modulations of components of facial mimicry. Alternatively, models of social contagion are thought to fall into separate classes of behavioural responses (Hodas & Lerman, 2014; Dodds & Watts, 2004). There is a growing body of evidence suggesting that contagion is dependent upon different variables from that of mimicking or imitation (Yoon & Tennie, 2010). These include the level of exposure, a novel experience or one experienced before, and single or successive exposures, depending on the contagious entity. Some contagion models assume that the contagious entity determines the types of contagion, whether simple or complex (Weng et al., 2013; Kramer et al., 2014). There has been a limited amount of quantitative analysis of the components that establish these differences, between what is considered simple or complex. A systematic understanding of how we should decompose the constructs that contribute to models of contagion is necessary and it seems that this would have to include the possible impact empathy has on the contagious process. Many types of imitation appear to be understood as social mirroring, in particular, those instances in which the purpose seems to be some type of empathy or mutual identification. Monkeys recognise if they are being imitated, but they are incapable of learning by imitation. Indeed, imitation could be understood as two separate dimensions: a social mirroring one, which would be in those instances when actions have a clear social benefit, and they are equated in their entirety; and another dimension by which learning relies on copying. As Byrne states, this is "when new behavioural routines are acquired by observation" (Byrne, 2005). The terms mimicking, imitation and copying seem to be occasionally used indistinctively in the literature. However, the definitions of these terms, their significance and, consequently, their use, vary without a clear distinction or reference to the abundant theoretical approaches to models of imitation. Furthermore, models on contagious behaviours are not in such abundance in social, cognitive or neuropsychological fields.

Imitation mechanisms and social matching play a central role in developmental stages, communicative and social interactions, acquisition of knowledge and culture. The exploration of these mechanisms in different agents (animals, humans, and robots) has already influenced the way we understand the nature and the roots of both social human and artificial intelligence. Although such matters have traditionally been explored in subjects such as biology, psychology, palaeontology and ethology, it is clear that a 'constructive approach' towards copying or imitation and social learning, using artificial agents, can offer vital understandings into the systems involved. Thus, this can create agents that are instructed and taught by imitation, simple demonstration, and complex social interactions, as well as by explicit programming and algorithmic operations. There is however, a common conception about the differences between imitative and contagious behaviour. Although a formulation of a model is certainly needed, and a complete reformulation is beyond the scope of this work, findings reported here may well serve as a basis to develop an appropriate new model. The studies in this thesis attempt to shed some light on the behavioural consequences of contagion, while beginning to draw some possible paths to follow, in the route to develop plausible approaches and clear models that address the seemingly overlooked differences between these behaviours.

1.6.5 Contagious yawning

The contagious aspect of a yawn is a curious behavioural phenomenon, one which has been observed in several primate species, including humans (Provine 1986; Baenninger 1997; Campbell et al., 2009; Palagi et al., 2009). The spreading of the behaviour from one individual to another, regardless of species, could guide us towards a better understanding of social cognition in general, not just in the animal kingdom. Contagion has been described as the short-term spread of a behaviour (Thorpe, 1963), by which a stimulus serves as a releaser to the unlearned behaviour of others (Zentall, 2001). According to several neurobiological (Cooper et al., 2012; Haker et al., 2013), psychological (Lehmann, 1979; Platek et al., 2003) and ethological (Campbell & de Waal, 2011; Campbell & de Waal, 2014; Romero, Konno & Hasegawa, 2013) findings, yawn contagion is regarded as an empathy-related phenomenon. Furthermore, some authors specifically consider yawn contagion to be a form of emotional contagion as observed by the “Russian Doll Model” in de Waal (2008), Preston and de Waal (2002), and Hatfield, Rapson and Lee (2009), even though there is no evidence of yawning carrying any emotional component.

A study whereby human participants were shown a video stimulus of yawning faces found that 50% were affected by yawn contagion (Provine, 1986), with some regarding these occurrences to be based on a perception-action mechanism (Preston & de Waal, 2002; de Waal 2012c), which consists of the involuntary re-enactment of an observed facial expression, creating shared representations (Palaggi et al., 2014). Unfortunately, this description, by referring to a re-enactment as the result of an observation, which by definition would have to be through visual perception, fails to include other perceptual modalities, such as an auditory contagion demonstrated in several species (Massen, et al et al., 2015). Furthermore, contagious yawning (CY) is elicited simply by sensing or thinking about the action (Provine, 2005).

The views presented so far are shared by many authors, whose studies investigated the developmental onset of contagious yawning in children (Anderson & Meno, 2003; Millen & Anderson, 2010; Hoogenhout et al., 2013), since CY is thought by many to develop in parallel with empathy-related capacities (e.g., Perner & Lang, 1999). Initially, Senju et al. (2007), Giganti and Ziello (2009) and Helt et al. (2010) reported the absence of contagious yawning in children with autism spectrum disorder. At the time the authors claimed that their findings supported the supposed connection between yawn contagion and empathy. However, a subsequent study by Senju's group reported the contradictory results of autistic individuals yawning contagiously as much as a normally-developed individual, as long as they were instructed to look at the eyes of the yawner. The authors argued that their previous results may have been a consequence of the reduced tendency of autistic individuals to spontaneously attend to others' faces (Senju et al., 2009; Usui et al., 2013). Contradictory results raise several questions, for example, whether eye contact is such an indispensable part of the stimulus to be contagious? If so, is this the case for anyone, and any species, susceptible to yawn contagion in the first place? How indispensable is the assumed empathy-reliant mechanism in a potentially contagious scenario that involves a non-emotional action?

Contagious yawning (CY) has been found in several group-living species, which suggests it plays a role in social interactions. Unequivocal indication of CY has been shown in humans (Provine 1986; Anderson & Meno 2003; Platek et al., 2003, 2005; Arnott et al., 2009; Giganti & Ziello 2009; Helt et al., 2010). In the first study to explore contagious yawning across species, Joly-Mascheroni et al. (2008) found that domestic dogs (Canis lupus familiaris) catch yawns when observing a human yawning. Later, similar results were found with puppies (Madsen & Persson, 2013; Silva et al., 2012; Romero et al., 2013), and with budgerigars - Melopsittacus undulates (Miller et al., 2011). Further indications of CY have been found in chimpanzees - Pan troglodytes (Anderson et al., 2004; Campbell et al., 2009; Campbell & de Waal 2011; Massen et al., 2012; Madsen et al., 2013), bonobos - Pan paniscus (Demuru et al., 2012), and gelada baboons - Theropithecus gelada (Palagi et al., 2009). By contrast, the only solitary species tested for CY, the tortoise, Geochelone carbonaria, has shown no evidence of yawn contagion (Wilkinson et al., 2011). This may suggest, although indirectly, that, instead of incrementing arousal, “yawning may be a form of communication that evolved to synchronize group behaviour” (Daquin et al., 2001).

So far, social modulation of yawn contagion has only been demonstrated in adult individuals. Neither young dogs (Madsen & Persson 2013), nor juvenile chimpanzees (Madsen et al., 2013) have shown a familiarity-bias on heterospecific CY. This has led to the suggestion that the effect only emerges at later stages of development (Madsen & Persson, 2013), which is supported by evidence of familiarity-biased heterospecific yawn contagion in adult dogs (Silva et al., 2012; Romero et al., 2013). Nonetheless, young chimpanzees have only been explicitly tested when viewing the yawns of humans in a (live) social context, while adult chimpanzees have been tested with respect to conspecific yawn contagion (Campbell & de Waal 2011; Massen et al., 2012) and, more recently, heterospecific yawn contagion (Campbell & de Waal, 2013), using videotaped yawn stimuli. The difference in results pertaining to chimpanzees may thus not owe exclusively to developmental issues, but to the nature of the stimulus: whether the yawns derived from humans or conspecifics, and whether they were presented in a live social context or on video.

1.7 Facial expressions in Humans and Primates

Humans appreciate objects, artefacts and material things, however small or large. We produce objects through industrial and artistic means, appreciate these on their general aesthetic nature and may even worship them on religious grounds. Humans’ emotional and practical involvement with things or objects are tangible and, generally, somehow explicable. This adoration for objects is not an example of irrationality in humans. Instead, it points to a deep-rooted human relationality with things and objects (Bowlby, 1969, 1973; Robb, 2010). Human characteristics, such as aesthetic appreciation, category distinction, or quality appreciation, are indeed considered to be typically and exclusively human. However, as will be shown in the studies here, some of these category distinctions may not be exclusively human. It will be shown that in regards to others' faces (and in one study, objects with characteristically human faces), facial actions, behaviours or gestures, this recognition may not be an essential part of an exclusively human nature and adaptation capacity. Instead, some of these capacities might have been present in our evolutionary ancestors too.

Many researchers have posited the existence of multiple recognition systems, each of which support the recognition of one or more visual categories (Tarr et al., 2003). The most popular distinction has been that there are separate systems for faces and non-face objects (Farah, 1992). This dichotomy is based on intuitions, such as the inherent social significance of faces and the difficulty of discriminating individual faces, as well as the following evidence: (1) A visual preference for face-like stimuli in neonates (Goren et al., 1975; Johnson et al.,1991), (2) Face-specific effects in behavioural measures of visual processing (Yin et al.,1969; Tanaka et al., 1993), (3) Face-selective neurons (Perrett et al., 1992; Duchaine et al., 2010), brain areas and neural signals (McCarthy et al., 1997), (4) Dissociations between face and object recognition in brain-injured patients (Farah et al., 1995; Moscovitch et al., 1997).

Although these arguments make a seemingly convincing case for there being separate systems for faces and objects, they are based on the questionable assumption that there are characteristics and modes of processing that are exclusive to faces and face recognition. Alternatively, these properties may be ones that faces happen to have, but they could also be true for other object categories, including some (such as in the case of two of the studies here) that are non-biological objects. This is especially the case if these non-biological objects represent biological faces. Thus, if the characteristic underlying neurological and behavioural mechanisms involved are not necessarily face- specific or even biologically specific, it is possible that either a single or several systems in humans, and again, a single or several, albeit rudimentary, but still similar systems, may be present in animals. These systems might support recognition of facial motion and gestures, and facial characteristic motion of objects. Indeed, when factors other than the visual category are considered, such as the specificity of the recognition judgment and the degree of expertise with that category, faces and objects elicit similar patterns of neural and physiological responses in humans. In the case of the studies presented here, this includes behavioural responses in animals.

Empirical evidence has been provided by Hadjikhani et al., (2009) showing that human beings are neurologically ‘wired’ (in the fusiform gyrus) making them particularly alert to faces and facial expressions. The authors state that this could explain why we tend to ‘see’ ‘faces’ in all sorts of objects and arbitrary stimulus complexes (Hadjikhani et al., 2009). Similarly, inanimate objects may sometimes appear as animate ones, in the sense that they may seem to act independently. This is possibly due to the fact that we are psychologically and neurologically compelled to be alert to motion, to interpret movements as ‘willed’, and to attribute agency and intentionality to whatever has the capacity to move, especially so, if that agent has features that bear resemblance to a face. This propensity made our ancestors alert to the presence of predators and other humans (Tinbergen, 1951; Atran & Norenzayan, 2004). Visual recognition of non-biological objects is an immensely difficult problem, which biological systems solve effortlessly. In the studies here, the references are those of objects and faces. Ample evidence indicates that the task demands and learning arising from different forms of feedback determine which computational routines are recruited automatically in both object and face, feature and motion recognition. One classification for object recognition is reliant on the fact that objects can often be placed into distinct categories, based on their visual appearance (Tarr & Cheng, 2003). Therefore, the objects used in these studies are of biological appearance, but are non-biological in nature. The intention of doing this is based on the certainty that both humans and animals would have no problem in recognising, in the stimulus, the distinction between a human looking object and an object representing a facial gesture motion.

The most influential sources of inspiration for contemporary studies on human recognition of faces, its different forms or expressions, and their respective meanings

(Basic Emotion Theory (BET), see Ekman, 1982; Ekman & Oster, 1979) assume that “recognition” means detecting a message with adaptive value for senders (and potentially for receivers). Thus, for BET, the sender’s expression launches some sort of essential and immediate connection between the sender’s and the receiver’s emotional experience. In the same vein, Ekman pointed out that:

> *“The initial translation of an expression into some meaning […] is likely to be so immediate that we are not aware of the process we go through […] I think we use emotion words—anger, fear, disgust, sadness, etc.—as a shorthand, an abbreviated way to refer to the various events and processes which comprise the phenomenon of emotion”* (Ekman, 1997).

In contrast to contemporary research, which focusses on emotional aspects, this work explores facial expressions that do not necessarily involve an emotion, or at least that the emotion-related message sent or received is not intended as such. In order to clarify the different emotional and non-emotional potential intentions reflected in someone’s facial expression, it will be helpful to start by looking at the similarities and differences in the face morphology of humans and chimpanzees.

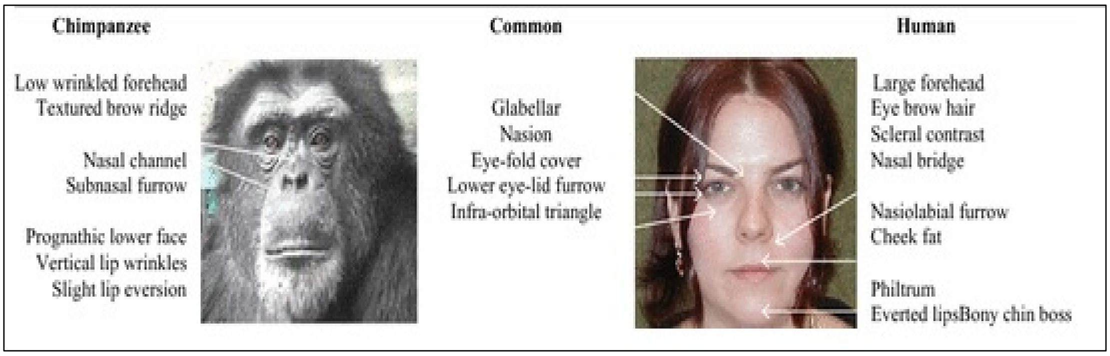


Figure 1.3 Similarities & Differences in Facial morphology between Humans & Chimpanzees Adapted from *Vick, S. J., Waller, B. M., Parr, L. A., Pasqualini, M. C. S., & Bard, K. A. (2007). A cross-species comparison of facial morphology and movement in humans and chimpanzees using the facial action coding system (FACS). Journal of Nonverbal Behavior, 31(1), 1-20.*

Facial recognition studies are based on two slightly different but complementary hypotheses (but see Fernández-Dols, 2013 for alternative arguments). On the one hand, most facial recognition studies are aimed at showing that some facial expressions are, for evolutionary reasons, universal adaptations shared with other primates going back at least six million years. On the other hand, facial recognition studies also assume that these primitive facial expressions have specific meanings (i.e. a precise correspondence with some concepts of emotion and the words that refer to these concepts).

It seems plausible to question some of these assumptions (i.e. facial recognition has preverbal and evolutionary roots allowing us to apply specific verbal referents to expressions), as we would be falling into a theoretical hindsight bias and not acknowledging that there are many facial actions, gestures and behaviours initiating in the facial motor act that are not well understood. By continuing to accept previous conceptions, we would be assuming that, six million years ago, hominids with preverbal brains were already capable of segmenting their facial behaviour into a precise set of fixed facial expressions (Fernandez-Dols, 2013) and they may very well have been able to do so, anticipating—several million years later—Homo sapiens' categories of emotion, such as contempt (Ekman & Friesen 1988; Izard and Hayes 1988) or shame (Tracy & Matsumoto 2008). Even though Darwin's lists were strikingly heterogeneous, given the supposed basic approach of such repertoires, the general assumptions about the significance of some facial gestures were far from simple. They included expressions of hunger, determination, love, devotion (Darwin 1872/1965), remorse, revenge, and madness (Bell 1924). As an example of Darwin's Zeitgeist, physician and anthropologist Paolo Mantegazza (1883) was determined to find the facial expressions that were indices of benevolence, religious feelings, or vanity. Current research has, it seems, adopted approaches that are reliant on deduction and speculation, to provide sets of facial expressions of emotion, also adopted such a deductive and speculative approach, although there isemotions often an unexplained variabilityresulting in a wide variation of their lists (See Ortony & Turner 1990). Tomkins and McCarter's (1964) pioneering study on the recognition of emotion through facial expressions included eight primary affects (interest, enjoyment, surprise, distress, fear, shame, contempt, and anger) with two different levels of intensity. In Tomkins and McCarter's set, sadness was not even mentioned, while disgust was referred to as "intense contempt". The first validation of the Facial Affect Scoring Technique (FAST, Ekman et al., 1971), an observational method for describing facial behaviour, included only six categories (happiness, sadness, surprise, anger, disgust, and fear), all of which were related to emotions. Although Ekman's technique has proven extremely useful for many years, it is probably time to move on and include other methods of exploring facial expressions. Firstly, it is important to distinguish some differences in the apparent emotional feeling of some animals and those expressions to which we would attribute these feelings in humans. As one example, (see figure 1.4 below) where the human face expression of laughter appears to be strikingly similar to that of the chimpanzee counterpart, when the actual emotion the chimpanzee is expressing is one of screaming terror.

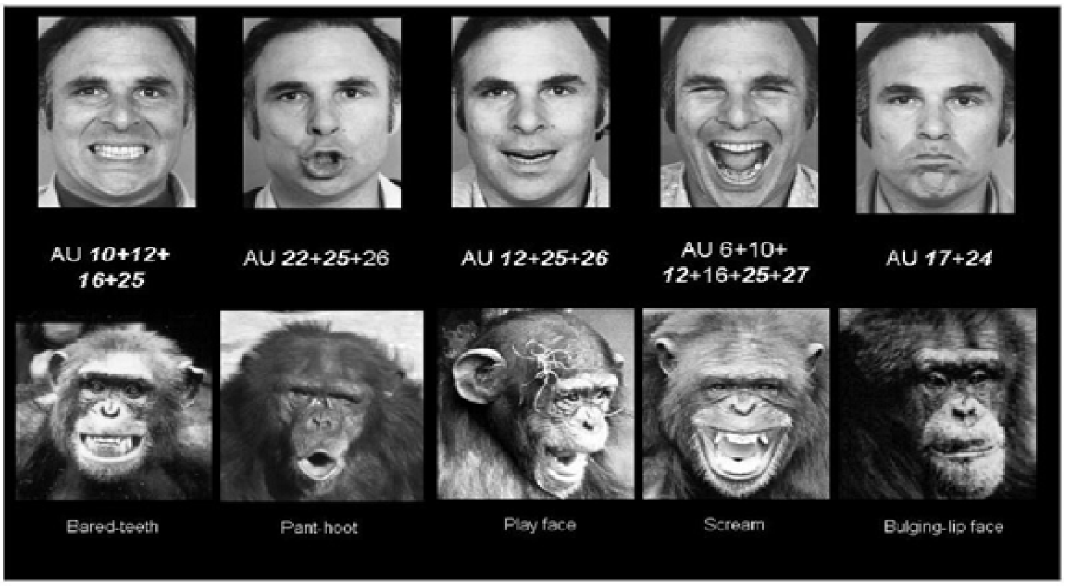


Figure 1.4 Prototypical chimpanzee facial expressions and homologous facial movements in a human (Ekman et al., 2002).

Secondly, the continuity in the choice of a restricted set of exaggerated expressions, such as in the Ekman faces, or those from Le Brun through Darwin to Tomkins, raises the question of whether this research tradition captures something other than emotional behaviour, which would allow us to disentangle other puzzles related to facial expressions and the potential underlying human and animal behaviour.

1.7.1 Social dynamics and familiarity

There are innumerable types of social interactions between primates, and this is certainly the case in chimpanzees. It is worth noting from the start that some ethologists' references for within-species social behaviours are beyond the scope of this thesis. This is partly because the interactions referred to here are not only across species, but also across agents, given that the stimulus behaviour performed in the first study was by humans, (familiar and unfamiliar) and in the second by an android (unfamiliar agent). However, there will be some reference that touches upon two of the main social communicative behaviours: Affiliative => A=B of equalitarian and positive connotations of social interactions, and Agonistic => A≠B where the scenario includes a dominant and a subordinate socially interactive partner. Furthermore, the reason behind the selection of these two social communicative behaviours was to make sure there were no signs at all on the part of the humans or artificial agent interacting with the animals, of reinforcing either of these two types of interactions. Some of the many potential interaction behaviours in such highly social and hierarchal animals include grooming, socio-sexual, socio-inspection and socio-enrichment behaviours. None of these apply within the context of this work. Therefore, the emphasis within this thesis will be on non-reflexive, but essentially automatic communicative behaviours, either perceived or performed by the animal. These will be behaviours resulting from their observation of others (humans and objects).

Current cross-species research seems to show that humans and non-human animals are more likely to catch yawns from those with whom they are familiar or already socially bonded. This would mean they contagiously catch yawns at a higher rate from those they like or would affiliate with, and, according to previous research, this is the case in humans (Norscia & Palagi 2011), chimpanzees (Campbell & de Waal 2011), bonobos (Demuru et al., 2012), gelada baboons (Palagi et al., 2009) and dogs (Silva et al., 2012; Romero et al., 2013). However, there are methodological issues pertaining to the study regarding social bonding and CY in chimpanzees (see Madsen et al., 2013). This means that ascertaining whether CY in chimpanzees is influenced by relationship quality, or only by a less fine-grained in-group bias, out-group bias, and even other species or agents, would benefit from further research. Chimpanzees yawn contagiously in response to videos of yawning in-group, but not out-group members (Campbell & de Waal 2011), although the degree of social bonding (as measured by grooming and proximity patterns) with in-group members does not appear to affect susceptibility to yawn contagion (Massen et al., 2012).

Another reason for the possible absence of yawn contagion in some findings can be inferred from the fact that chimpanzees are well known for displaying antagonistic behaviours towards unknown groups, denoting a strong sense of ‘us versus them’. This is possibly because chimpanzees are also extremely territorial, when two groups meet in the wild it would very rarely be a friendly encounter (Nishida et al., 1985; Wilson & Wrangham, 2003). Such aggressive responses towards an unfamiliar individual may, first of all, inhibit potential empathic reactions (as has also been reported in humans: Singer et al., 2006), thereby reducing potential imitative behaviours and, in turn, yawn contagion. This is demonstrated by a lack of contagion in response to videos of unfamiliar chimpanzees yawning (Campbell & de Waal, 2011).

By contrast, chimpanzee interactions with unfamiliar humans are typically not automatically aggressive or competitive, and, in line with this, heterospecific yawns do not elicit a familiarity effect on juvenile chimpanzee yawn contagion (Madsen et al., 2013). Similarly, Campbell & de Waal provided evidence that showing adult chimpanzees videos of humans yawning elicits a contagious yawn response of equal magnitude to that of videos of yawning in-group conspecifics (Campbell & de Waal 2011), which were obviously familiar individuals.

Overall, findings seem to suggest that, while chimpanzees may target their empathic reactions in interactions with conspecifics (and consequently, randomly catch yawns from familiar conspecifics), when observing videos of humans, they seem to apply what might be regarded as a more generalised, undefined type of empathic behaviour, if indeed it can be categorised as empathy at all. While chimpanzees, either in captivity or in the wild, would rarely interact or engage in competition with humans, there are no studies that have explored this type of cross-species, live chimp-human interaction.

1.7.2 The social/communicative hypotheses of yawning

In contrast to evidence from human studies, non-human primate yawns are often classified according to the context in which they are detected, and these vary greatly. Darwin (1872) viewed Old World monkeys yawning as a form of ritualised display. He described it as an expression of passion and anger at the same time, both in baboons and other Old-World monkeys. This view still exemplified that yawning was regarded as a form of communication. Guggisberg et al. (2010) attempted to explain the social function of contagious yawning by proposing yawning as a communication signal that spread to other people for survival purposes (i.e., the social or communication hypothesis of yawning).

Before we delve into the different positions about the communicative nature of the behaviour, it is worth noting that the summary of the views provided in this section of the chapter will be of two kinds: (1) observational, of experts such as ethologists, biologists etc. and (2) experimental, for which research has been rather limited, and has employed many different paradigms and settings.

Some non-verbal behaviours displayed by humans and animals constitute a large part of key social interactions and communication processes. Our closest relatives in the animal world, Pan Troglodytes (chimpanzees), which we know are highly social, also display communicative behaviours through audible vocalisations, visual body postures and facial expressions and tactile interactions such as grooming. From an evolutionary perspective, it is important to explore whether our current communicative behaviours were employed by our ancestors, as some of these could have been the precursors of language. Broadly speaking, social interactions are exchanges of visual and auditory signals. Some of these signals, such as spoken words or tone of voice in the case of humans, and vocalisation and facial gestures in chimpanzees, often represent different types of information exchanges. Exploring the automaticity with which we perform some of these communicative actions, and how often we humans and animals display behaviours without awareness or intention, is a potential route to learning more about the important role this non-verbal behaviour had in human evolution. Actions perceived in a communicative social interaction are sometimes unintentionally repeated and performed by the interacting partner. Contagious yawning seems to represent an example of a potentially communicative, still non-verbal or non-language-based, behaviour, which appears to trigger in the interactive partner the urge to perform the same action.

1.7.3 Sensory modalities and sensory impairment

Up until now, investigations of yawn contagion, have been mostly restricted to the visual modality. The present studies will show that other sensory modalities such as the auditory and the tactile are sufficient to trigger yawn contagion. If we consider any type of perception, which is not a passive but rather an active set of mechanisms, and which may be initiated in any of our sensory modalities, we are acknowledging that whether the perceiver is a human or an animal, the perception will be subjected to an information processing practice that is somehow dependent on both experience and expertise. A previous experience of having dealt with the particular sensorial event provides us with knowledge, and the repeated experience makes us ‘experts’ in dealing with the event. Behavioural studies mostly focus on visual perception, however, the tactile perception expertise of blind individuals is not entirely due, as legend has it, to an enhancement of the other sensory modalities, such as audition, smell or touch, and neither solely to compensatory attributes of their perceptual abilities. Blind individuals’ extensive expertise in tactile, smell or auditory perception (Pasqualotto & Proulx, 2012) is not just due to their inability to see either. Noë (2004) stated that blind individuals do not consider their blindness as an absence of a sensory modality, but rather a “modified kind” of information processing. This is empirically demonstrable in retinal pathologies, such as cataracts or injury to the visual cortex. There is also a possible blindness condition presented as an inability to integrate sensorial information, which would lead to a disrupted stimulation perception pattern, even though the perceptual mechanism, such as retinal performance, may be intact. This particular inability to see has been called experiential blindness (Noë, 2004). According to Noë, this experiential blindness occurs as a consequence of either an incapacity to conceptually integrate information obtained via a coupling of thoughts and sensorimotor experience, or a breakdown at a particular level of the cognitive processing of that information.

There will be further references to this concept later on, but for the purposes of this introductory note, it is important to emphasise that the phenomena described in this thesis, in relation to both blind and vision-intact individuals, are intrinsically related to a type of perceptual experience, and therefore eventual expertise, which is acquired as a result of a combinatory mechanism between sensorimotor knowledge provided by the previous experience and the perceptual event. This is coupled with the experiential essence of the corresponding motor activation that leads to the behavioural response. Previous research suggested that the mirror neuron system holds a motor representation of the actions of others, which can be elicited through sensory mechanisms, normally regarded as supramodal. In Calvo-Merino et al., (2006), expert dancers displayed a greater premotor and parietal activation when watching videos of moves that formed part of their own repertoire, when compared with activation displayed when watching a different dance movement or style, or moves performed by someone of the other gender (Calvo-Merino et al., 2006). Therefore, the studies here aim to fill a gap in the literature, while addressing the same principles as in previous studies, but this time focusing on the auditory and tactile modalities too.

Statistical maps reported by Riccardi et al. (2009) showed that the Mirror system response is greater for motor familiar than for unfamiliar action sounds, and that the activated brain regions are also greater, while listening to familiar actions as compared to environmental sounds, and during the motor pantomime of action as compared to the rest. In both sighted and congenitally blind individuals, aural presentation of familiar actions, as compared to the environmental sounds, elicited similar patterns of activation involving a left-lateralised premotor, temporal and parietal cortical network, see figure 1.5 below.

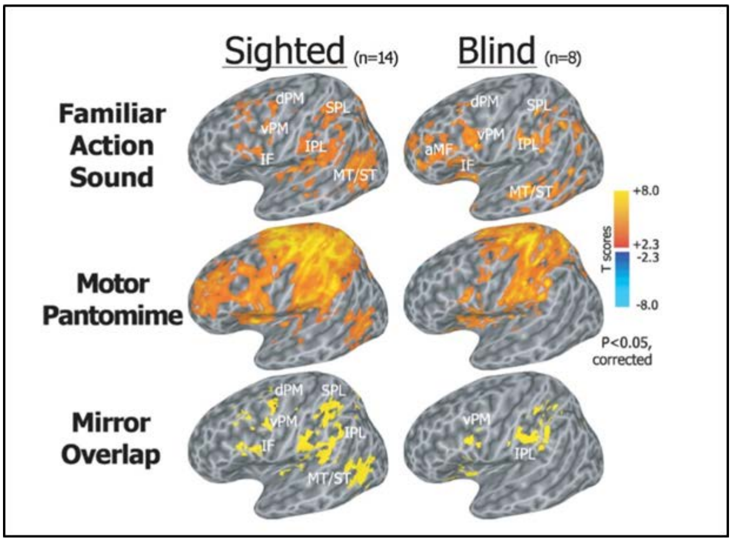


Figure 1.5 Statistical maps showing brain regions activated during listening to familiar action compared with environmental sounds, and during the motor pantomime of action compared with rest (corrected p<0.05) reproduced from (Riccardi et al., 2009)

1.7.4 Use of robotics in social cognition

In the fields of psychological and neuroscientific research, artificial agents, human-robot and animal-robot interactions are helping us elucidate evolutionary acquired capacities of interpersonal communication and social information processing. While the initially developed avatars and artificial devices have been employed to focus on emotional aspects of face perception studies, as well as exploring natural language, or socio-emotional intelligence, this work is mostly focused on non-emotional and non-verbal behaviours. This shift in attention by the cognitive sciences would enable us to part from extremely valuable, and widely used techniques, such as Ekman faces. Although Ekman, arguably one of the most influential figures in emotion recognition research until today, and his facial expressions have been successfully been implemented as stimuli in many face perception studies, the posed aspect of that particular work has also attracted criticism (Damasio, A. 2004), and the faces are portrayed in black and white.

Given the technological advances employed in the production of visual stimuli, there is a possibility that these could be improved in some respects. For example, modern colour versions facilitate techniques such as morphing facial stimuli. The implementation of virtual reality stimuli and indeed robotic physical stimuli, may have provided an alternative facial expression and for some studies may have been satisfactory as an experimental tool, although these may not have been able to avoid all problems either (Leys, R. 2017). Here, the emphasis on new robotic devices aims to support the argument that this type of stimulus provides an enhancement in ecological validity, by for example, adding colour and motion to the expression as well as the obvious three-dimensional and physical presence of the stimulus. By maximising the benefits of latest technological developments, the use of robotic devices should in turn reflect upon further advances in psychology and cognitive neuroscience research.

The argument proposed is that by equipping machines with social communicative features, we will get closer to the goal of these devices helping to interpret subtle non-verbal cues in humans. In turn this can enhance the understanding of how we respond to these social affordances, and in turn how to create emotionally intelligent, non-verbal or even language-based communicative devices. In particular, it is proposed that the use of credible, realistic-looking humanoid robots defines the ultimate test for our understanding of human and animal communication and of social cognition, thus providing the perfect research tool to improve our knowledge about the underlying psychological processes and neurological mechanisms of human and animal behaviour.

The idea to simulate motor functions of biological systems through technology is also eminent in the field of Biorobotics (Webb, 2018). The domain essentially addressed here is that of embodiment and non-verbal communication. Along with the above, embodiment, as employed here with regard to the robotic stimulus, will refer to the features of artificial agents defined as the live presence and equipped with human-like physical properties, which enable the transmission of non-language-based signals (Bente et al., 2008). Embodiment would, in principle, be present in any face to face interaction, as opposed to that of a human-screen interaction, such as with avatars.

Although artificial reconstructions of human-looking beings present the potential problem of anthropomorphising the agent, it can also be considered as a means of embodying the technology. It has also been assumed to render Human-Technology Interactions (HTI) more natural, in the sense that humans can intuitively rely on their everyday communication routines and thus perform interactions with greater ease (Duffy, 2008; Krammer & Bente, 2005). The mere technical feasibility of the use of these realistic human-looking robots represents a clear real-time communicative capability, certainly not present in a screen-based interaction and virtual environments. The development of this device, which is both visual and tactile, also represents an alternative and useful way to explore other non-visual communicative channels and is an exceptional tool to explore nonverbal cues, such as facial gestures, expressions, facial movements and facial displays of non-emotional expressions (Vogeley et al., 2010; Kramer 2006).

1.7.5 How to present yawning as a reliable stimulus for contagion

Drastically different methods and procedures have been employed in previous lab-based explorations, thus preventing suitable comparisons. Furthermore, in a previous heterospecific (human-chimp) investigation, methodological choices may have even confounded the results. Although live models have been reported to have elicited CY in 35% of four-year-old children (Helt et al., 2010), neither videos nor stories, in which the protagonist repeatedly yawned, have elicited CY in children below 5 years old (Anderson & Meno et al., 2003). However, theory of mind, and the acquisition of cognitive capacities that relate to the interpretation of others' thoughts or feelings, are only attained at 4 to 5 years old.

As was mentioned above, comparisons are restricted by the differences in methodologies and procedures. Furthermore, while dogs have shown CY in three of four experiments involving live models (Joly-Mascheroni et al., 2008; O'Hara & Reeve 2010; Madsen & Persson 2013; Romero et al., 2013), they have failed all tests involving videoed (conspecific and human) yawn stimuli (Harr et al., 2009; O'Hara & Reeve 2010). Thus, there is some indication that the medium may influence yawn contagion in younger and non-human subjects, or that video stimuli may reduce contagion effects. Except for one study (Madsen et al., 2013), tests of CY in chimpanzees have deployed videoed (Anderson et al., 2004; Campbell & de Waal 2011; Massen et al., 2012) or computer-animated yawn stimuli (Campbell et al., 2009). To preclude potential issues relating to video stimuli reducing contagion effects, and to enable comparison with our previous study of heterospecific CY in dogs and young chimpanzees, live stimuli were employed to test yawn contagion in this study with adult chimpanzees.

In many species in the animal world, adult male yawning is seen in agonistic, tense situations of conflict, but, as the behaviour is also displayed when hormonal level changes are known to occur, the showing of canine teeth displayed by monkeys in these circumstances has also been interpreted as a social status demonstration (Depute 1994). Zuckerman, S. (1932) described 'bachelor' Hamadryas baboons about to engage in conflict situations also yawning, noting an association with teeth grinding, grimacing and staring at the intended target of the aggression. Remarking how the act of yawning clearly displayed the large canine teeth of the adult males, Hall and DeVore (1932) proposed a secondary intimidating effect for the yawning behaviour in baboons. It would be reasonable to argue that a distinction should be made between the feeling of stress and that of emotion. They are distinguishable sensations or feelings that do not necessarily have to occur simultaneously. These studies aim to make a small contribution towards this goal.

1.7.6 Brain areas related to yawning

Research on yawning has yielded brain activation in several regions. These include various structures and networks, some of them involved in triggering the release of hormonal and biochemical substances affecting yawning and the inhibition of the behaviour. Regarding the brain areas active during spontaneous yawning, clinical and pharmacological evidence indicates that the hypothalamus (mainly the paraventricular nucleus), the bulbus and the region around the pons with frontal connections, are involved in triggering the yawn. The numerous connections between these bulbus areas and the ascending reticular activating system, largely involved in the sleep wake rhythm and the modulation of arousal levels, suggest the relationship between yawning and sleepiness (Giganti et al., 2010). Among the several neurotransmitters and neuropeptides that have been reported to be involved in the control of yawning, adrenocorticotropin, α-melanocyte-stimulating hormone, acetylcholine, dopamine, nitric oxide, excitatory amino acids and oxytocin, all have a facilitatory effect, while serotonin and noradrenaline have different effects (facilitatory or inhibitory) according to the receptor involved. Furthermore, GABA and opioid peptides have an inhibitory effect (Argiolas et al., 1998). Again, it is well known that many of these substances are involved in sleep-wake regulation (Argiolas et al., 1998).

A good number of clinical and pharmacological studies indicate that yawning involves the hypothalamus, particularly the paraventricular nucleus (PVN), the brainstem, and the cervical medulla (phrenic nerve C1–4 and motor supply of inter costal muscles) (Krestel et al., 2015). The neuroanatomical localisation of the brainstem motor pattern, which orchestrates yawning, is still disputed (Askenasy 1989; Walusinski 2006). According to Krestel and colleagues, at least three distinct neural pathways have been identified that participate in the induction (and control) of yawning. These are (1) subsets of oxytocinergic neurons in the PVN, which either project to the hippocampus or to the brainstem; (2) neurons in the PVN, which are activated by adrenocorticotropic hormone and a-melanocyte-stimulating hormone (a-

MSH), and also project to the medial septum where they activate cholinergic septohippocampal neurons; (3) direct activation of septohippocampal/hippocampal neurons; and (4) a serotonergic-cholinergic pathway (e.g., to the hippocampus) whose brain localisation has not yet been identified (Collins & Eguibar 2010; Sato-Suzuki et al., 1998; Argiolas & Melis 1998) (Krestel et al., 2015).

1.7.7 Brain areas related to action perception

When vision is intact, human development is practically guided by learning through the perception of others' behaviours, looking at and observing their actions. It is through visual perception that we achieve most of our understanding of the purpose of others' actions. Areas of the premotor and inferior parietal cortex are active during passive observation of particular actions, including during execution of those same actions (Gallese, Fadiga, Fogassi & Rizzolatti, 1996). This type of neuron, originally discovered in the monkey premotor and parietal cortex, were found to discharge both when the monkey performed hand, goal-directed actions and when the animal visually perceived and observed another individual performing the same hand action. Those neurons in the macaque monkey were named "mirror neurons" (Gallese et al., 1996; Rizzolatti et al., 1996; Rizzolatti and Fadiga, 1998; Rizzolatti & Craighero, 2004). A similar "mirror" system has been identified in humans, and is not just considered to play a major role in action perception and the understanding of the intention behind that action, but also in learning by imitation, empathy, and language development (Iacoboni et al., 1999; Carr et al., 2003; Buccino et al., 2004 a, b; Rizzolatti and Craighero, 2004; Rizzolatti, 2005; Fabbri-Destro & Rizzolatti, 2008; Rizzolatti & Fabbri Destro, 2008; Rizzolatti & Sinigaglia, 2008). Functional brain studies showed that the human mirror system responds similarly to the primate mirror neuron equivalent, relying on inferior frontal, premotor, and parietal cortical networks (Buccino et al., 2004 a, b; Gallese et. al., 2004; Dapretto et al., 2006; Chong et al, 2008; Keysers & Gazzola, 2009). An elegant example of this was demonstrated by Calvo-Merino, who showed that this mirror system is more activated when dancers observe movements for which they have developed a specific competence and expertise (Calvo-Merino et al., 2005, 2006; Cross et al., 2006). It is also found in musicians listening to musical pieces they have rehearsed, compared with music they had never played before (Lahav et al., 2007). These brain areas have been found activated in many motor mimicry behaviours. Therefore, many researchers believe automatic imitation is mediated by the mirror neuron system (Longo et al., 2008). This system is widely believed to connect action perception with action production in a “direct” way—without, for example, the mediation of higher cortical processes (but see, e.g., Csibra, 2008). However, motor mimicry is thought to be unconscious and unintentional (Heyes, 2005).

This type of brain activation in animals, which was later found in humans, was taken as representative of neuronal activity as a result of visual perception. There is a limited amount of research that focused on these types of brain activations through auditory perception, thus it is still unclear whether these results can be extended to other sensory modalities, such as touch.

Neuroimaging studies of CY, using blood oxygen level dependent functional magnetic resonance imaging (BOLD-fMRI), have shown inconsistent results with regards to which brain regions are activated through the visual perception of someone yawning. The finding of posterior cingulate and precuneus activations by (Platek et al., 2005) suggests that CY involves theory of mind (ToM) or empathy networks, with a study by (Schurmann et al., 2005) finding right superior temporal sulcus (STS) activation. Both studies noted a lack of activation, during CY, in mirror neuron areas, such as the inferior frontal cortices, when compared with similar noncontagious motor acts, which did in fact activate mirror neuron areas.

The absence of significant activations in mirror neuron areas suggests that highly stereotyped motor patterns, like CY, do not necessarily require a true imitation process, as regarded when exploring mirror neuron activations on the observation of hand actions. Instead, yawning is not performed with the hands but is, instead, a mostly a facial action that happens to be merely accompanied by a stretching of the arms. This might be a possible reason why previous authors failed to find that the perception of a yawning behaviour would not activate the same mirror neuron brain areas. Specifically associated with the viewing of a spontaneous yawn was an area of activation in the ventromedial prefrontal cortex (Nahab et al., 2008). These findings suggest a role for the prefrontal cortex in the processing of yawning and, perhaps, in the triggering of contagion while demonstrating a unique automaticity in the processing of contagious motor programs in a more general way, which, as the authors state, would take place independently of mirror neuron networks (Nahab et al., 2008). Despite divergent reports on the recruitment of the human motor neuron system (MNS), there is general consensus that contagious yawning recruits the neural network involved in cognitive empathy.

Previous research has elucidated the neural correlates of the mechanisms that allow humans and animals to perceive, interpret and interact socially. These perceptual mechanisms form a large part of social and communicative processes. One of these processes is the mental state attribution of other individuals. Until recently, when we referred to ‘the other individuals’ potentially involved in social interactions, we could only be referring to other humans or animals. Therefore, most research has concentrated on exploring the social cognitive processes associated with a network of brain regions sometimes referred to as the ‘social brain’ (Brothers, 1990; Frith & Frith, 2010). This group of brain regions comprises the medial prefrontal cortex (mPFC), the temporoparietal junction (TPJ), the anterior cingulate cortex (ACC), the inferior frontal gyrus (IFG), the inferior parietal lobe (IPL), the intraparietal sulcus (IPS), the superior temporal sulcus (STS), the amygdala, and the anterior insula (Blakemore 2008; Figure 1.6 below)

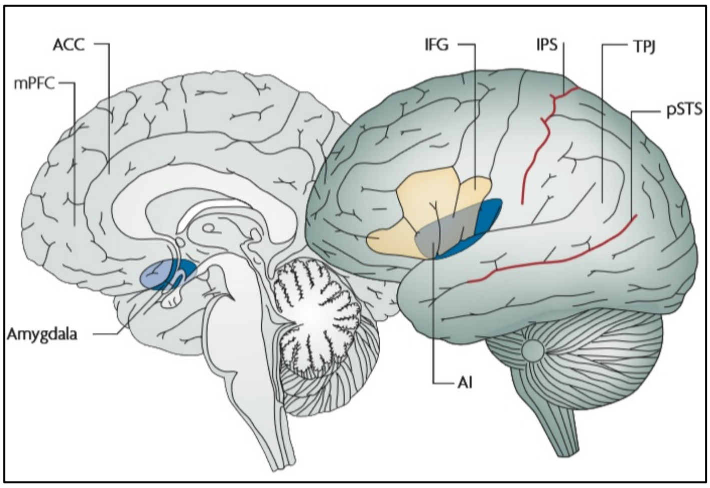


Figure 1.6 Regions of the social brain that are involved in social cognition, including thinking about the mental states of others, and regions involved in the observation of faces and biological motion perception adapted from Nature Reviews Neuroscience (Blakemore, 2008).

The brain regions known to be involved in communicative social interaction situations, and other higher-order cognitive functions, are highly interconnected

(Adolphs, 2001). The communication between these regions relies on the intact functioning of the relevant brain area. Providing the whole perceptual modality is in good working order too, this would then lead, in the case of the occipital cortex, for instance, to processing visual information. However, the intercommunication between these visual cortical areas is sometimes taken to mean that an impairment in one brain area has been shown to be compensated for by the activation of a neighbouring one, or even an area that would normally be involved in dealing with information processed in another sensory modality. It’s worth noting that higher-level functions, such as social reasoning, will not be assessed in much depth here. Instead, the focus of this thesis is mostly on lower-level socio-cognitive mechanisms, apart from the occasional cases of reference to lesions in some relevant brain areas caused by a stroke.

2 GENERAL METHODS

The historical background and State of the Art have presented a comprehensive description of the path followed so far by this area of research. The following sections will provide a general description of the methods used in the studies presented in this thesis. It will clarify the reasons behind the methodological choices made in this work, and it will lay out some necessary methodological considerations.

2.1 Overview of the studies in this thesis

Human and animal action perception mechanisms have been generally assessed in explorations of automatic imitation, or movements seen as copying, mimicry or any other equivalently automatic behavioural response. Employing live presentations in three of the four studies presented in this thesis, the focus is on the perception of the particular action of a wide opening of the mouth and closing of the eyes (Yawn); a matched control stimulus with a less wide opening of the mouth and eyes remaining open (Gape); and the third control condition, where the eyes are open but the mouth remains closed (Close). Although these actions are sometimes considered reflexive, the focus in these studies is on distinguishing the potential mechanisms that may apply to the understanding of contagion, and we will only be able to speculate on how dissimilar these are from imitation or copying. Specific attention will be paid to (a) the concept that action contagion can trigger potentially similar social interaction mechanisms, in both animals and humans, and (b) to exploring the possibility that action contagion can be triggered through different sensory systems (i.e. Visual, Auditory and Tactile).

This thesis presents four studies exploring contagious yawning both in humans and non-human primates (chimpanzees). In the two studies involving non-human primates, a series of factors are explored that may influence the contagious response, one of them including different levels of familiarity with the observed agent. In the two studies involving humans, we explore the concept of yawning as a multisensory stimulus, hence the inclusion of blind individuals. These last two studies measure physiological responses through electromyography during the perception of actions that include yawning.

The first study explores yawn contagion across species between humans and adult chimpanzees. Addressing previous debates in the literature related to the use of videos, this study employs live presentations. Given the previous commonly-held belief that empathy exerts an impact on yawn contagion, the experiment investigates the possibility of a modulatory effect on yawn perception, driven by familiarity with the perceived stimulus. This was tested by assessing if the animals catch more yawns from a familiar human (the keepers), rather than from a person who is unfamiliar to them. These chimpanzees were very close to the keepers, relying on them for feeding and care, while the experimenters were unfamiliar to the animals. Both the keepers and experimenters had to produce the three different facial actions that constituted the experimental conditions. The investigation also includes a test of yawn contagion through a solely auditory modality.

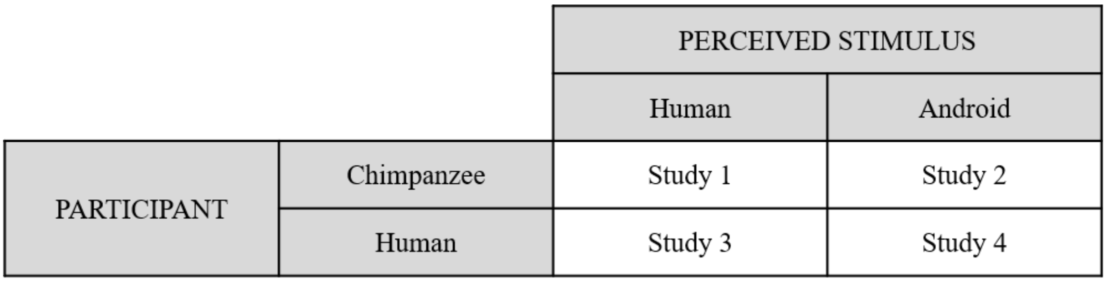
The second study explores the possibility of yawn contagion across agents, this time employing the live presentation of a yawning android. Given the live aspect of the presentation, in comparison with previous studies, this represents an enhancement of the ecological validity of the stimulus. This study tests yawn contagion between a human-looking robot and adult chimpanzees, which constitutes the first time a potential contagion is investigated when elicited by a man-made object, an android. Although yawn contagion between humans is well known, and the stimulus so strong, only a few studies have explored it empirically. Previous findings have not yet met a general consensus regarding exactly what components of humans' facial features exert an impact on the contagious process, i.e. the eyes or the mouth region. Perhaps because contagious yawning research has been rather limited, and different methodologies and set ups have been employed, it has, so far, been difficult to establish fair and reliable comparisons.

The third study, therefore, addresses this question, and, again, in order to enable comparisons, employs the same paradigm used in the other studies in this thesis. Here, participants provide an immediate self-report, while electromyography is implemented to measure the urge to perform the same action observed.

Simultaneously, eye tracking is used to investigate eye gaze and fixation patterns directed towards the regions of interest.

The fourth study explores, for the first time, yawn contagion through tactile perception and with blind participants. This is achieved with the android as a tactile stimulus, to test, again, if yawn contagion is present across agents, this time, between humans and an artificial agent.

Table 2 Schema representing the differences between the four studies. 1st Study: Chimpanzee study I (across species, chimpanzees and humans); 2nd Study: Chimpanzee study II (across agents, chimpanzees and android); 3rd Study: Humans study I (within species, humans with intact vision); 4th Study: Humans study II (across agents, blind humans and android).



		PERCEIVED STIMULUS	
		Human	Android
PARTICIPANT	Chimpanzee	Study 1	Study 2
	Human	Study 3	Study 4

2.1.1 Participants

The participants in the first two studies were rescued chimpanzees housed in Mona Chimpanzee Sanctuary in Girona, Catalunya Spain. The Mona Foundation cares for these rescued chimpanzees, and other primates, where they can live the rest of their lives in the most natural environment possible. The primates have all been rescued and rehabilitated from abusive or unsuitable situations. Many of them come from the pet trade or entertainment industries, where they are likely to have lived through extremely traumatic events, such as seeing their family killed or suffering physical abuse. Unfortunately, it is impossible to return them completely back to the wild, but at MONA they try to offer them the next best thing: an enriched and natural environment in a group of their peers, with lifetime care and support. The sanctuary offers them a new life of recovery with physical and psychological care, giving them the respect and space, they deserve. The animals would collaborate and participate in the study only if they would want to and no animal was forced or reinforced in any way.

The chimpanzees were only separated and placed in a room on their own strictly for the duration of testing and with the purpose of addressing the possible confounding issue of yawning contagiously between themselves. The participants were 14 chimpanzees (see Figure 2.1). A brief outline of their demographic data is detailed here and further information in the studies (Table 3 in the next page).

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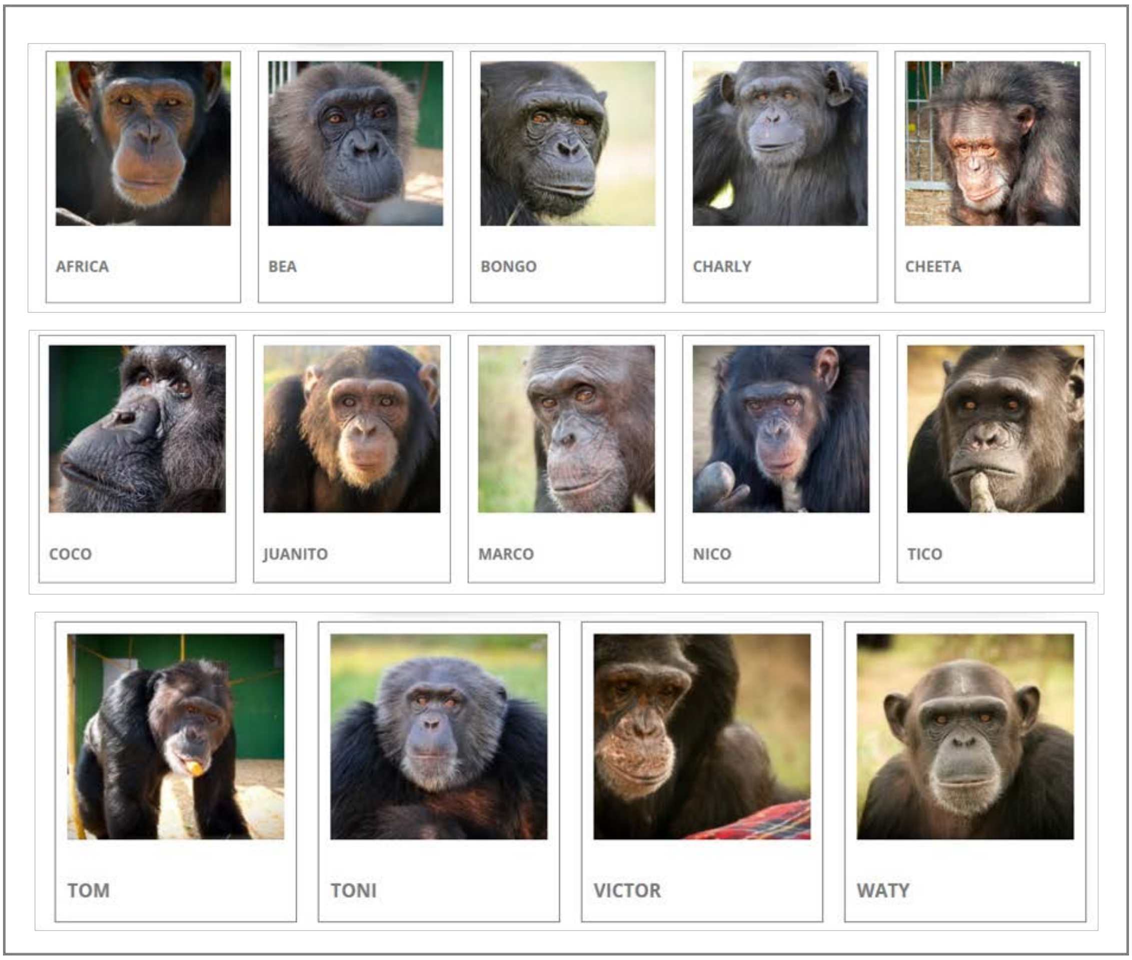
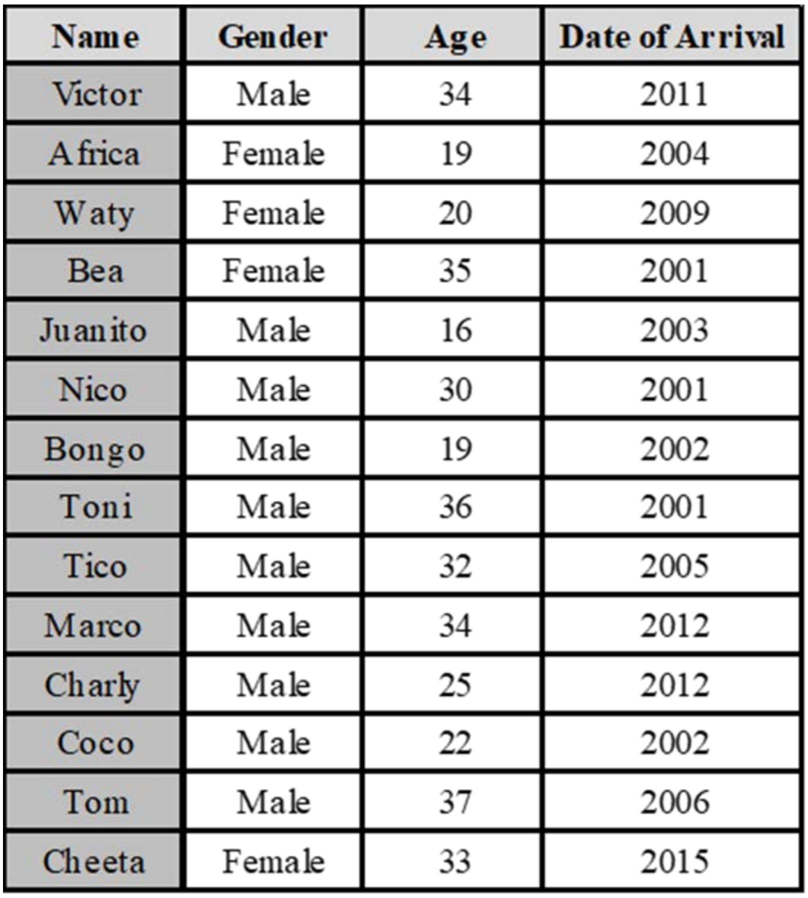


Figure 2.1 Photographs of the chimpanzees rescued and rehabilitated at Mona Chimpanzee Sanctuary, Girona, Spain.

Table 3 Demographics of Chimpanzees participating in the study



Name	Gender	Age	Date of Arrival
Victor	Male	34	2011
Africa	Female	19	2004
Waty	Female	20	2009
Bea	Female	35	2001
Juanito	Male	16	2003
Nico	Male	30	2001
Bongo	Male	19	2002
Toni	Male	36	2001
Tico	Male	32	2005
Marco	Male	34	2012
Charly	Male	25	2012
Coco	Male	22	2002
Tom	Male	37	2006
Cheeta	Female	33	2015

The participants in the third study were psychology undergraduate students from City University of London. All had intact or corrected vision. Demographic information can be found detailed in the study.

The participants in the fourth study were blind individuals recruited from institutions, such as The Royal National Institute for Blind People (RNIB), Blind Veterans UK, East London Vision, ONCE (Spain), School N33 for Blind Students (Argentina) and many blind individuals who did not belong to any of these organisations, but volunteered to participate in the study and be part of trials of the Sound and Tactile biofeedback prototype development. See Table 4 for schematic description of all studies in this thesis.

Table 4 Schematic description of participants and stimulus for all four studies in this thesis

	Conditions	Presentation Format	Stimulus Type	Sensory Modality	Participants
Study 1	Close Gape Yawn	Live	Humans Familiar & Unfamiliar	Visual & Auditory	Chimps Across Species
Study 2		Live	Android	Visual	Chimps Across Agents
Study 3		Videos	Humans Unfamiliar	Visual	Humans Within Species
Study 4		Live	Android	Tactile	Blind Humans Across Agents

2.1.2 Stimuli: Development of the android

Gray’s anatomy teaching was instrumental in the emulation of a robotic equivalent of the human facial anatomy. Animatronic experts in the field of special effects, who were instrumental in the incredible achievements of legendary films including Star Wars, Harry Potter, and The Lord of the Rings, helped recreate the human equivalent of facial expressions choreographed in the “motoric” movement of each of the android’s 33 servos.

Figure 2.2 The final developed android. (see video in the following link)

These movements exemplify the robotic emulation of an initial set of human facial expressions. These first examples of robotic movements aimed to, as accurately as possible, match the commonly used expressions of simple communicative, non-linguistic human facial gestures. All of the thirty-three mini servos acting as “muscle activity simulating motors” were used in the production of the android’s facial expressions. The facial movements were programmed to last a total of 10 seconds, from onset to offset. The back of the androids’ head was transparent, to display the internal mechanism as an artificial agent. Of these 33 servomotors used in the internal mechanism of the robotic heads, almost half were employed to form and maintain a neutral facial expression, i.e. the first facial gesture the android displays when it is not in motion. The neutral expression was surprisingly difficult to portray, given the amount of energy needed to replicate the artificially created equivalent to the architectural front part of a human skull (Figure 2.2). The eight mini servos placed in the eye brow regions were designed to exemplify the corrugator muscle movement. Six mini servos work to facilitate and create the internal space necessary for the next move command, which would also correspond to the motion of zygomaticus major area muscle activity in a happy/smile expression in humans. All motion resemblance, and actual motion, was controlled in such a manner that all movements shared the same basic patterns of activation, start instance or onset. Biological motion characteristics were emulated during the actual movement. Length of motion time, speed, velocity and trajectory, as well as maintenance and modification of motion pattern, was emulated in an artificial, non-biological equivalent to that of human facial, biological motion. Duration (exact length of motion) and end instance or offset were intended to respect that of the equivalent human facial motion. The android represents a visual stimulus that is novel for the chimpanzees, who are intelligent enough to realise that, although the stimulus looks like a human, it is in fact an object that is placed in front of them (Figure 2.3).

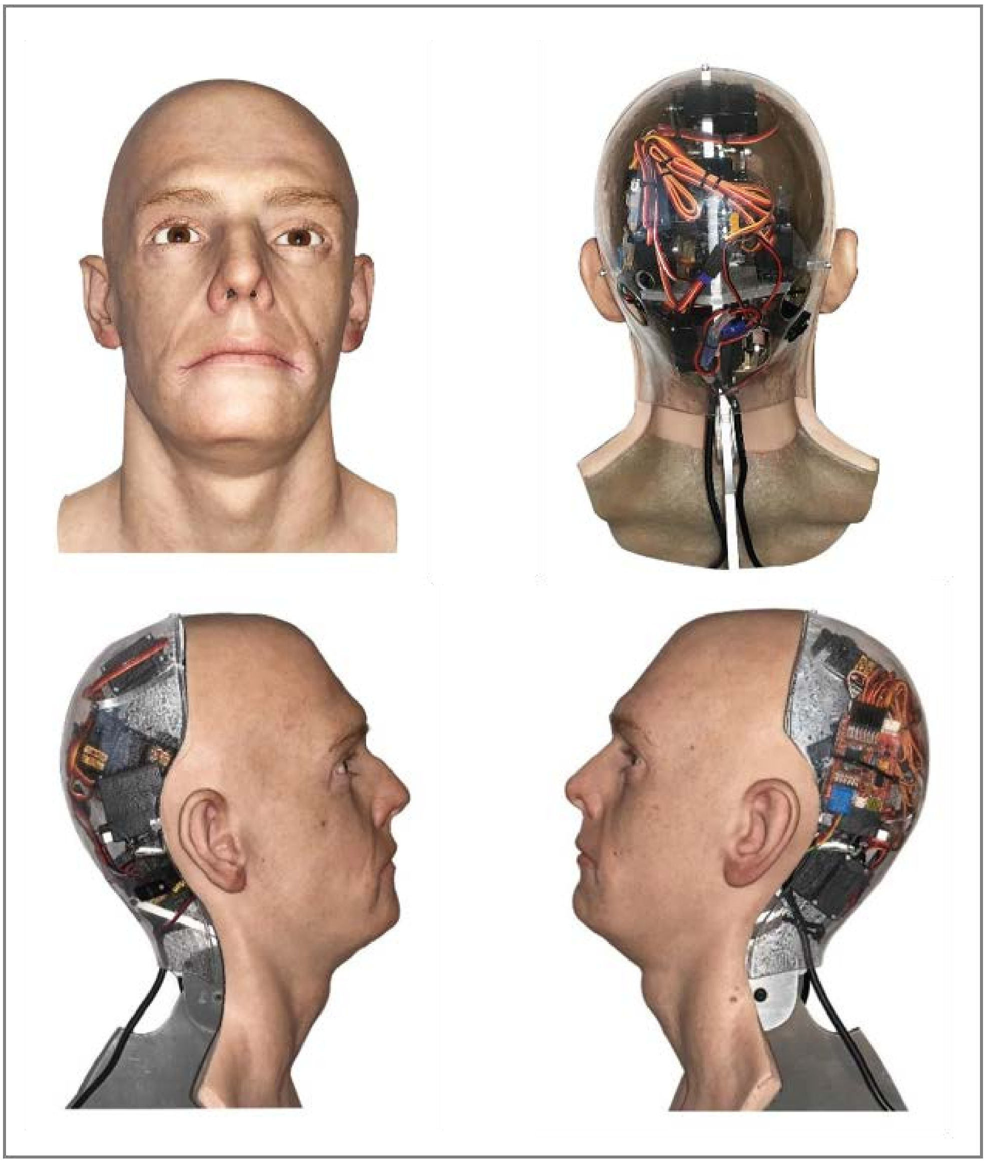


Figure 2.3 Representation of the android in all orientations (back front, and profiles).

https://www.youtube.com/watch?v=2M0NuU4_gqg&t=71s

The animals were unfamiliar to the device; therefore, they would have no emotional or behavioural attachment to it. In the case of blind participants, the device is part of the sound and biofeedback tool developed as part of this thesis, which represents the perfect stimulus for the tactile perception of facial expressions being performed through an algorithm that is programmed to be loyal to the specification needed for purpose, always respecting the characteristics of the movement within the parameters it was designed for; start/onset, duration/length, and end/offset of motion for all conditions.

2.1.3 Stimuli: Digitally recorded actions

The facial expressions were aimed to be as clear as possible, even when, for example, the yawning expressions would obviously have to be a ‘pretend yawning action’. In the case of the close (closed mouth) expression, the chances of being interpreted as any other expression were almost none. With regard to the gape, the morphology of the expression was that of a less wide opening of the mouth and, again, the aim was to minimise the possibility of the expression being interpreted as an emotional expression, as well as an attempt to minimise the chances of it relating to any particular symbolism or meaning. See examples of the three conditions in Figure 2.4:

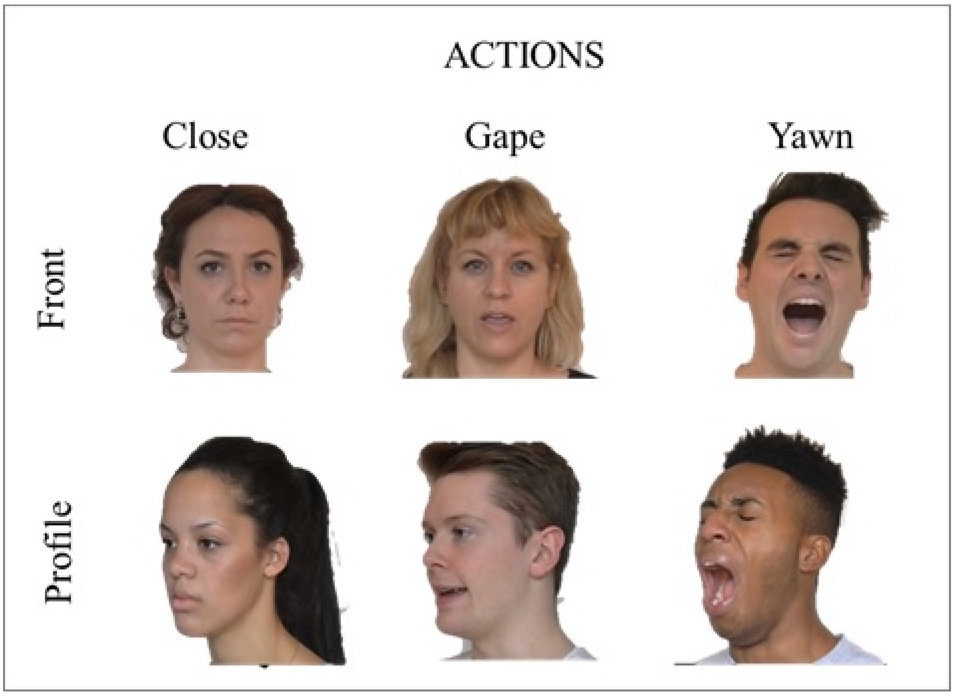


Figure 2.4 Still of the digitally created videos of human actors in Front and Profile for all conditions.

2.1.4 Eyetracking

Combining eye tracking with EMG represents another novel and complementary route in exploring precisely which area of another’s face the perceiver is looking at, while muscle activity is being measured (Figure 2.5).

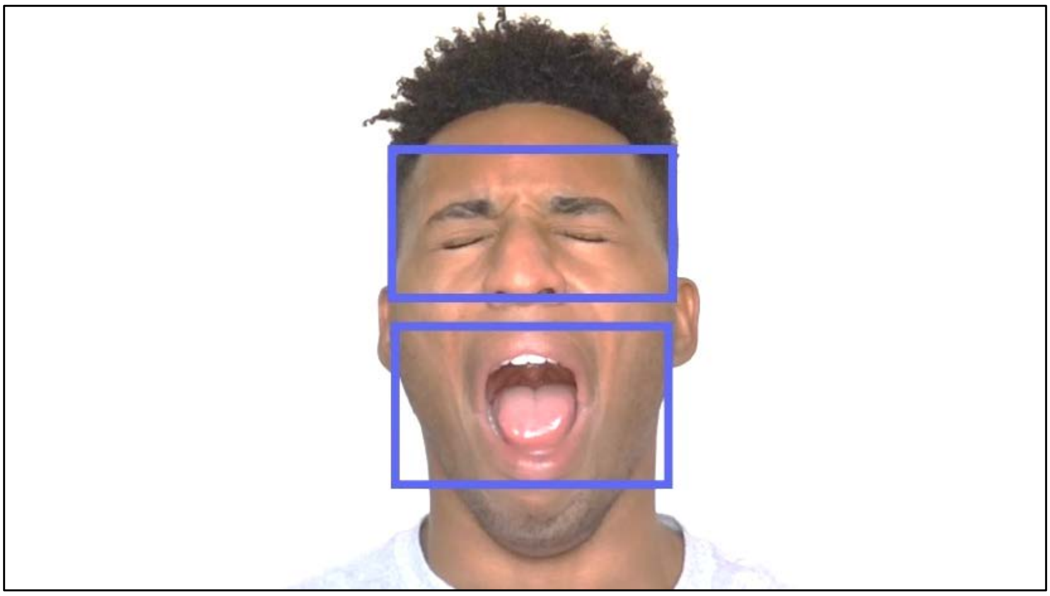


Figure 2.5 Blue boxes represent the regions of interest (ROI) for eye gaze and fixation patterns.

2.1.5 Electromyography (EMG)

Skeletal muscles do the majority of the work for locomotion and support of the animal and human skeleton. Each muscle is made up of individual muscle fibres organised in fascicles (Figure 2.6). Each individual fibre is innervated by a branch of a motor axon. Under normal circumstances, a neuronal action potential activates all of the muscle fibres innervated by the motor neuron and its axonal branches. The motor neuron, together with all of the individual muscle fibres that it innervates, is termed a motor unit (Figure 2.6) This activation process involves the initiation of an action potential (either voluntarily, or as the result of electrical stimulation of a peripheral nerve), conduction of the action potential along the nerve fibre, release of neurotransmitter at the neuromuscular junction, and depolarisation of the muscle membrane with resultant contraction of the muscle fibres.

Electromyography is a technique that measures the electrical activity of muscles and the nerves controlling the muscles. The data recorded provides a depiction of the timing and pattern of muscle activity during complex or simple, and minute or large, movements.

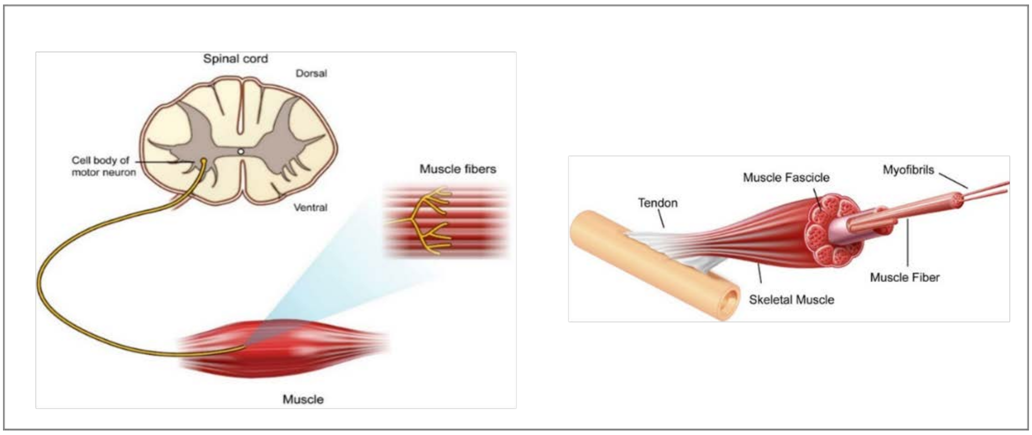


Figure 2.6 Skeletal muscle structure (left) and components of a motor unit (right).

The raw surface EMG signal reflects the electrical activity of the muscle fibres active at that particular time. Motor units fire asynchronously, and it is sometimes possible, with exceedingly weak contractions, to detect the contributions of individual motor units to the EMG signal. As the strength of the muscular contraction increases, the density of action potentials also increases, and the raw signal at any time may represent the electrical activity of perhaps thousands of individual fibres. This is partly why the decision here is to be both cautious and rather conservative as to the significance of the measurements and regard the signal as incoming from the muscle area, given that there is a possibility that the fibres could be extensions from another adjacent muscle.

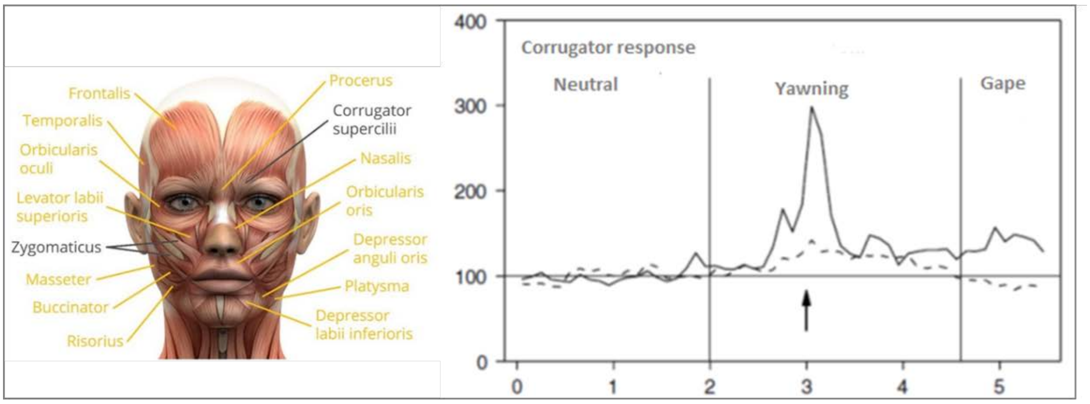


Figure 2.7 Facial muscles (left) and example of electromyography signal sample (right).

The raw EMG signal, during voluntary contractions, may be processed in various ways to indicate the intensity of EMG activity. In the method used here, the negative-going portions of the EMG are inverted and then the whole signal is integrated in such a way as to smooth out individual spikes, making the time course of changing activity much clearer.

The facial muscles, the group of skeletal muscles lying under the facial skin, mostly originate from the skull or fibrous structures and radiate to the skin through an elastic tendon. Contrary to the rest of the skeletal muscles, they are not surrounded by a fascia (except the buccinator). Although there are many obvious benefits from employing skin surface sensors instead of needle electrodes to measure the activity in these facial muscles, the primary benefit here is that one can detect the pre-motor activity in the facial muscles, when perceiving an embodiment-inducing action, such as a yawn. This is true even whether the person is reporting it or not. As mentioned above, there are also difficulties in being extremely precise about exactly from which muscle the activity is reaching the sensors.

2.2 Aims and Hypotheses of the studies

The main aim of the **first study** is, using a live presentation, to explore whether chimpanzees are susceptible to heterospecific yawn contagion. In addition, this experiment investigates a possible impact of two potentially modulatory effects, namely familiarity/unfamiliarity and visual/auditory perception.

Therefore, the following hypotheses were set up:

(H1) Adult chimpanzees yawn contagiously when visually perceiving an adult human yawning, and do not show contagious behaviour when observing the control conditions, gape and close (closed mouth, no movement).

(H2) It is hypothesized that chimpanzees' contagious response to yawning behaviour is modulated by the level of familiarity that the animal has with the observed human. It is expected that yawn contagion will increase with familiarity.

(H3) It is hypothesized that yawn contagion occurs through other sensory modalities apart from vision, i.e. auditory perception. The expectation is that yawn contagion will be induced through a merely auditory perception of the stimulus.

The main aim of the **second study**, using a live presentation, this time that of an android, is to test yawn contagion between a human-looking robot and adult chimpanzees, to explore whether chimpanzees are susceptible to a different type of heterospecific yawn contagion, one never explored before, i.e. across agents (note that objects cannot be categorized as species).

(H4) It is hypothesized that adult chimpanzees yawn contagiously when visually perceiving an inanimate agent (android) moving in a manner that simulates yawning. This yawning behaviour is predicted in the yawn conditions, but not in the control condition gape and close (closed mouth, no movement).

(H5) Depending on the results from (H1), it is hypothesized that after being exposed to the yawning stimulus, the animals will display behaviours that denote experiential contagion. The expectation is that there will be differences in the duration spent lying down across the three main experimental conditions.

The main aim of the **third study** is to investigate contagious yawning in humans, by providing both physiological evidence and eye tracking data denoting contagion and thereby extending previous findings of contagious yawning through visually perceiving videos of conspecifics. In addition, this study aims to explore a possible relation between empathy and susceptibility to yawn contagiously.

(H6) It is hypothesized that when an adult human visually perceives someone else yawning, there are physiological measurements, provided by EMG, that can denote presence of contagion, internal simulation, embodiment, resonance, evidenced by their own facial muscle activity. Measures are taken from two major muscles areas, zygomaticus Major (Muscle ZM) and the corrugator supercilii (Muscle CS) and the expectation is that the mouth region (A) will denote higher activation than the eye muscle region (B).

(H7) It is hypothesized that in yawn contagion scenarios, some facial regions are more important than others. This is tested by exploring whether there are mean differences in eye tracking measurements (gaze orientation fixation time and other patterns) between the eyes and mouth areas.

(H8) It is hypothesized that there is no relation between empathy scores and yawn contagion. Therefore, the expectation is that there will be no correlation between the EMG activity denoting contagion and high empathy quotients.

The main aim of the **fourth study** is, using a live presentation, again that of an android, to explore if blind humans catch yawns through tactile perception.

In addition, the study aimed to explore the potential and previously reported relation between empathy and susceptibility to yawn contagiously.

(H9) It is hypothesized that when an adult blind human perceives a yawning stimulus through tactile perception, there are physiological measurements, provided by EMG activity, that can denote presence of contagion, of internal simulation, embodiment and resonance, evidenced by their own facial muscle activity. The expectation is that there will be differences in muscle activity following a pattern of being lower in the close condition, and highest in the yawning condition.

(H10) It is hypothesized that there is no relation between empathy and yawn contagion through tactile perception.

3 STUDY 1 CROSS-SPECIES CONTAGIOUS YAWNING IN CHIMPANZEES

3.1 Introduction

Humans communicate signals through body language, physical gestures and facial actions. Even though we are the only animals who socially interact predominantly through language, many non-verbal behaviours displayed by humans and by animals constitute part of key social interactions and communications processes. Our closest relatives in the animal world, Pan Troglodytes (chimpanzees), that are highly social, also display communicative behaviours through vocalizations, body postures and facial expressions. From an evolutionary perspective, it is important to explore whether our current communicative behaviours were employed by our ancestors, as some of these could have been the precursors of language. Generally, social interactions include exchanges of visual and auditory signals. Some of these communicative signals, such as spoken words or tone of voice in the case of humans, and vocalization and facial gestures in chimpanzees, often represent different types of information exchanges. Exploring the automaticity with which we perform some of these communicative actions and how often we humans and animals display behaviours without conscious awareness or intention is a potential route to learning more about the important role these non-verbal actions had in human evolution.

Actions perceived in a communicative social interaction are sometimes unintentionally repeated and performed by the interacting partner. Contagious yawning seems to represent an example of a potentially communicative, still non-verbal or non-language-based behaviour, that appears to trigger in the interactive partner the urge to perform the same action.

The level of affinity between the interacting partners in a communicative scenario, is thought to influence the extent of a mirrored response (Arnott et al., 2009; Platek et al., 2003). As shown in the introduction, contagious yawning has already been confirmed in several social animals, and authors suggested it may play a role in their social interactions (Provine, 1986; Anderson & Meno, 2003; Platek et al., 2003, 2005).

Although the ultimate function of yawning remains disputed (see Guggisberg et al., 2011), it has been suggested that it serves thermoregulatory (Gallup & Eldaker, 2012), stress-reductive and non-verbal communicative purposes, to be related to states of rest, arousal and focus of attention (Walusinski, 2013), and its contagiousness to synchronise group behaviour (Deputte, 1994). Whatever the physiological function of spontaneous yawning is, previous studies results provide evidence of a different phenomenon present in contagious yawning. Not all actions are contagious, so is there something particular about the action of yawning that distinguishes it from others?

Yawning contagiously has been suggested to be primarily linked to, and modulated by, empathy (e.g. Platek et al., 2003; Anderson & Matsuzawa, 2006; Palagi et al., 2009; Campbell & de Waal, 2011; Demuru et al., 2012; Romero et al., 2013). Other researchers have emphasised that CY represents a fixed action pattern, for which the releasing stimulus is another's yawn (Provine, 1986); a primary mechanism, which may subsequently be modulated by dispositional and social factors, also possibly related to empathy (Preston et al., 2002).

Humans, chimpanzees and dogs gradually develop susceptibility to yawn contagion, which becomes prominent in these species around the ages of 4 years, 5 years and 7 months, respectively (Anderson & Meno, 2003; Helt et al., 2010; Millen & Anderson, 2011; Madsen & Persson, 2013; Madsen et al., 2013). The emergence of yawn contagion concurs with the development of Level 2 perspective taking (children: Gzesh & Surber, 1985; chimpanzees: Povinelli et al., 1994; dogs: Maginnity, 2007) and it has been implied that it relies on the development and interaction of several cognitive capacities, such as perspective-taking, attention to and identification of others' states, and also to a particular type of empathic reaction sometimes referred to as affective empathy (Deputte & Walusinski, 2002; Madsen et al., 2013).

Yawn contagion has also been interpreted as a type of emotional contagion. Theories to support this interpretation rely on two inter-linked processes: non-conscious mimicry and afferent feedback. Non-conscious mimicry (the so-called 'chameleon effect': Chartrand & Bargh, 1999, see also Yoon & Tennie, 2010) is the tendency to mirror the behaviours (postures, facial expressions, etc.) of others, without either individual’s awareness or intent. Studies exploring social interactions found that body language and facial expressions can influence emotional experiences providing afferent feedback, e.g. smiling (Soussignan, 2002), and body posture (Briñol et al., 2009; Adelman & Zajonc, 1989). These previous studies may have offered insights into the contagiousness of laughter or crying, but those findings cannot be extended to the contagiousness aspects of yawning. Laughter has an emotional component attached to it, whereas yawning has not. Some types of non-conscious mimicry have been reported to give rise to emotional contagion, whereby mimicking someone’s movements, or imitating their facial expressions has been found to lead individuals to converge emotionally (Hatfield et al., 2009). Nevertheless, there is no strong evidence of a causal relationship between contagious yawning and emotion-related feelings as such. Given that spontaneous yawning tends to occur in the transitional periods between rest and arousal, there is no evidence to suggest that these stages relate to a particular emotional feeling. Mimicking or imitating (as opposed to contagion) have indeed been found to serve a positive function in social interactions, by exerting an emotional feedback loop in affiliative relationships (Carpenter et al., 2013). Thus, in humans, being mimicked increases affinity, liking and empathic reactions, as well as prosocial behaviours towards both the mimicker and people not directly involved in the mimicry situation (Lakin & Chartrand, 2003; Van Baaren et al., 2004; Carpenter et al., 2013). In humans, holding positive emotional feelings towards someone, or simply liking them, increases non-conscious facial mimicry (McIntosh, 2006). Although social motivations, such as the desire to bond with another, have also been found to increase non-conscious mimicry in humans (Lakin & Chartrand 2003), suggesting that mimicry is a (non-conscious) strategy to affiliate with others (Chartrand et al., 2005). Nevertheless, one ought to be cautious when extending these assumptions and evidence to the animal kingdom.

In many animal species, we may see the offspring copying or imitating their parents (Mc Elreath, R., & Strimling, P. (2008); Over, H., & Carpenter, M. (2013)), for example, in techniques such as hunting or self-cleaning. These types of mimicking behaviours are a phylogenetically old phenomenon that seem to constitute the basis for animal and human learning (Jones, S., (2017). We know that imitation is not restricted to humans. For instance, capuchin monkeys (Cebus apella) prefer to affiliate and interact with humans who imitate them (Paukner et al., 2009). These types of socially positive effects of imitation, have also been found in children as young as 18 months of age, with whom Carpenter observed that pro-social behaviour increases, relative to the level of mimicking behaviours (Carpenter et al 2013).

In line with evidence that humans are more likely to mimic those they like or would affiliate with (Norscia & Palagi, 2011), chimpanzees (Campbell & de Waal, 2011), bonobos (Demuru et al., 2012), gelada baboons (Palagi et al., 2009) and dogs (Silva et al. 2012; Romero et al., 2013) are more likely to catch yawns from those with whom they are familiar or already socially bonded. Chimpanzees yawn contagiously in response to videos of yawning in-group, but not out-group members (Campbell & de Waal, 2011), although the degree of social bonding (as measured by grooming and proximity patterns) with in-group members does not appear to affect susceptibility to yawn contagion (Massen et al., 2012). Nonetheless, methodological issues pertaining to the study regarding social bonding and CY in chimpanzees (see Madsen et al. 2013), means that ascertaining whether CY in chimpanzees is influenced by relationship quality, or only by a less fine-grained in-group bias, out-group bias and even other species or agents, would benefit from further research.

Social modulation of yawn contagion has only been demonstrated in adult individuals. Neither young dogs (Madsen & Persson, 2013), nor juvenile chimpanzees (Madsen et al. 2013) have shown a familiarity-bias on heterospecific CY. This has led to the suggestion that the effect only emerges at later stages of development (Madsen & Persson, 2013), which is supported by evidence of familiarity-biased heterospecific yawn contagion in adult dogs (Silva et al., 2012; Romero et al., 2013). Nonetheless, young chimpanzees have only been explicitly tested, when viewing the yawns of humans in a (live) social context, while adult chimpanzees have been tested with respect to conspecific yawn contagion (Campbell & de Waal, 2011; Massen et al., 2012), and more recently, heterospecific yawn contagion (Campbell & de Waal, 2013) using videotaped yawn stimuli. The difference in results pertaining to chimpanzees may thus not owe exclusively to developmental issues, but to the nature of the stimulus: whether the yawns derived from humans or conspecifics and whether they were presented in a live social context or on video.

Chimpanzees are well known for displaying antagonistic behaviours towards unknown groups, denoting a strong sense of ‘us versus them’. Possibly because chimpanzees are also extremely territorial, when two groups meet in the wild, it would very rarely be a friendly encounter (Nishida et al. 1985; Wilson & Wrangham 2003). Such aggressive responses towards an unfamiliar individual may, first of all, inhibit potential empathic reactions (as has also been reported in humans: Singer et al., 2006), thereby reducing potential imitative behaviours and, in turn, yawn contagion, as demonstrated by a lack of contagion in response to videos of unfamiliar chimpanzees yawning (Campbell & de Waal, 2011).

By contrast, chimpanzees’ interactions with unfamiliar humans are typically not automatically or necessarily aggressive or competitive, and, in line with this, heterospecific yawns do not elicit a familiarity effect on juvenile chimpanzee yawn contagion (Madsen et al., 2013). Similarly, Campbell & de Waal provided evidence that showing adult chimpanzees videos of humans yawning, elicits a contagious yawn response of equal magnitude to that of videos of yawning in-group conspecifics (Campbell & de Waal, 2011), which were obviously familiar individuals.

Overall, findings seem to suggest that, while chimpanzees may target their empathic reactions in interactions with conspecifics (and consequently, randomly catch yawns from familiar conspecifics), when observing videos of humans, they seem to apply what may be regarded as a more generalised, or at least still undefined type of empathic behaviour, if it can be categorised as empathy at all. While chimpanzees, either in captivity or in the wild, would rarely interact or engage in competition with humans, there are no studies that have explored this type of cross-species, live chimp-human interaction.

Drastically different methods and procedures have been employed in previous lab-based explorations, thus preventing suitable comparisons. However, in the only previous heterospecific (human-chimp) investigation, methodological choices may have even confounded the results. Firstly, the familiarity of 14 individuals of another species, such as humans, may be difficult to distinguish in a video played to the chimps on a small iPod display (7.5 cm x 5 cm), a method used in the study that found no familiarity bias on heterospecific CY in chimpanzees (Campbell & de Waal, 2013).The generalisation of the yawn response, and lack of differentiation between familiar and unfamiliar human yawns, may simply derive from the medium.

Moreover, the assumption that video stimuli are in a one-to-one correspondence with live stimuli is problematic (e.g. Persson et al. 2008). Whether this critique has any bearing on the critical cues required for yawn contagion, however, is unknown, but empirical data suggest that it might have. Although live models have been reported to have elicited CY in 35% of four-year-old children (Helt et al. 2010), neither videos nor stories, in which the protagonist repeatedly yawned, have elicited CY in children below 5 years old. (Anderson & Meno et al. 2003). However, theory of mind and the acquisition of cognitive capacities that relate to the interpretation of others' thoughts or feelings, are only attained at 4 to 5 years old. As was mentioned above, comparisons are restricted by the differences in methodologies and procedures. Furthermore, while dogs have shown CY in three of four experiments involving live models (Joly-Mascheroni et al. 2008; O'Hara & Reeve 2010; Madsen & Persson 2013; Romero et al. 2013), they have failed all tests involving videoed (conspecific and human) yawn stimuli (Harr et al. 2009; O'Hara & Reeve 2010). Thus, there is some indication that the medium may influence yawn contagion in younger and non-human subjects, or that video stimuli may reduce contagion effects. Except for one study (Madsen et al. 2013), tests of CY in chimpanzees have deployed videoed (Anderson et al. 2004; Campbell & de Waal 2011; Massen et al. 2012) or computer- animated yawn stimuli (Campbell et al. 2009). To preclude potential issues relating to video stimuli reducing contagion effects, and to enable comparison with our previous study of heterospecific CY in dogs and young chimpanzees, live stimuli were employed to test yawn contagion in this study with adult chimpanzees.

3.2 Hypotheses

Here, several questions were examined and led to following hypotheses:
The main aim of this study is to explore whether chimpanzees are susceptible to heterospecific yawn contagion, and to explore if this behaviour is modulated by familiarity and by the modality the yawn is perceived. Therefore, the following hypotheses were set up: -

(H1) It is hypothesized that adult chimpanzees yawn contagiously when visually perceiving an adult human yawning, and do not show contagious behaviour when observing the control conditions, gape and close (closed mouth, no movement).

(H2) It is hypothesized that chimpanzees' contagious response to yawning behaviour is modulated by the level of familiarity that the animal has with the observed human. It is expected that yawn contagion will increase with familiarity.

(H3) It is hypothesized that yawn contagion occurs through other sensory modalities apart from vision, i.e. auditory perception. The expectation is that yawn contagion will be induced through a merely auditory perception of the stimulus.

In this study, the question of whether human yawns are contagious to adult chimpanzees is addressed. The yawns of humans and dogs are often accompanied by an auditory component, and the mere sound of a yawn is contagious (Arnott et al. 2009; Silva et al. 2012; Romero et al. 2013). In contrast, chimpanzees frequently yawn without audible sounds. This raises several questions. Firstly, whether a visual stimulus is necessary for chimpanzee yawn contagion. Secondly, whether previous research suggesting a possible connection between yawn contagion and mirror neuron activity holds true in a facial action as opposed to a hand action, as previously tested in macaques (Iacoboni et al., 1999). Thirdly, any effect of a reduction of yawning cues was explored, by exposing the animals to a solely auditory perception of a yawn, and to the visual perception of a less wide-open mouth (gape). Would this go some way to either eliciting yawn contagion or triggering the same gaping action in the chimpanzees? A previous study of yawn contagion in young dogs (Madsen & Persson, 2013) and chimpanzees (Madsen et al. 2013) showed a trend of gape stimuli evoking more yawns than a baseline condition, where the participants interacted with an experimenter merely talking. Gape stimuli may thus go some way to act as a releasing stimulus that potentiates a possible type of fixed action pattern different from that manifested in a yawn contagion response. Would yawn frequency increase, when the stimuli include more components of a full, typical (human) yawn? The prediction would be a decrease of yawning in the following order:

The higher number of episodes of contagious yawning would be in response to the visual presentation of yawn stimuli;

Quantity of yawns diminishing and contagiousness occurring after a time delay for the solely auditory yawn stimuli (requiring the animals to identify the stimuli as yawning sounds, after some cognitive processing);

Further decrease of yawning in response to gape stimuli (viewing a human opening the mouth, not as wide as in a yawn, and then closing it). Importantly, gaping portrays an action that conveys neither an emotional nor any other informational or instructional cue;

Least amount of yawning in response to a closed mouth stimulus (where the human's mouth was closed and lips were sealed). As such, this study represents the first to address the possibility of auditory contagious yawning in non-human primates, a response previously only observed in humans (Arnott et al. 2009) and dogs (Silva et al. 2012).

In relation to hypothesis (1) the present study employed a live presentation of humans (familiar & unfamiliar) portraying the three experimental conditions, also addressing potential confounding issues regarding the use of videos.

In relation to hypothesis (2) the present study explored whether chimpanzees' contagious response to yawning behaviour is modulated by the level of familiarity that the animal has with the observed human. It is expected that yawn contagion will increase with familiarity. In order to test whether developmental or species/stimuli-related issues underlie the contrasting research results of yawn contagion in juvenile (Madsen et al., 2013) and adult chimpanzees (Campbell & de Waal, 2011), cross-species CY in adult chimpanzees was examined, using the same basic design and paradigm, previously used in testing adult dogs (see Joly-Mascheroni et al., 2008). Since yawn contagion in juvenile chimpanzees is not biased towards familiar humans (and there is evidence to suggest that this is also the case for adult chimpanzees, albeit found by using qualitatively different stimuli (Campbell & de Waal, 2011), it was predicted that adult chimpanzees would also denote a generalisation of their CY response to unfamiliar humans. In a previous study of cross-species yawn contagion (Madsen et al., 2013), juvenile chimpanzees produced more than twice as many yawns in response to unfamiliar, compared to familiar, yawn stimuli (albeit the difference was found to be statistically non-significant). The context of that experiment involved the chimpanzees interacting with a familiar and an unfamiliar person (playing with leaves and branches), an interaction that the authors reported the chimpanzees seemed to enjoy, as it evoked grooming sounds and (chimpanzee) laughter. To explore if yawn contagion in chimpanzees might be modulated by familiarity, this study tested whether adult chimpanzees responded differently to the yawns of a familiar human (keeper) and an unfamiliar human (experimenter), while striving to make the interaction between chimp-familiar human and chimp-unfamiliar human as equal as possible during testing.

In relation to hypothesis (3) the study explored whether yawn contagion occurs through other sensory modalities apart from vision, i.e. auditory perception. The expectation is that yawn contagion will be induced through a merely auditory perception of the stimulus. The literature in the field proposes that the triggering of responses is via observation, and the word observation, by definition, refers to visual perception. There are only a limited amount of studies that explored motor contagion through sensory modalities other than vision.

3.2.1 Experiential contagion vs simple motor contagion

There are theoretical and empirical grounds to suspect that CY represents emotional contagion. Theoretically, CY has been suggested to serve the adaptive function of synchronising group behaviour in social animals (Deputte, 1994). Empirically, anecdotal observations of dogs indicate that yawning transfers states of drowsiness (Madsen & Persson, 2013). However, can a state of drowsiness be considered an emotion as such? There is some suggestion that yawn contagion provides an afferent feedback and elicits a similar state in the observer.

To explore if chimpanzee yawn contagion represents a case of state sharing or as might be referred to as ‘experiential contagion’, we tested the behaviours displayed when the chimps observed facial expressions that did not contain any emotional component. It is fair to assume that chimpanzees have already had the experience, the sensation and the feeling triggered by the action of yawning. They can, therefore, relate to that experience, and when they visually observe or recognize it through auditory perception, this may trigger that same sensation or experience. In this experiment, this concept of an experiential contagion was tested both through visual and solely auditory perception.

We examined, behaviourally, if the chimpanzees exhibited signs of drowsiness/relaxation/stress or simply motorically displayed similar or different behaviours in each of the experimental conditions. We tested whether an ‘experiential contagion’ was displayed, when exposed to a mouth closed, a gape or a yawn stimulus. If so, behaviours would denote the possible feeling or sensation that would be accompanying that experience. Furthermore, we measured and compared the duration in which the chimpanzees displayed certain behaviours, for example, how long they spent lying down across the conditions.

The paradigm may offer a contribution to discussions in the literature of the neighbouring field of imitation and on the correspondence problem, on which psychologists working in the field for nearly a century, have come up with two kinds of solution. It is worth noting here, that we are aware that these theories address issues primarily related to learning and imitation but we believe they can, at least indirectly, provide evidence of, and support for, new theories on contagion. These theories, which are transformational and associative (Heyes et al., 2002), suggest that “the correspondence problem is solved by mechanisms that convert a visual representation of the model’s action, derived from observation, into a ‘symbolic’ or ‘intermodal’ representation, and that this intermediate (neither visual nor motor) representation enables observers both to produce the same actions as the model and, as a means to this end, to recognize the similarity between their own actions and those of the model” (Heyes, 2016). On the contrary, associative theories suggest that direct connections between motor and visual representations of those actions solve the correspondence problem, enabling the observer to reproduce the same action as the model, as Heyes calls it, “blindly”. Importantly, she adds, “without explicitly representing the relationship of similarity or dissimilarity between the model’s action and the observer’s actions” (Heyes, 2016).

Spontaneous primate yawns are typically distinguished according to context (rather than form), and related to physiological arousal (Hinde & Rowell, 1962;

Altmann, 1967; Redican, 1975; Deputte, 1994; Vick & Paukner 2010). ‘True yawns’ are observed during rest-wake transitions (correlating with drowsiness and relaxation) and thermoregulatory brain processes (Gallup & Eldaker 2012). By contrast, ‘tension yawns’ co-occur with changes in vigilance and levels of what some authors call “emotional arousal”, such as elevated stress levels during conflict situations, and are considered a displacement behaviour (Goodall 1968; Maestripieri 1992; Baker & Aureli 1997). In this study, the possibility of evoking ‘tension yawns’ was minimised by engaging the chimpanzees in bouts of calm, friendly and playful interactions through the bars of their enclosure. It would be reasonable to argue that a distinction should be made between the feeling of stress, and that of emotion. They are distinguishable sensations or feelings and they do not necessarily have to occur simultaneously. By exploring the behaviours these animals display when exposed to others’ actions, it might be possible to take those behaviours as potential evidence of an association between what is being perceived, either through visual or auditory modalities, with another event that had already been experienced by the animal before, hence ‘experiential contagion’. This study aims to make a small contribution towards this goal.

3.3 Methods

3.3.1 Participants

Participants were 14 adult chimpanzees (Pan troglodytes spp., 10 – 31 yr., mean age ± SD = 21.93 ± 7.43 yr., 10 males, 4 females, see Table 3). The chimpanzees were housed at Fundació Mona Sanctuary (Spain), where they had spent between 1 and 18 years (mean = 7.93 ± 4.21 yr.). The chimpanzees at Mona were rescues from private zoos and homes.

3.3.2 Design and procedure

The study used a repeated measures design, with two independent variables: model familiarity (unfamiliar and familiar human model: a researcher and a familiar keeper, with whom the chimpanzees had a positive relationship) and model behaviour (none/baseline, yawning, auditory yawning, gaping, closed mouth). Each participant received four sessions of 15 min each, with both the familiar and unfamiliar model. A session consisted of a 5-min baseline phase followed by a 5-min phase, where the model repeatedly either yawned in full view of the participant, yawned behind an occluding screen (auditory yawning), gaped or kept her mouth closed. Each phase was followed by a 5-minute post-stimulus observation phase, during which social interaction continued, without the inclusion of the key behaviours (yawning, auditory yawning, gaping, and closed mouth). In all phases the model encouraged the participant to engage in calm interactions through the bars of the enclosure (by blowing soap-bubbles, drawing, showing magazines, teddy-bears etc.).

Yawn: The model repeatedly yawned while being within the participant's 'full' or 'peripheral' field of vision (defined, respectively, as the visual field approx. 0-45° and 45-110° from the sagittal plane between the animal's eyes). Models yawned as naturally as possible, with yawning defined as opening the mouth fully, drawing in air, lifting the shoulders, tilting the head and body backwards, closing the eyes, and producing a vocalisation during exhalation, for a total duration of 5-10 s.

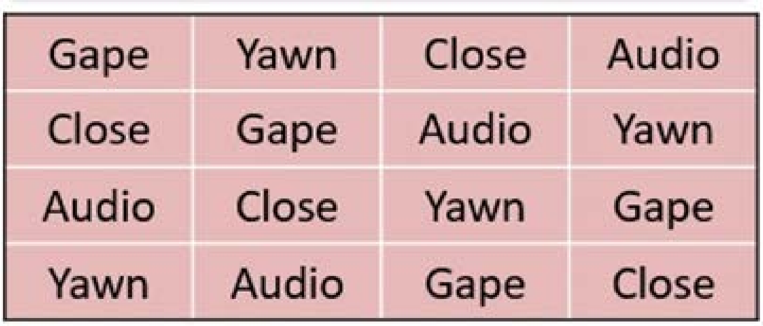
Auditory yawn: The model walked behind a cardboard screen (1.60 x 1.40 m), 1m away and yawned with a vocalisation (see Figure 3.1).

Figure 3.1 Auditory yawning condition behind a screen.

Gape: The model performed repeated (non-yawning) mouth openings, but still opening the mouth (not as wide as in a yawn) and closing it, without audible inhalation and exhalation of air (approx. 4 to 7 seconds), while within the participant's 'full' field of vision.

Closed mouth: The model maintained an expressionless face with mouth closed and lips sealed for the duration of the 5-min phase. Models aimed to expose participants to 15 instances of each behaviour, yet given the restive nature of the animals, yawns and gapes were sometimes produced outside the participants' field of vision. In such cases, the behaviour was repeated, while within the participants' field of vision but never exceeding the max number of 20 behaviours in each condition. The 5-minute conditions were presented in an order determined by a balanced Latin Square.

Table 5 Latin Square order of testing conditions



Gape	Yawn	Close	Audio
Close	Gape	Audio	Yawn
Audio	Close	Yawn	Gape
Yawn	Audio	Gape	Close

Individual sessions were separated by a minimum of 5 minutes and a maximum of 15 days (for 33 % of the sessions, there were more than 12 hours between sessions), depending on how long the participants could be encouraged to engage with the model (sessions conducted on the same day, were separated by a mean of 17.86±4.59 minutes. Participants received two full sequences of sessions, one with the familiar and one with the unfamiliar model, with a minimum 24-hour interlude. All conditions (except for the baseline phase) were counterbalanced across participants, including sessions with the familiar and unfamiliar models (see Table 1 for details). The chimpanzees were tested, individually, between 9.30 h and 18 h in an indoor enclosure. The frequency of yawning in the baseline and yawn condition was not influenced by the time of day of testing (9-12, 12-15, 15-18, Friedman test, Baseline: X2(2) = 1.72, P = 0.423; Yawn: X2(2) = 0.56, P = 0.756). Sessions were recorded (by a Canon Legria HF G25, Sony HDR-305 CX740VE and Panasonic Lumix DMC-FZ200) and scored from videos.

3.4 Analysis

Individual phases (yawn, auditory yawn, gape, closed mouth) and the subsequent five-minute post-observation phases were used as means of comparisons.

Given that chimpanzees yawn at different times of the day, and those yawns would be regarded as spontaneous ones, the rating of the behaviour was subjected to the phase in which the animals were observed, i.e. any yawns found in the gape condition would not be counted as a contagious yawn. Please note the description of the behaviour in primates is exactly the same as in humans i.e. a wide opening of the mouth, accompanied by a long inspiration, followed by a brief acme and a short expiration.

Three independent blind (i.e. not aware of the tested hypotheses) scorers were chosen from a list of raters who were palaeontology students at the Mona Fundation. Observer inter-rater reliability, (that is, the number of agreed scores divided by the total number of scores) of the number of chimpanzee yawns was high (agreement = 99.17%, Cohen's Kappa = 0.99, 36% of sessions scored). Inter-rater reliability with respect to the time that chimpanzees laid down (when a shoulder touched the ground) was perfect (agreement 100%, 21% of sessions scored). Chimpanzee gapes and yawns across the conditions were analysed as the number of behaviours per 5-minute condition. The duration of the baseline (5 min) was the same as all other experimental conditions (5 min) including the post-experimental observation condition (5 min). These baseline phases were taken as measures that were intended to be representative of how much the animal would spontaneously yawn during the day, therefore the baseline phase taken for analysis were the visual and auditory yawn and post yawn conditions respectively. General linear models (GLM) were used to assess the effect of model behaviour, model familiarity and interaction effects.

Participant identity was controlled (random effect) and robust covariances and a Satterthwaite correction were used as approximation (due to the small sample size). Friedman's ANOVA and Wilcoxon signed ranks tests were used for post-hoc comparisons of number of yawns per condition and across conditions. Kruskal-Wallis tests were used to test for order effects. Data were analysed using SPSS Statistics 22 for Windows (IBM Inc.). Values are also reported as the mean ± SEM of spontaneous yawns or gapes per condition, and number of contagious yawns per condition in the yawning, auditory yawning and post auditory and visual yawning phases. All tests were two-tailed and significance levels set at α= 0.05. Ethics Statement: Experimental procedures were non-invasive and complied with the ethical guidelines of the Animal Behaviour Society Guidelines for the Use of Animals in Research. The boards of Fundació Mona Sanctuary reviewed and approved the study.

3.5 Results

Sixty-four per cent (9 of 14) of the chimpanzees exhibited yawn contagion (i.e. yawned more in the yawn than in the baseline condition). The yawn condition elicited in excess of three times as many yawns (N = 99, mean = 7.07±2.26) as the gape (N = 30, mean = 2.14±0.65) and closed (N = 25, mean = 1.79±0.74) conditions (Figure 3.2). A difference in the number of yawns across conditions, including the baseline (0.10), yawn (0.35), auditory yawn (0.15), gape (0.11) and closed phases (0.09, Friedman test: X2(4) = 10.47, P = 0.033), reflected that chimpanzees were more likely to yawn in the yawn phase than in all other phases (Wilcoxon test: yawn vs. baseline: N = 14, z=2.63, P = 0.009; yawn vs. gape: N = 14, z = 2.49, P = 0.013; yawn vs. closed: N = 14, z = 2.43, P = 0.015; yawn vs. auditory: N = 14, z = 1.96, P = 0.050).

About 50% (n = 7) yawned more in the auditory than in the baseline condition, while only 14% (n = 2) yawned more in the baseline than in the auditory condition (Figure 3.2). Overall, chimpanzee yawn frequency across the conditions showed a trend, following the pattern described below, and in Figure 3.2: yawn phase (0.35±0.11) > auditory yawn (0.15±0.06) > gape (0.11±0.03) > closed (0.09±0.04). There was no difference in the total number of yawns to familiar and unfamiliar stimuli across conditions (familiar: mean per min = 0.13±0.04, unfamiliar: mean = 0.17±0.05, Wilcoxon test, N = 14, z = 1.49, P = 0.135), yet unfamiliar yawn stimuli (mean = 0.44±0.14) elicited significantly more yawns than familiar yawn stimuli (mean = 0.27±0.09, Wilcoxon test: N = 14, z = 2.32, P = 0.020).

A similar pattern emerged when comparing the number of individuals that yawned more to unfamiliar than familiar yawn stimuli (50%, 7 of 14 chimpanzees) with those that yawned more to the familiar than unfamiliar yawn stimuli (7.14% 1 of 14, McNemar test, P = 0.034). There was no significant familiarity effect on the number of yawns elicited by auditory yawns (familiar: mean = 0.10±0.04, unfamiliar: mean = 0.21±0.10, Wilcoxon test: N = 14, z = 1.02, P = 0.307), although there was a clear trend of chimpanzees responding more to unfamiliar auditory stimuli (Figure 3.2 and Figure 3.3).

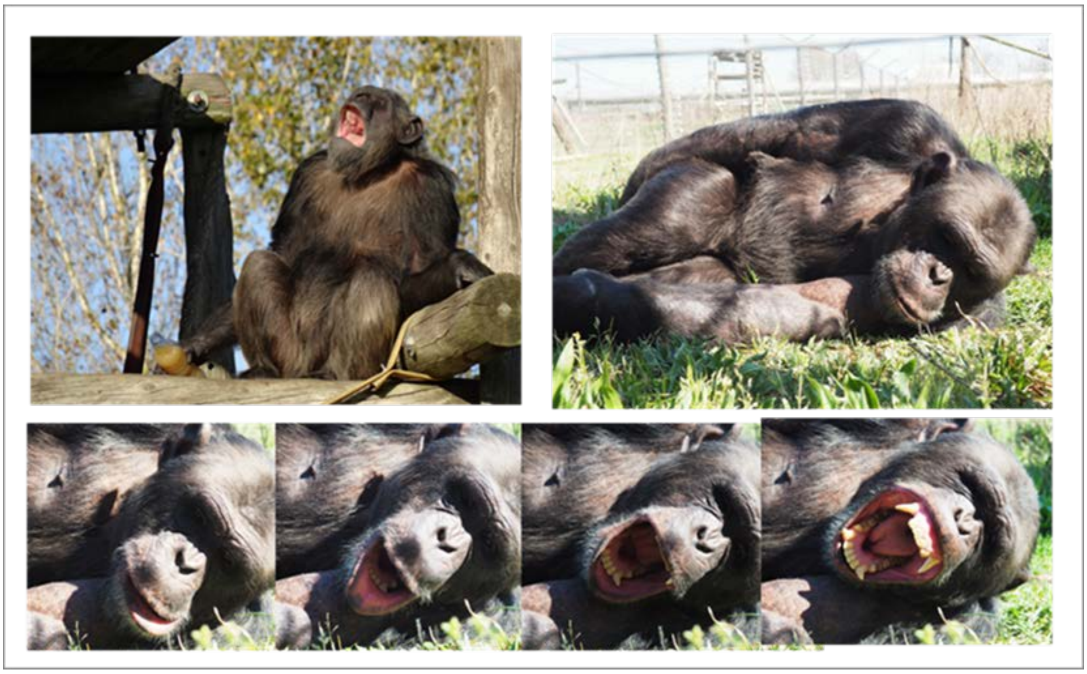


Figure 3.2 Example of Yawning and lying down behaviour.

Furthermore, exploratory post-hoc analyses indicated that chimpanzees were more likely to lie down during both the yawn (5.49±8.81) and auditory phases (8.58±13.70) than the closed mouth phase (1.08±4.01, yawn vs. closed: N = 14, z = 2.37, P = 0.018; auditory vs. closed: N = 14, z = 2.67, P = 0.008). In contrast, there was no difference between time spent lying down in the yawn and auditory yawn phases (N = 14, z = 1.33, P = 0.182), nor between the yawn/auditory phases and the gape phase (5.06±8.71, yawn vs. gape: N = 14, z = 1.18, P = 0.237; auditory vs. gape: N = 14, z = 1.60, P = 0.110), or indeed, between the gape and closed phases (N = 375 14, z = 1.52, P = 0.116).

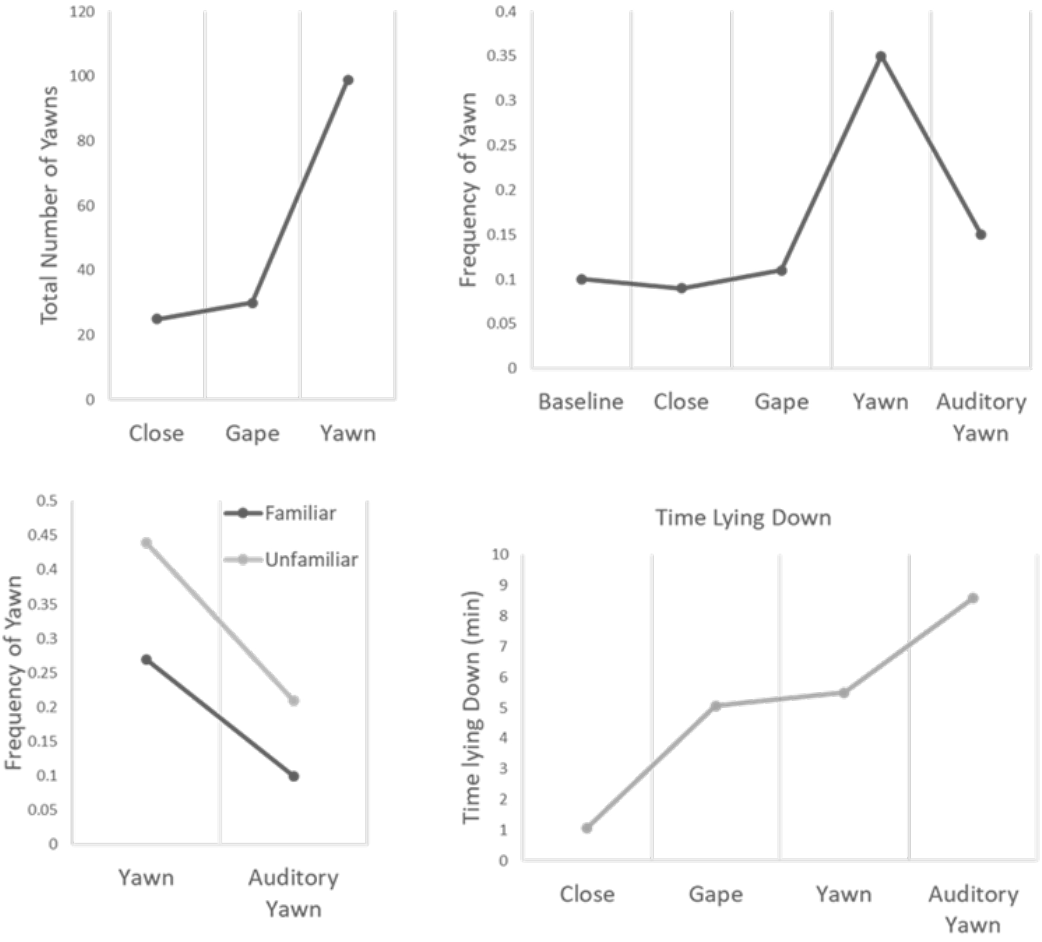


Figure 3.3 Mean number of Yawns (Top left); Number of visual Yawns (Top right); Number of auditory Yawns (Bottom left); Time spent lying down (bottom right)

Finally, there were no order effects (i.e. the frequency of yawning in the yawn condition was not influenced by order of presentation, with yawn condition presented as first, second, third or fourth condition after the baseline: Kruskal-Wallis test: H = 0.97, P = 0.809).

3.6 Discussion

This is the first study to explore contagious yawning across species in a live presentation between chimpanzees and humans, and we found that 64% of the adult chimpanzees exhibited heterospecific (across species) yawn contagion in a live presentation. Adult chimpanzees displayed yawn contagion through auditory perception and they displayed behaviours such as lying down in the yawning and post-yawning condition while displaying signs of drowsiness and making their beds.

The chimpanzees were more likely to yawn contagiously in the yawn phase than in all other phases. It’s worth clarifying that chimpanzees, as do humans and all animals, may yawn at different times of the day and those are regarded as spontaneous yawns, as these are behaviours displayed naturally and not as a response to being exposed to someone yawning in front of them, whether in the closed, gape or baseline conditions.

Overall, yawning across the conditions fitted the predicted pattern. Results, although statistically non-significant, still denote a trend that followed a continuum from contagious yawning rates at its highest when the stimuli included more components of a full, typical yawn, and yawning diminished when those components were absent. That is, the rate of yawning was greatest in response to yawns, followed by the condition of minimalist clues of mere auditory perception of a yawn, followed by gapes and finally, closed mouth stimuli. During typical yawns, the eyes of the yawner (Familiar and Unfamiliar) are briefly closed, but in the gape condition, the eyes remained open. In line with these results, children with autism spectrum disorder who lack spontaneous attention to others’ faces (e.g. Kikuchi et al., 2011), unless they are primed to fixate on the eye region of the yawner (Senju et al. 2009; Usui et al. 2013), show no contagious yawning (Senju et al., 2007; Giganti & Ziello, 2009; Helt, 2010). In Senju’s study, when autistic children were instructed to look at the eyes of the yawner in the video, they yawned contagiously at the same rate as that of typically developed individuals (Senju et al., 2007; see also Giganti & Ziello, 2009; Helt, 2010).

Overall, the chimpanzees did not yawn more in the auditory phase than in the baseline, closed mouth and gape phases. Nonetheless, in line with evidence that only some individuals (be they humans, chimpanzees or dogs) exhibit yawn contagion, while others seem immune or do so at a lower rate, some chimpanzees showed clear evidence of auditory yawn contagion. Fifty per cent of chimpanzees yawned more in the auditory than in the baseline phase, while only 14% yawned more in the baseline phase. This baseline phase was only tested as a measurement to be taken as representative of their yawning rate during the normal day. The proportion of chimpanzees that exhibited heterospecific yawn contagion (to full human yawns, 64%) was comparable with that of adult dogs (72%), found by using the same basic experimental design (Joly-Mascheroni et al. 2008). Like humans and dogs (see

Madsen & Persson 2012), chimpanzees show a developmental increase in susceptibility to yawn contagion, as the combined results from the present study and a similar study of young chimpanzees (Madsen et al. 2013), suggest that infant chimpanzees are immune to CY (0 of 12 exhibited CY), while 48% (N = 21) of juveniles and 64% (N = 14) of adults have shown heterospecific yawn contagion.

To explore if heterospecific contagious yawning represents a type of experiential contagion and involves afferent feedback, this study examined if the chimpanzees showed signs of synchronisation of states of drowsiness or relaxation. Overall, the chimpanzees were more likely to lie down when the human yawned either behind an occluding screen or in full view of them, than when either the keepers (familiar) or experimenters (unfamiliar) kept their mouth (and lips) closed. Moreover, the duration of lying down followed the pattern of auditory yawn > yawn > gape > closed mouth. In contrast to prediction, however, there was no statistically significant difference between the time that the chimpanzees spent lying down during the yawn/auditory yawn phases and the gape phase. Nonetheless, the overall pattern of results suggests that the duration of the rest response when perceiving the human yawned differed from when the human gaped: the rest response in the gape phase was statistically indistinguishable from when the human simply kept her lips closed, while the chimpanzees were more likely to show a rest response in the yawn/post yawn and auditory yawn/post auditory yawn phases, than when the human kept her mouth closed.

Thus, results show evidence that perceiving human yawns elicited signs of drowsiness or relaxation in the chimpanzees, as previously found in humans (Provine et al., 1986), dogs (Joly-Mascheroni et al., 2008) and puppies (Masden & Persson, 2013). Furthermore, in this study, when chimpanzees perceived yawns, they tended to gather leaves, and lie down as they do in the wild. These results seem to suggest there is a transference of a ‘signal’ or message sent across to the perceiver, in this case emitted by the human and picked up by the chimpanzees. It remains to be discussed, whether the seeming transfer of such a signal is a sharing of states, in the act of yawning and in the perception of someone else yawning. Furthermore, the result of the present study may represent sufficient grounds to suggest that future investigations of this signal transfer should be further explored. This would reconfirm that the signal transferring in this context, can include an actual synchronisation of states, as in the present findings, drowsiness behaviour was displayed by the animals, and was not included in the stimuli. It is worth noting that, in the present set up, neither the familiar nor the unfamiliar stimuli included a laying down or drowsiness display. Nevertheless, these findings could still be regarded as the basis of what could be defined as an ‘experiential contagion’. This type of contagiousness can only occur when there is a recognition of the signal emitted, and the perceiver has had a previous experience of that state.

The primary aim of this investigation was to elucidate some of the causes of the differences found in results of studies of juvenile and adult chimpanzee contagion of yawns from humans and conspecifics, and also to implicitly examine if the experiential contagion effect may operate in heterospecific yawn contagion contexts. In domestic dogs, the bias to selectively catch yawns from familiar humans emerges only at later stages of development (Madsen & Persson., 2013; Silva et al., 2012; Romero et al., 2013) and the study therefore examined whether a heterospecific familiarity bias might also develop gradually in chimpanzees, or if chimpanzee yawn contagion is simply not biased towards familiar humans, at any age.

We found that there were overall a greater number of yawns to unfamiliar rather than familiar human yawns. Unfamiliar yawn stimuli also elicited yawns from more chimpanzees, than did familiar yawn stimuli. Similarly, although there was no significant familiarity effect on the number of yawns elicited by auditory yawns stimuli, there was a clear trend in that direction. Chimpanzees did respond more to unfamiliar auditory yawn stimuli. One possibility is that the context of the experiment, during which the chimpanzees showed signs of enjoyment (laughing and grooming behaviours), predisposed them to preferentially catch yawns from the unfamiliar individual, by drawing attention towards the new and unknown individual. This meant that the chimps, by being more attentive, made more eye contact and thereby observed/perceived more yawns. Another possibility could be explored through a full test of whether the chameleon effect modulates contagious yawn contexts. This requires a comparison of the strength of yawn contagion to an unfamiliar individual who is either passive or engages in fun games with the participant. Future research could involve a test in which participants are exposed to the yawns of familiar and unfamiliar individuals across two contexts: (1) a neutral interaction with a passive model, (2) a fun interaction. It could be expected that yawn contagion would increase in accordance with the degree of interaction, and differences in the strength of contagion would denote a bias towards an unfamiliar human, only in the context of fun interaction.

Hatfield and her colleagues have proposed that, as people attend to others, they continuously and unconsciously mimic the other's fleeting emotional expressions and synchronize their facial, vocal, postural, and instrumental expressions with those to whom they are attending. The afferent feedback generated by this mimicry produces a simultaneous congruent emotional experience. Hatfield and her colleagues have termed this process "emotional contagion" and define it as "a tendency to automatically mimic and synchronize expressions, vocalizations, postures, and movements with those of another person's and, consequently, to converge emotionally"(for a review see Hatfield et al.,1994) The capacity for "the imaginative transposing of oneself into the thinking, feeling, and acting of another" (Allport, 1937/1961) requires sufficient cognitive development to differentiate the psychological attributes of oneself and others and the ability to assume the psychological role of another (Eisenberg & Miller, 1987; Feshbach, 1978). These theories apply to human behaviour and particularly with regards to mimicking and imitation. In contrast, contagion has not been sufficiently explored in connection with actions that do not include emotions. The experience of having performed an action does not necessarily have to include the emotion that one would consequently feel after performing that action. Imagine you see someone with tears running down their cheeks. This is likely to lead you to believe that the person might have been crying. Depending on the facial expression that the individual portrays, you might be able to guess if that individual was crying out of sadness or after having laughed out loud. One might even experience an emotional, (happy or sad) feeling that accompanies the visual or auditory perception of actions such as someone crying. However, the emotional component that may or may not be attached to the visual or auditory perception of crying is not present in the perception of yawning. The visual perception of someone crying, may or may not necessarily make us feel like crying. Nevertheless, if we hear, but cannot see someone crying, we might still be able to deduce if the person was crying out of sadness or happiness. Although laugher and crying contagion goes beyond the exploration of the present study, the example serves to demonstrate the accompanying feeling that has to be attached to the perception of an action in order to be considered an emotional contagion. To summarise, we introduce the concept of experiential contagion, in order to differentiate between the experiencing of an action that would be associated with an emotion and that of the perception of an action that triggers the sensation of having previously experienced how it feels to perform that action.

Given the possible link between behavioural contagion and empathy, we suggest that the variability in chimpanzee yawn contagion to different species and across contexts may reflect empathetic flexibility and the extent to which particular contexts and classes of individuals may or may not evoke empathy. If empathy is one of the factors that would have an impact on yawn contagion, we propose that chimpanzees may exhibit a targeted type of empathy in interactions with conspecifics (resulting in yawn contagion biased towards in-group members: Campbell & de Waal 2011), and a more generalised type of empathy towards humans (resulting in there being no difference in the contagion of yawns from familiar and unfamiliar humans, if they simply view video stimuli of humans yawning, without any accompanied interaction: Campbell & de Waal in press, see also Madsen et al. 2013). However, the live presentation here, shows the medium may have had an impact on the response in previous studies. Therefore, further explorations where comparisons are made between videos and live presentations might be a fruitful route for future studies to take. Finally, the results of the present study suggest that chimpanzee yawn contagion is biased towards unfamiliar humans, if the context is one of interacting with a new individual, that they may wish to bond and foster a relationship with and this may indicate a possible relationship with the chameleon effect. We therefore suggest that, the prosocial consequences of the chameleon effect may extend to non-conscious mimicry and contagion in non-humans, and that chimpanzees are more susceptible to behavioural contagion from individuals, with whom they may wish to affiliate. Therefore, this might constitute proof that distinctions be made between mimicking, imitation, and experiential contagion.

4 STUDY 2. BEYOND HUMAN: CONTAGIOUS YAWNING IN PRIMATES ELICITED BY AN ANDROID

©Ramiro Joly-Mascheroni

4.1 Introduction

Humans, the only animals who socially interact predominantly via spoken language, also communicate through physical gestures, facial actions and body language. All animals display non-verbal behaviours, too, and these often constitute a key part of their social interactions and communication processes.

Social interaction and communication is only thought to be possible between animate living beings, particularly between group-living social animals. But, what if one of the interacting partners was an inanimate agent? A humanoid robot was created to provide an artificial stimulus which visually looked human, but would not be a screen-based avatar and would be able to repeat actions with strict accuracy and according to time-dependent variables. This device was created to explore potential underlying processing mechanisms in the human and animal brain, when perceiving communicative actions of other agents. That is, when perception is not that of other humans' actions but rather that are similar-looking to humans, but are, in fact, man-made objects. The android's facial movements are similar to those of humans, in terms of dynamics, configuration, kinematics and some biological motion features, such as velocity. Simulating biological systems, those of animate/living entities, by building a human-like machine that reproduces human behaviours, may serve to show us how both humans and animals deal with events around them, and the plausible mechanisms involved in the perception, processing and understanding of the actions of others. These explorations may provide us with guiding principles that may help us better understand our own evolution and that of animals. We chose the embodiment-inducing act of yawning, to explore further the contagious aspects of this non-goal directed and non-object directed (intransitive) action, and in this case, an act performed by a non-human agent, an android.

Although the ultimate role of spontaneous yawns remains disputed (see Guggisberg et al., 2011), it has been suggested that it serves many physiological functions such as a thermoregulatory one (Gallup & Eldaker, 2012), stress-reductive and non-verbal communicative purposes. Spontaneous yawning has also been claimed to be related to states of rest, arousal and focus of attention (Walusinski, 2013) and its contagiousness serving to synchronise group behaviour (Deputte, 1994).

Humans, chimpanzees and dogs develop susceptibility to yawn contagion gradually, and it becomes prominent in these species around the ages of 4 years, 5 years and 7 months, respectively (Anderson & Meno, 2003; Helt et al., 2010; Millen & Anderson, 2011; Madsen & Persson, 2013; Madsen et al., 2013).

A possible relationship between CY and empathy has been established when the emergence of yawn contagion was found to concur with the development of Level 2 perspective-taking (children: Gzesh & Surber, 1985; chimpanzees: Povinelli et al., 1994; dogs: Maginnity, 2007) and it has been implied that it relies on the development and interaction of several cognitive capacities, such as perspective-taking, attention to and identification of others’ states, and also to a particular type of empathic reaction sometimes referred to as affective empathy (Deputte & Walusinski, 2002; Madsen et al., 2013).

Yawn contagion has also been interpreted as a particular type of emotion contagion. Theories to support this interpretation claim that contagious yawning relies on two inter-linked processes: non-conscious mimicry and afferent feedback. Non-conscious mimicry, the so-called ‘chameleon effect’ (See Chartrand & Bargh, 1999 and Yoon & Tennie, 2010) is the propensity to mirror others’ behaviours that in social interactions we may emulate, such as physical postures, facial expressions, leg positions or limb movements, without particular purpose, individuals' awareness or conscious intent. Studies exploring social interactions found that body language and facial expressions can influence emotional experiences of the particular communication, in some cases providing an afferent feedback, e.g. reciprocating smiling: (Soussignan, 2002); or in a more general whole-body posture: (Briñol et al., 2009, see also Adelman & Zajonc, 1989). Results of previous studies may offer insights into laughter or crying contagion, but those findings cannot be extended to yawn contagion, as laughter often has an emotional component attached to it, whereas yawning has not. Some types of non-conscious mimicry have been reported to give rise to emotional contagion, whereby mimicking someone's movements or imitating facial expressions has been found to lead individuals to converge emotionally (Hatfield et al., 2009). Nevertheless, there is no evidence of a direct causal relationship between contagious yawning and emotion-related feelings. Furthermore, spontaneous yawning tends to occur in the transitional periods between rest and arousal. Moreover, there is no indication to suggest that these in-between stages would necessarily relate to any emotional feeling. As opposed to contagion, mimicking or imitating have indeed been found to serve a positive function in social interactions, by exerting an emotional feedback loop in affiliative relationships (Carpenter et al., 2013). Thus, in humans, being mimicked increases affinity, liking, and empathic reactions, as well as prosocial behaviours towards both the mimicker and people not directly involved in the mimicry situation (Lakin & Chartrand, 2003; Van Baaren et al., 2004; Carpenter et al., 2013). Furthermore, social motivations, such as the desire to bond with another, have been found to increase non-conscious mimicry in humans (Lakin & Chartrand, 2003), suggesting that mimicry is a (non-conscious) strategy to affiliate with others (Chartrand et al., 2005). Nonetheless, this study shows that we ought to be cautious when we extend these assumptions and evidence to the animal kingdom.

In many animal species, we see the offspring copying or imitating their parents in, for example, hunting or self-cleaning techniques (Over & Carpenter, 2013). These types of mimicking behaviours are a phylogenetically old phenomenon that constitutes the basis for animal learning. We know that imitation is not restricted to humans. For instance, capuchin monkeys (Cebus apella) prefer to affiliate and interact with humans who imitate them (Paukner et al., 2009). These types of socially positive effects of imitation have also been found in children as young as 18 months, with whom Carpenter observed that pro-social behaviour increases relative to the level of mimicking behaviours (Carpenter et al., 2013).

In line with evidence that humans are more likely to mimic those they like or would affiliate with, (Norscia & Palagi, 2011), chimpanzees (Campbell & de Waal, 2011), bonobos (Demuru et al., 2012), gelada baboons (Palagi et al., 2009) and dogs (Silva et al., 2012; Romero et al., 2013) are more likely to catch yawns from those with whom they are familiar or already socially bonded.

Social modulation of yawn contagion has only been demonstrated in adult individuals. Neither young dogs (Madsen & Persson, 2013) nor juvenile chimpanzees (Madsen et al. 2013) have shown a familiarity-bias on heterospecific CY. These previous findings seem to suggest that CY only emerges at later stages of development (Madsen & Persson, 2013), which is supported by evidence of familiarity-biased heterospecific yawn contagion in adult dogs (Silva et al. 2012; Romero et al., 2013). Nonetheless, young chimpanzees have only been explicitly tested when viewing the yawns of humans in a live social context, whereas adult chimpanzees have been tested with respect to conspecific yawn contagion (Campbell & de Waal, 2011; Massen et al., 2012), and more recently, heterospecific yawn contagion (Campbell & de Waal, 2013) using videotaped yawn stimuli. The difference in results pertaining to adult chimpanzees may thus not depend exclusively on developmental issues, but on the nature of the stimulus: whether the yawns derived from humans or conspecifics and/or whether they were presented in a live context or on video.

Computer animations have been successfully employed in previous studies with chimpanzees (Campbell, Carter, Proctor, Eisenberg & de Waal, 2009), and results have been interpreted to study animal and human behaviour and cognition. Presentation of video images of real behaviour has also proven to be both useful and to have several limitations, see Campbell & de Waal (2014). It is the large differences between setups and multitudes of paradigms exploring yawn contagion that seem to be one of the main contributors to the ongoing debate. Here, to address this particular problem, and in order to provide the chance of performing reliable comparisons, we employed the same live presentation technique, previously used in our studies with dogs, chimpanzees and humans (Joly-Mascheroni et al., 2008; Joly-Mascheroni et al., submitted).

At the outset, robots and artificial physical agents, differ from computer animations in the obvious fact the subject can interact and share the same environment (Franklin & Graesser, 1996). The successful marriage of artificial intelligence and computer science has made possible to create robots and agents with humanlike capabilities, such as lifelike gestures and speech. Typically, "robot" refers to a physically–embodied system whereas "agent" refers to a software system. Some examples of humanlike robots are NASA's Robonaut, a humanoid that can hand tools to an astronaut (robonaut.jsc.nasa.gov/robonaut.html), Honda's Asimo, and Hiroshi Ishiguro's android, Gemini. Software agents include other versions of animated icons such as Clippit, the Microsoft Office software assistant that has now become Cortana, and used to offer voice conversational help and still keeps the three-dimensional characteristic presence, predecessor of avatars and 3D video presentation and the newer version Alexa. Robots have started to provide cognitive neuroscience with a unique opportunity to observe human and animal interactions with technological "species or agents", and use as a window to human and animal social cognition (Scassellati, 2004). Humans tend to incorporate their common habits and attitudes into these interactions with robotic agents. Human stereotypic responses to these robotic stimuli can vary greatly and generally seems to depend on their humanlike faces (Yee, Bailenson, & Rickertsen, 2007). For example, authors reported that humans think that baby-face looking robots are sociable and friendly (Powers & Kiesler, 2006). Human participants also tend to attribute knowledge to robots such as landmarks, and depending on the nationality, knowledge of dating depending on whether its voice is male or female (Powers et al., 2005). A human face on a software agent induces participants to cooperate with it as much as they do with a real person (Parise, Kiesler, Sproull, & Waters, 1999). Participants have been reported to recognize extroverted and introverted synthetic speech on a book buying website and reveal similarity–attraction responses in their book reviews and reviewer ratings (Nass & Lee, 2001). Mimicry in an agent (Bailenson & Yee, 2005) and perspective taking in a robot (Torrey, Powers, Marge, Fussell, & Kiesler, 2006) lead to more favourable attitudes. Nonetheless, not all behavioural or perceptual events can explain the entirety of possible social scenarios and potential aspects of anthropomorphism. Thus, we are only beginning to employ these agents in our investigations of human and animal behaviour. Psychology researchers are starting to realise the potential benefits towards a better understanding of both animal and human brain activation, cognitive processes, and strictly related to the present work, animal behavioural responses. Therefore, just being aware of previous findings pointing out possible limitations or offering cautionary attitudes is sufficient, but should not be a deterrent to continue using these agents to explore animal and cognitive issues with the help of man-made machines.

Although there is a growing body of research that employs robots as experimental stimuli in action observation tasks, the cognitive neuroscience literature on the perception of robots has inconsistencies (Kilner et al., 2003; Chaminade & Hodgins, 2006; Chaminade et al., 2007; Gazzola et al., 2007; Oberman et al., 2007; Press et al., 2007; Saygin et al., 2012; Urgen et al., 2013). Nevertheless, this route seems to represent a reasonable next step from previous techniques employed incorporating technological advances in the exploration of human behaviour. Some studies reported that perception of robot actions results in similar activity in the MNS (as compared to that for human actions), whereas others have argued that the MNS is not responsive to nonhuman actions (Tai et al., 2004).

For example, in a previous experiment, participants who owned a dog were more cooperative with a doglike software agent than those who did not own a dog (Parise et al., 1999). When participants were asked to imagine “their own dog” or “a neighbour’s dog” enacting the identical behaviour, some explained their imagined own dogs’ behaviour more anthropomorphically; this difference held even among those who did not actually own a dog (Kiesler, Lee, & Kramer, 2006). This result mirrors people’s tendencies to attribute more complex human qualities to people they like (Leyens et al., 2000). Following this comparative perspective, if our relationship with an animal or object changes how we anthropomorphize it (Kiesler, Lee, & Kramer, 2006), then a context–sensitive process of anthropomorphizing machines and animals would seem to exist, and run in parallel to perceptual and behavioural processes. Perhaps such a process evolved as humans learned to protect and value other people and animals (Caporael & Heyes, 1997). If anthropomorphism is partly a value prescription process that facilitates potential interaction, then face–to–face interaction with a humanlike machine may prompt greater anthropomorphism of the machine, but this may not be such a bad result if the findings provide insights into general or particular social interaction theories. However, this may or may not be the case in animals' behavioural responses to machines. This is something we still don't know. We do know, that authors previously stated that two important attributes of face–to–face interaction are that one's partner is embodied and that he or she is physically present (Kiesler et al 2008). The actual presence of others is physiologically arousing, and potentially provoking a kind of "social facilitation" (Zajonc, 1965). This assumption was made long before any of today's technological devices were invented. Therefore, there is a possibility that an embodied behaviour and actual physical presence of the artificial agent could make a machine more salient and raise the importance of the event. Consequently, the animal may look at it more or pay more attention to it, but these would be positive consequences of the use of these stimuli, even if they may also encourage anthropomorphism on the part of the animals, which is something we may never know.

In this study, we explored yawn contagion "across agents". Our aim was to test if an artificial agent yawning represented a stimulus that was sufficient to induce yawn contagion in animals, as this would occur in such an encapsulated manner that could not be modulated by any potential social contextual factor. Results, therefore, would warrant further explorations of the impact empathy may have on yawn contagion. Importantly, we examined whether chimpanzees yawn contagiously when observing an unfamiliar human-looking robot, which from an anthropological perspective, aimed to assess the possibility that the act of yawning, and its contagious feature could have represented a rudimentary form of communication before humans acquired language.

4.1.1 Hypotheses

The main aim of this study is to explore whether chimpanzees are susceptible to a different type of heterospecific yawn contagion, one never explored before, i.e. across agents, (note that objects cannot be categorized as species).

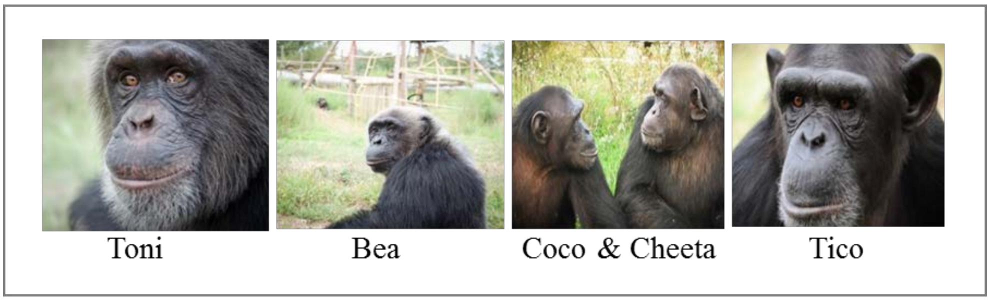
(H4) It is hypothesized that adult chimpanzees yawn contagiously when visually perceiving an inanimate agent (android) moving in a manner that simulates yawning. This yawning behaviour is predicted to be stronger in the yawn condition, than in the control condition gape and close (closed mouth, no movement).

(H5) Depending on the results from (1) it is hypothesized that after being exposed to the yawning stimulus, the animals will display behaviours that denote experiential contagion. The expectation is that there will be differences in the duration spent lying down across the three main experimental conditions.

4.2 Methods

4.2.1 Participants

Participants were 14 adult chimpanzees (Pan troglodytes spp., 10 – 31 yr., mean age ± SD = 21.93 ± 7.43 yr., 10 males, 4 females, see Table 3). The chimpanzees were housed at Fundació Mona Sanctuary (Spain) where they had spent between 1 and 12 years (mean = 7.93 ± 4.21 yr.). The chimpanzees were rescues from private zoos and homes. Experimental procedures were non-invasive and complied with the ethical guidelines of the Animal Behaviour Society which establish the standard and safe Guidelines for the Use of Animals in Research. The ethics board of Fundació Mona Sanctuary and the Psychology Department Research Ethics Committee of City, University of London, reviewed and approved the study. See in Figure 4.1 some of the participants.



Toni Bea Coco & Cheeta Tico

Figure 4.1 Some of the chimpanzees that participated in the study.

4.2.2 Design and Stimuli

The study used a within-subjects design, with an independent variable of observation of an android depicting a yawn, a gape or a close mouth. A human-looking robot head was created (Android), with realistic biological features and motion dynamics. Thirty-three servo motors were used in the production of the robotic head in order to create the movements. When the android is switched on, its neutral expression constitutes the close (closed mouth) condition. All the robotic head's facial movements are programmed to last a total of 10 seconds from onset to offset. Only 9 of the 33 motors were employed for the neutral expression, and to specifically portray the non-expressive nature of a neutral expression. A total of 12 out of the 33 servos were active during the gape expression. Two on each side on the top of the mouth and two on each side on the lower part of the mouth. The rest of the active servos act as support for the rest of the facial expression to remain static. Eight mini servos placed around the eye brows regions, were designed to exemplify the corrugator muscle movement, which forms part of the yawning expression. The Yawn condition required 6 mini servos to create the internal space necessary for the movement command. These "space facilitator servos", are placed in the back of the cheek area to maintain the facial structure in the same position and therefore prevent the portrayal of more than one expression at the same time. Motion time, speed, velocity, muscle simulator motion pattern, motion parameters, modification adjustment and maintenance were programmed, recorded and automatically adjusted for each of the android's facial expressions (Figure 4.2).

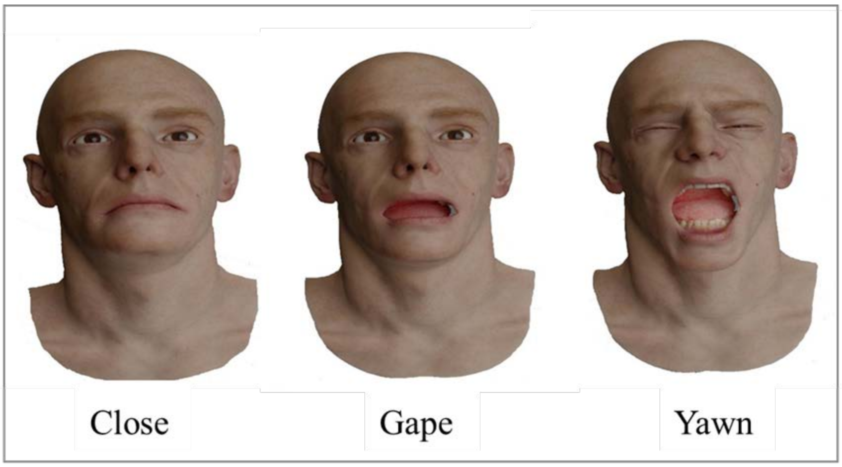


Figure 4.2 Android in the Close, Gape and Yawn conditions

Modifications to the motion patterns were intended to emulate, in an artificial-non-biological manner, those of the human facial biological motion parameters. Although all the previously-programmed movements for each target facial expression, and for all conditions, were restricted to a maximum duration of 10 seconds, the motion length periods were intended to respect those of an equivalent human facial motion for each respective expression. That is, although a robotic movement would never look as natural and biological as a human movement, the smoothness of the trajectory of the simulated muscle area was reproduced as human-like as possible. Given that the android's face is composed of several layers of strong silicone, there are inevitable differences between how a human facial skin would look and feel, and that of a robotic replication. The artificially-produced materials could never equal the qualities of the human skin. Nevertheless, the android does looks realistic, but still possessed features that denoted it was an artificial agent, such as a transparent back, that displayed the internal mechanism. It was placed on a base, which showed it could never be a real human face.

There were three observation conditions and an initial baseline measurement was obtained when the box where the android lived was covered with a black cloth:

Close: The model maintained an expressionless face with mouth closed and lips sealed for the duration of the 5-min phase.

Gape: The model performed repeated (non-yawning) mouth openings. This involved opening the mouth, not as widely as in a yawn, and keeping the expression in that open mouth (gape) position. The android portrayed the gaping expression for the similar duration to that of a yawn, (approximately 6 to 8 seconds) and then closed its mouth. The whole movement took 10 seconds from start to finish.

Yawn: The model repeatedly yawned while being within the participant's 'full' visual field approx. (0-45°) or 'peripheral' field of vision (defined, as 45-110° from the sagittal plane between the animal's eyes). The android model repeatedly displayed a yawning action, with yawning defined as, opening the mouth fully, simulating drawing in air, closing the eyes, then opening them while its mouth closed. The whole movement took 10 seconds, and the action was displayed repeatedly for a total duration of 5 minutes. The android actions were activated a minimum amount of 15 times and a maximum of 20 times per condition by the experimenter who was concealed behind a screen and not visible to the animal. The motion control was achieved by a previously programmed routine of pressing one of 3 buttons on the control panel of the android (Close, Gape, Yawn). This would activate the facial movement portraying the particular expression programmed for the condition.

4.2.3 Procedure

Each participant received four sessions of 15 min each. A session consisted of three phases. All sessions started with and 5-min baseline phase. This was followed by a 5-min observation phase, where one of the three actions performed by the android was performed (close, gape or yawn). Each observation phase was followed by a 5-minute post-stimulus observation phase, during which there was no interaction between the experimenters and participants, and the android box was covered, to avoid any further interaction.

In all phases, the model was covered until the condition started, which was the time when the front panel covering the android was lifted, revealing the android that could only be seen within a 45° angle. It is important noting that the chimpanzees were free to wander within the limits of their enclosure, and this consequently meant that if they chose to remain away from the android, this would mean they might not have been able to see the android’s movements from where they chose to sit or lie down. See Figure 4.3 for representation of angle of view. To control for the fact that some participants would not even look at the stimuli, we measured the time that each chimpanzee spent looking in each of the conditions.

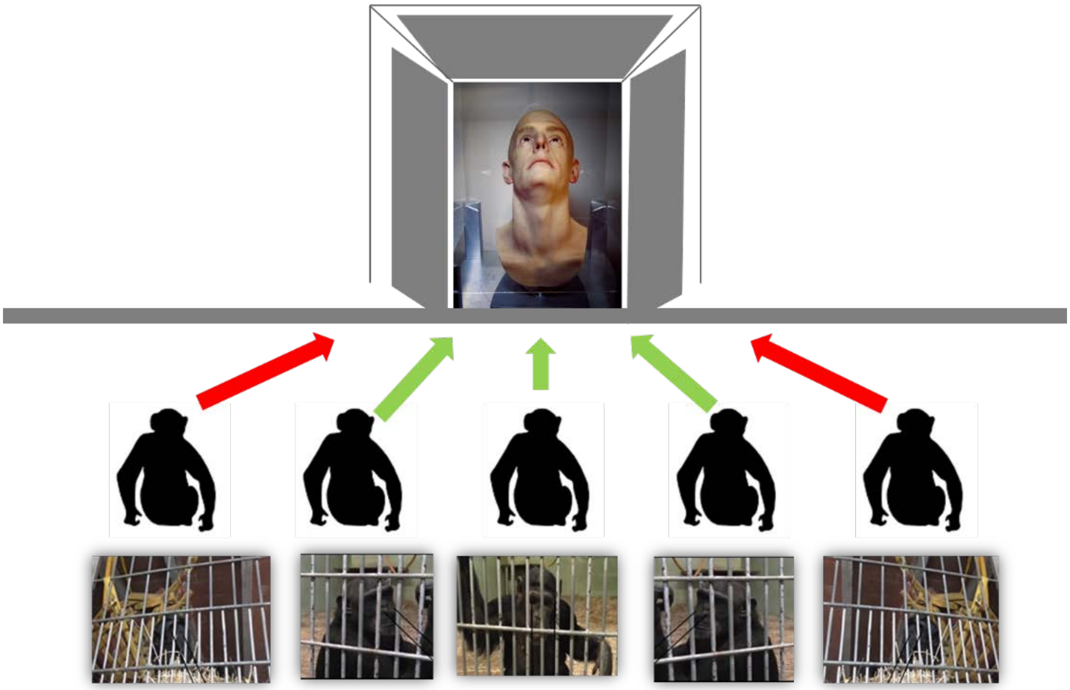


Figure 4.3 Schema representing the angle of vision. Android head was placed in an opaque box, only visible from the front. Chimpanzees would freely move and position themselves where they could either see the android (green arrows) or not (red arrows).

Participants were exposed to 15 instances of each behaviour, yet, given the restive or agitated nature of the animals, yawns and gapes were sometimes produced outside the participants’ field of vision. In such cases, the behaviour was repeated, while within the participants’ field of vision, but never exceeding the maximum number of 20 behaviours in each condition.

Individual sessions were separated by a minimum of 5 minutes and a maximum of 15 days (for 50 % of the sessions, there were more than 12 hours between sessions). In order to minimize interference with the Sanctuary´s routines, sessions conducted on the same day, were separated by a mean of 30 minutes. All conditions (except for the baseline phase) were counterbalanced across participants, (see Table 6 for details).

Table 6 Latin square for order of condition.

		Order of condition		
Victor	Baseline	Closed	Gape	Yawn
Africa	Baseline	Gape	Yawn	Closed
Waty	Baseline	Yawn	Closed	Gape
Bea	Baseline	Yawn	Gape	Closed
Juanito	Baseline	Closed	Yawn	Gape
Nico	Baseline	Gape	Closed	Yawn
Bongo	Baseline	Closed	Gape	Yawn
Toni	Baseline	Gape	Yawn	Closed
Tico	Baseline	Yawn	Closed	Gape
Marco	Baseline	Yawn	Gape	Closed
Charly	Baseline	Closed	Yawn	Gape
Coco	Baseline	Gape	Closed	Yawn
Tom	Baseline	Closed	Gape	Yawn
Cheeta	Baseline	Gape	Yawn	Closed

The chimpanzees were tested, individually, between 09.30 h and 18:00 h and in an enclosure the animals were familiar with. The frequency of yawning in the baseline and yawn condition was not influenced by the time of day of testing (9-12h, 12h-15h, 15h-18h, Friedman test, Baseline: X2 (2) = 1.72, P = 0.434; Yawn: X2 (2) = 0.56, P = 0.890). Sessions were recorded (by a Canon Legria HF G25, Sony HDR-305 CX740VE and Panasonic Lumix DMC-FZ200), two Go Pro cameras, and scored from videos.

4.3 Analysis

Figure 4.4 Examples of some of the chimpanzees own facial expressions.

Independent observers (3) analysed the videos and rated the number of yawns, gapes, and lying down responses. Lying down was defined as: whole body in a horizontal position either on the ground or in their enclosure’s hammocks. If on the ground, at least one shoulder should be in contact with the floor. Chimpanzee yawns across the conditions were analysed as the number of yawns per 5minute phase. Each observation phase (closed mouth, gape and yawn) and the subsequent five-minute post-observation phase.

Observer inter-rater reliability of the number of chimpanzee yawns was extremely high (agreement = 99%, Cohen's Kappa = 0.99, 75% of sessions scored). Inter-rater reliability with respect to the time that chimpanzees laid down (defined as when a shoulder touched the ground), and did not include their hammocks, was perfect (agreement 100%, and 100% of sessions scored).

Generalised linear models (GLM) were used to assess the effect of the different model behaviours, and to later explore potential interaction effects. We controlled for participant identity (random effect) and used robust covariances and a Satterthwaite approximation (due to the relatively small sample size). Friedman's ANOVA and Wilcoxon signed ranks tests were used for post-hoc comparisons of Kruskal-Wallis assessments were used to test for order effects. Two Spearman's correlations were performed to examine the relationship between the number of seconds lying down in the Yawn condition (During + Post exposure) and the time lying down in the Closed condition (During + Post exposure); and between the number of seconds lying down in the Yawn condition (During + Post exposure) and Gape condition (During + Post exposure). A final Spearman's correlation was run to examine the relationship between the time looking at the stimuli (collapsed across all three conditions) and number of yawns in Yawn plus Post Yawn.

Data were analysed using SPSS Statistics 23 for Windows (IBM Inc.). Values are reported as the number of yawns per condition, as the mean ± SEM number of yawns per condition and the total number of yawns and gapes across all conditions.

Finally, analysis was also performed collapsing the experimental and post experimental phases for exploration purposes. All tests were two-tailed unless specified, and significance levels set at $\alpha = 0.05$.

4.4 Results

Chimpanzees displayed behaviours denoting yawn contagion by observing the yawns of an android, an inanimate agent. A large number (57.1 per cent N=14) of the chimpanzees exhibited yawn contagion (i.e., yawned contagiously at a higher rate in the yawn condition than in the baseline condition). The yawn condition elicited 22 yawns, and, 23 yawns were observed in the post yawn condition. The gape condition elicited 16 gapes in the gape experimental condition (N = 14, mean =1.143) and 7 gapes (N = 14, mean =0.5) where observed in the post gape condition. There were no yawns observed in the closed condition and 4 spontaneous yawns were displayed in the post closed condition (mean =0.286) (See Figure 4.5). Upon inspection of raw data (Figure 4.6) and Shapiro-Wilks tests of normality, it was clear that all variables, except for Time spent looking (TL) total (p=.582) were significantly different from normality (p<.05). Therefore, non-parametric tests were used for analyses.

A larger number of yawns were displayed by the chimpanzees in the Yawn + Post Yawn conditions together (total =45 yawns), than in all the other conditions, such as Baseline (total= 5 yawns), Closed + Post Closed (total=4 yawns) and Gape + Post Gape (total=13 yawns), (Wilcoxon test: yawn vs. baseline: N = 14, Z=-2.81, P =.005; Yawn + Post Yawn vs. Gape + Post Gape vs. Closed + Post Closed: N = 14). Overall, chimpanzee yawn frequency across the conditions showed a clear yawn contagion trend, following the pattern described below and in Figure 4.5. The yawning condition elicited contagious yawning in the yawn phase (N_{yawns}= 22) > gape phase (N_{yawns}=0) > & closed phase (N_{yawns}=0), Friedman's X^2 =10.46, P=.005.

Follow up Wilcoxon tests showed significant differences between Yawn + Post Yawn vs Closed + Post Closed (N =14, Z=-2.503, P=.012) and Yawn + Post Yawn vs Gape + Post Gape (N=14, Z=-2.047, P=.041).

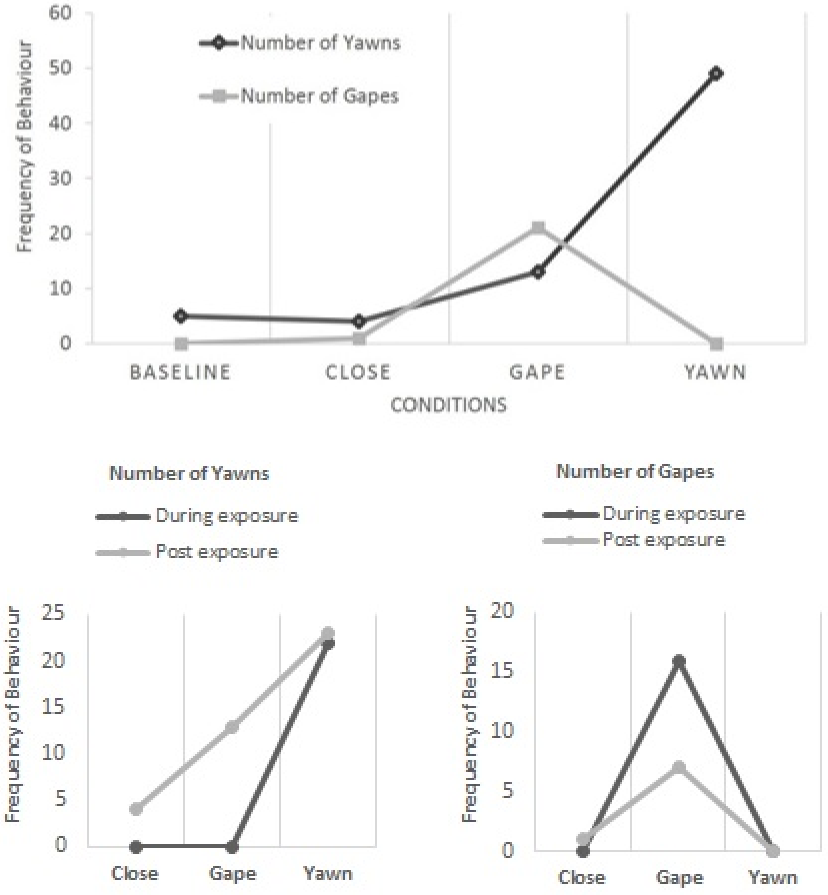


Figure 4.5 Total number of behaviours displayed. Top panel shows frequency of number of yawns and gapes in the four experimental conditions (Baseline, Close, Gape, Yawn). Bottom left panel shows frequency of yawns during the exposure and post exposure period (5 min each). Bottom right panel shows frequency of gapes during exposure and post exposure period (5 min each).

In order to explore chimpanzees´ behaviours that denoted signs of relaxation or drowsiness when exposed to either Yawn, Gape or Close mouth stimuli, we compared the duration (reported in seconds per condition) spent lying down across the three main experimental conditions. Yawn vs. Closed, Wilcoxon test, (Z=-2.55, p=.011); Yawn vs. Gape was also statistically significant, (Z=-2.56, p=.011). Closed Lying down vs. Yawn Lying down Wilcoxon test, (Z=-2.02, p=.043).

In contrast, there was no statistically significant difference between time spent lying down in the closed and gape conditions (N = 14, z =-1.46, P=0.144). These results were reflected in the means, as mean time spent lying down in Yawn + Post was 108.83 sec > 88.25 sec in the gape condition > 62.77 sec in the closed condition >0 sec during the baseline.

A positive correlation was found between the total Time Looking at the stimuli and Yawn plus Post Yawn, (r_s=.564, p=.035). Inspection of the means showed that chimpanzees were more likely to look (TL) during the Gape (TL =1141 sec) and Post Gape conditions (TL=675.5 sec), total TL=1816 sec, as compared to the Yawn (TL=1367sec), and Post Yawn phases (TL=318.5sec) Total (TL=1685.5 sec), and Close (TL=910 sec) and Post Closed phase (TL=352 sec) Total TL= 1262 sec). Spearman's correlations revealed that there was a significant, positive correlation between the number of seconds Lying down in the Yawn condition (During + Post exposure) and the time Lying down in the Closed condition (During + Post exposure): r_s=0.58, p=.028; and a significant, positive correlation between the number of seconds lying down in the Yawn condition (During + Post exposure) and the number of seconds lying down in the Gape condition (During + Post exposure): r_s=0.55, p=.042. The time spent Lying down was highest in the Yawn condition (LD=639.9 sec) + Post Yawn phase (LD=883.8 sec) (Total LD=1523.7 sec), than in the Gape condition (LD=590.5 sec) + Post Gape phase (LD=645.1 sec) Total (LD=1235.6 sec); in the Closed condition (LD=340.4 sec) + Post Closed condition (LD=538.4 sec) Total (LD=878.8 sec), and Baseline (0 sec) (Figure 4.6).

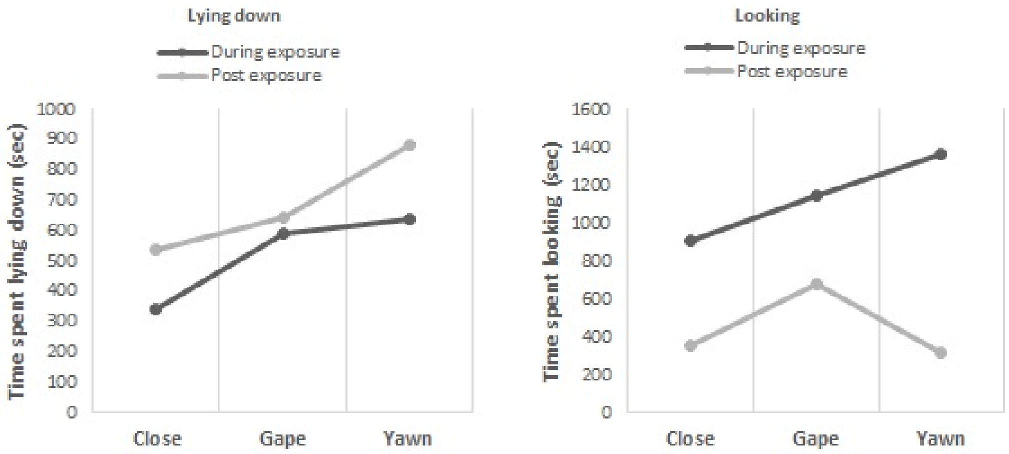


Figure 4.6 Time spent lying down (left) and looking at the android (right).

The animals seemed more likely to yawn contagiously and/or lay down if the android was within view distance, that is, within the 45° angle (Figure 4.3).

Figure 4.7 Example of a participant in a lying down position.

Finally, any potential order effects were controlled by using a Latin square method order of presentation to each condition and (i.e., the number of yawns in the yawn condition was not influenced by the order of presentation, whether the yawn condition was presented as the first, second, third or fourth (post) condition after the baseline: Kruskal-Wallis test: H = 0.97, P = 0.809).

4.5 Discussion

This is the first study to explore contagious yawning in a live presentation, between chimpanzees and an inanimate agent, an android. Findings show that a robust number, 8 chimpanzees (N = 14, 57%) of the adult chimpanzees exhibited across-agent yawn contagion. That is, when the animal was in front of, or within the angle of view of, an object that simulates a yawn, they tended to yawn contagiously. The chimpanzees were more likely to yawn contagiously in the yawn phase, than either yawning spontaneously or not yawning at all, in any of the other conditions. Adult chimpanzees displayed behaviours such as lying down in the yawning and post-yawning condition, while also showing signs of drowsiness and making their beds, by gathering leaves and lying down on them, whereas the animals did not display these behaviours either in the gape or closed conditions, or in the baseline phase.

Overall, yawning across the conditions fitted the predicted pattern. Findings followed a continuum from contagious yawning rates at its highest when the stimuli displayed a full, typical yawn, to no yawning when the action was absent (baseline), or from a non-yawn (gape) android facial action. That is, the rate of yawning was greatest in response to yawns, followed by the post yawn condition. No yawning was displayed in either the closed or post closed condition. Overall, the chimpanzees yawned contagiously more in the yawn phase than in the baseline, closed mouth or gape phases. As mentioned earlier, 8 out of 14 chimpanzees yawned more in the yawning than in the baseline phase, while only 1 chimpanzee yawned more in the baseline phase. Note that baseline measurements were taken as representative of their yawning rate during a normal day.

We implemented the same paradigm set up by Joly-Mascheroni et al (2008) with dogs, to address the common problem in the literature of difficulty of comparing results, when testing procedures and methods differ so greatly between studies, and when assessing if this type of heterospecific, or rather across-agent (Animal – Android) contagious yawning, also manifests itself as a type of experiential contagion. The proportion of chimpanzees that exhibited across-agent yawn contagion from yawns simulated by an android was lower (57%) but still comparable with that of adult dogs (72%), found by using the same basic experimental design to that of Joly-Mascheroni et al (2008).

Furthermore, behaviours displayed, especially during the Yawn and Post Yawn conditions, could not be explained by tiredness or boredom, as the chimpanzees would have been more likely to get bored when they were exposed to no movement or to a gape (face actions that have no meaning or purpose) from the android, than to a yawn produced by the robotic head.

We investigated if the behaviours displayed also involved any afferent signal feedback, by exploring whether chimpanzees showed signs of synchronisation of states (behaviours displaying signs of drowsiness or relaxation), depending on the condition to which they were exposed. Overall, the chimpanzees were statistically significantly more likely to lie down when the android yawned in their full view, than when they chose not to interact with it, and either ignore it completely or randomly look at it from a side angle. So, as expected, we found that time spent looking at the android had an impact on the rate of yawn contagion. Chimpanzees yawned contagiously when the android yawned and importantly, no chimpanzee yawned when the android's mouth (and lips) were closed. Moreover, the duration of lying down followed the pattern of yawn > post yawn > gape > post gape >closed mouth > post closed phase. Interestingly, and in line with predictions, statistically significant differences were found between the time that the chimpanzees spent lying down during the yawn/post yawn phases and the gape/ post gape phase. Nonetheless, the overall pattern of results suggests that the duration of the rest response when visually perceiving the android´s yawns, differed from when the android gaped. The rest response in the gape phase was statistically non-significant and indistinguishable from the closed and baseline condition, while the chimpanzees were more likely to show a rest response in the yawn/post yawn than when the human-looking android’s mouth was kept closed.

There is some evidence that perceiving yawns elicits signs of drowsiness or relaxation in the chimpanzees as previously found in humans (Provine et al., 1986), dogs (Joly-Mascheroni et al., 2008) and puppies (Masden & Persson., 2013). Furthermore, chimpanzees tended to gather leaves, as they do in the wild, and lie down both in this study and in the study with live humans, found in our previous study Joly-Mascheroni et al (submitted).

Chimpanzees yawning contagiously, making their bed by gathering leaves, and lying down when observing certain inanimate agent´s actions (an android yawning), and not others, seems to confirm the transference of a signal which is picked up and interpreted by the animals. Results suggest that chimpanzees denoted there was an information processing mechanism in action, and were able to perceive and interpret a signal produced by an unfamiliar model, humanlike in appearance, but ultimately an android. This finding represents important evidence of relevance to evolutionary theories, and offers grounds for further comparative across-species and across-agents research on action perception and action understanding. This is the first study to show that our genetically closest primate displays the urge to perform the same action that it is observing being performed by an object. Animals’ embodied experience with that object may denote that, regardless of the agent that performs the action, there is an embodiment-inducing component of the movement that is reflected in the contagious behaviour displayed by the animal. The implications of this finding could be interpreted in many ways: one of them could be that the phylogenetically old phenomenon of contagious yawning may have been a part of a pre-language form of communication and/or may have had a functional role in information processing mechanisms implicitly used, and therefore maintained through evolution. A yawn, regardless of its unknown primary role, may have always carried a non-verbal communicative function, and its contagiousness aspects may help us find out more about how humans and animals developed adaptive functions, ways of communication, synchronization and social interaction. Findings warrant further studies of android, human and other animals’ action perception and interaction.

These findings present us with the need of clarification of what is meant by a contagious action. What exactly in the perceived behaviour do we consider contagious? This finding reconfirms the necessity of a clearer term that would encompass different types of contagion processes. We propose calling this form of contagion, an "Experiential Contagion" and define it as "the tendency to automatically and almost simultaneously synchronize expressions, vocalizations, postures, facial or body movements, with those of another intercommunicative agent, and, consequently, to converge experientially". These findings suggest that chimpanzees may have the capacity to imaginatively transpose their embodiment of another´s action, even when that other is an artificial agent. Furthermore, the animals displayed behaviours that denoted a cognitive information processing mechanism in action. The chimpanzees’ immediate response could be interpreted as a result of an immediate and uncontrollable urge to both re-enact and/or react. In the case of perceiving a yawn, they re-enact by immediately yawning as well, but they also seem to react by behaving as if they were perceiving the yawning as a message that tells them it was the place and time to lie down and rest. The information could only have been inferred, given that the android was not lying down or making a bed, and the chimpanzees did not display this behaviour in the gape condition. Until now, we thought that this capacity was characteristically and exclusively human, and would therefore only occur between humans. Our genetically nearest ancestors seem to have undergone sufficient cognitive development that has enabled them to interpret the significance of other agents´ actions. If the action perceived is an embodiment-inducing one, then the information processing mechanism triggers their own embodiment and the consequent behavioural response. Equally importantly, these results also suggest that chimpanzees seem to possess the ability to construe the potential meaning of the behavioural roles of another agent, even if this agent is in fact an object.

Experiential contagion could be triggered through sensory modalities such as visual, auditory and tactile. In one of its most basic forms, it could be represented by an embodiment-inducing action that does not necessarily have an emotional component attached to it. It is proposed that Experiential Contagion could be prompted by the mere perception of an action that generates the recognisable sensation of having previously experienced how it feels to perform that action.

Given the possible link between behavioural contagion and empathy, these results seem to suggest that chimpanzee yawn contagion is not necessarily reliant solely on empathic behaviour. The finding that this animal species shows yawn contagion triggered by an android that looks as if it is yawning, may mean that the contagion may not have necessarily been evoked by a targeted empathic behaviour. If indeed empathy is one of the factors that could potentially have an impact on the rate of yawn contagion at all, what a perceiver might be empathising with, would be the actual sensation resulting from having themselves experienced how it feels to perform the embodiment-inducing action they are in that case observing in others, and not empathising with the actual agent performing that action. This scenario could still be considered as a type of Experiential Contagion with the consequent inevitable urge of performing the same behaviour as a response.

Finally, in the case of this study, the context was that of an interaction with a new agent that was neither human nor animal, one with which they may or may not have wished to bond. This suggests it is not a sign of mimicking behaviour or a chameleon effect. Even though the prosocial consequences of the chameleon effect may extend to non-conscious mimicry and contagion in non-humans, and that chimpanzees seem to be susceptible to behavioural contagion from man-made objects, these results should not be taken as a sign that the animals may have wished to affiliate with this agent. This may warrant further studies exploring the potential differences between mimicking, imitation, and possible different types of Experiential Contagion.

5 STUDY 3. PHYSIOLOGICAL EVIDENCE OF CONTAGIOUS YAWNING IN HUMANS WITH NORMAL VISION

5.1 Introduction

Human social interaction and effective communication relies on the perception and accurate interpretation of the actions and behaviours of others. When we socially relate to each other, we employ a wide range of facial actions and gestures, which are often non-linguistic compositions (Cartmill, Beilock & Goldin-Meadow (2012)). Some of our facial actions, although not intended to be communicative gestures, when perceived by others, may almost immediately trigger the urge to produce the same action. One example of these behaviours is that of yawning, which is characterised by being contagious. It is important to study how humans comprehend and respond to others' facial gestures in general and, in particular, to these types of communicative signs or non-goal directed actions. The puzzling phenomenon of contagious yawning is considered here as a type of information transference. It seems possible that yawning represents a kind of signal that gets sent, by one communicative agent, to a social interacting partner, whose automatic response after perceiving this sign is to immediately yawn contagiously. Elucidating the behavioural cognitive and physiological mechanisms underlying these particular human behaviours will help us understand how and why this specific, seemingly communicative interaction, may occur. In turn, by exploring these types of specific cases of social interactions, it would help us better understand other communicative processes underlying social cognition and their common behavioural responses.

The ability to infer the emotional states of others is important for social interaction. A large amount of facial perception studies has focused, understandably, on exploring the intricate processes involved in emotion perception (Henry, Phillips, Crawford, Ietswaart & Summers, 2006). However, facial gestures do not always involve emotions. Therefore, the understanding of others' actions, particularly facial actions and gestures, involves exploring relevant aspects of human behaviours that are commonly related, and instrumental, to non-verbal communication. The large majority of research investigating responses to emotional expressions regards this kind of social interaction, based on facial gestures, as reliant on modulations of components of facial mimicry, whereas models of some types of social contagion are thought to denote different classes of behavioural responses (Christakis & Fowler, 2013, Levy & Nail, 1993).

There is a growing body of evidence suggesting that contagion is dependent upon different variables from those of mimicking or imitation, and correlations are not being found Genschow, et al., (2017). “Many researchers believe that automatic imitation is mediated by the Mirror Neuron System” (Heyes, 2011; Longo et al., 2008). Furthermore, research is lacking on issues such as the level or the characteristics of the exposure to the contagious entity (rumour, disease or behaviour), i.e. whether it is a novel stimulus or one that has been experienced before, whether contagion occurs after a single or successive exposure. In the past two decades, contagion has generally been referred to in connection with: behavioural economics or financial crises (Goodhart et al., 2002); legal and/or ethical challenges; the spread of a financial crisis from one country to another (Liang et al., 2009); the contagion of crises in financial networks within groups (Allen et al., 2000) and of course, contagion in disease transmission (Stanton et al., 2016). It is worth noting that there is either a general misconception about the meaning of contagion, or there is a general ambiguous use of the term contagion by several disparate disciplines.

Some contagion models assume that contagious entity determines the types of contagion, whether simple or complex (Weng et al., 2013, Kramer et al., 2014). There has been little quantitative analysis of the components that establish these differences between what we should consider simple or complex. A systematic understanding of how we should decompose the constructs that contribute to models of contagion is necessary to understand what constitutes a contagious entity. Here, the focus on contagion will be from a psychological perspective and only in relation to yawning. According to previous research, it seems that when considering the implications of contagious models in relation to the behaviour of yawning, the impact that empathy may have on the contagious process needs to be explored further.

Empathy relies on a perception-action mechanism (Preston & de Waal, 2002). Despite having such a poor understanding of why yawning is contagious, the fact that it shows a delayed developmental pattern (Madsen & Persson, 2012, Madsen et al., 2013, Palagi et al., 2009), seems to have indicated to many authors that this reflects some high-level social cognitive capacities (Arnott et al., 2009, Norscia & Palagi, 2011, Norscia et al., 2016, Palagi et al., 2014, Platek et al., 2003; 2005). The original proposed link between CY and empathy stems from a monograph on yawning that was published around 40 years ago (Lehmann, 1979), and more recently by its inclusion in the above-mentioned Perception-Action-Model (PAM), proposed by Preston and de Waal (2002, see also de Waal & Preston, 2017). In that original work, Lehmann (1979) notes that yawning is a sign of boredom (cf. Provine & Hamernik, 1986), considering the latter an emotion. Subsequently, he concludes that CY constitutes emotional contagion (Lehmann, 1979). If the contagious process is part of the progression of an emotional sense, then CY within an empathic processing would represent a primitive form of the state matching mechanism proposed by Preston and de Waal in 2002, whereby the simple observation of an emotional state in another elicits the same emotion in the observer (Massen & Gallup 2017). However, there is a debate in the literature as to whether these processes are as simple as they are described, and whether CY indeed constitutes an emotion-transferring mechanism.

5.1.1 Empathy

On the one hand, empathy is a complex construct, representing the ability to understand, share and be affected by the state and/or feelings of others (Singer et al., 2004). On the other, the particular case of perceiving the yawns of others, which can trigger the urge to perform the same action in response, cannot, by simple association, be regarded as indicating the transmission of an emotion. Instead, previous authors consider contagious yawning to be due to a type of nonconscious mimicry or, at least mechanistic at an even lower-level, resulting from ‘simple’ behavioural contagion (Thorpe, 1963; Yoon & Tennie, 2010; Zentall, 2001). Again, nothing is simple in that view, either. In order to contribute to a common aim in the relevant literature, that of achieving a systematic understanding of how we should decompose the constructs that contribute to models of contagion and specifically regarding the contagious aspects of yawning, we would have to include the possible impact empathy may have on this type of contagious process. Therefore, some of the possible links to empathy-related responses will be addressed here.

Previous research exploring gender differences in empathic behaviour has yielded inconsistent results. In some cases, observed gender differences in empathy may have arisen from males' reluctance to report their empathic feelings, rather than a real difference in their ability to feel empathy. For example, studies that used emotion perception tasks, such as "Reading the Mind in the Eyes," which rely on the accurate judgment of emotions from observing the eyes, reported a female advantage (Baron-Cohen, Wheelright, Hill, Raste, & Plumb, 2001). Assessment of nonverbal data using neuroimaging techniques, such as functional magnetic resonance imaging (fMRI), provided little support to theories of gender differences in empathic abilities (Wager et al., 2003). There is, however, plenty of evidence to suggest that within a second of seeing a facial expression that denotes an emotion, humans tend to match that expression (e.g. Moody et al., 2007). These rapid facial reactions (RFRs), are often termed mimicry, and are thought to be implicated in emotional types of contagion in social perception generally (Hatfield et al., 1994). They can also be found in embodied affect processes, in particular (Chartrand & Bargh, 1999). Given the uncertainty that remains regarding the involvement of these mechanisms in contagious yawning, embodiment, RFRs, the possibility that there is a nonaffective motor response involved in this process, is explored in the present study. Here, corrugator supercilli and zygomaticus major muscle area activity is measured through Electromyography (EMG), in order to explore the induction of the yawning behaviour, not to mention the consequent urge to produce the same action observed and embodied by the perceiver. Most researchers that study RFRs also use the term mimicry to describe these reactions (e.g., Hess & Blairy, 2001; McIntosh et al., 2006). This is because mimicking can imply that the action is merely a matching of the observed expression, therefore ignoring that the response in question is that of an individual perceiving the particular behaviour of yawning. Previous theories seem to fail to account for other possible mechanisms that may potentially be involved in the urge to produce the same action as perceived, such as additional possible aspects of the others' facial expression that may be inducing the embodiment mechanism in the perceiver. Muscle activity represents a productive route to explore these mechanisms, and the study addresses these questions directly in a way that hasn't been addressed before.

5.1.2 Physiological measurements: EMG

Much of the previous research made tacit or explicit assumptions regarding the mechanism(s) leading to the reactions of an observer. For example, Hatfield et al. (1993, 1994) base their theory of emotional contagion on an assumed automatic and, strangely enough, non-emotional rapid facial matching of observed emotional expressions. On the other hand, Dimberg (1997) suggests that these rapid reactions are the result of emotional processes rather than simple reflexive processes. The understanding of what these rapid facial reactions represent varies across studies and theoretical perspectives. The fact that there are several untested, or slightly contradictive, assumptions about the mechanism(s) that may underlie contagious yawning, underscores the need for a focused approach to understanding and documenting the nature of these embodiment-inducing behaviours, not to mention these particular embodied responses. This should relate to what it is that influences them and which components of the facial expression are relevant in the yawn contagion process.

5.1.3 Familiarity

The majority of studies in the field, including one in this thesis, have tested the supposed link between CY and familiarity biases in responses. In the case of humans, the principle is that empathy is supposed to increase with the degree of familiarity between the individuals concerned (see Preston and de Waal, 2002 for a review). If CY is indeed a proxy for empathy, by presenting only unfamiliar stimuli to adult humans of both genders, the correlation should be high between the contagious yawning rate and those highly empathic individuals, even though they are unfamiliar to each other. In order to avoid any other confounding variables, and to address the contrasting results attributed to different methodologies between studies, the same paradigm was employed in all the experiments presented in this thesis, with only unfamiliar actors used as stimuli in the present study. In fact, this unfamiliarity is expected to be helpful in conjunction with an Eye tracking measurement, given that humans' gaze avoidance has been described as common among strangers in both natural and experimental contexts (Zuckerman et al., 1983; Laidlaw et al., 2011). Additionally, in-group faces are perceived more holistically than out-group faces

(Michel et al., 2006). This might mean that specific areas of the face, as opposed to a gestalt approach in looking at the stimulus face, would provide indications of the principal components of the yawn contagious process. Previous findings have not met a general consensus yet regarding which of the humans' facial features, such as the eyes or the mouth region, exert an impact on the yawn contagion process.

Studies suggested diminished susceptibility to contagious yawning in children with Autism Spectrum Disorder (ASD) (Senju et al., 2007). Although the authors' initial suggestion was that their results may have been driven by atypical attention to the face, the authors later tested this hypothesis by exploring whether children with ASD yawned contagiously when their attention was navigated to yawning faces. Senju et al., (2009) reported to have used exactly the same experimental design as Senju et al., (2007), except that a small cartoon animation was presented in the location where the eyes of the facial stimuli appeared, and, in another experiment, where the mouth would appear just before the presentation of each face, and children were instructed to fixate on this animation. If fixation on the eyes plays a critical role in the processing of a yawning face, and given that for the normally developed, 'Faces are releasers of contagious yawning' (Provine, 1989), in individuals with ASD, the authors expected, and indeed claimed to have found contagious yawning when their attention was navigated to the eyes in their first experiment, but also when their attention was drawn to the mouth in their second experiment. The authors concluded that atypical fixation on the face could not explain all previous reports, including those absent of contagious yawning in ASD. Consequently, the debate in the literature persisted with regards to what areas of the others' face would exert an impact on yawn contagion. It is possible that eye contact affects the observers' behaviours in ways that are not yet very clear. We do know that gaze direction is a communicative signal, one which conveys the sender's communicative intention, and may enhance visual learning (Csibra & Gergely, 2009).

5.1.4 Neural correlates of visual perception of faces

In the cerebral cortex, object recognition, face perception, and other social interaction behaviours, have shown that visual learning is thought to be mediated by the ventral visual pathway. This pathway runs from the primary visual cortex, V1, over the extrastriate visual areas V2 and V4, on route to the inferotemporal cortex. This has its beginnings in simple unitary cells in V1(Parker, 2001), which only have a small, limited specific receptive field, preferentially responding to oriented bars. Later on in this path, other types of neurons along the ventral stream show an increase in receptive field size, as well as the complexity of their preferred stimuli (Poggio et al., 2004). At the top of the ventral stream, in the anterior inferotemporal cortex (AIT), neurons respond optimally to complex stimuli, such as faces and other objects. The tuning of the neurons in anterior inferotemporal cortex probably depends on visual experience (Tanaka, 1993). In addition, some neurons show specificity for a certain object, such as faces, and certain orientations. See figure 5.1 for a graphical representation of this.

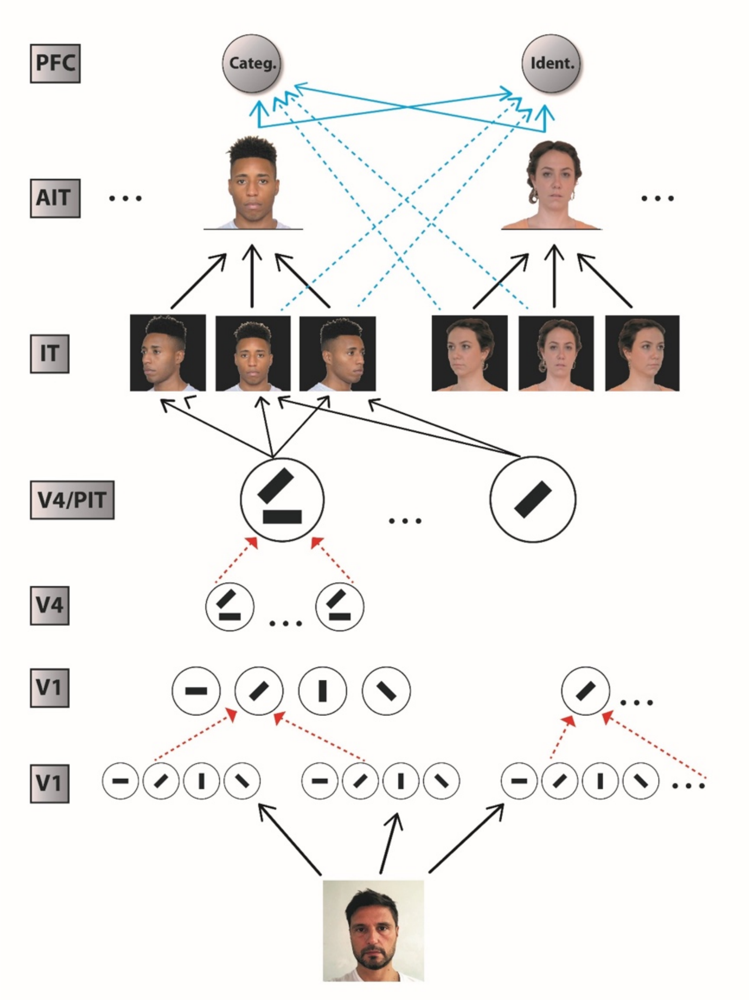


Figure 5.1 A model of the type of visual perception explored in this study, adapted from the model of visual learning by Tomaso Poggio1 & Emilio Bizzi in Nature Insight review (2004) model of vision and motor control

The model summarises, in quantitative terms, other models and much data about visual recognition in the ventral stream pathway in the cortex. The correspondence between layers in the model and visual areas is an oversimplification. Circles represent neurons and arrows represent connections between them; the dots signify other neurons of the same type. Stages of neurons with bell-shaped tuning (with black arrow inputs), which provide example-based learning and generalisation, are interleaved with stages that perform a max-like operation (denoted by red dashed arrows), which provides invariance to position and scale. In the motor cortex, time also plays an important role. Most of our motor commands deal with time-dependent motions, not just with static postures, but also dynamic rapid or slow gestures. In visual perception, time can be introduced in a direct way. For example, it is presented here, in videos, by assuming that visual neurons respond to ‘snapshots’ of a motion and are selective for a sequence of snapshots that form the particular motion pattern. In the motor control equivalent, the assumption is that these motor activations are time-dependent, too (Logothetis et al., 1995). With this circuitry, active snapshot neurons pre-excite neurons that encode temporally subsequent configurations and inhibit neurons that encode other configurations. Significant activity can arise only when the individual snapshot neurons are activated in the ‘correct’ temporal order.

There seems to be a strong analogy between vision and motor control in the time-dependent case, where the basic strategy is to combine locally-tuned units with time-dependent properties (Giese et al 2003). In the motor areas of the frontal lobe, neurons with similar preferred direction are interleaved with mini-columns having nearly orthogonal preferred directions (Amirikian et al., 2003). This discovery indicated that the motor cortex is endowed with functional modular structures, not unlike those described for the visual cortex (Hubel et al., 1962; 1965), the somatosensory cortex (Mountcastle, 1957) and the auditory cortex (Merzenich et al., 1973). Neuronal activity in the frontal cortical areas, such as the primary motor cortex, the supplementary motor areas, and the dorsal premotor areas, change during adaptation and visuo-motor learning (Wise et al., 1998); visual perception and motor control (Paz et al., 2003). These assumptions, made by previous authors, have not been addressed in the context of the action of yawning before, and therefore are relevant to be addressed in the present study, which uses an EMG quantification, that offers high temporal resolution and eye tracking to reliably measure a facial motion perception, and the corresponding immediate muscle activation on the fast motor and/or pre-motor response.

5.1.5 Eye tracking

There are two clear facial components that are relevant in the movement of yawning: the mouth and the eyes. However, previous literature does not clarify what facial component is being processed the most during an observation of yawning. Combining eye tracking with EMG represents another novel and complementary route in exploring precisely which area of another's face the perceiver is looking at, while muscle activity is being measured.

5.1.6 Intracortical inhibition and facilitation in the facial M1 and other motor and premotor areas

The facial motor system has several unique features. Facial muscles carry few or no muscle spindles (Voss, 1956; Lovell et al., 1977). The facial muscles are under both voluntary and emotional control (Lees, 1988). Dissociation between voluntary and emotional movements may occur in patients with supranuclear lesions, suggesting that they are under the control of separate descending pathways (Hopf et al.,1992). Since the upper face is usually spared in patients with hemispheric lesion, the upper facial muscles are considered to have bilateral cortical innervation (Brodal, 1981). However, it is the subject of controversy whether there are projections from the primary motor cortex (M1) to the upper facial muscles in humans (Chen et al 2010). While some authors reported responses in the upper and lower facial muscles with TMS of the facial M1 area, the latencies were similar to the first component (R1) of the blink reflex, with the central delay significantly longer for facial muscles compared to limb muscles or muscles innervated by other cranial nerves (Benecke et al., 1988; Cruccu et al. 1990b). Therefore, timing is important for the measuring of muscle activity, which is sometimes considered as a reflexive response of the others' facial actions, and the aim is to address this here by incorporating the EMG recording of the potentially contagious facial action in the yawning motion. By doing so, in conjunction with the eye tracking information, we can also indirectly measure the potential paths the information has been transferred across, (i.e. from the visual area to the relevant motor, premotor and/or somatosensory cortices) and before the signal is sent to the facial muscle area representing the contagion, by inducing the urge to perform the same action.

In humans, due to the complexity of facial expressions, the anatomy of corticofacial pathways has not been studied in detail, thus the cortical areas that control facial muscles remain controversial (Paradiso et al 2005). Dissociation of emotional and voluntary movement is frequently observed in facial paralysis, resulting from supranuclear lesions (Monrad-Krohn,1924; Taverner,1969; Topper et al., 1995). Although the pathways responsible for these two types of facial activity are not well understood, it has been suggested that volitional activity may be mediated by the M1 and the descending pyramidal tract, whereas emotional movements may be mediated by the anterior frontal-thalamo-pontine connection that descends in the anterior limb of the internal capsule (Hopf et al., 1992). Is there a possibility that the yawn contagion process is modulated by inhibitory or facilitatory circuits? Since the cingulate cortex is part of the limbic system that is associated with emotional expression, the mesial frontal cortex may be responsible for emotional facial expressions (Morecraft et al., 2001). Some findings do suggest that there are M1 projections to contralateral upper and lower facial muscles in humans (Paradiso et al., 2005). The authors also suggested that the facial M1 representation has been reported to be under the influence of short interval intracortical inhibitory and intracortical facilitatory circuits, similar to the arm and leg areas of the M1. Given the evidence of the facilitatory and inhibitory circuits possibly being involved in some reflexive motor activation, there is a potential connection here with other reflexive motor activations that would not be easily inhibited. Furthermore, a difference in activation by a facilitatory circuit, or a short interval of no intracortical inhibition, could lead to the reflexive motion being present in a relevant facial muscle area. Some facial mimicry effects remain present even during participants’ active behavioural inhibition of facial movement (Korb et al., 2008). Given these findings in mimicry situations, it is relevant to explore these effects in a contagion scenario, instead of a purely imitational one.

Previous findings provide only indirect evidence for or against a relation between the MNS and unconscious mimicry. Here, only an indirect relationship would also be claimed between certain motor and premotor activation areas and the EMG activity captured in the facial muscles. However, there are only very few studies that have directly examined the neuronal correlates of contagious facial responses to others’ non-emotional facial expressions and, to the best of our knowledge, none in the manner conducted here, such as incorporating EMG and eye tracking, which are both high temporal resolution techniques. Studies mentioned above, which examined conscious mimicry, instructed participants to imitate a seen facial expression deliberately and compare their reactions in that condition with those from a passive viewing condition. In other studies, which do not test mimicry, but rather a passive viewing condition, participants would probably still display some mimicry in their response, given that this facial mimicry reaction is known to be unconscious. Hence, Schilbach et al. (2008) evaluated through EMG the spontaneous facial muscular responses, together with the blood oxygen level dependent (BOLD) physiological response to dynamic facial expressions of virtual characters in an fMRI scanner. The instructions to participants were to view the presented expressions passively. The authors reported an enhanced BOLD activation in the precentral cortex area, the precuneus, the hippocampus, and the cingulate gyrus, all within the same time window in which non-conscious facial mimicry occurred. However, Schilbach et al. (2008) did not assess muscular activity and BOLD response in the same participants and at the same moment in time. Thus, there is, up until now, neither specific empirical evidence about the neuronal structures involved in automatic spontaneous mimicry (Likowski et al., 2012), nor in automatic responses, which could be seen as contagion rather than mimicry. In the current study, previous findings regarding the neuronal path the visual information follows has been used to address the questions of which features of someone else’s facial gestures affect gaze and fixation patterns and, in turn, the rate of behavioural contagion. Facial expressions are a special type of action. Experiments that have examined the neural structures, involved in both the observation and resonance of embodiment of dynamic facial expressions, are in agreement that, akin to observing hand actions, observing the facial expressions of others vicariously activates ventral sectors of Ba2 and/ or SII that are involved in sensing self-produced facial expressions. Secondary questions, such as: does the position or orientation front or profile exert any difference in the rate of contagion; do these orientations affect gaze patterns towards the eyes or the mouth regions, are equally important.

A previous study tested the hypothesis that the human mirror neuron system (MNS) is activated by visually perceived yawning using fMRI and comparing signal-dependent changes in blood oxygen levels when subjects viewed videos of yawning faces, as opposed to faces with a neutral expression (Haker et al., 2012). The authors report finding components of empathy (motor empathy), which underlie the development of cognitive empathy, and concluded that these results emphasised the connection between the MNS and higher cognitive empathic functions, including mentalising. Furthermore, from these findings, they deduced, CY was based on a functional substrate of empathy. Unfortunately, some aspects of their analysis of the participants’ responses might have been confounded. For example, the authors rated behaviours as contagious if minimal signs of yawning - such as yawning-like visible muscular activity around the mandible or deep breaths - were detected in the participant even without fully apparent yawning. However, the manner in which those possible minimal signs were analysed was not reported. Furthermore, by asking participants to respond after each session finished, the subjects must have had to rely on their memory and accurate recollection of their previous sensations, whereas responses related to the neutral videos were requested after each neutral video.

Here, one of the aims was to better define the individual contribution and roles of various factors in susceptibility to, and rates of, contagious yawning. Employing the same basic paradigm as in the previous studies in this thesis, consistency was ensured, by employing the same conditions and assessing them with the same parameters. Direct eye contact, and gaze straight to the eyes, has been shown to have different effects in certain social interactions. Although gaze shifts to left or right (i.e., averted gaze) seem to trigger a reflexive shift of spatial attention towards the gaze direction (Friesen, Moore, & Kingstone, 2005), eliciting joint attention to the objects of other's interest (Emery, 2000; Kleinke, 1986), direct gaze has also been shown to facilitate face processing (Conty, Tijus, Hugueville, Coelho, & George, 2006; Hood, Macrae, Cole-Davies, & Dias, 2003), person perception/evaluation (Kampe, Frith, Dolan, & Frith, 2001; Macrae, Hood, Milne, Rowe, & Mason, 2002; Mason, Tatkow, & Macrae. 2005), and action understanding/monitoring (Becchio, Bertone, & Castiello, 2008; Kilner, Marchant, & Frith, 2006; Castiello, 2003; Conty, Gimmig, Belletier, George, & Huguet, 2010; Schilbach et al., 2012). There has been a considerable amount of research advocating explorations of mimicry behaviours and their importance in human non-verbal communication and social interaction. Although mimicry is not normally consciously controlled, this extensive research suggests that mimicry is flexible and context dependent (Brass, Ruby, & Spengler, 2009; Heyes, 2011). Contagion, however, seems to be less flexible, but still context dependent. Wang, Newport, & Hamilton (2011) found behavioural evidence that mimicry can be rapidly modulated by eye contact in a hand moment task. The authors term this the eye-contact-mimicry (ECM) effect. Participants observed a direct or averted gaze, followed by a hand opening or closing action. They responded by opening (in some blocks) or closing (in other blocks) their own hand as fast as possible. The authors reported to have found that direct gaze led to faster reaction times for congruent actions only, demonstrating that eye contact causes a rapid and specific enhancement of mimicry responses.

Some researchers have attempted to explore these mimicry findings with facial stimulus rather than hand-centred (Wang, Newport, et al., 2011 Study 2). However, according to some of the above-mentioned previous studies (e.g. Usui et al 2013), it is still not clear if the eyes or mouth regions are the facial area of most importance when it comes to a contagious yawning process (Senju et al 2007), or, as the authors put it, “merely a mimicry effect”. This study, therefore, addressed this question in the following ways. Firstly, by presenting actors in front and profile orientations to explore whether frontal eye contact made any difference in gaze and fixation patterns, and consequently in the rate of yawn contagion. Secondly, a profile orientation provides the chance to explore the contribution of gaze and fixation patterns to the same muscle area activation in the participant’s facial muscles, both when the orientation would mean an angled visual input, with consequential information processes potentially following a particular neural path, which provides invariance to position, and the EMG measurement is consistently performed in the same muscle area.

To sum up, the present study was designed to (1) assess the influence of adult’s empathic traits upon their physiological and behavioural response patterns in their perception of an unfamiliar person yawning. Eye-tracking and EMG were incorporated into the paradigm in order to (2) provide physiological evidence for internal simulation and therefore contagion experience. Although no specific prediction was made for the present study, according to previous research, it is reasonable to expect that dissimilar facial expressions, and facial orientations, would be perceived and processed differently. Responses would, therefore, denote individual and distinguishable muscle activity according to the behaviour visually perceived. Self-report through a Visual Analogue Scale (VAS) was employed in order to (3) obtain a measurement of the participants' self-reported urge to perform the same action as observed. This response is requested immediately after the visual perception of the stimuli. The eyes and mouth areas of the face were considered as regions of interest ROI on the eye tracking data, in order to (4) investigate any potential relation between the embodiment-inducing effect, arising from the contagious component of the visual perception, and differences in gaze orientation and fixation patterns between regions of a facial stimulus. Lastly, (5) questionnaires were provided: two different measures of Empathy Quotients. A sleepiness scale, and Alexithymia scores were also obtained.

5.2 Hypotheses

The main aim of this study is to investigate contagious yawning in humans, and provide physiological evidence of contagion and thereby extend previous findings of contagious yawning through visually perceiving videos of conspecifics. The second aim of this study is to explore a relation between empathy quotients and susceptibility to yawn contagiously.

(H6) It is hypothesized that when an adult human visually perceives someone else yawning, there are physiological measurements, provided by EMG, that can denote presence of contagion, internal simulation, embodiment, resonance, evidenced by their own facial muscle activity. Measures are taken from two major muscles areas, zygomaticus major (Muscle ZM) and the corrugator supercilii (Muscle CS) and the expectation is that the mouth region (ZM) will denote higher activation than the eye muscle region (CS).

(H7) It is hypothesized that in yawn contagion scenarios, some facial regions are more important than others. This is tested by exploring whether there are mean differences in eye tracking measurements (gaze orientation fixation time and other patterns) between the eyes and mouth areas.

(H8) It is hypothesized that there is no relation between empathy scores and yawn contagion. Therefore, the expectation is that there will be no correlation between the EMG activity denoting contagion and high empathy quotients.

5.3 Methods

5.3.1 Participants

Forty healthy volunteers participated in the study. All participants had normal or corrected-to-normal visual acuity and no history of neurological illness. Participants' mean age was 25.83 (10.22) years. There were 9 males (22.5%) and 31 females (77.5%) in this study.

The study was approved by City, University of London Research Ethics Committee and participants' written informed consents were collected.

5.3.2 Apparatus

Stimulus presentation was performed by e-prime 2.0 software (Psychology Software Tools, Inc.) and MATLAB with the Psych Toolbox (version 3.0.11; Brainard, 2006) running on a Windows PC. Participation was video recorded with a Panasonic HC-V110 video recording camera, and using an iTrust web camera which allowed the experimenter to remain occluded from the participant view and broadcast the image to the Biopac system. This method also allowed the experimenter to place markers directly in the EMG signal when gapes and wide mouth-opening yawns occurred. Stimuli were presented on a Tobii TX300 eye monitor at a resolution of 1920 by 1080 pixels and a refresh rate of 60 Hz. The Tobii TX300 eye tracker running at 300 Hz was used for eye tracking adults' gaze and any eye movements. The TX300 is capable of recording at 0.4° accuracy (binocular) and 0.14° precision under ideal conditions. The Tobii SDK was used for communication between E-prime, the eye tracker and the Biopac software. Preceding the visual experiment was a 5-point calibration sequence. Each calibration and validation stimulus consisted of a red coloured dot on a black background, sequentially presented in the four corners and the centre of the screen. The order of points was random each time the calibration was run. The dot moved from either the top right or left corner of the monitor, to the opposite end either right top, bottom left or bottom right, ending at the centre of the monitor. This was the exact position where the fixation point would appear in consequent experimental trials. After the calibration procedure was deemed successful, a central static fixation point or attention getter (i.e. cross) preceded each trial.

5.3.3 Stimuli

In this study, the possibility of the orientation of the head exerting an impact on the visually perceived event is, in part, addressed by presenting the faces of the actors in the videos in front or profile positions, with respect to participants’ view angle (see Figure 5.2). Videos of male and female drama students performing three different facial actions were recorded. Videos were displayed in the Tobii TX300 24" monitor screen. Actors portrayed three expressions A neutral (Closed) mouth expression, A non-emotional (Gape) opened mouth expression, A (Yawn) opened mouth yawning expression. All expressions were presented from a Front orientation, and a Profile orientation. Viewpoints, lighting conditions, contrast and luminosity remain constant across all videos. Actors faced the camera at a distant of 1.5 metres, portraying the facial actions from a Front position (straight to camera) and from a Profile position (on their right profile). These simply added variability to the stimuli and provided two different angles of view, where the profile position meant the participants would not have the same full view of what would normally be regarded as an eye contact position.

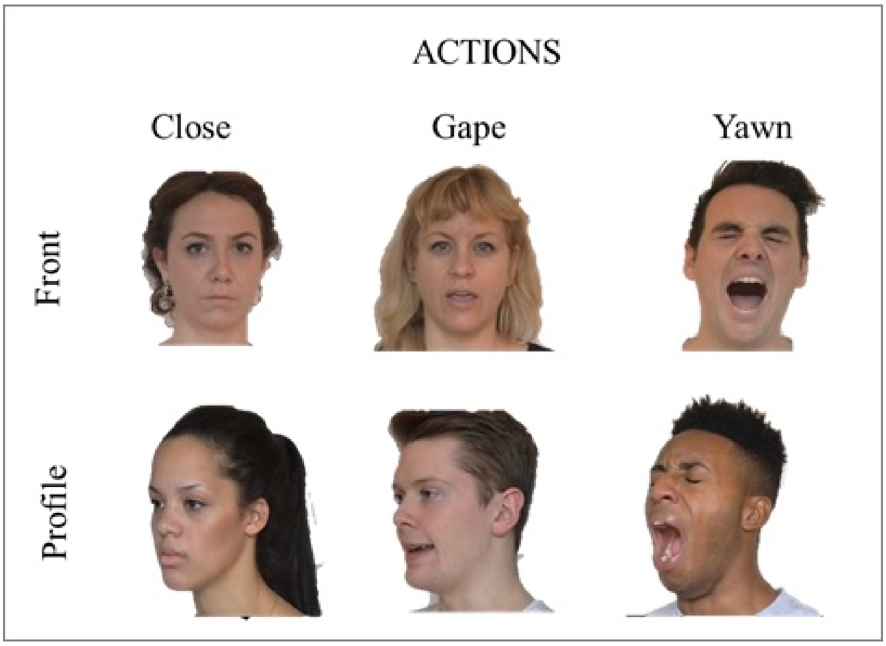


Figure 5.2 Still of digitally created videos of human actors in Front and Profile for all conditions.

5.3.4 Procedure

Upon arrival at the laboratory, participants were informed about the experimental procedure and invited to sign a consent form. Participants sat in a comfortable chair while physiological sensors were attached to their face. The experimental procedure consisted of two simple tasks: First, observing the 10 seconds long videos, when the actors performed one of the randomised actions, and secondly responding, with no time limit, to the rather ambiguous question “Rate how much you felt the urge to perform the same action that you have just observed”. The answers were taken using a visual analogical scale (VAS) ranging from “not at all” (0) to “very much” (100) with the range of possible ratings between 0 and 100 occluded by a black bar (Figure 5.3). Responses were subjected to the participant’s estimation of at which number their mouse-clicking fell. Although the task was very simple, each participant started with three practice trials in order to enable the participants to familiarise with themselves with the procedure. Each trial started with a central fixation cross lasting 500ms, followed by the video stimuli presentation, which lasted 10 seconds.

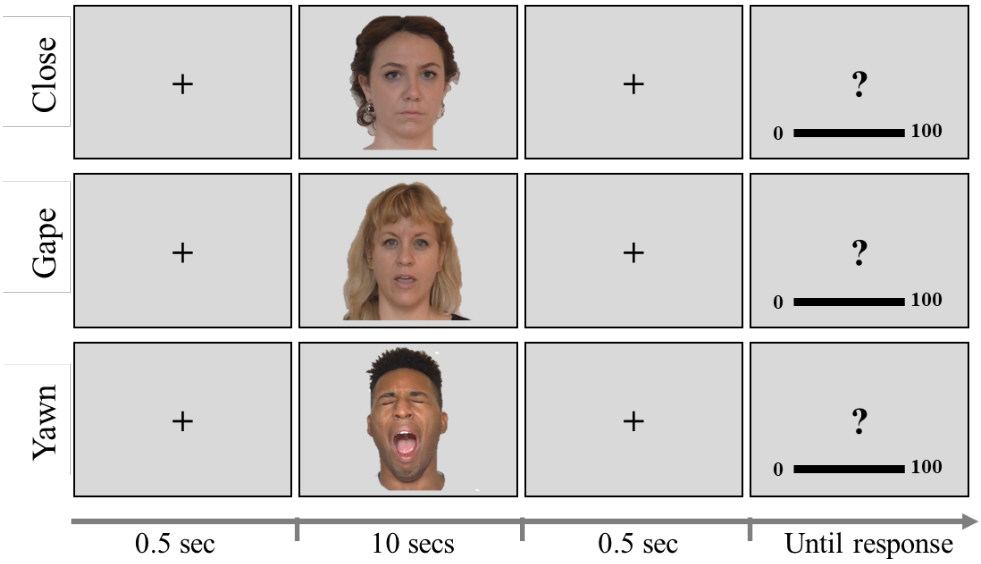


Figure 5.3 Schema of a trial. Figure show an example of each experimental condition (close, gape, yawn). At the end of each trial (when the question mark appeared), participants had to rate how much they felt the urge to perform the same action that they had just observed.

The set up was composed of three blocks, each comprising three mini-blocks, in which the order of Close, Gape, Yawn conditions and Front vs Back orientations were randomised and counterbalanced across participants.

After each video presentation, the task question and VAS scale appeared at the bottom of the screen. The next trial began immediately after the participants' no time-limit answer. E-Prime 2.0 software (Psychology Software Tools, Inc.) was used for stimuli presentation.

5.3.5 EMG: Zygomaticus major (ZM) and Corrugator supercilii (CS)

Participants' facial electromyographic activity (EMG) was recorded simultaneously with the video recording or the participants' response in order to guarantee online and post-hoc congruency between muscular activity and adherence to instructions. Four disposable Ag/AgCl surface electrodes (4mm) were placed on participants' facial muscles, with one on a non-muscle area to act as ground. Two electrodes were placed over the Corrugator Supercilii and two electrodes on the Zygomaticus Major muscle area, on the left side of the participants' face, following Fridlund and Cacioppo's (1986) guidelines. Before being attached over muscle regions, the electrodes were filled with gel electrode paste and the participants' skin was cleaned with a non-alcohol solution, which reduced impedance. Facial EMG was recorded at 1000 kHz with a two-channel amplifier (Biopac System). Off-line, data were submitted to a 20–1000 Hz band-pass filter to reduce movement related artefacts and environmental noise. Data were then visually inspected and trials with remaining artefacts, which coincided with participants' non-contingent movements (e.g., coughing, talking or head movements), were marked and excluded from the analysis. There was no participant for whom the number of excluded trials exceed 10% of total trial numbers (total of 108 trials). The averaged EMG response of the two muscles was calculated via the root-mean-square method.

Activity of the M. zygomaticus major, and the M. corrugator supercilii was recorded on the left side of the participants' face using bipolar electrodes and according to the guidelines established by Fridlund and Cacioppo (1986). The EMG raw signal was measured with a Biopac amplifier, digitised by a 16-bit analogue-to-digital converter, and stored on a personal computer with a sampling frequency of 1000 Hz. The EMG data was post-processed offline using Acknowledge software (Version 4.3). Following gradient artefact correction, the raw data were rectified and filtered with a 30 Hz low cut-off filter, a 500 Hz high cut-off filter, a 50 Hz notch filter, and a 125ms moving average filter. The EMG scores are expressed as change in activity from the pre-stimulus level, defined as both the mean activity during the 10 seconds from the stimulus onset to the peak value, minus the initial first sample, and again up to the 10 seconds offset or 1000ms stimulus duration. Trials with an EMG activity below 0.01 μV, or above 8 μV, during the stimuli presentation, were excluded (less than 2%). Before statistical analysis, the EMG data was computed for each of the 108 trials, and responses were averaged over the 10s of stimulus exposure to provide an example snapshot of the raw and the filtered zygomaticus and corrugator EMG data.

5.4 Questionnaires

5.4.1 Empathy

The Interpersonal Reactivity Index (IRI) (Davis, 1980) is currently one of the most widely used and validated measures of dispositional empathy. The IRI is generally a 28-item self-report measure which consists of four 7-item subscales, each tapping into a differing facet of the universal notion of empathy. This has been largely defined as a degree of reactivity to others. The four subscales are Perspective Taking (PT), which relates to the propensity to assume the psychological point of view of another; Fantasy Scale (FS), related to the inclination of individuals to transpose themselves imaginatively into the feelings and actions of fictitious characters in books, movies, and plays, and was removed because it was not relevant to the content of the study; Empathic Concern (EC), which assesses feelings of sympathy and concern for unfortunate others; and Personal Distress (PD), which measures feeling of personal anxiety and unease in tense interpersonal settings. Participants are divided by the median averaged IRI score into low and high IRI group for purposes of analysis, followed by the median split analyses, correlation and multiple regressions analyses.

5.4.2 Sleep

The Circadian Energy Scale (CIRENS) (Ottoni, Antoniolli & Lara, 2011) is a two question chronotype measure based on self-report energy levels throughout the day. The difference between the evening and morning scores determined the overall chronotype score, ranging from 24 (most marked morning preference) to +4 (most marked evening preference). It has previously been shown that differences between chronotypes, or sleep-wake rhythms, affect yawning susceptibility.

5.4.3 VAS

The visual analogue scale (VAS) is the scale used here to measure subjective responses by participants specifying their level of urge to perform the same action they have observed. Participants respond by indicating a position along a continuous line from zero to hundred as known end-points. The superiority of this method over other analogue scales is that this discrete measurement does not allow the respondent to see exactly where within the scale they would place the response because the individual points forming the scale are not shown. This means the participant has to provide a response that is representative of at least three general areas, which are bottom, middle and top end of the scale. In this case, it is particularly useful to be able to compare the subjective self-report response with the physiological measurement of their facial muscle activation, which is accurately measured through EMG. Therefore, VAS represents a useful instrument for subjective measurements and complements both the physiological information measured by EMG and the gaze and fixation pattern information obtained with the Eye tracker.

Mean scores were computed for VAS across conditions (Close, Gape and Yawn) regardless of orientation (Front or Profile). A one-way ANOVA was carried out to explore differences in Self Report VAS measures between conditions, irrespective of block.

5.4.4 Alexithymia scores

The Toronto Alexithymia scale (Bagby, Parker, & Taylor, 1994) was employed to measure Alexithymia indexes, (= difficulties identifying and describing one's own feelings). The twenty-item Toronto Alexithymia Scale-I. Item selection and cross-validation of the factor structure was employed to assess emotion recognition in the present cohort of healthy participants and reconfirm that subjects would have been able to recognise and report if an emotion was present in the stimulus and, importantly, that they would have recognised the emotion in their own feelings. Generally, emotion recognition is assessed using photographs depicting posed facial expressions of different emotions and participants are categorised into high, moderate and low alexithymia groups. Previous results showed that there are no effects of gender on the ability to recognise facial emotions (Parker et al., 1999). However, a high score in the alexithymia scale would denote the presence of deficits in the perception of nonverbal expressions of emotion in the videos employed here, instead of effects found from the visual perception of static pictures generally used in the literature (Parker et al., 2014; Bagby et al., 1992).

5.5 Statistical analyses

5.5.1 Descriptive statistics

For all continuous measures, means and standard deviations were obtained and are reported below. For categorical measures, frequencies and percentages were obtained and are reported below.

5.5.2 Eye tracking Data quality assessment

The most common practice criteria to exclude Eye tracking data, which are cited in the literature, includes the percentage of zero values in the raw data samples. Holmqvist et al. (2011) conclude around 2-5% of the data from a population of average, non-pre-screened Europeans needs to be excluded due to participant-specific tracking difficulties. This number varies significantly, depending on the authors, such as (Todd (2000); Pernice & Nielsen (2009) and Schmidt & Mast (2011)), who excluded participants' data due to calibration and tracking issues. Our data quality assessment was a conservative assumption, derived from the standardisation procedure, followed by the latest accuracy and precision measures achieved by tobii, the manufacturer of the tobii TX300 eye tracker used in this study. These reports of precision values reflect the Root Mean Square (RMS) of inter-sample distances, with averages and standard deviations as follows: Calibration Accuracy Average achieved was that of the manufacturer's suggested values of 0.32◦ and SD 0.11◦ Precision just before end of recording 0.21◦ 0.06◦. Given our target sizes, and clear parameters established for the ROI, we can confidently assume our data complies with the standardised methods used in the majority of these type of studies. The acquisition value was the recommended for a 23'' screen (with the test subject at a distance of 60 to 65 cm from the eye tracker). This corresponds to a 31º visual angle from the centre of the eye tracker unit when no head movements were evident or recorded, we can again confidently assume minimisation of outliers and/or erroneous interpretation of missing data points, or data falling outside the regions of interest.

The quality of eye-tracking data is sensitive to a variety of factors. Therefore, eye movements were analysed using several methods. Tobii Studio was used in conjunction with e-prime extension for presentation of stimuli. E-prime extensions software was used in conjunction with the Biopac Acknowledge Software system for the emission of the trigger sent to the EMG system as soon as the video was presented in the eye tracker monitor. Customised MATLAB routines were employed to extract the durations, latencies, and co-ordinates of all gaze patterns and fixations lasting a minimum of 100ms from the raw data. Tobii software was used to calculate how many gaze samples were correctly identified as belonging to the fixations, or saccades, as a percentage of the total number of identification attempts made by the software for the corresponding region of interest. Combined, these methods offered a robust tool to identify which recordings should be included in the analysis of the results and which should not, relating to data quality issues and the regions of interest established for the stimuli.

5.5.3 Global interpolation of Missing Points

The face of the actors was divided into two same-size regions of interest. Therefore, gaze and fixations outside the face were considered outside the region of interest and establishing the position within the x-and y coordinates was helpful to ensure the correct exclusion of this data. Thus, due to blinking or falling outside these regions of interest, a variable amount of points were appearing as zeros and therefore considered missing (Walker 2018). The average loss of datapoints by blinking was determined in normal vision participants before and found to be 10 milliseconds at 300 Hz. Temporal and spatial processing of the visual input such as fixation time, as clustering within the ROI’s were subsequently plotted. The average amount of time participants oriented and fixated their gaze towards the areas of interest was measured consistent with previous literature (e.g. Kovic et al., 2009).

The main analysis for eyetracking consisted of one three-way (3x2x2) within-subjects ANOVA. The dependent variable (DV) was fixation time and condition, orientation and ROI were the independent variables (IVs). Interaction and main effects were followed up with relevant tests where necessary.

5.5.4 EMG

For muscle ZM area of the zygomaticus (zygomaticus major) and for muscle CS area (corrugator supercilii) separately, the main analysis consisted of a 3x2 within-subjects ANOVA, with mean area activation as the dependant variable (DV), and orientation and condition as independent variables (IVs). Interaction and main effects were followed up with the appropriate paired comparisons.

5.5.5 Artefact control and data preparation

The physiological measures of EMG data were offline rectified and smoothed. The video records for each trial and each participant were visually inspected for non-stimulus-related artefacts (e.g., movements such as yawning, which were counted, and coughing or sneezing, which were noted) that could disrupt the EMG measures

5.5.6 Questionnaires: EQ, TORONTO, TAS, CIREN

Frequencies and percentages were obtained for each questionnaire overall. In addition, gender specific frequencies and percentages were calculated for EQ, TORONTO and TAS. Three one-way ANOVAs were performed to explore potential gender differences in these measures. Not all participants completed the questionnaires, and therefore 38 participants completed the EQ, Toronto and CIREN (n=2 missing) while 34 completed the TAS (n=6 missing).

Median split analysis

Participants were grouped into one of two categories, split by the median value of the EQ score (median=53). Participants were also placed into two groups; those with scores lower than 53, and those with scores equal to or higher than 53.

For the primary analysis, the focus was on whether or not the participants yawned in response to the video stimulus portraying a closed mouth, a gape or a yawn. After participants were split into Low (n=17) and High (n=21) empathy categories (as per the median split), a one-way between-subjects ANOVA was performed to explore potential mean differences in the number of yawns between the groups. The same procedure was followed for the Toronto scale, with participants split into Low (n=18) and High (n=20) as per the median = 49. Subsequently, a one-way between-subjects ANOVA was performed to examine whether there were differences in the EMG activity indicating a potential variation in the number of yawns by Toronto category. The CIRENS measured the general energy level of subjects in the morning for those who participated in morning sessions, and, accordingly, the general energy level in the afternoon or evening for those who participated in afternoon or evening sessions.

5.6 Results

5.6.1 Main Results. Eyetracking: Mouth and Eye areas

The 3x2x2 within-subjects ANOVA (visual videos, orientation, ROI), that is, [yawn/gape/close vs. front/profile vs. mouth/eyes]) showed that there was no main effect of visual videos F (2, 74) = .472, p=.625, partial η^2 = .013, nor was there a main effect of orientation, F(1,37)=.116, p=.735, partial η^2 =.003. The main effect of ROI was, however, highly significant, F (1, 37) = 24.188, p=<.001, partial η^2 = .395, which represents a medium effect **(**Richardson, 2011). As can be observed in Figures 5.4 and 5.5, there were no clear differences for mean fixation time between front and profile orientations across all three conditions. There was a non-significant two-way interaction between condition and orientation, F (2, 74) =.739, p=.481, partial η^2 = .020. Figures 5.4 & 5.5 show that participants' fixation times were similar across both Front and Profile orientations. Figure 5.4 shows that, in the front orientation, the highest mean fixation time was in the Gape-mouth condition, with the next highest means observed in Yawn-mouth and the smallest means in Close-mouth. The 2-way interaction between condition and ROI was highly significant, F(2,74)=53.129, p<.001, partial η^2 =.589, but the interaction between orientation and ROI was not significant, F(1,37)=3.606, p=.065, partial η^2 =.089. The means strongly supported the two-way condition by ROI interaction (Figures 5.4 and 5.5), such that means were generally higher for profile orientation and the mouth region than the front orientation. Additionally, the 3-way interaction between condition, orientation and ROI was highly significant, F (2, 74) = 33.697, p<.001, η^2 = .477, which was a medium effect (see Figures 5.4 and 5.5).

This 3-way interaction was followed up with three two-way ANOVAs by condition (close, gape, yawn) to examine whether there were differences in ROI or orientation by condition. Within the close condition there was a significant main effect of ROI, F (1, 37)=4.646, p=.038, but not of orientation, F (1,37)=.710, p=.405.

This was supported by the means, such that the largest mean was observed in close, front orientation in the mouth ROI (mean=6915.03) vs. the smallest mean observed in close, front orientation in the eyes, ROI (mean=4218.94). In the gape condition there was a highly significant main effect of ROI, F (1, 37) =47.154, p<.001, but no effect of orientation, F (1,37)=.300, p=.587. Again, this was reflected in the means, as the highest mean was observed in gape, profile orientation, mouth ROI (mean=8271.55) vs. the lowest mean in gape, front orientation, eyes ROI (mean=2991.43). A two-way ANOVA in the yawn condition revealed a highly significant main effect of ROI, F (1, 37)=32.167, p<.001, but no main effect of orientation, F (1,37)=.270, p=.606. Again, these results were supported by the pattern of means, whereby the largest mean was in yawn, profile orientation, mouth ROI (mean=7628.84) vs. the smallest mean in yawn, profile orientation, eyes ROI (mean=3369.59).

Gender differences were also explored for total fixation time of each condition, orientation and ROI. Results of a between-subject analyses of variance (ANOVA) revealed no significant gender differences (all p>.05).

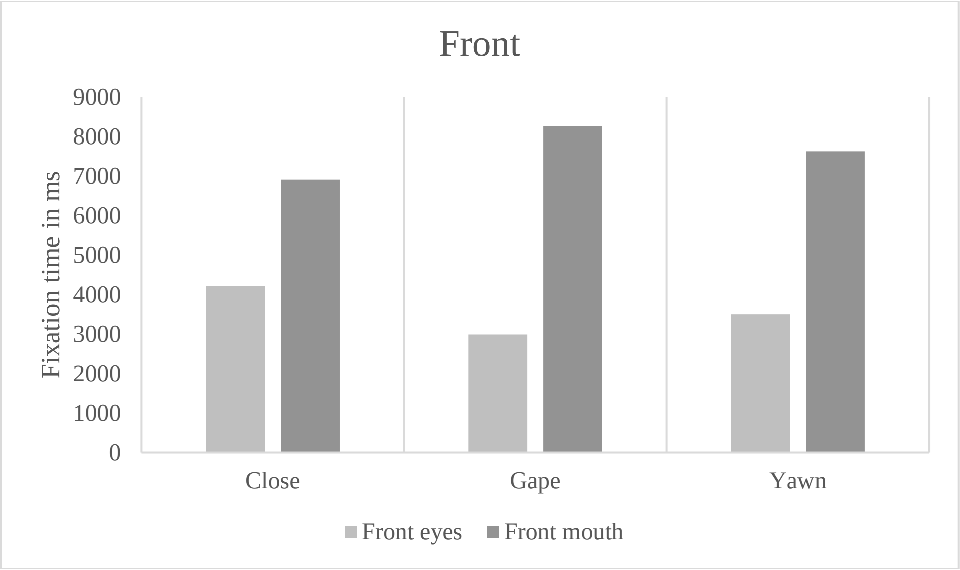


Figure 5.4 Mean fixation duration across all visual video conditions (Close, Gape, Yawn) for each region of interest (Eyes, Mouth) in Front orientation.

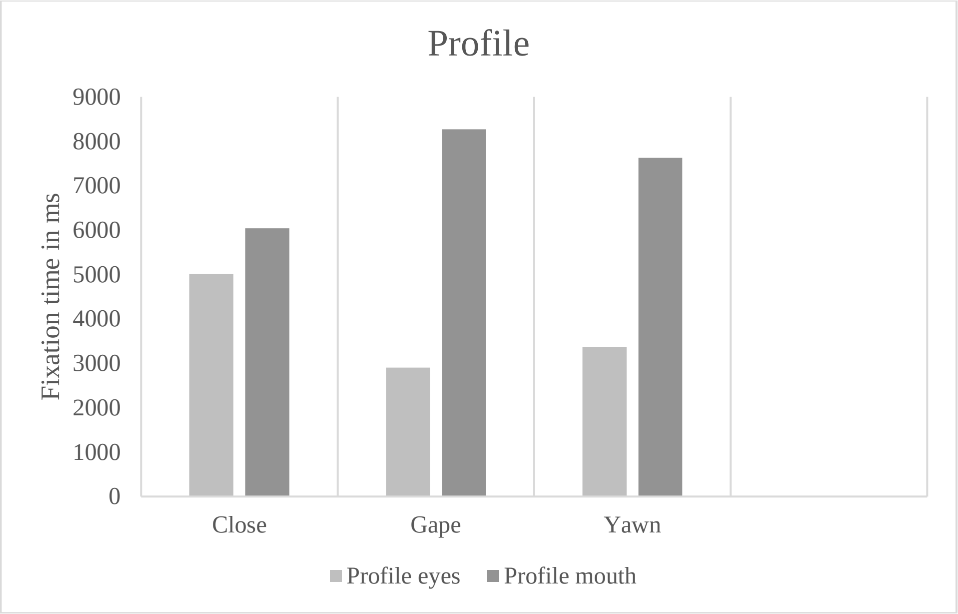


Figure 5.5 Mean fixation duration across all visual video conditions (Close, Gape, Yawn) for each region of interest (Eyes, Mouth) in Profile orientation.

5.6.2 Main results EMG

5.6.2.1 Muscle zygomaticus major (ZM)

3x2 Analysis of Variance (ANOVA)

The ANOVA showed that there was a significant main effect of visual video condition, F (2, 66) = 7.814, p=.001, partial η^2=.191. Upon close inspection of the means for each visual Video condition (Figures 5.6) it could be seen that these were substantially higher for the yawn condition, irrespective of orientation (Front vs. Profile), in comparison to the means for close and gape conditions. There was, however, no main effect of orientation, F (1, 33) = 2.251, p=.143, partial η^2=.064, nor was there a two-way interaction between visual video condition and orientation, F (2, 66) = .524, p=.595, partial η^2=.016.

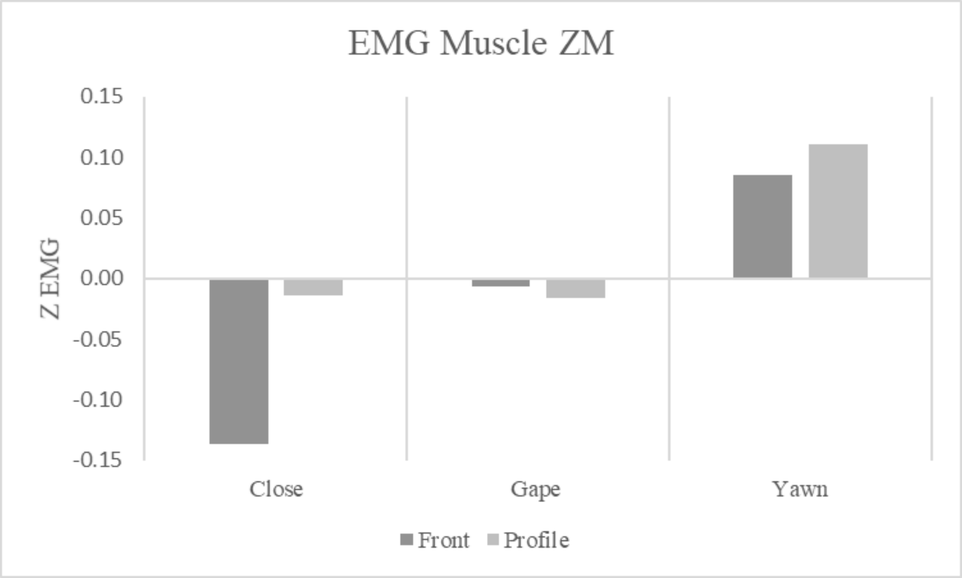


Figure 5.6 Mean activation in zygomaticus major (ZM) for each visual video condition (Close, Gape, Yawn) and orientation (Front and Profile).

5.6.2.2 Muscle corrugator supercilii (CS)

3x2 Analysis of Variance (ANOVA)

The ANOVA showed that there was a significant main effect of visual video Condition, F (2, 66) =3.982, p=.023, partial η^2=.108. Upon close inspection of the means for each condition (Figure 5.7) it could be seen that these were substantially higher for the yawn condition, irrespective of orientation (Front vs. Profile), in comparison to the means for close and gape conditions. There was, however, no main effect of orientation, F (1, 33) =.040, p=.629, partial η^2=.007, nor was there a two-way interaction between visual video condition and orientation, F (2, 66) =.517, p=.599, partial η^2=.015.

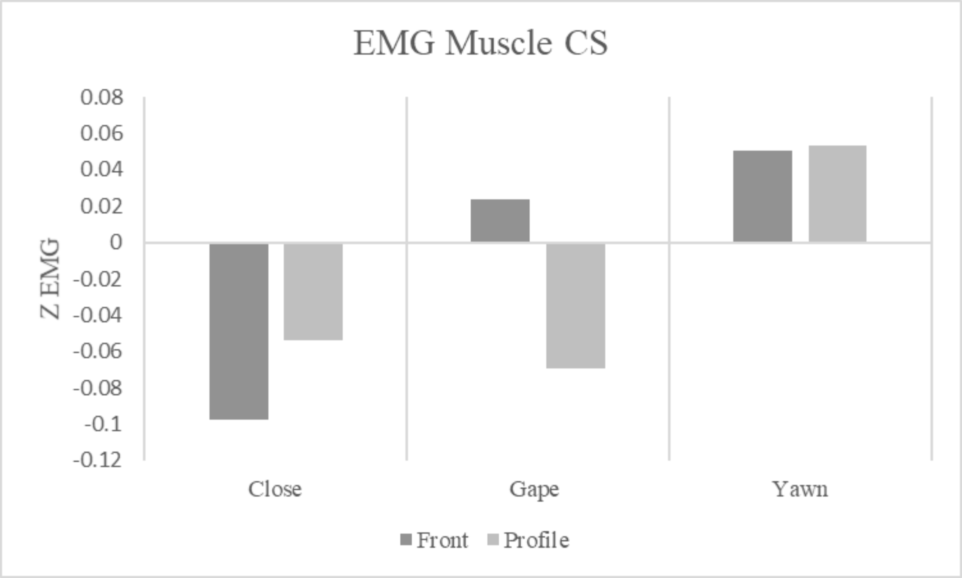


Figure 5.7 Mean activation in corrugator supercilia (CS) for each visual video condition (Close, Gape, Yawn) and orientation (Front and Profile).

5.6.2.3 Muscle zygomaticus major (ZM) & Muscle corrugator supercilii (CS)

3x2 Analysis of Variance (ANOVA)

An omnibus ANOVA including as a factor muscle did not show a main effect of muscle. An 3x2 ANOVA collapsing over muscle showed ANOVA showed that there was a significant main effect of Condition, F (2, 66) =7.394, p=.001, partial η^2=.183. Upon close inspection of the means for each condition (Figure 5.8) it could be seen that these were substantially higher for the yawn condition (M=.075, SD=.528), irrespective of orientation (Front vs. Profile) in comparison to the means for close (M=-.075, SD=.412) and gape conditions (M=-.017, SD=.495). In addition, three one-way ANOVAs showed that there were no significant differences in EMG activation in Yawn or Closed conditions (p>.05). However, there was a significant difference between males and females in the Gape condition, F (1,32) = 4.399, p=.044.

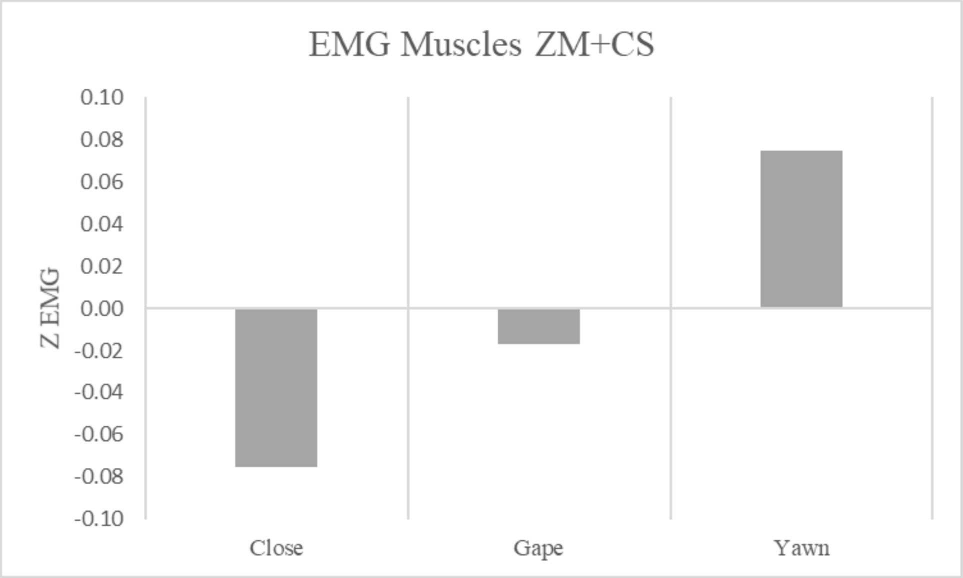


Figure 5.8 Total Mean activation in muscles ZM + CS for each visual video condition (Close, Gape, Yawn).

5.6.2.4 Questionnaires

Empathy Quotient (EQ), Toronto Questionnaire, TAS and CIREN

Participants' mean score on the EQ was 52.42 (SD=8.086), whilst the mean scores on the TAS and Toronto were 28.71 (SD=11.527) and 48.11 (SD=6.685), respectively. There were three categories that participants fell into, with 28 (70%) classed as morning type, 7 (17.5%) classed as afternoon and 3 (7.5%) in the evening category.

Table 7 Mean Gender differences for EQ, TAS and Toronto scores

Measure	EQ (SD)	TAS (SD)	Toronto (SD)
Males	49.33 (8.675) n=9	24.33 (7.124) n=9	43.11 (9.239) n=9
Females	53.38 (7.803) n=29	30.28 (12.492) n=25	49.66 (4.916) n=29
Total	N=38	N=34	N=38

Note. (SD) = standard deviation.

Gender differences in questionnaires

The one-way ANOVAs for EQ and TAS scores showed that there were no significant gender differences in these measures (both $p>.05$). However, there were significant gender differences in scores on the Toronto scale, $F(1, 36) = 7.789$, $p=.008$, $\eta^2 =.178$.

5.6.3 VAS

Findings from the one-way ANOVA using as a factor the three visual condition showed there was a highly significant difference in VAS mean scores between Close, Gape and Yawn conditions, $F(2,72) = 8.819$, $p<.001$, partial $\eta^2=.197$. This can be explained by a higher score in the conditions VAS Yawn = 39.143 (SD=20.806), followed by the VAS Close = 30.585 (SD=24.365) and finally the Gape = 26.083 (SD=18.216). However, the results of the follow up three paired t-tests in between each condition showed no significant differences between VAS scores (all $p>.05$).

5.6.4 Empathy quotient (EQ), Toronto scale and EMG signal

The between-subjects ANOVA showed that there was no significant difference in number of yawns between the Low (n=17) and High (n=21) EQ categories, $F(1, 32) = .015$, $p=.905$. Also, a between-subjects ANOVA comparing Low (n=18) and High (n=20) Toronto categories' number of yawns yielded a non-significant difference, $F(1, 32) = 3.384$, $p=.059$.

Toronto coefficient indicated that females are on average higher on the empathy quotient compared to males, which mirrors the results of other studies (e.g. Chan and Tseng 2017, Norscia et al. 2016, Willer et al. 2015). However, our data does not support the notion that the susceptibility to contagious yawning, measured by an increase in the EMG signal, is directly related to higher empathy quotients.

The CIRENS measured the general energy levels of subjects in the morning for those who participated in morning sessions and, accordingly, the general energy levels in the afternoon or evening for those who participated in afternoon or evening sessions. Findings showed that none of these indicators has an effect on the empathy score or signs such as an increase in activation of muscles used in yawning and consequently denoting yawn contagion.

5.7 DISCUSSION

A thorough assessment was conducted of the impact of multiple factors that could potentially affect susceptibility to, and rate of, contagious yawning. Firstly, a clear pattern of an increase in the EMG signal, showing activation of muscles used in the action of yawning, reconfirms the well-known fact that yawning is contagious and, for the first time, physiological evidence is presented. Secondly, as expected, participants contagiously yawned, when watching videos of unfamiliar individuals yawning. Therefore, one might infer that familiarity is not a necessary factor of CY. The physiological evidence supports the argument that these results show evidence of muscle activation as a consequence of a contagion effect and does not support the possibility that participants were mimicking or imitating the observed action, given that the findings showed a statistically significantly higher level of muscle activity in the Yawn condition than in the Gape or Closed conditions. Lastly, the level of yawn contagion (measured in increases of physiological EMG activity in muscles used for yawning) found in healthy human volunteers with intact vision was in line with previous studies, both in the human literature and in the behavioural animal experiments in this thesis, within and across species respectively (Provine 1986; Joly-Mascheroni et al., 2008; Joly-Mascheroni et al., 2019 submitted).

The results of the current study showed that there were no gender differences in EMG activation in the Yawn and Closed conditions. However, there was a gender difference when participants watched videos in the Gape condition.

Previous studies reported to have found indirect evidence that baseline empathy level was an indicator of an individual's susceptibility to yawn contagion (Norscia et al. 2016, Norscia and Palagi 2011). These used video recordings to count and code behaviours. A potential problem with these studies is that the methods of counting would only be able to account for overt wide mouth opening yawns. Most people can stifle yawns. The present study is the first to provide physiological evidence measured through EMG instead of relying on visual judgment and offering a more robust indicator of the participant’s response. Other studies argued that contagious yawning is a signal of empathy “but the signal is not very strong or clear” (Franzen et al., 2018). They also point out that the Bartholomew and Cirulli (2014) experiment did not include a control condition, therefore their findings of no relationship between empathy and yawn contagion was obscured by methodological constraints (2018). Although Bartholomew and Cirulli (2014) were criticised for not having included a controlled condition, unfortunately, experiment 1 in Franzen et al., (2018) did not involve a control condition either. Hence, they reported that without a control condition, it was unclear if the yawning observed had been elicited by contagion or the yawning had been spontaneous and would have happened even if the subjects had not watched yawning faces (Franzen et al., 2018). Although (Franzen et al., 2018) still reported to have found clear evidence that the susceptibility to contagious yawning was related to empathy, according to the results in this study, differences in empathy scores had no impact on the level of EMG activity and therefore on the rate of yawn contagion.

As mentioned before, other studies have identified correlations between high empathy quotient and increased susceptibility to yawn contagion (Anderson et al., 2003; Lehmann 1979, Norscia et al 2016, Palagi et al. 2009, Provine 1986, 2005). However, the present study used two different measures of empathy and, although one scale showed that females scored higher, there was no evidence of empathy exerting a higher impact on the physiological EMG measurements and consequently on yawn contagion. This suggests that findings warrant further explorations to clarify discrepancies in the literature, with regards to the generally-held view of the effect empathy may have on susceptibility to yawn contagion.

Following the results presented in the previous chapters on explorations of contagious yawning across species between humans and chimpanzees, where unfamiliar individuals were found to trigger yawn contagion at a higher rate than familiar individuals, it was relevant for this investigation to only include unfamiliar individuals as it still remained unclear which features of the others' unfamiliar faces are important in the yawn contagion process. These results demonstrated, through physiological EMG measures and eye tracking data, that humans with intact vision either fully yawn contagiously, or at least present a higher level of EMG-measured physiological activity when observing unfamiliar humans yawning. The investigations of the eye and mouth areas, as regions of interest, showed that physiological evidence of muscle activation was clearly higher in the Yawn condition, and a lower amount of activation in the Close or Gape conditions, when participants were still fixating their gaze on the mouth area of the facial stimulus.

The findings of the present study do not fully support the special role of fixation on the eyes to elicit a higher rate of yawn contagion (Provine, 1989). As expected, eye tracking results showed that fixation time was higher when directed towards the mouth area, even though the videos lasted 10 seconds, which provided enough time and opportunities for participants to saccade from the mouth to the eyes if they wished to. Furthermore, the eyes of the actors in the videos only closed in the yawning condition and not in the close or gape conditions.

In previous studies, such as in Haker et al. (2009), participants were aware of the goal of the stimulation-inducing contagion by yawning and were thus instructed to pay full attention to the videos, avoiding any head movements. In their experiment, the authors also requested that the participants suppress overt yawning, by keeping their mouths closed. After each yawn sequence (consisting of repetitions of the same stimulus), the participants had to indicate whether they had 'felt a contagion', by pressing one button indicating contagion, or another indicating no contagion. By not asking each participant to respond until after each session had finished, it is likely that the participants would have had to rely on memory and an accurate recollection of their previous sensations, whereas responses related to the neutral stimulus were requested after each video. Although the authors claimed that their procedure was set up in this manner to avoid additional motor activation, the results may still have been confounded, given that they asked participants not to perform yawning motions in order to avoid movement artefacts in the scanner.

This potentially confounding factor of the design of previous studies was both addressed and avoided in the present study by requesting participants to provide a self-report measure immediately after each video. Importantly, in the current study, EMG activity was measured while participants were watching the videos. Furthermore, there is a strong possibility that in Haker's study, motor inhibition could also have led to activation of the IFG region, particularly because both factors (motor inhibition and mirror neuron activity) may be associated with IFG activation (Rowe and Siebner, 2012; Bien et al., 2009). The current study aimed to address other limitations of Haker et al., 2009, which in this case were acknowledged by the authors themselves, such as the task-imminent inequality between the two sets of dynamic stimuli, especially concerning the amount of biological motion. Therefore, the videos in the present study were constructed in such a way that the amount of motion in the Gape and Yawn conditions were practically equal, with the gape displaying a less wide opening of the mouth. Also, all videos maintain the same duration of facial movement. Furthermore, whenever a task is designed to provide differentiated stimuli in the manner set up in Haker's fMRI study, one cannot entirely exclude the possibility that the extra activation in BA 9, found in the yawning condition, would have been merely due to additional facial motion.

Even though aspects of emotion perception and response were considered beyond its scope, one limitation of the present study is that emotion-related actions could have provided the chance to explore potential differences in resonance in the participants' facial muscle area in an emotional and non-emotional contagion scenario. Perhaps a direction for future studies would be to complement this paradigm with the inclusion of a condition portraying emotional actions, to which behavioural responses could be compared with responses to non-emotional conditions that were similar to, or the same as, the actions presented here. Future investigations could examine the effect of inhibitory and facilitatory effects arising from the perception of others' behaviours, specifically exploring whether these particular actions would modulate activation of cortical areas. For instance, fMRI studies that analyse effective connectivity between visual cortex and somatosensory and premotor areas could be used to investigate which of the possible anatomical connections and neuronal paths, mentioned in the introduction here, could trigger contagious or mimicry-related activity in somatosensory cortices, as a result of the activity produced by either the visual perception and activation of the visual cortex or auditory perception and auditory cortex. It would be interesting to explore these findings further by including emotional actions, such as laughter, which is considered a contagious behaviour too. Given that there would be emotion involved within the action of laughing, there could be some preferential activation of one, the other, or both brain hemispheres, and therefore it would be possible to explore whether each somatosensory cortex may convey people’s reported experience. It would be interesting to know if there are correlations between the pre-motor activation, somatosensory cortex and even motor cortex, and participants self-report of what they consider funny. This could perhaps be examined during electrostimulation of each of the somatosensory cortices, combining analysis of changes in people’s perception of others facial actions during the manipulation of activity in these regions using TMS.

5.8 Conclusion

From the results of the present study, the empirical evidence on whether contagious yawning is related to empathy seems to be in contrast with previous inconclusive studies, such as that of Massen and Gallup (2017). The present findings do not necessarily provide clarification to the debates in the literature, partly because findings showed no gender differences in empathy quotients and the highest empathy scores did not trigger a higher rate of yawn contagion. Therefore, taken together, the existing evidence continues to appear, at best, contradictory. The present study did, however, show clear physiological evidence denoting human visual yawn contagion, based both on EMG and eye tracking measurements, the results of which could not be attributed to mimicking or imitation behaviour. The main effect of Yawn condition together with the high score on the participants’ self-report of the urge to produce the same action, denotes contagion in the yawn condition and not in Gape or Closed mouth. There was neither intentional nor unintentional imitative or mirroring behaviourally displayed or physiologically measured. The highest EMG activity measured when perceiving a yawn and not a Gape or Closed mouth cannot support the possibility of participants mimicking or imitating the facial actions in these conditions. This study represents an important finding that indicates potential routes for future research. Firstly, susceptibility to yawn contagion does not appear to be related to high empathic abilities. Secondly, results show no gender differences in the rate of yawn contagion, and thirdly, not surprisingly, that the mouth appears to be the area of the face that is most important in visual yawn contagion, as opposed to previous findings where the focus was on the eye contact (Senju et al 2009). Results confirm that previous findings denoting eye contact as necessary for yawn contagion were relevant in autistic individuals as the profile view of Yawning action here showed high fixation patterns and highest EMG mouth area muscle activity. These findings raise several questions for future research where emotion perception and contagion could be explored jointly, employing an adaptation of the paradigm of the present study investigating the contagious aspects of laughter. Since findings reconfirm yawn contagion through visual perception, and there is evidence of contagious yawning through auditory perception, an interesting question would be: which other sensory perceptual modality would the puzzling phenomenon of yawn contagion apply to? Therefore, the next study explores yawn contagion though tactile perception in blind individuals.

6 STUDY 4. PHYSIOLOGICAL EVIDENCE FOR CONTAGIOUS YAWNING THROUGH TACTILE PERCEPTION IN BLIND INDIVIDUALS

6.1 Introduction

Tactile perception has been difficult to define ever since the period of the great Greek Philosophers. Perceptual modalities, Aristotle argued, are to be individuated by their intentional object. The difficulty, however, is that “prima facie tactile objects do not constitute a natural class” (De Anima, 422b17-424a16). “Let us call the proper object of a sensory modality, the entity that we directly perceive through this modality only; and its primary object, the entity that we directly perceive through it as a matter of necessity” (Sanford, 1976). The importance of the tactile sensory modality for blind individuals, however, remains as great as ever, and the benefits in exploring the relationship between tactile perception and social interaction, has not been investigated thoroughly. Therefore, this study examines the relations between the tactile sensory modality and the perception of others’ facial actions, and the consequences of these connections relative to contagion.

The primary focus here is to explore, for the first time, if yawning is contagious through tactile perception. Touch seems elusive to study in isolation from other sensory modalities. The difficulties appear to be associated with the conceptual delineation between what is purely and solely tactile perception, and what is restricted to contributions of experiences acquired through other sensory perceptual modalities. The experiences blind individuals acquired through their first social interactions are normally with the primary carer. During childhood, it would be permissible for a blind child to be able to touch the faces of parents. But in adulthood and normal social interactions, it is of course more difficult for blind individuals to have the chance to explore the facial features of another person through tactile perception. Obviously, for individuals with intact vision, using a mirror is how they perceive their own facial expressions. However, for blind individuals, not only is interpreting others’ facial actions and gestures a real challenge, but learning to portray their own accurate facial expression, one that conveys precisely what they are feeling, is often just as difficult.

To this aim, this study explores if the physiological response of facial muscle activation (measured using electromyography -EMG), is sensitive to tactile perception of an embodiment-inducing action (yawning) which can potentially trigger the urge to produce the same action i.e. is contagious. A follow up aim is to investigate if this response is modulated by individual empathy levels (measured via subjective questionnaires) or the subjective experience or “urge” to perform that movement. With this aim in mind, an android head was built able to simulate several human facial actions (yawning, gape). Therefore, another important element of this study is to explore if experiential contagion may result from the tactile perception and interactions with a yawning non-biological stimulus, namely, an android. Overall, this would constitute the first study to investigate yawn contagion through tactile perception of a non-biological agent.

The use of an android as a tactile stimulus raises a few considerations. Touch is considered by some authors as “bipolar” (e.g. Katz, 1925), and their proposals generally rely on the common assumption that tactile perception always involves some experience of our own body, in conjunction with the experience of external objects. This bipolarity attributed to tactile perception is related to the specific nature of touch, which consists of our awareness of our own body, along with that of others, in the process of interacting with the whole environment around us. In this study, the approach goes beyond this notion of bipolarity, to include both biological and non-biological entities. Objects around us, are generally non-biological entities, and so the tactile perception of a facial action that is, in fact, performed by a non-biological inanimate agent, represents a novel way of exploring the intricate mechanisms underlying these interactions. This agent is of course a very particular object, one that has the capacity to portray movement and therefore, by also characterising a facial gesture, represents a non-biological stimulus, but a very similar one, to that of a human facial movement or gesture.

Several apparently contradictory conceptions should be addressed first. One important characteristic of the stimulus used here, is that paradoxically, it looks and feels like an inanimate agent. It is understood that this may sound contradictory, in several ways. Through tactile perception, the stimulus developed for this study might naturally feel inanimate, simply because it is made of silicone. However, it may also feel naturally biological, because it moves. Another apparent contradiction may arise because the “object” in our study, is, literally, an object, an android. But it is an inanimate object, that portrays human facial expressions, and, for the main purpose of our explorations with blind individuals, it represents the perfect stimulus for the study of potential embodiment-inducing mechanisms, a process referred to here as experiential facial action contagion. A secondary purpose of this work is that for stroke victims, it constitutes a sound biofeedback system, which can help with the arduous process of rehabilitating exercises of facial gestures and expressions.

6.1.1 Tactile perception in blind individuals

Our interaction with the world around us is through all sensory modalities. Although this is not necessarily in equal quantities, in the case of blind individuals, due to their lack of visual feedback, tactile/haptic experience becomes an indispensable part of their everyday life. According to Loomis and Lederman (1986) the phrase “haptic perception” refers to the combined use of cutaneous and kinesthetics’ sense, and generally, it is an “active experience under the individuals’ own control” (see also Lederman & Klatzky, (2009).

The receptive field capability of tactile perception cells, makes them important in transmitting local spatial discontinuities and are known to be helpful for detection of edge contours and Braille, so their use is maximised here in these studies for the accurate reading of marks, given that being selectively sensitive to points, edges and curvatures, the cells’ capabilities make them perfect in recognising the wrinkling of a silicone-based structure and form of the android’s facial contours and motion. The receptive field areas of the sensory peripheral regions such as hands, can potentially exert and impact on the electrical stimulation of those tactile sensory areas as a whole. The actual receptive field encompasses the sensory receptors that would feed into the corresponding sensory neurons and therefore can also influence a collection of receptors which are capable of generating an activation of other neurons via synaptic and post synaptic connections (Levitt 2010) The accuracy at which a tactile stimulus is detected depends on both the density of receptors and the size of their receptive fields. The greater the density and the smaller the receptive field, the higher the tactile acuity (Cattaneo et al., 2011). It is not surprising that studies found that cutaneous receptors, are more densely present on the tips of the glabrous digits and in the perioral region (d'Annunzio, G. 2011).Legge et al., 2008). Accordingly, receptive fields are smaller on the finger tips, where each receptor serves an extremely small area of the skin. However, at a cortical level, densely innervated body parts, such as the hands and the face, are represented by a large number of neurons occupying a disproportionately large part of the somatosensory system's body representation. This is also another important feature of the perceptual and physiological composition of our brain structures and regions exerting an impact upon our cognitive and behavioural responses. Proprioceptive receptors are located in our muscles. They provide the brain with sensory information, coded by these cutaneous and proprioceptive receptors to convey it through the dorsal column medial-lemniscus pathway. This pathway has been shown to underlie the capacity for fine form and texture discrimination, and again, particularly importantly for us, form recognition of three-dimensional objects, and motion detection, as well as transmitting information about conscious awareness of body position in space (Fonseca et al., 2014).

The receptive field capability of these proprioceptive receptors makes them important in transmitting local spatial discontinuities and are known to be helpful for detection of edge contours and Braille, so their use is maximised here for the accurate reading of marks, given that being selectively sensitive to points, edges and curvatures, the cells' capabilities make them perfect in recognising the wrinkling of a silicone-based structure and form of the android's facial contours and motion. Although Ruffini corpuscles have a smaller spatial resolution due to their large and less localised receptive fields, they are still critical in providing the brain with motion signals from the whole hand and whatever they are in contact with.

The human brain, as well as that of the chimpanzees, animal by which we share a common ancestor and the primates that were participants of the first two studies in this thesis, is not entirely composed of a predetermined conglomeration of neuronal cells, each tackling a function that is extremely and irrevocably specific. Neither is it composed of areas whose functions we are unable to change completely or significantly. Rather, many studies have showed that we can modify many of these neurons' functions and specialities, and that, in fact, the whole brain has an extraordinary capacity to reorganise itself (Chang, Y. 2014), in response to external variables, such as the quality or quantity of sensorial experience or capacity. Furthermore, regardless of the extent to which a specific sensory modality has been affected and diminished, plasticity occurs at different organizational levels of the central nervous system, from the genetic to the molecular, and from the neural to the cortical levels (see Shaw & McEachern, 2001). The "other sensory areas" do get reorganised. The expansion of the representation of the fingertips in the sensorimotor within somatosensory cortex of many blind Braille readers is a great example of intramodal plasticity (e.g. Pascual-Leone & Torres, 1993).

Depending on the particular behaviour for which we need to utilise the sensory modality, such as that of the auditory perception employed to achieve a level of musical ability, whether playing an instrument, listening to a particular music style or further becoming an expert player/listener, blind individuals can acquire expertise in recognising other peoples' facial expressions and in accurately portraying their own. It is not normally thought that these abilities could be acquired through tactile perception. This study aims to take advantage of the general reorganization phenomena that takes place in blind individuals (for reviews see Grafman, 2000; Roder and Neville, 2003) and expand the field to explore how combination of crossmodal information can be integrated in the blind individual. In this study, the focus is on the ability to embody actions thought tactile perception. Other interesting avenues that need to be followed will maximise the available information from functional existing sensory modalities. These can positively affect blind individuals' everyday social interaction and communication. For example, the further development of sensory substitution devices (SSDs) can help intramodal changes to occur in the same cortical regions that are normally devoted to processing information in a specific percept, and these brain areas can further be trained to be used by an alternative sensory modality. Although not immediately apparent, the effects of visual sensory impairment and/or complete lack of visual perception, are similar effects to those resulting from a stroke (provoking limited mobility of a body part, e.g. facial muscles). This research may lead to a further enhanced reliance on the improved alternative sensory abilities for both population cohorts. In the case of the blind, this would be by maximising the tactile and auditory domains, and, in the case of the neurologically lesioned, this may represent a way of improving facial motion and expression, through visual and auditory perception of their own limited range of facial movement and gestures. Further details related to the use of SSDs will be discussed in the general discussion and implications.

6.1.2 Cortical reorganisation and intramodal cortical plasticity.

Significant amount of research conducted to study the pattern of connectivity between different brain regions has shed light on the many neural pathways that mediate the functional and behavioural changes incoming from actual changes in the occipital cortex of blind individuals (Tanabe et al., 2009). Given that functional plasticity can be induced both by sensorial deprivation and by higher practice in the spared modalities, studies on sighted individuals highly trained in a specific field, such as professional musicians (Pantev, Oostenveld, Egelien & Ross, 1998) have provided us with clarification of the effects that intense perceptual training might exert on brain plasticity and compensatory mechanisms. Critically, cortical reorganisation can either result from an unmasking of previously silent connection and/or from a sprouting of new neuronal conglomerating elements from those areas that previously existed as connected areas of the brain. These underlying mechanisms also result in morphological alterations in blind individuals, such as changes in the volume of grey and white matter, cortical surface and cortical thickness and consequent reorganisation. Previous results show that it is reasonable to expect beneficial effects from the use of the tools developed as a result of the present study (Voss, Pike, & Zatorre, 2014).

A phenomenon called “map expansion” refers to the enlarging of functional brain regions, as a result of actual functional requirements, usually due to sensory impairment (Grafman et al, 2000). Authors have proven, for example, that an intramodal expansion of the tonotopic representations in the auditory cortex of blind individuals has been consistently reported to be the subservient means on the increased auditory capacities often associated with blindness (Elbert et al., 2002). It is not that blind individuals are normally exposed to more auditory information than sighted individuals, but it might be that they do eventually receive more stimulation, given that, in order to effectively socially interact with others and within the environment, they do have to rely more heavily on the right interpretation of the auditory and tactile input.

Somatosensory cortical plasticity refers to the capacity of the sensory and motor “homunculus” to change in response to tactile experience. For instance, the repeated use of fingertip for Braille reading induces an enlargement in the fingertips-representation within the homunculus (e.g. Pascual-Leone & Torres 1993; Schweizer, R., et al 2008).Burton, Sinclair & McLaren, (2004). Accordingly, a TMS experiment has shown that motor-evoked potentials in the first dorsal interosseus muscle of expert Braille readers can be induced by stimulating a larger area of the motor cortex than that of the non-reading hand of the same participant and compared to both hands of control participants (Pascual-Leone and Camarota et al., 1993). There are several lines of research that showed how neurological disorders or lesions can present the same clear maladaptive or positively adapted plasticity, in other conditions that are not related to sensory impairment.

Comparisons have been shown plausible as Sterr et al. (1998) and Pujol et al. (2000) demonstrated in this regard (e.g. movement-disorder that causes involuntary contractions of muscles, which paradoxically are also often seen in blind children and adults) “but may sometimes not co-occur with increased cortical representation, and might also be subtended by a change in firing pattern of the involved neural population” (see Hotting & Roder et al., 1999, 2009). This may suggest a possible involvement of inhibitory and hyperactivation processes in yawn contagion underlying mechanisms. Another example was provided by findings showing tactile imagery even through Braille reading in blind subjects’ induced task-related activation in the occipital cortex. This suggested that the somatosensory input was redirected toward occipital areas; these results were later confirmed using SPECT and regional cerebral flow measurement (Uhl, F. et al., 1994). Furthermore, Burton and colleagues demonstrated occipital activation in early and late blind subjects, both during embossed uppercase-letter reading (Burton et al., 2006). The authors conclude that a blind individual’s perceptual system is re-organized in a similar manner to that of a full-sighted individual, except that the initial input for recognition is not being provided by the visual modality but by the tactile (Burton et al., 2006).

The causal role of the activation of visual areas during tactile processing in blind individuals has been demonstrated by single case studies and TMS experiments

(Florio & Haggard, 2005; Bolognini, Rossetti & Maravita, 2011). In particular, Hamilton and colleagues (2000) have reported that an infarction of the bilateral occipital cortex induced alexia in an early blind Braille reader (Merabet, L., et al 2005). This lady was congenitally blind and happened to have learned Braille when she was only six years old. Later, when she was sixty-three, she suffered from a bilateral occipital ischemic stroke. Importantly, she was still able to detect tactile stimuli without any relevant loss in her tactile sensitivity. However, critically, she was unable to recognize Braille characters. This finding has been regarded as clear confirmation of the causal role of the occipital cortex in Braille reading. Further support for this view was provided not just by case studies, but also by many experiments using TMS, allowing researchers to investigate the need of a specific cortical region for a particular task, by inducing a sort of reversible “virtual lesion” (Walsh, V. & Pascual-Leone, A., 2003). Virtual lesions approaches have also been employed to study cortical plasticity phenomena in blindness and other somatosensory perception mechanisms as the crossmodal reorganisation evidence in sighted people. Boroojeredi et al., (2000) showed that, after subjects were blindfolded for five days, visual cortex excitability increased after 60 minutes. This finding was accompanied by increased tactile acuity. Interestingly, sighted individuals showed increased tactile acuity after only 90 minutes of visual deprivation (Facchini et al., 2003). Pantev and colleagues (2003) reported that when lips of trumpet players were stimulated while being presented at the same time with a trumpet tone, activation in the somatosensory cortex increased more than during the sum of the separate lip and trumpet-tone stimulations, indicating that somatosensory cortices of these players had learned to respond to auditory stimuli (Pantev et al., 2003).

In addition, there is also robust evidence of occipital cortex activation in blind individuals during auditory processing. For example, several studies using EEG have reported that the topography of auditory-related evoked potentials in blind individuals is shifted towards posterior (occipital) regions. When ERPs were recorded during a free-field sound localisation paradigm in blind subjects, the N1 and P3 components not only peaked at their usual position but were also present over occipital regions, suggesting that blind individuals’ occipital cortex might be involved in very early stages of auditory processing (at around 100ms after sound presentation) (Kujala et al., 1992; Leclerc et al 2000).

Finally, further evidence of crossmodal brain activation in blind individuals is provided by speech and music studies. Enhanced speech perception capabilities in a blind listener, have also been associated with activation of the fusiform gyrus and primary visual cortex (Hertrich et al., 2009). According to Hertrich, the left fusiform gyrus, known to be involved in phonological processing, may provide the functional link between the auditory and visual systems. Gaab and collaborators (2006) compared the neural correlates of absolute pitch perception in a group of blind and sighted musicians, reporting that the former relied on a different neural network in pitch-categorization, including visual association areas (Pascual-Leone et al., 2004), thus possibly explaining the higher incidence of absolute pitch in blind compared to sighted musicians (Hamilton et al., 2004; Pring et al., 2008).

6.1.3 Tactile perception and action observation

Several lines of evidence from visual perception studies seem to point to an important involvement of the motor system in supporting processes traditionally considered to be "high level" or cognitive, such as action understanding, mental imagery of actions, and perceiving and discriminating objects. One of the first examples was provided by the discovery of a population of neurons in the monkey ventral premotor cortex (mirror neurons) that discharge both when the monkey performs a grasping action and when it observes the same action performed by other individuals (Gallese et al., 1996; Rizzolatti et al., 1996a). In those visual studies the mirror neurons were regarded as responsible for providing the neurophysiological evidence for the capacity of primates to recognize different actions made by other individuals. A short summary of the mirror neuron mechanism in humans have been provided in earlier chapters of this work. This visual-motor matching mechanism in the visual studies with monkeys was regarded as a motor matching of the visual perception.

The current study employs physiological measures taken from the facial muscle, during the perception of facial actions. Because of the classic mirror neurons assumption, the same motor pattern which characterizes the observed action is evoked in the perceiver who activates its own motor repertoire, it is assumed that the recorded facial muscle activation would be an indirect measure of internal simulation of the perceived action, and by extension, a representation of sensorimotor activation. Moreover, if research of action perception of visually-impaired participants shows actions and behaviours can be perceptually recognized, even when the percept is acquired through touch, we would then assume that tactile perception of facial actions can evoke an internal sensorimotor response (enactment of the tactile perceived action) measurable by electromyographical activity of the correspondent facial muscles.

The aim here was to measure the enactment of the (tactile) perceived action by recording facial muscles using electromyography (EMG). Muscle activations measured by electromyography (EMG) are detected employing small skin surface electrodes. Signals are decomposed into their constituent motor unit action potential trains (MUAPTs). The MUAPTs that essentially constitute and are the main components of an EMG signal provide information regarding the temporal behaviour and morphological layout of individual motor units and specific face muscle area contractions during facial action, and in the case of our study here, during facial perception. Finally, beside revealing how classical internal simulation mechanisms respond to tactile perception, we will use similar measurements to those employed in study 3, regarding individual levels of empathy and subjective feelings of reproducing the observed facial contagious action, to investigate how they relate to when embodiment is tactually probed.

6.2 Hypotheses

The main aim of this study is to explore if blind humans catch yawns through tactile perception. The study also aimed to explore a potential and previously reported relation between high empathy quotients and a higher susceptibility to yawn contagiously or show a strong indirect index of yawn contagion.

(H9) It is hypothesized that when an adult blind human perceives a yawning stimulus through tactile perception, a physiological response measured by EMG in the participant facial muscles will be present. The prediction is that in this cohort of blind participants, there will be differences in the strength of the facial muscle activity between the experimental yawning conditions and the control conditions. A lower EMG response is predicted in the close condition, incrementing in the gape condition and stronger in the yawning condition. This modulation will denote presence of contagion, of internal simulation, embodiment and motor resonance by tactile perception.

(H10) Based on our results from study 3, it is hypothesized that there is no relation between empathy scores and intensity of the yawn contagion. Therefore, the prediction is that there will be no significant correlations between the strength of the EMG response denoting contagion and empathy quotients scores.

6.3 Methods

6.3.1 Participants

Given that the previous study explored the same action perception mechanisms as in the present study but through visually perceiving means, this experiment focused on blind participants. It might be worth clarifying that participants were all diagnosed medically and classified legally as blind. This meant congenitally blind humans unless mentioned differently. These participants were totally blind or had at most some light perception without pattern recognition and the majority apart from two participants, since birth. Most participants became blind because of peripheral lesions (e.g. retinopathy of prematurity, retina degeneration) or an atrophy of the optic nerve but they had neither direct lesion in the brain nor any neurological disease.

Thirty-six blind participants took part in this study. Participants' mean age was 44.04 (SD=15.29) years and there were 20 males (55.56%) and 16 females (44.44%). The study received ethical approval from the City, University of London, Research Ethics Committee and participants written informed consents were collected.

6.3.2 Tactile Stimulus

The tactile stimulus was an android head able to move and portray three different actions. This android was previously employed in study 2 (please refer to the general methods section in chapter 2 or study description in study 2 for full details). The actions portrayed by the android were (1) yawning, (2) gape, (3) close (no-movement).

The android was placed in front of the participants, so they were able to touch it and examine it with their hands. The android was placed in two different orientations with respect to the participant: front and back. The front orientation allowed the participants to perform the tactile examination as if they were touching another person facing them. The back condition allowed a tactile examination that resembled one we can do of our own face, or when we touch the face of a person while we are behind them (see an example of the stimuli in Figure 6.1). Trials and blocks were in a randomised.

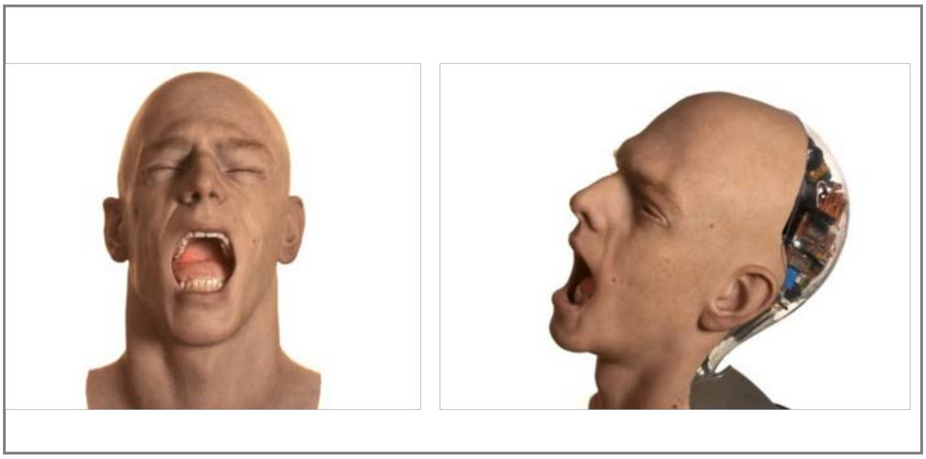


Figure 6.1 Visual image of the android depicting one of the experimental conditions (yawning).

6.3.3 Measures

6.3.3.1 Facial Electromyogram (EMG)

Bipolar EMG was recorded over the left eyebrow and cheek targeting the corrugator supercilii (CS) and zygomaticus major (ZM) muscle areas (Fridlung and Cacioppo, 1986). Data were sampled at 1000HZ with DC- 1.6 kHz bandwidth using a BIOPAC System. Using both Matlab and Aknowledge software, data were filtered (20-500HZ), down sampled to 500Hz, full-wave rectified, and segmented (-500 ms pre-stimulus to +2000 ms post stimulus onset). The baseline was corrected employing the pre-stimulus period, and smoothed with a sliding average window of 3 frames (TFs, 6 ms). Trials with baseline amplitudes over 30mV had to be excluded as a threshold needed to be consistent and as similar as possible to normal vision participants in the previous study.

In this study EMG measures were taken during tactile perception of the android portraying the three types of actions in two orientations (front and back). Participants' facial electromyographic activity (EMG) was measured and video-recorded with a Panasonic HC-V110, simultaneously with their tactile perception, in order to investigate the online congruency between muscular activity and tactile perception denoting contagion. Four disposable Ag/AgCl surface electrodes (4mm) were placed in participants facial muscles, and one on a non-muscle area to act as ground and two electrodes on the Zygomaticus Major muscle area (from now on referred to as Muscle ZM), and two electrodes were placed over the Corrugator Supercilii (from now on referred to as Muscle CS) on the left side of the participants' face, following Fridlund and Cacioppo's (1986) guidelines (Figure 6.2).

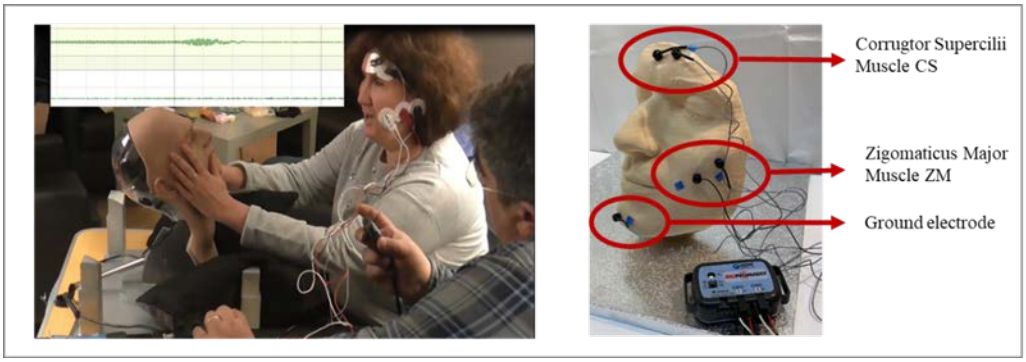


Figure 6.2 Schema illustrating the localization of electrodes during the EMG recording.

6.3.4 Questionnaires

6.3.4.1 Empathy questionnaire:

The Interpersonal Reactivity Index (IRI) (Davis, 1980) is currently one of the most widely used measures of dispositional empathy. The IRI is generally a 28-item self-report measure which consists of four 7-item subscales, each tapping into a differing facet of the universal notion of empathy. This has been largely defined as a degree of reactivity to others. The four subscales are Perspective Taking (PT), which relates to the propensity to assume the psychological point of view of another;

Fantasy Scale (FS), related to the inclination of individuals to transpose themselves imaginatively into the feelings and actions of fictitious characters in books, movies, and plays, and was removed because it was not relevant to the content of the study; Empathic Concern (EC), which assesses feelings of sympathy and concern for unfortunate others; and Personal Distress (PD), which measures feeling of personal anxiety and unease in tense interpersonal settings. Participants are divided by the median averaged IRI score into low and high IRI group for purposes of analysis, followed the median split analyses, correlation and multiple regressions analyses.

6.3.4.2 Sleep questionnaire:

The Circadian Energy Scale (CIRENS) (Ottoni, Antoniolli & Lara, 2011), is a two-question chronotype measure based on self-report energy levels throughout the day. The difference between the evening score and morning score determined the overall chronotype score, ranging from 24 (most marked morning preference) to +4 (most marked evening preference). It has previously been shown that differences between chronotypes, or sleep-wake rhythms, affect yawning susceptibility.

6.3.5 Procedure

Participants were sat on a chair in front of the android. Before the experiment they were asked to touch the android head to get familiar with its morphology and reduce any effect related to novelty. Once they were comfortable with the tactile stimulus and the experimental setting, the experiment started. Participants instructions were provided in audio format, in braille and verbally. Participants were instructed to perceive tactually the stimuli in front (android) every time they heard the auditory instruction that indicated a trial was starting

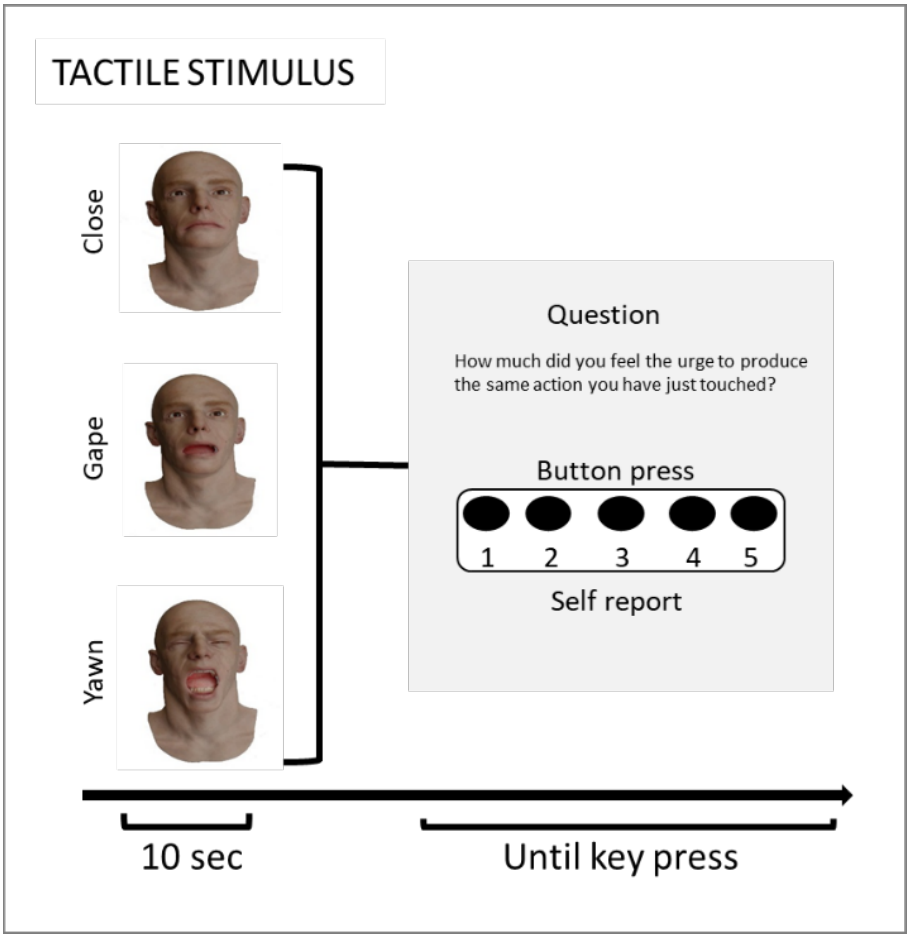


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Figure 6.3 Trial structure for study 4. Participants were instructed to touch at the beginning of each trial (auditory instructions). After tactile inspections of the android during 10 seconds, participant had to rate in a 5-button box how much they felt to produce the action they have just touched.

Every trial commenced with a 10 seconds stimulus (yawn, gape or close) in one of the two possible orientations (front or back). While participants tactually examined the performed action, EMG was recorded from two facial muscles (corrugator supercilii (CS) and zygomaticus major (ZM). Each trial lasted ten seconds. After each trial participants had to indicate “how much they felt the urge to produce the movement they have just touched” using a 5-button response box in front of them (see trial procedure in Figure 6.3). This physical 5-button box was the equivalent of the Visual Analogical Scale (VAS) used in study 3.

The study commenced with three practice trials and was composed of 36 trials of each action condition (Yawn, Gape, Close) in randomised blocks. Half of trials were presented in the front orientation and half of them in the back orientation. The order of presentation was also counterbalance across participants. Overall, the study had 111 trials including the three practice ones at the beginning. Once the practice session was completed, participants filled out the questionnaires that were provided in an audio accessible format.

6.3.6 Data analyses

6.3.6.1 EMG

For muscle ZM area of the zygomaticus (zygomaticus major) and for muscle CS area (corrugator supercilii) separately, the mean area was calculated for each ten seconds trial and data were normalized using Z scores. The mean area activation was the dependant variable (DV), and condition (Close, Gape, Yawn) and orientation (Front, Back) were independent variables (IVs). For each muscle, we performed a 2x3 within-subjects repeated measured ANOVA including factors: perceived action (Close, Gape, Yawn) and orientation (Front, Back). Additionally, follow up paired comparisons were performed and corrected for multiple comparison using Bonferroni to reduce Type-1 error.

6.3.6.2 Questionnaires analyses:

The three questionnaires (EQ, TORONTO, CIREN) were scored according to their instructions. Two types of analysis were performed in with the questionnaires. An initial overall correlation between each questionnaire score was perform together with the amplitude of the EMG signal in each muscle. We also correlated these individual scores with the number of behavioural yawns. All participants (N=36) completed the TAS questionnaire, whilst n=26 completed the CIRENS, n=25 completed the Toronto and n=33 completed the EQ questionnaires. Due to n=11 not completing the Toronto questionnaire this was excluded from the analyses.

A second analysis used a median split to investigate if participants that naturally fall into high or low empathy scores would show differential response at the EMG measuring physiological contagion. In the EQ questionnaire, participants were grouped into one of two categories which were split by the median value of the EQ score (median= 53), those with scores lower than 53, and those with scores equal to or higher than 53. This resulted in two groups of Low (n=14) and High (n=19) empathy categories (as per the median split). A between-subjects ANOVA was performed to explore the intensity of the contagious responses (measure by the EMG) in the different conditions.

The same procedure was followed for the Toronto scale, with participants split into Low (n=11) and High (n=13) as per the median = 36.55. This was a questionnaire that not all participants filled out completely and some not at all. As this was a secondary supplementary measure, given that the EQ questionnaire was the main empathy measurement, the results had to be discarded. Subsequently, a between-subjects ANOVA was performed to examine if the intensity of the contagion responses (measured by an increased level in the EMG-measured signal of yawning-related muscle activation) in all conditions.

6.3.6.3 Self-report urge to move

Mean scores were computed for the self-report urge scores across conditions (Close, Gape and Yawn) regardless of orientation (Back or Front). A one-way ANOVA was carried out to explore differences in Self Report VAS measures between conditions. Amplitude of the EMG signal and self-reported urge scores were correlated to investigate the relationship between subjective self-perception of contagion and physiological evidence of contagion.

6.4 RESULTS

6.4.1 EMG Muscle zygomaticus major (ZM)

3x2 Analysis of Variance (ANOVA)

The 3x2 ANOVA on tactile condition and orientation (gape, yawn, close x front, back) showed a significant main effect of Tactile Condition, F (2, 64) =3.705, p=.030, partial η^2=.104, which represents a small effect size (Richardson, 2011). From an inspection of Figure 6.4 displaying the means for each condition it could be seen that these were substantially higher for the yawn condition, irrespective of orientation (Front vs. Back), in comparison to the means for close and gape conditions (Figure 6.4).

There was, however, no main effect of orientation, F (1, 32) =1.744, p=.196, partial η^2=.052, nor was there a 2-way interaction between condition and orientation, F (2, 64) =.616, p=.543, partial η^2=0.19.

6.4.2 EMG Muscle corrugator supercilii (CS)

3x2 Analysis of Variance (ANOVA)

The ANOVA on tactile condition and orientation (gape, yawn, close x front, back) showed that there was a significant main effect of Tactile Condition, F (2, 64) =6.999, p=.002, partial η^2=.177. Upon close inspection of the means for each condition (Figure 6.8) it could be seen that these were substantially higher for the yawn condition, irrespective of orientation (Front vs. Back), in comparison to the means for close and gape conditions (Figure 6.4).

There was no main effect of orientation, F (1, 32) =.254, p=.619, partial η^2=.008, nor was the interaction between condition and orientation, F (2, 64) =.735, p=.483, partial η^2=.022.

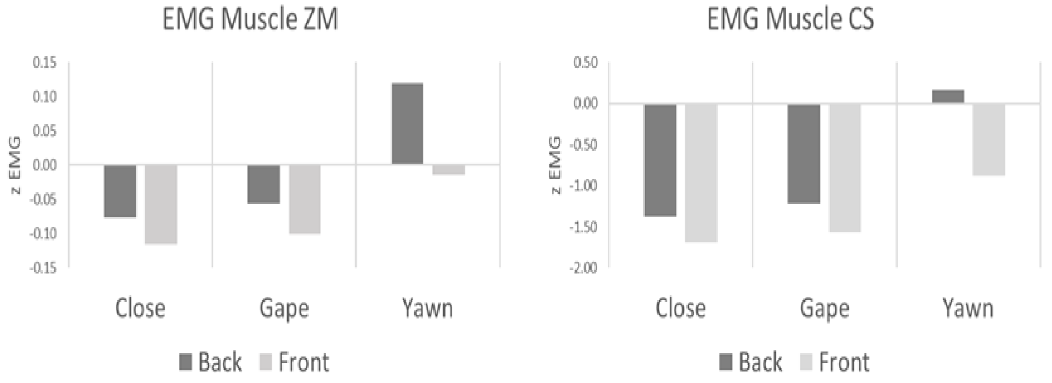

Figure.6.4 Mean activation in muscle zygomaticus major (left) and corrugator supercilii *(*right) by condition and orientation

6.4.3 EMG zygomaticus major (ZM) and corrugator supercilii (CS)

3x2 Analysis of Variance (ANOVA)

The ANOVA on tactile condition and orientation (Close, Gape, Yawn, x Front, Back) for both muscles together revealed a significant main effect of Tactile Condition, F (2, 64) =5.829, p=.005, partial η^2=.154. Upon inspection of the means for each condition (Figure 6.4) it could be seen that these were substantially higher for the Yawn condition, irrespective of orientation (Front vs. Back), in comparison to the means for Close and Gape conditions (Figure 6.4).

There was no main effect of orientation, F (1, 32) =1.753, p=.195 partial η^2=.052, nor was the interaction between condition and orientation, F (2, 64) =.787, p=.459, partial η^2=.024.

6.4.4 Questionnaires

6.4.4.1 Empathy Quotient (EQ), Toronto Questionnaire, TAS and CIREN

Participants' mean score on the EQ was 52.45 (SD=8.33), whilst the mean score on the TAS was 44.92 (SD=10.36) and on the (discarded) Toronto was 50.16 (SD=8.07). For the EQ the total number of valid cases was n=33 (n=3 missing), whilst for TAS and Toronto there were n=24 and n=25 valid cases, respectively and n=12 missing for TAS and n=11 missing for Toronto. For the CIREN questionnaire there were n=25 valid observations and n=8 missing. There were three categories that participants fell into, with 19 (76%) classed as morning type, 4 (16%) classed as afternoon and 2 (8%) in the evening category.

Correlations between total scores in Toronto Questionnaires and EMG amplitude signal was not significant for all conditions (Close r=0.134; Gape r=0.196; Yawn r=0.200).

6.4.4.2 Gender differences in questionnaires

The results of the three ANOVAs show that there were no significant gender differences (all p>.05). These were clearly supported by the means: 50.81 (SD=7.67) and 51.12 (SD=10.49) on the TORONTO questionnaire, for Males (n=11 valid and n=3 missing) and Females respectively (n=8 valid and n=2 missing); 51.33 (SD=8.08) for Males (n=12 valid and n=2 missing) and 52.44 (SD=10.40) for Females (n=9 valid and n=1 missing) on the EQ questionnaire; and on the TAS questionnaire means were 45.29 (SD=10.75) and 44.40 (SD=10.35) for males (n=14 valid and n=0 missing) and females (n=10 valid and n=0 missing), respectively.

6.4.4.3 Self-report urge to move

Findings from the one-way ANOVA showed there was a highly significant difference in mean scores in the three conditions (Close = 2.18 (SD=1.16); Gape = 2.84 (SD=1.1); Yawn = 3.07 (SD=1.39). the main effect of condition was significant F (2,64) = 10.39, p<.001, partial η^2=.24. The partial η^2 indicates that this is a medium effect.

6.4.4.4 Number of Yawns results

The number of yawns, accounted for by the increase in the EMG signal, varied substantially across conditions, such that, as expected, participants yawned the most in the Yawn condition. In total 93 yawns were recorded, of which 56 were in the Back orientation and 37 in the Front orientation (Figure 6.5). In the Close condition participants yawned a total of 2 times (both in the back orientation) and in the Gape condition participants yawned a total of 7 times, 5 in the Back and 2 in the Front orientations.

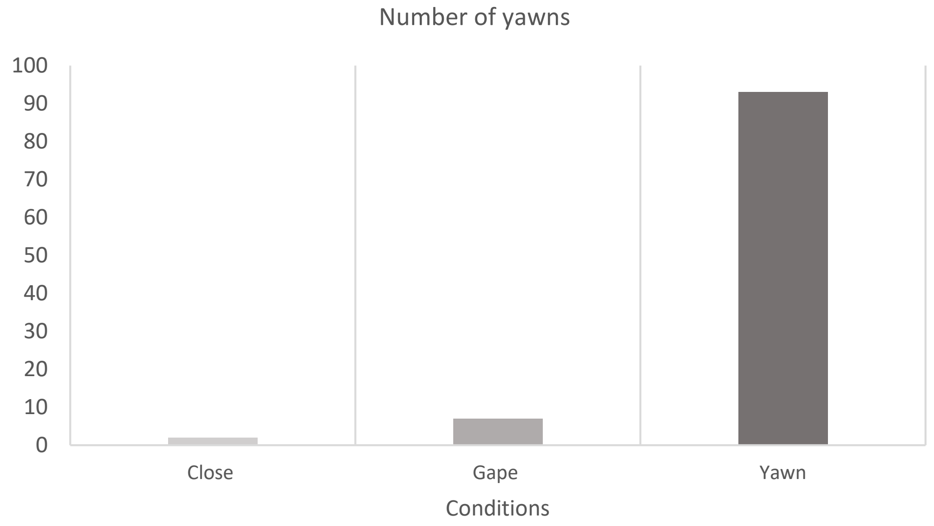

Figure 6.5 Number of yawns in tactile perception of android action across all conditions: Close (+ post Close), Gape (+ post Gape) and Yawn (+ post Yawn) in Front plus Back orientations.

6.4.4.5 Empathy quotient (EQ), Toronto scale and number of yawns

The between-subjects ANOVA showed that there was no significant difference in number of yawns between the Low (n=14) and High (n=19) EQ categories, F (1, 31) = 1.53, p=.225 partial η^2=.46. Although the Toronto categories eventually had to be discarded, a between-subjects ANOVA comparing Low (n=12) and High (n=13) number of yawns yielded a non-significant difference, F (1, 23) = .023, p=.881.

6.5 DISCUSSION

The main aim of this study was to explore if yawning is contagious through tactile perception. The main analysis looking at the size of the electromyographic response in facial muscles as an index of contagion showed a significant stronger response in the Yawn condition, compared to the gape and close condition. This suggests that the internal mechanism for embodiment or internal simulation is sensitive to the tactile perception of a contagious action.

The present data showed a differential modulation of the EMG activity for the different type of behaviours represented by the artificial stimuli. How should these findings be interpreted in the light of the recent experimental evidence? There is a possibility that EMG activity measured from facial muscles does not directly reflect the activity of either the premotor cortex, motor or somatosensory cortex, which has been the focus of most previous studies. Instead, facial EMG, may be partially reflecting the activity of the primary motor cortex, for some facial actions and not reflect it in the same way that it was observed before in hand actions. Hoffree et al., (2014) suggests EMG can also be susceptible to other influences, such as the contribution in the mechanics of action observation, showing greater activation in the contralateral hemisphere. Greater motor cortex activity in the contralateral side, i.e., the right motor cortex, might then have produced greater muscle activity in the left arm in Hoffree's study. Those results would only be partially relevant, as the reference is towards observation, rather than tactile perception, and to arm movements, rather than facial gestures. Inhibitory processes, though, may have had an impact on the results, but in convoluted or less straightforward ways. For example, in certain situations, one might stifle a yawn, but the facial muscle activity is still present. One message we can take from these results is that differences between observation and other types of perception such as tactile perception, should be taken into account when exploring these types of muscle activation, and the potential underlying mechanisms being present, but perhaps not noticeable at a behavioural level. These mechanisms may still be present at a sensory and pre-motor or motor cortex level, and inhibitions of facial muscles might be reliant on a completely different type of mechanism, of which we are still not fully aware. The activations seen here, might indeed reflect an inhibition too, perhaps even at a motoric level that is reflected in the muscle activity as a result of an earlier inhibition at a cortical, even a subcortical level, e.g. in an emotion perception or expression.

In order to understand perceptual mechanisms resulting from a tactile perception rather than from visually perceived actions, artificial intelligence, robotics and comparisons with biological and conventionally-used stimuli, can provide neuroscience with a novel and enhanced ecological validity, that would be extremely useful for exploring the boundary conditions for motor activation in the perception of contagious behaviours, as noted by Hoffree et al., (2011), when referring to motor simulation (Chaminade et al., 2007; Saygin and Stadler, 2012)

Despite a recent increase in the use of robots and avatars as stimuli, most research explores action observation tasks and therefore, by definition, these can only relate to visual perception. As the results of this study show, other sensory modalities can represent a fruitful path, specifically to address inconsistencies already reported in the literature (Kilner et al., 2003; Gazzola et al., 2007; Oberman et al., 2007; Saygin et al., 2012). Some studies showed that perception of robotic actions may result in MNS activity that is similar to that of human actions (Cook et al., 2011), whereas others have argued that some brain structures usually associated with MNS are not responsive to nonhuman actions (Tai et al., 2004). Given the present results, another useful route to follow, would be to further investigate these possible inhibitory processes in the context of contagion, rather than imitative actions as is generally explored (see Kilner and Frith 2007; Borroni et al., 2008). This potential factor of the presence of inhibitory influences during action observation was highlighted by Cross et al., (2013). However, in general, this area of research mostly concentrates on hand actions. Although lateralization mechanisms are simpler to study in arms and hands, there is a possible comparison to be explored in facial muscles which would still address premotor and motor cortical processing and the potential relationship to facial muscle activity that may contribute to solving a complex neuro-computational problem (Baldissera et al., 2001; Fadiga et al., 2005; Churchland et al., 2012; Shenoy et al., 2013). Future studies could explore differences in facial EMG activity when perceiving emotionally-charged actions and actions that are not carrying an emotional component attached to them, while muscle activity is measured on both sides of the face.

Cumulatively, these findings offer compelling evidence that contagious yawning can be considered either as amodal, or even supramodal, specifically with regards to the sensory modality, through which the contagion can occur, and now it can be confirmed that this includes tactile perception. At the same time, together with findings of the previous studies in this thesis, which explored auditory and visual perception of a yawning stimulus, these tactile perception results show that yawn contagion may represent a cross agent, (given that an android is an inanimate object), and across sensory modality signal transference of a facial communicative action. The tactile perception of the yawning stimulus trigger in the blind perceiver neuronal activation that, in turn, emits a muscle activation signal which has a resonance, producing the same facial muscle activity in the perceiver, to that perceived in the facial motion of the artificial agent. High empathic quotient scores were not a significant predictor of susceptibility to yawn contagiously. Therefore, the current findings are in relative contrast to some of the previous studies in the literature, that identified correlations between contagious yawning susceptibility and empathic abilities (Anderson et al 2003; Platek et al 2003; Haker et al 2009). This was in line with previous findings in this thesis, suggesting that contagious yawning might not be as strongly related to empathic processing as previously thought (Senju et al 2007; Platek et al., 2010).

6.6 CONCLUSION

It is well known that severe visual impairment and complete blindness can result in plasticity change in early visual areas such as the striate cortex (Sadato et al., 1996; Cohen et al., 1997). For instance, transcranial magnetic stimulation (TMS) over the early visual cortices reduced performance accuracy of Braille reading in early blind subjects (Cohen et al., 1997). A large number of neuroimaging studies have shown that the functional organization of other brain regions is highly similar, regardless of visual experience: the ventral visual pathway (Amedi et al., 2007; Mahon et al., 2009; Reich et al., 2011; Wolers et al., 2011; Stiem-Amit et al., 2012); dorsal visual pathway (Poirier et al., 2006; Ricciardi et al., 2007; Matteau et al., 2010); limbic areas (Klinge et al., 2010); and the action-understanding network (Ricciardi et al., 2009). Results here extend these findings by demonstrating, for the first time, physiological evidence of potential yawn contagion through tactile perception. These results may suggest that cortical areas beyond the somatosensory, premotor and motor areas might be functionally organized in a supramodal fashion for representing particular facial expressions. Given the participants' report of an urge to produce the same action as touched, and therefore denoting yawn contagion, this could mean that subcortical structures might be involved in the tactile perception of particular facial expressions beyond the ones studied here.

7 GENERAL CONCLUSION & FUTURE DIRECTIONS

The current work sets out to explore a particular type of action perception and action understanding by human and non-human primates. Even though humans are the only animals who predominantly use language for social interaction, there are a great proportion of social cues that are transferred through body language, physical gestures or facial expressions. Those cues can be processed in an explicit and in an implicit way and may contribute to the basis of what we call social cognition. Exploring implicit cues is not only important for questions that aim to understand further particular social cognition processes, they can also contribute to evolutionary and developmental questions.

Comparing how implicit cues can vary in their modality contributes further insights about multiple realisations of information processing. Contrasting human behaviour with that of chimpanzees can show that we rely on similar procedures.

In this thesis, contagious yawning was chosen as a paradigmatic example for several reasons. Firstly, yawn contagion presents a stable stimulus-response relation that enables controlled experimental settings. Secondly, yawning is a well-defined behaviour, which can therefore can be distinguished from other similar behaviours. Thirdly, the contagion can be manifested and therefore tested in several modalities (visual, auditory and touch). Fourthly, yawning can be perceived and processed in a variety of circumstances. The contagion is normally automatic and unintentional; it can be triggered by an internal representation elicited by just thinking about the action of yawning. It may also be the object of inhibition, although the power to inhibit the contagion seems to be limited. Importantly, as was shown here, the physiological activity, denoting premotor and motor activation can be measured independently of self-report.

The thesis aimed to explore cognitive, behavioural and physiological mechanisms underlying these particular type of implicit processing cues. In the studies with human participants, this work included both individuals with intact vision and those who are blind. This helped investigate the phenomenon of yawn contagion through possible different sensory modalities. Within a comparative perspective, and through indirect but well-established routes, such as electromyographic activity measurements, eye tracking techniques, and employing the latest advances in robotics and artificial intelligence, it attempted to address existing debates in the literature about this common behaviour, one which humans and animals perform several times a day.

Based on the review of the literature, and the State of the Art described in **Chapters 1 & 2**, several open questions were addressed. In the following section, a description of the extent to which these questions have been answered is presented and possible future directions are suggested.

Experiment 1 investigated yawn contagion across species. First, it addressed the question of whether human yawning is contagious to adult chimpanzees. In previous studies with chimpanzees, yawn contagion has produced contrasting results and has been primarily linked to empathy. In the first study to employ live presentations, the experiment found that adult chimpanzees yawn contagiously when observing an adult human yawning. The second open question was related to a possible modulatory effect, which is potentially implicit in the yawn contagion behaviour. This question was inspired by a bias previously observed in adult chimpanzees, where contagion was restricted to times when the subjects were viewing the yawns of conspecifics, and not the yawns of heterospecifics, and the fact that CY in humans has been primarily linked to empathy.

Chimpanzees tested here are rescued animals that get close to their keepers, who look after and feed them every day. The animal keepers acted as the familiar stimulus for the experimental condition, and the researchers, who were unknown to the animals, represented the perfect sample for the unfamiliar stimulus in the experimental condition. Surprisingly, and contrary to expectations, the results showed that chimpanzees were more likely to catch yawns from a new and unknown, rather than a familiar human.

This study also explored whether this type of heterospecific yawn contagion occurs through other sensory modalities, such as mere auditory perception. And if so, whether there was a modulatory effect exerted by this auditory perception of human yawns. Findings showed, for the first time, that chimpanzee yawn contagion also occurs through a solely auditory perception of a human yawn, even though chimpanzees do not emit sounds when they themselves yawn. The overall results showed that yawn contagion frequency increased, when the stimuli included more components of a full yawn: rate of yawn contagion was greatest in response to visual perception of human yawns, followed by the mere auditory perception. This confirmed a possible modulatory effect exerted by the perceptual sensory modality. As expected, the gape condition did not produce yawning responses. This less wide opening of the human mouth, served to support the argument that the findings denoted contagion rather than mimicking or imitation. The setup of this study provided the opportunity to explore whether the chimpanzees would display any other behavioural response to the stimulus. Yawning cues triggered a form of soporific behaviour when the different human actions were perceived by the animals: chimpanzees lay down, gathered leaves, made their beds and displayed drowsiness, only when they were exposed to visual and auditory yawn stimuli, and not when humans gaped or kept their mouths closed. This exemplified the concept of Experiential Contagion and differentiates it from an imitative or copying behaviour. This warrants further investigations of other actions, and with behaviours of animals of different species. The modulation found by unfamiliarity and sensory modality, suggests that the impact empathy may have on heterospecific yawn contagion, also ought to be further explored.

The rather surprising results found in the first study raised the questions of what role empathy might have, if any, in the yawn contagion process and if these findings would be restricted to contagion between chimpanzees and humans.

Experiment 2 employed the same paradigm as in experiment 1, but this time, the stimulus was a yawning android and therefore the exploration constitutes one we choose to term “across agents”.

The main hypothesis was set up to test yawn contagion, in a live presentation, between a human-looking robot and adult chimpanzees. Given the results of the previous study, the android represented an ideal stimulus. Chimpanzees are extremely clever animals and, after having submitted them to a pilot test and habituation to the covered container over a table that they were familiar with, it is possible to assume they were perfectly aware that the android was an object placed in front of them. Furthermore, it is also fair to assume that the animals would not have expected to be fed by the object, and they had certainly never seen anything remotely similar. Therefore, the stimulus represented an unknown entity: an object that was definitely not familiar and which should not induce, at least in theory, any type of empathy-modulated response. As the impact of empathy on yawn contagion had already been questioned in the previous study, it was then relevant to explore yawn contagion in chimpanzees with an inanimate agent as a triggering stimulus. Results showed that chimpanzees do indeed catch yawns from an android. These animals displayed different behaviours, when they were exposed to the experimental and control conditions, that is, when the android's facial expression was a less wide opening of the mouth (gape), or when the mouth was closed (close). Interestingly, chimpanzees displayed the same behaviours as in the previous study, laying down, gathering leaves to make their beds and displaying drowsiness, only when exposed to yawn stimuli, but not to a gape or closed mouth. This synchronisation of a state of drowsiness, displayed by the chimpanzees in an identical form to that in the previous study, suggests the same form of Experiential Contagion, but this time elicited by the android yawning.

For the first time, it was shown that animal yawn contagion can be elicited by a man-made object. These results raise the need to re-examine the relation between yawn contagion modulation and empathy attributions, and suggest new routes to explore and increase our understanding of contagion in general, yawn contagion in particular, and the possibility of considering the existence of a different type of contagion phenomenon, a general experiential contagion effect. For future directions, other researchers may explore the differences and similarities between other contagious human behaviours, and their equivalence in the animal world. For example, laughter. We know that chimpanzees laugh and primatologists have confirmed their distinctive sound and facial expression portrayed when displaying the positive emotion behaviour. If yawning is contagious in humans, as is commonly thought, it would be interesting to explore if laughing behaviour is also contagious in chimpanzees.

Human research on gender differences in empathy has yielded inconsistent results. Some behavioural and physiological studies have stated that their observed gender differences in empathy may have arisen from males' reluctance to report their empathic feelings, instead of having found a real difference in males' diminished ability to feel empathy, in comparison with their female counterpart. According to the present studies, findings show no gender differences in the rate of yawn contagion. Although one of the empathy questionnaires used here, indicated higher scores for females, susceptibility to yawn contagion does not appear to be related to these empathic abilities.

Even though the phenomenon of yawn contagion in humans is well known, and the stimulus so strong, only a very limited amount of studies have explored it empirically. Findings up until now have not met a general consensus regarding, for example, exactly which components of humans' facial features exert an impact on the contagious process, such as the regions of the eyes or the mouth. These potential impacting factors were assessed through eye tracking. Eye gaze and fixation patterns showed, as expected, that the mouth area was the most prominent facial part in a yawn-catching scenario. The present study found a clear physiological activity arising from the perception of an embodiment-inducing action, which, in turn, manifested itself in a contagious behaviour as a response.

Due to the fact that contagious yawning research has been rather limited, and different methodologies and paradigms have been employed, so far it has been difficult to establish fair and reliable comparisons. For instance, an fMRI study studies exploring yawn contagion in humans asked participants to remember how much they felt like yawning, in reaction to certain stimuli, such as having viewed videos of people yawning and control videos. However, the question was asked after they had come out of the scanner (Schürmann, et al. (2005)).

In **experiment 3**, the participants also watched videos, but this time they provided an immediate self-report, while electromyography was simultaneously measured. Findings reconfirmed the need for further explorations of the debatable relationship between empathy quotient and contagious yawning susceptibility. Although contradictory to this generally held assumption about empathy, present findings are in line with our previous results with dogs and adult chimpanzees, all tested with the same paradigm and one which, for the same purpose of consistency and comparability, was also used in all studies in the present thesis (Joly-Mascheroni et al., 2008; Joly-Mascheroni et al., 2018 (submitted)).

Given that the results here showed clear contagion through visual and auditory modalities, it became pertinent to investigate whether yawn contagion could occur through another sensory modality.

Thus, **experiment 4** explored, for the first time, yawn contagion through tactile perception. Findings did confirm the existence of tactile contagious yawning in blind individuals. This result of tactile transmission of a signal, in this case between an android and a blind human, raises new lines of enquiry. The discovery of a possible contagion through tactile perception, certainly confirms several of the expected outcomes, whatever the significance we decide to attribute to the particular social interaction. One thing we may all agree on is that, on the part of both interacting partners, which, in this scenario, are an inanimate object, and a human with a sensory impairment, there is an unintentional information processing mechanism that they both take part in, and an unintentional transference of a signal embedded in that information, which gets sent from one communicative agent towards the other interacting partner. This type of signal or particular kind of information, may carry either detailed or rather vague data about an event. On a higher level one may interpret the significance of this event as denoting a set of circumstances in which these behaviours are displayed, i.e. as some blind participants stated, “this portrayal is that of an expression of tiredness”. Others said, “this motion must be exemplifying how human faces may ‘look’ like”. Some even expressed, “this must be how humans (through their facial expressions) portray that they are bored or sleepy”. However, the interacting partner transferring this signal is not a human. It is in fact an inanimate object that portrays a facial motion, gesture or expression. A thing cannot be tired, and an object cannot be bored. So, what kind of message is being transferred across, and what exactly is the information inherent within it, is not one hundred per cent clear yet for either the blind participants, or for those investigating it. Although this is beyond the scope of this work, what does seem to be evident, is that there is a transference of some kind of information, and a response arising as a result of this, which certainly triggers in the recipient the urge to re-enact that motion or facial expression. Sometimes this is accompanied by a stretching of the arms, which is well known to occur simultaneously with the wide opening of the mouth in a yawn. This, again, exemplified the experiential contagion effect seen across species and across agents. It shows that experiential contagion could be prompted by the mere tactile perception of an action that generates the recognisable sensation of having previously experienced how it feels to perform that action. That the potential significance of these actions is not known or clear, does not change the fact that we now know that contagion through tactile means can occur.

From a psychological perspective, future studies could look at other social interaction scenarios, both beyond the action of yawning, and the contagion aspect of the behaviour.

All these studies concentrated specifically on contagious behaviour, and explored if contagion should be differentiated from imitation, mimicry or any other, perhaps equally automatic behavioural response, to the perception of the facial actions of others. However, there is a possibility that contagion is not as automatic as other imitative responses. Furthermore, future explorations could also expand to include other actions or behaviours apart from the facial ones investigated here maybe using other parts of the body. One limitation of the present studies is the impossibility of investigating if time, from the instance of the perception to the actual behavioural response, has an impact on the strength of the premotor activation, regardless of a potential contagion-mediated or modulated response. That is, the response to other behaviours may not necessarily be strictly related to, or as a result of, an urge to perform the same action as perceived. There is another possibility that the EMG activity threshold established in these studies, was not sensitive enough to minimal muscle activations which could have still represented a predisposition to perform the same action. Furthermore, a more stringent time measurement would be more accurate in establishing if the response immediately after the perception of an action (one that would trigger a semi-automatic response similar to the one found in contagion) could be one that would indeed incite a re-enactment. This possible embodiment, induced by the perceived actions of others, might still be reflected in an internal representation. This representation would be responsible for the relevant neuronal activation, which in turn, in the case of somatosensory, premotor and motor cortices, would be responsible for a predisposition or readiness to provoke a similar muscle activation to the one that is perceived. According to the present results, it would be possible to speculate that these scenarios could apply in visual, auditory and tactile perceptions. In this potential scenario of a multisensory perception of another's action, it would be plausible to expect an interaction, of which we are unaware, between sensory modalities, given that it is normally the case, when our senses are intact, that we perceive the world around us through more than one modality. The interaction may favour one modality; simultaneity of sensory perception may exert another impact on the percept, and timing differences in the sensory modalities may become the strongest modulatory effect on either the physiological or even behavioural response.

There are several possible accounts for the role played by the potential brain structures from which physiological activity measured here may be incoming. For instance, Inferior Frontal Gyrus (IFG) and Medial Temporal Gyrus (MTG) have been shown to be active in the haptic identification and recognition of facial expressions (Kitada et al 2013). There is a possibility that these brain regions might be related to cognitive processing of different aspects of face perception, including facial expressions that do not denote emotions. For instance, Tsao et al. (2008) demonstrated that the ventral prefrontal cortex and the superior temporal sulcus in the non-human primates contain regions (patches) selectively active during observation of faces. In the equivalent neuroimaging studies performed with human participants, a number of them have shown that observation of faces (relative to the other categories of common objects) selectively activates regions in and around the superior temporal sulcus (e.g., Puce et al., 1996; Haxby et al., 1999). It is plausible to expect that the IFG and MTG, which are active in the processing of face perception, may also contribute to the formation of resonance activity and representations of embodiment-inducing behaviours which may already be underlying the recognition of basic facial expressions.

The interpretation of the results obtained here should be limited in terms of how much one should speculate about their meaning and, importantly, how much one can generalise these results for the interpretation and responses of the perception of other facial actions. This caution in generalisation should perhaps also be extended to other populations that are not severely visually impaired or blind. Nevertheless, they may serve to propose that, in the absence of visual experience, future consideration should be applied to the exploration of haptic recognition as early as possible during development. It is known that early visual deprivation can delay the development of social cognition (Keeler, 1958; Wing, 1969; Brown et al., 1997; Hobson et al., 2010). Many behavioural studies have shown that early visual deprivation reduces voluntary control of facial expressions, a limitation that extends into adulthood (Webb, 1977; Marshall and Peck, 1986; Rinn, 1991; Galati et al., 1997). For consideration in future studies, it would be sensible to propose that haptic recognition of a caregiver's facial expressions may potentially serve as a valuable substitute for visual recognition, as a means by which early blind adults could reduce, if not overcome, current difficulty in interpreting and portraying facial expressions voluntarily. This is specifically the case for those expressions which they mean to voluntarily employ in certain circumstances. Such a haptic approach to intervention may further facilitate the development of social cognition, which is typically mediated by vision.

Another limitation of these studies was the impossibility of measuring a possible impact of attention, awareness and conscious or unconscious components associated with the behavioural responses that could potentially be inhibited. It was argued here that, in a contagion scenario, there might be an absence of inhibitory processes normally present in most action perception mechanisms. For example, what is different in the visual perception of someone else yawning from that of someone else walking? Observing someone else walking, does not trigger the urge to stand up and walk. What inhibitory processes are not present when one sees someone else yawning? Although this was beyond the scope of the present study, investigations of inhibition of response, have generally been associated with components of conscious awareness. Future physiological explorations may clarify why some of these processes are not consciously perceived, or why, at least sometimes, they are not reported as such.

In the recent past, there has been some increase in research exploring contagious behaviours related to political orientation, behavioural economics, and decision-making scenarios. Yawning is generally regarded as an intransitive, nonintentional, and non-goal directed action. It is often considered as a banal inconsequential behaviour. However, the fact that such a simple, supposedly unimportant action, when perceived, through vision, touch or audition, performed by human or a robotic entity, can trigger the same behaviour in the perceiver, may be a sufficient reason for future studies to explore what other inconsequential or perhaps rather more important actions, humans and animals would be automatically repeating almost instantaneously and/or immediately after perception.

In fields such as Neuroscience, Robotics and Artificial Intelligence, there is increasing interest in exploring the acceptability of, and reactions to, artificially created inanimate objects, such as androids and robots. This android yawning was sufficient to elicit yawn contagion in chimpanzees and blind humans. The inanimate agent’s motion seem to have conveyed a message which was picked up by both animals and humans. Results of our study suggested chimpanzees are capable of elucidating a communicative signal produced by an unfamiliar model, humanlike in appearance, but ultimately an android. A yawn, regardless of its unknown primary role, may have always carried a non-verbal communicative function, and its contagiousness aspects may serve to find out more about how humans and animals developed adaptive functions, ways of communication, synchronisation and social interaction.

8 FURTHER DEVELOPMENTS ARISING FROM THIS WORK

8.1 TRAINING AID: Auditory and Tactile biofeedback system

A prototype has been developed as a result of the experiments reported in this thesis.

To follow are the legal descriptions and specifications declared for the intellectual property rights.

Field

A first aspect of the present invention relates to a training aid. In one implementation, the training aid can be employed to help users (particularly, but not exclusively, blind or partially sighted users) to adopt a desired fascial expression. A second aspect of the present invention relates to apparatus for providing a representation of a human face with a desired facial expression. Background The ability to portray the right facial expression is very important in social interaction and communication. Blind individuals often have difficulties in portraying and/or interpreting other peoples' facial expressions. Given the lack of visual feedback, blind individuals' ability to recognise emotions and other facial expressions is often affected. This can often have a negative impact on their social interaction and communication. This problem affects over two million people in the UK, who live with sight loss, or in other words, approximately one person in 30. Of these, around 360,000 people are registered with their local authority as blind or partially sighted. It is predicted that by 2020 the number of people with sight loss will rise to over 2,250,000.

Importantly, 90% of people suffering from sight loss will never work for more than six months in their lives, which increases their isolation and reduces their opportunity for social interaction. Moreover, one in four visually impaired children under the age of twelve suffers from depression, due to isolation and lack of social inclusion. These children are twice as likely as their sighted peers to be bullied at school, often due to their lack of facial expressions. One aspect of the present invention has been devised with the foregoing problems in mind.

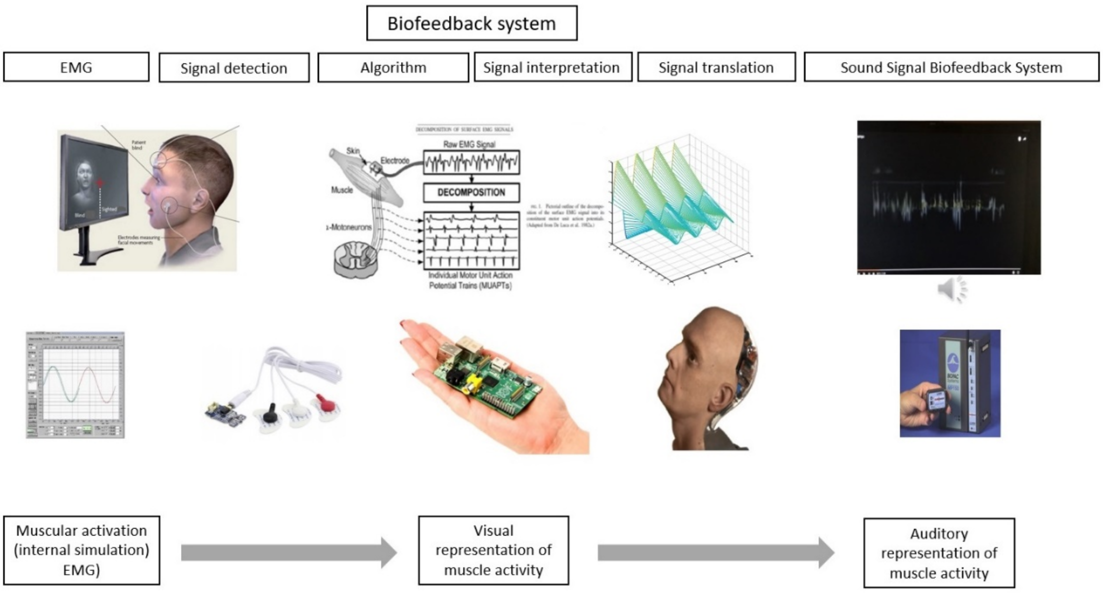

Figure 8.1 Auditory & Tactile Biofeedback system, from signal acquisition to representation.

8.2 Summary & Submitted Patent Application **Ref: P003055GB**

One aspect of the present invention provides a training aid comprising: a plurality of sensors for attachment to a user's face, the sensors being operable to acquire signals representative of muscle activations in said user's face; a controller configured to receive said signals from said sensors, to derive from said signals a measure of how well a user's fascial expression achieves a desired predetermined fascial expression, and to generate a feedback signal representative of said measure; and feedback apparatus configured to receive said feedback signal and provide said user with feedback concerning how well their fascial expression achieves a desired predetermined fascial expression. In one envisaged implementation, said feedback apparatus comprises a tactile representation of a human face, said tactile representation including a plurality of actuators that are operable to provide said tactile representation with a fascial expression, said tactile representation being operable to activate said actuators in accordance with said feedback signal to provide said user with a tactile representation of their fascial expression. Alternatively, or additionally, said feedback apparatus may comprise a speaker operable to generate an audio signal that indicates to said user how well their fascial expression achieves a predetermined desired fascial expression. Another aspect of the present invention provides apparatus for providing a representation of a human face with a desired facial expression, said apparatus comprising: a resiliently flexible member configured to provide a representation of a human face, a plurality of actuators each operable to move a respective part of said flexible member, and a controller for operating one or more of said actuators to move said associated part or parts of said flexible member so that said flexible member adopts a desired facial expression. The apparatus may further comprise a speaker so that a user can play audio messages to a child looking at the flexible member. The apparatus may comprise a motion sensor that is operable to detect motion and in response operate one or one or more of said actuators to move said associated part or parts of said flexible member so that in response to movement said flexible member adopts a desired facial expression. The apparatus may include a microphone and a communications module so that sound may be detected and transmitted to a monitoring station, for example a remote speaker.

Other aspects, features and advantages of the teachings of the invention will be apparent from the following detailed description of preferred embodiments.

Brief Description of the Drawings

Various aspects of the teachings of the present invention, and arrangements embodying those teachings, will hereafter be described by way of illustrative example with reference to the accompanying drawings, in which: Fig. 1 is a schematic representation of a training aid; and Fig. 2 is a photograph of an animatronic head.

Detailed Description

Fig. 8.2 is a schematic representation of a training aid 1. The aid 1 comprises a plurality of sensors 3 for attachment to a user's face and are operable to acquire signals representative of muscle activations in the user's face. The aid also comprises a controller 5 that is configured to receive signals from said sensors 3. In one implementation the controller is wired to the sensors, but it is envisaged that the controller could be wirelessly coupled to the sensors 3. The controller 5 includes an input interface 7 through which signals are received from the sensors 3, a processor 9, an output interface 11 through which signals are output to feedback apparatus 13. The controller also includes a power source 15 (such as a rechargeable battery) for powering the components of the controller 5.

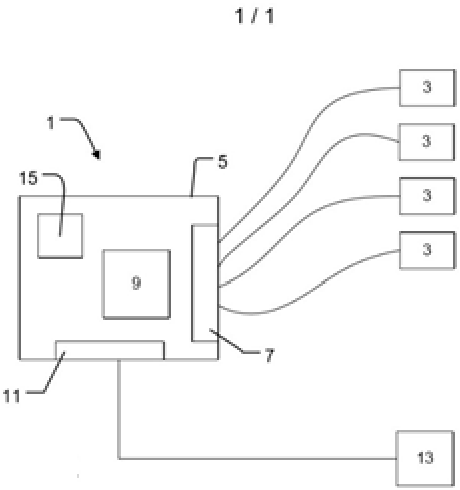

Fig. 8.2 Schematic representation of a training aid 1.

In one envisaged implementation the controller is embodied in a so-called Raspberry piTM or an ArduinoTM. The sensors are configured to pick up Electromyography (EMG) signals resulting from muscle activations in the user's face. Muscles are composed of very fine fibres, and these fibres are organised into groups known as motor units. Motor units are innervated by a single motor neuron and then they activate together during muscular contraction. The nervous system activates the motor unit by sending an electrical impulse along the motor neuron axon. The nervous system controls the force of the muscular contraction by turning the motor units on and off and by modulating the discharge rate. Each nerve impulse triggers an electrical discharge or action potential. When the motor unit discharges the electrical potential from all the muscle fibres, it produces a compound potential known as the motor unit action potential (MUAP). The EMG signal is the sum of the discharges of all the MUAPs within the pickup range of a given sensor 3. The signals from the sensors 3 are processed by the processor 9. In particular, the processor amplifies the signals, rectifies and smooths them. The processor then derives (from the amplified, rectified and smoothed signals) a measure of how well a user's fascial expression achieves a desired predetermined fascial expression, for example by comparing the derived measure against a stored measure for a desired predetermined fascial expression. The processor 9 is configured, once it has determined how well the user's expression achieves a desired predetermined fascial expression, to generate a feedback signal for passing to feedback apparatus 13. In one implementation of the teachings of the invention, the feedback apparatus 13 comprises an audio feedback device – such as a speaker. In this implementation of the teachings of the invention, the feedback signal generated by the processor may comprise control signals configured to cause the audio 4 feedback device to sound a first tone that is representative of the desired fascial expression, and a second tone that is representative of the user's fascial expression.

From this information, the user can then adjust their fascial expression until the tones are similar, at which point the user will have a fascial expression that achieves the desired fascial expression (at least approximately). Through repeated use of the training aid the user should then be able to train their fascial muscles to achieve a desired fascial expression without needing feedback.

In other envisaged implementation of the teachings of the invention, the feedback apparatus comprises an animatronic human head (or alternatively only the face of a head). In this implementation of the teachings of the invention the feedback signal may comprise control signals that cause actuators in the animatronic head or face to move a resiliently flexible membrane to achieve a fascial expression that approximates the user's fascial expression. The user can then determine by feel how well their expression achieves a desired fascial expression (which the animatronic head or face may have previously presented). In a preferred implementation the animatronic head or face may be configured to adopt a predetermined desired expression and then adopt the user's expression, so that the user can judge how well their expression achieves the desired expression and adjust their expression accordingly. Fig. 2.2 is a photograph of an animatronic head that could be used in such a manner. As will be appreciated, such an aid can be used by persons who are blind or partially sighted to help them achieve fascial expressions. Given the similarities of the difficulties between patients with vision loss and patients suffering from acquired paralysis or other neurological disorders (such as craniofacial, dimorphisms and Moebius Syndrome) that manifests itself primarily in facial paralysis and an inability to smile or frown, the training aid could also be used with this population. As such, the potential use and benefit of this device goes beyond blind or partially sighted individuals. Potentially, it could also benefit individuals within the Autism Spectrum Disorder as well as this population also have difficulties in conveying and recognising emotional expressions. In another implementation of the teachings of the invention, apparatus for providing a representation of a human face with a desired facial expression is provided. In this aspect of the invention, the apparatus comprises: a resiliently flexible member configured to provide a representation of a human face (more preferably, a representation of a particular person's face (for example, the face of a child's mother)), a plurality of actuators each operable to move a respective part of said flexible member, and a controller for operating one or more of said actuators to move said associated part or parts of said flexible member so that said flexible member adopts a desired facial expression.

According to the World Health Organisation, an estimated 15 million babies are born prematurely (before 37 weeks of gestation) every year. Of these, one in 20 is likely to be born blind or with severe loss of vision, a rise of 22% in the past decade. In neonatal units, along with sensorimotor and neurological training, time in the incubator during babies first periods of extrauterine life is considered to be of utmost importance. These first months, when babies rely completely on the incubator to survive, are also a vital opportunity to achieve significant rehabilitation of their underdeveloped visual system. At present, early interventions in neonatal units consist of visually exposing and training eye gaze using two and three-dimensional emoticon type pictures and objects. However, it has also previously been proposed that it is important for babies to be exposed to human features. Babies follow and prefer human faces to objects, and they recognise their mother’s voice and facial expressions even when they are born extremely early in their uterine maturation process. Unfortunately, immunological risks and other issues often prevent parents from spending invaluable time in the tiny babies’ sensorineural and emotional development. This overall has an impact on the baby’s development, as from early age they are deprived of the essential social and maternal contact. This period has been proven to be important not only in the level of attachment, but also in the babies’ global progress. The aforementioned second aspect of the present invention deals with the aforementioned issues. In particular, in this second aspect the mother of a given child may have her face cast in a resiliently flexible material, for example silicone. Actuators are then fitted beneath the silicone cast and are arranged so that they can be actuated to move the cast so that it adopts a desired fascial expression.

The cast may be backlit, and the apparatus may be configured for mounting inside an incubator. In this way, a baby inside the incubator may be presented with a representation of its mother's face, and that face may be moved to smile at the baby (or make some other desired facial expression) – for example in response to detection of sound or movement within the incubator. In this way, the apparatus can provide a child with maternal contact in circumstances where the mother cannot be at their child's beside. This aspect of the present invention is not limited solely to incubators. Rather, the teachings of this aspect of the present invention could readily be provided with the functionality of a conventional baby monitor so that all children can be provided with maternal contact when the mother concerned is not present. It will be appreciated that whilst various aspects and embodiments of the present invention have heretofore been described, the scope of the present invention is not limited to the particular arrangements set out herein and instead extends to encompass all arrangements, and modifications and alterations thereto, which fall within the spirit and scope of the invention. Lastly, it should also be noted that whilst particular combinations of features have been described herein, the scope of the present invention is not limited to the particular combinations described, but instead extends to encompass any combination of features herein disclosed.

Summary report of preliminary advances in Biofeedback system

Ramiro M. Joly-Mascheroni & Dr Beatriz Calvo-Merino

Reference:	09/1718
Internal transfer code:	48001GN
Project title:	Human-Robotics & AI in Healthcare: Helping Blind people hear a smile
Project mentor:	Tia Khan
Award:	£22,680

Summary:

This project aims to help emotion recognition and facial expression portrayal in blind individuals by combining state of the art technology, Robotics, and Artificial Intelligence, with research from the Neuroscience domain, developed in our laboratory (Cognitive Neuroscience Research Unit, Psychology Department). The core of the project lives in the use of other sensory modalities to compensate for the lack of vision. When working with blind individuals, focusing on emotion perception and expression, this multisensory approach, is novel and timely. The grant has provided us with the invaluable chance to start the projects we have been planning and working on for several years.

Social interaction and the ability to interpret and express emotions are very important factors in our lives. Blind individuals often have difficulties in portraying and/or interpreting other peoples' facial expressions. Given the lack of visual feedback for the blind, their emotion recognition and facial expression is often affected. This has a negative impact on their social interaction and communication. This problem affects over two million people in the UK, who live with sight loss.

Results:

A Robotic facial reproduction of a blind person emulates the expressions produced by the user. Through the employment of algorithms that recognise and translate facial muscle activity into sound, the blind user hears the expression they are portraying while he/she can simultaneously touch his/her own expression portrayed in their own robotic face.

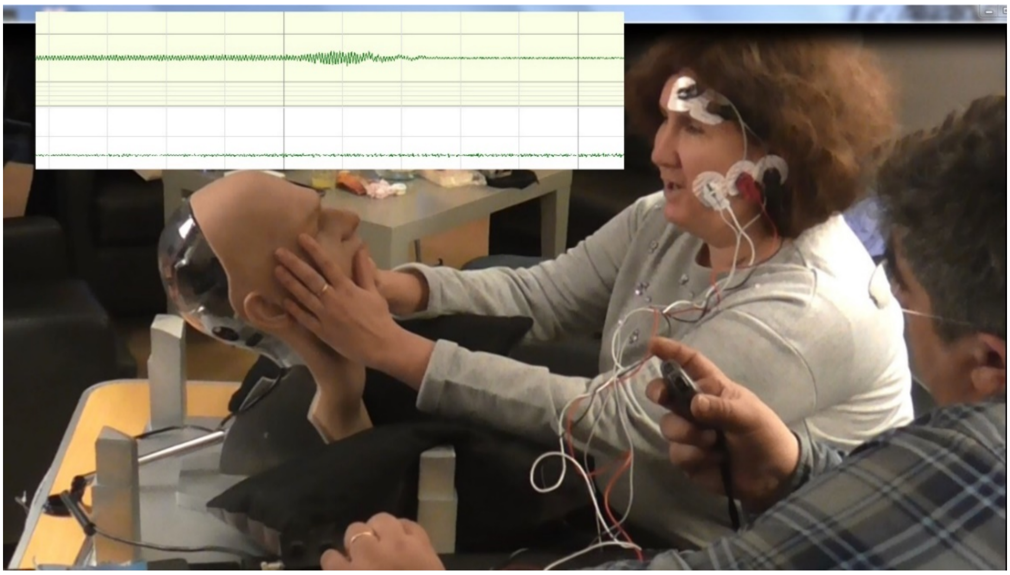

Figure 8.3 Representation of the prototype in use by a blind individual’s perception of a robotic facial expression and measurement of the EMG (electromyographic signal).

Our solution is inspired by our current research that uses Robotics and Artificial Intelligence to provide alternative pathways of training emotion recognition and portrayal in blind individuals. In the case of Adult blind and stroke sufferers, we developed a device that acts as an “Audible and Tactile Mirror”. This mirror aids the training and the recognition of how it feels to portray or recognise a smile and other facial expressions. We have developed a simple but novel EMG (Electromyography) biofeedback system. This system is based on 2 steps: (1) Using skin surface facial electrodes (EMG), activity from the movements of facial muscles (e.g. during a smile), can be recorded using a small but sophisticated microprocessor that is attached to the facial sensors, employing raspberry pi technology (see picture below). (2) Using Artificial Intelligence, we produce an algorithm through which the muscle activations (EMG signal), is translated online into an audible signal.

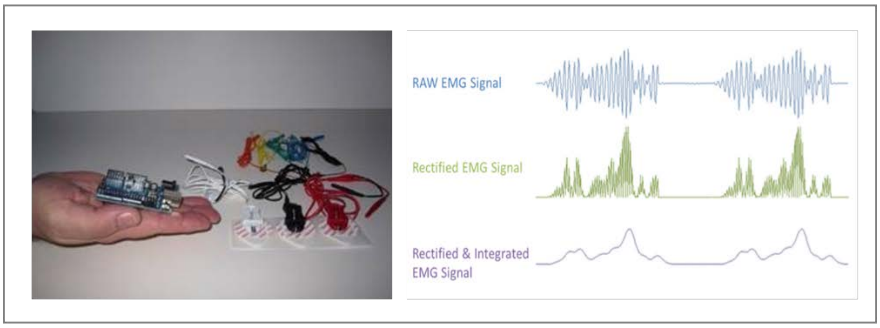

Figure 8.4 (left) Electromyography example of muscle activation signal (right) Raspberry Pi technology for the biofeedback System**.**

Importantly, this audible signal can be heard and interpreted by the blind. Incorporating the robotic simulation of a blind individual’s facial expression, blind users can become aware of their own facial expressions, through the auditory perception of their facial muscle movements and the tactile perception of their own expression. Full-sighted individuals use mirrors to perceive their own visual facial gestures. The proposed audio-muscular feedback will allow blind individuals to hear their own smile and train to depict a truly emotional expression. In the case of stroke victims, this prototype is already in testing phase by physiotherapy and Neurorehabilitation clinics, where training and exercises are used to regain facial movement, in which practitioners are considering the implementation of the device in their treatment. The use of this device acquired at an economical price (less than £50) could potentially represent a form of treatment that may reduce waiting lists in hospitals. This represents a clear example of the use of Robotics and Artificial intelligence in healthcare, enabling these technological advances to be used in the home, and without the need to attend hospital appointments.

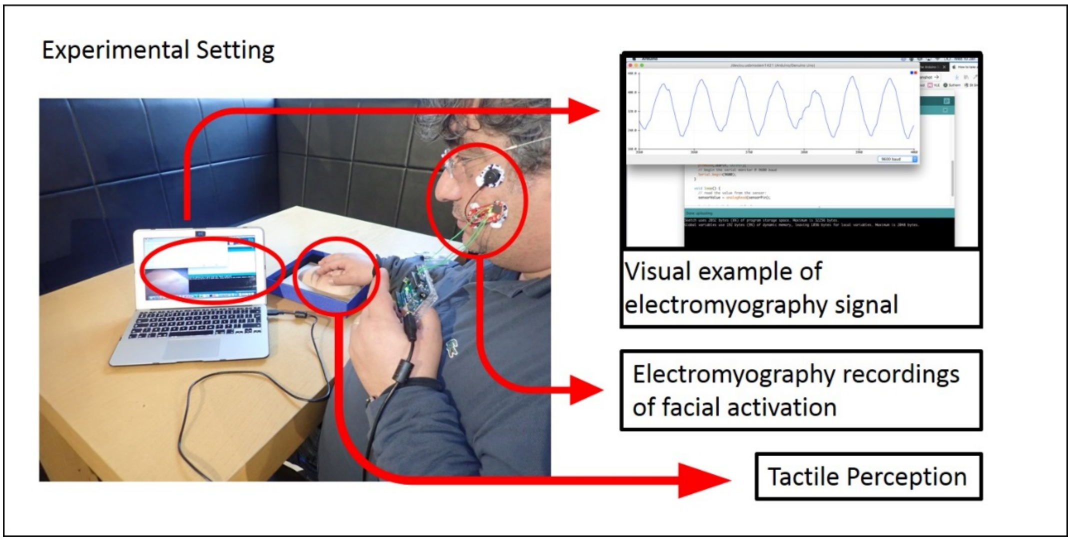

Figure 8.5. Prototype Trials with silicone facial model for tactile perception. Tactile & Auditory biofeedback system with a Robotic Tactile Stimulus

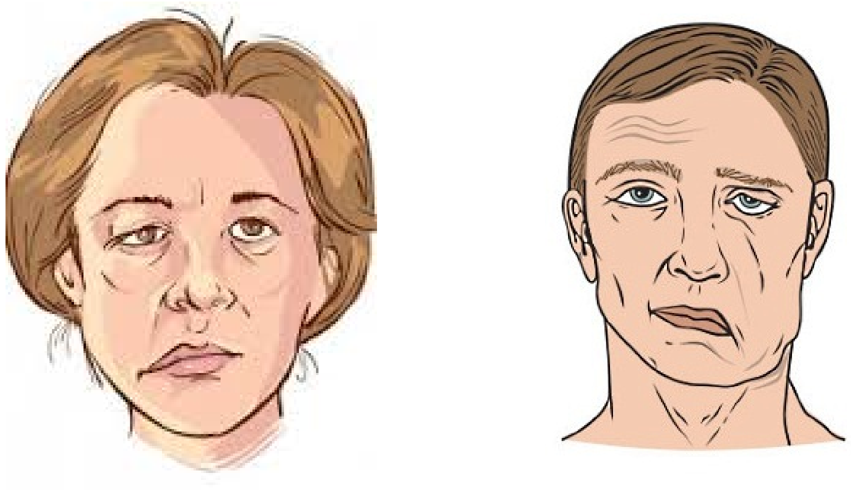

Figure 8.6 Figures exemplify typical stroke victim & Mobius Syndrome’s symptoms and gestural expression.

External engagement:

-Unfortunately, we still haven’t managed to secure funding for the next stage of the project. This will represent an indispensable step, which is the exciting prospect of launching the longitudinal study planned and further development work whereby children are trained and rehabilitated to perceive others and portray their own facial expressions accurately. Through the enlightening experience facilitated by this grant, we confirmed the extreme importance of providing an early intervention and tackling the difficulties shown in adults on their facial expression and interpretation. We therefore aim to prevent them reaching adulthood with a much bigger and more difficult problem to solve. We are therefore immersed in the search for external partners to help subsidise this next step in the project. Any help the Enterprise department can provide us with this difficult task would be extremely appreciated!

- **Presentation at the Research and Innovation Seminar Series Event**: “Life Beyond Sight Loss” Artificial Intelligence and Sensory substitution devices. 13-20 October Blind Veterans UK London Headquarters. The **“Life Beyond Sight Loss”** Seminar is the first in a series looking at various research and innovation ideas in relation to blind veterans, which can impact the whole of the visually impaired community. Guest speakers included internationally known ophthalmologists, academics and the Surgeon General of the British Defense Medical Services Vice Admiral Alasdair Walker**.**

- **Blind Veterans UK**: Presentation at the Technology Week 9-13 Brighton Headquarters. “Robotics, Artificial Intelligence and Assistive Technology for the blind”.

- **Presentation at the University of Sussex** Computer Human Interaction-SCHI LAB Multisensory Experience part of the Creative Technology research group February 6th. “Beyond Human” Human-Robotics & Artificial Intelligence in Healthcare: Helping Blind people hear a smile.

- **Invitation to present at the Seminar Series on behalf of the Systems and Cognitive Neuroscience Group, Department of Psychology at the University of Essex.** March 6th University of Essex “Beyond Human”. Human-Robotics & Artificial Intelligence in Healthcare: Helping Blind people hear a smile.

- **Human Brain Project Neurorobotics Workshop**: Does the body need a brain to be a body: A Human Brain Project Workshop at the University of Barcelona, in the Palau de les Heures, on the 8th and 9th of March 2018.

- **Widening Participation Projects** (Social Sciences Masterclass to 11 and 16-year-old underprivileged children) and **Research & Enterprise Marketing and Communication** at City University of London. Dissemination of research activities which led to a Widening Participation Outreach Award 2017 “Nomination for Student Workshop of the Year”, and “Outstanding Staff Contribution to Widening Participation”.

Feedback Received:

- "It was a pleasure to participate in this study. The goal of producing a biofeedback system that aims to help blind people (and potentially others such as those who have experienced a stroke) to better understand and possibly train their own facial expressions is extremely interesting. As a blind person, I know first-hand that my facial expressions are sometimes misunderstood by others, because my face does not always portray my real emotions. Being blind, I find it difficult to understand what different emotions look like on the face, or how to express them on my own face.

  Research that has the goal of producing a system that could help people like me better appreciate this, is potentially very interesting. It could help me understand facial expressions, and improve my own ability to communicate and be understood by others in professional and personal situations. I wish you well with your work."

- “As a PhD researcher in tactile experiences, as a late blind person as well as a potential user of the work around tactile and auditory exploration of faces, I’m excited to see where the work develops. Conveying emotions is not a trivial task for people with vision impairments. A smile, a frown, a surprised emotion can become more than just words, and therefore increase the emotional intelligence of some blind people who were born blind, or re-live experiences if one lost has lost sight later in life.”

- "in a world of sighted people, it is very important, for us as a blind individual to understand, how certain facial movements appear to the sighted person! I like to know, how the sighted person thinks, I look, when I open my mouth to smile, or narrow my eyes, I'm not able to touch the other person's face so to do that during the study, is very, very interesting, because we only concentrate on the facial expressions like movement of cheek bones, or eyes and nose.

  I liked to concentrate on this topic, and rethink, what certain facial expressions make me want to do. Or how to react.

  I'm certainly interested in emotions and how to bring them across and found the study very, very useful"

- “I really found your study very useful and specifically the activity involved. As I mentioned that it took me lots of practice to getting me smiling when taking photographs with my family. I can say your study will really benefit many people not only in the UK but internationally who are visually impaired. I really like to keep in touch and please let me know if I can be any further assistance in anyway. It would be very interesting to see the results of this study and please share when there are out. Good luck with your trip to Spain and hope to speak soon. Best wishes”.

“Thank you again for the brilliant workshops you delivered for us. The students got a lot out of the event”. (Rupa Lakhani Widening Participation Projects Officer City, University of London

FURTHER DEVELOPMENTS ARISING FROM THIS WORK II

Figure 8.7 Prototype preparation. Robotic Silicone casting of visual and tactile stimulus

Using expertise from the prosthetics team that worked on Star Wars, Harry Potter, Lord of the Rings and others, prototypes have been developed to reproduce the mother's face of a premature baby while they are having to stay in the incubator of the Intensive Care Unit.

This is part of a project we are working on in parallel, using similar technology, as a result of having won the Enterprise Competition 2017. (See details below)

Enterprise competition 2017
City, University of London

Project title: Soft mums for premature born babies. Mums' face, heart beat and soothing sounds.

Our Solution/ innovative idea:

We have developed "a pacifier system" designed to replace/work with the currently used 2-D and 3-D basic dimensional stimuli, and help soothe premature babies giving larger contact with social stimuli that evoke comfort and simultaneously train their visual gaze. The pacifier reproduces a 3-D face, and it is composed of a silicone replica of the baby's mother's face that produces facial expressions of pleasure, such as smiles and laughter and emits a soothing sound such as mum's heartbeat & lullaby.

Figure 8.8. Old Battery of 2D optotipos (Inside top left) New Battery of 3D Optotypes 3D scanned and 3D printed stimuli (right).

Figure 8.9 Premature baby in incubator looking at 3D optotypes.

Industry Partners

Raspberry pi. Cambridge, UK

Arduino. Ivrea, ITALY

Continuity of the activity at the end of present funding:

This pilot will lead to main study commencing in April 2018.

The main study will lead to a Longitudinal Study, following patients in clinic.

The grant provided the chance to pursue two studies on visual perception of different populations such as premature born babies in the Intensive Care Neonatal Unit, and severely visually impaired and blind individuals and stroke victims in their rehabilitation and training of facial gestures perception and portrayal.

Through the use of Robotics and Artificial Intelligence, the tools developed and protected by the Patent Filing Application, should have an impact on society in general and on these vulnerable population groups in particular.

We would like to thank again the Academic and the Research & Enterprise departments, Tia Khan, Caroline Sipos, Brigita Jurisic, Ms. Tanya Shennan for all the help and support. Last but not least, our immense gratitude goes to the mothers and babies, who, with their brave approach to life and their support for our work, are showing us that eventualities, even at this early stage of life, can be overcome and things will always get better!

Ramiro Joly-Mascheroni & Beatriz Calvo-Merino

Artificial Intelligence, Moral Dilemmas and Decision-making.

Might we, one day contagiously, perform a motor action that was executed by a ‘morally ignorant and ethically unaware’ android?

Might we find ourselves one day emulating an agent, not sufficiently ‘Artificially Intelligent’ to solve moral dilemmas?

In the case of the present work, it was only a yawn!

This android was designed and conceived by Ramiro Joly-Mascheroni and built with the help of award-winning prosthetics experts as a collaborative work with blind individuals, medical doctors, physiotherapists, teachers and other specialist educators, as part of a series of studies that go beyond the construction of tools for blind individuals to the extent of formulating some implications and consequences of technological advances. This presents us with important moral dilemmas that we may need to dwell on for the near future. For now, let us think about this possible scenario frequently implemented in decision-making research:

A driverless train is approaching a fork in the tracks. If the computer or robot driving the train allows it to run on its current track, a work crew of five will be killed. If the computer or robot steers the train down the other branch, a lone worker will be killed. So, what should the robot do?

It has been many years since trains without staff have operated on our railway tracks. Driverless cars have already crashed, causing fatalities. A robotic-operated surgery theatre was witness to a tragic mistake that caused the death of the patient. The current and increasing use of robots and artificial agents has raised important moral and ethical concerns. Some decision-making processes involve moral dilemmas. In most cases, moral judgements represent to us humans, enormously difficult challenges. Far too frequently, finding a solution to a moral dilemma, can appear to be practically unsolvable. Some argue for the eminent need to build artificial agents that would be capable of solving moral dilemmas. This intensifies the challenge ahead, as moral and ethical values would have to be somehow embedded into the computer software. How do we create an artificial agent that can solve the moral dilemmas we can’t solve ourselves? It seems evident that robots need to be capable of following some decision-making processes. Is it possible to contagiously perform a motor action executed by a ‘morally ignorant and ethically unaware’ android? We may unintentionally emulate an agent that is not sufficiently ‘artificially intelligent’ to solve moral dilemmas.

9 IMPACT STATEMENT

The main aim was to investigate contagious yawning assuming that this can provide a contribution to the work of researchers interested in visual perception, severe visual impairment and blindness, neurological lesions by stroke and premature birth, and last but not least, those working in the care and rehabilitation of abused primates. A secondary aim of this research, which is not fully described in this thesis, was the further development of alternative diagnostic, aid, rehabilitation and training tools for severely visually impaired and blind individuals. These are conformed by adaptations of existing sensory substitution devices which have already provided evidence of capability to provide an enhancement of the visual development of prematurely born babies.

The new battery of sensorial stimulation has been developed with the help of a grant by the Enterprise Department at City, University of London. Positive results have been presented in the Caixa Science Museum Barcelona Spain. Neonatology Intensive Care Units are already using our newly developed stimuli in their clinics. Preliminary results are extremely promising, and, in many cases, this early diagnosing, results vital to a possible regaining of a near to normal sensorial development.

Throughout the years advocated to this PhD work, the findings have been disseminated as they emerged, and have been presented in national and international conferences exhibitions and other educational events listed below. All the chapters in this thesis constitute part of manuscripts submitted for publication in scientific peer reviewed journals.

PUBLICATIONS

Publications based on work in this thesis

Joly-Mascheroni, R.M., Calvo-Merino B., Forster B. Cross-species contagious yawning in adult chimpanzees: Is it moderated by empathy and familiarity? (Submitted Animal Cognition)

Joly-Mascheroni R. M., Forster B., Calvo-Merino B. Beyond humans: contagious yawning in primates elicited by a non-human agent, an android. (Submitted to PNAS)

Publications arising from collaborative work related to this thesis

Joly-Mascheroni R. M., Forster B., Calvo-Merino B. Embodiment modulates multisensory perception of visual and tactile stimuli in motion submitted to Multisensory Research.

Joly-Mascheroni Dogs catch human yawns, 2008 Joly-Mascheroni, R.M., Senju, A., Shepherd, A. Biology Letters.

CONFERENCE PRESENTATIONS RELATED TO WORK IN THIS THESIS

- Joly-Mascheroni R. Human Adapt 2018 and the 2nd Harrison Memorial Lecture Oxford Natural History Museum
- Joly-Mascheroni, R. Beyond humans: contagious yawning in primates elicited by the visual perception of a non-human agent - an android." VI Primatological conference, Burgos, Spain 2016
- Joly-Mascheroni R. M. Beyond humans? Emulating a morally and ethically unaware android. The Visual Science of Art Conference Barcelona Spain 2016.
- Joly-Mascheroni R. M., Forster B., Llorente M., Calvo-Merino, B. Beyond humans: contagious yawning in primates elicited by the visual perception of a non-human agent - an android." European Conference on Visual Perception Barcelona, Spain 2016
- Joly-Mascheroni R. M. STARTS Prize 2016 Nomination. Grand prize of the European Commission honouring innovation in technology, industry and society stimulated by the arts. Prix Ars Electronica. Linz Austria 2016
- Joly-Mascheroni R. M., Forster B., Calvo-Merino B. Embodiment modulates multisensory perception of visual and tactile stimuli in motion CNS 23rd Annual Meeting Cognitive Neuroscience Society (CNS) New York 2016
- Joly-Mascheroni R. M., Forster B., Calvo-Merino B. Beyond humans: contagious yawning in primates elicited by a non-human agent (an android). Research in Imagery and Observation Conference RIO 10th Anniversary Meeting 6th – 7th April 2016 University of Manchester and Manchester Metropolitan University.
- Joly-Mascheroni, R.M., Calvo-Merino B., Forster B. Cross-species contagious yawning in adult chimpanzees: Is it moderated by empathy and familiarity? Shared Experiences: The Boundaries of the Social Brain. Aegina Greece 2014.
- Joly-Mascheroni, R. M. & Shepherd, A. Enhanced motion after-effects in migraine are related to display contrast: what does this tell us about precortical and cortical neural processing in migraine? Anglo-Dutch Migraine Association meeting, Brighton 2012.
- Joly-Mascheroni R. M. Developmental and Comparative Perspectives of Contagious Yawning. First International Conference on Yawning, Paris 2010.

Public engagements & Media Coverage

Slate/Panoply's podcast series –Dog Smarts, hosted by Dr. Brian Hare
BBC The Wonder of Dogs Episode 3 was produced in partnership with The Open University
(*) Joly-Mascheroni, R.M. et al. (2008) was featured in: BBC, ITN, Reuters, The Guardian,
The Daily Telegraph, The Daily Mail, The Daily Express, The Metro , The Scotsman, Science NOW, Science News, Milwaukee Journal Sentinel, Ynet , Los Angeles Times, Seattle Times,
ABC News, The Irish Times, ABC.net.au, The Hindu, 新华网 [English] ; 新华网 [English];nana10, Die Zeit, The Veterinary Record, Cães & Cia, Ladies' Home Journal, Weekly Reader, Greater Good Magazine, Scholastic Super Science Magazine
BBC Breakfast, BBC Radio 4, BBC Five Live, BBC World Service, BBC Radio Scotland, BBC Radio Cambridge, BBC Radio Newcastle, BBC Radio Northern Ireland, SPIN 1038, ZDF and Birkbeck, University of London
Pet dogs can 'catch' human yawns, BBC News Science.

Grants and Awards related to this work

Global Challenges Research Fund (GCRF) Institutional Strategy, Interdisciplinary and collaborative research generating impact. £5000

UK Government Industrial Strategy Challenge Fund, for research and innovation: Human-Robotics & Artificial Intelligence in Healthcare of premature babies in Intensive Care Units. £22,860

1st Prize winner of the Images of Research competition 2018 City University of London. £1,000

1st Prize winner of the Enterprise competition 2017 City University of London. £15,000**.**

10 APPENDIX Design and development of the Android.

Gray’s anatomy teaching was instrumental in the emulation of a robotic equivalent of the human facial anatomy. Physiological measurements from blind individuals guided the action path of the facial movements. These were represented by the motor input from the android servos and which would be incoming from an oversimplified and extremely basic robotic equivalent of the human brain. Animatronic experts in the field of special effects Coulier Creatures FX (https://www.couliercreatures.com/), who were instrumental in the incredible achievements of films such as Star Wars, Harry Potter, The Lord of the Rings and many others, helped recreate human facial expressions choreographed in the “motoric” (in the literal sense) movement of each of the android’s 33 servos. These movements exemplify the robotic emulation of an initial set of human facial expressions. These first examples of robotic movements aimed, as accurately as possible, to match the commonly used expressions of simple communicative non-linguistic human facial signals. The future purpose is to continue emulating basic emotions described in Ekman and Friesen’s FACS manual and to enhance the ecological validity of the currently-used stimuli in neuropsychological research. A further goal behind the robotic head is to incentivise the fields of psychology, in its cognitive, behavioural and neurophysiological investigations in their use of new technological advances for the production of visual, tactile and auditory stimuli.

The android’s face is composed of several layers of strong silicone. There are inevitable differences between how a human facial skin would look and feel, to that of a robotic replication, the artificial and human-made materials, never equalling the magnificent qualities of the human skin.

Thirty-three mini servomotors, acting as “muscle activity simulating motors”, were used in the production of the whole of the robotic head. An initial neutral facial expression is performed the moment the android is switched on, and remains in that position until a command is given from the main control panel. All movements are programmed to last 10 seconds from onset to offset. The first configuration is composed of 5 main sets of facial expressions: Neutral (closed mouth), Gape (small opening of the mouth), Frown (lowering of eyebrows and edge of mouth), Smile (raising edge of mouth), Yawn (large mouth and eyes opening and closing). Only 9 of the 33 motors were employed to set the non-expressive nature of the neutral expression. This neutral expression was of surprising difficulty, given the amount of energy that is needed to replicate the artificially created equivalent to human skull architecture, which has to be in place to sustain a moving, or in the case of the neutral portrayal, stationary expressionless face with the mouth closed. The 8 mini servos placed in the eye brow regions, were designed to exemplify the corrugator muscle movement. Initially, during the frowning expression (a movement which resembles corrugator muscle motion in the human expression of anger, worry or upset), 6 mini servos work to facilitate and create the internal space necessary for the next move command. These “facilitator engines” are placed in the cheek area, with two main purposes: Firstly, as mentioned above, to facilitate the creation of the physical space, that would be occupied by the new movement command to be executed. Secondly, to maintain cheek, mouth and eye movements, that should be as natural and as similar as possible to a human facial movement and expression. Length of motion time, speed, velocity and trajectory, as well as maintenance and modification of motion pattern, was emulated in an artificial non-biological equivalent to that of human facial biological motion. https://www.youtube.com/watch?v=2M0NuU4_gqg

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