



Published in final edited form as:

Emotion. 2006 August ; 6(3): 367–382. doi:10.1037/1528-3542.6.3.367.

Intramuscular Electrical Stimulation of Facial Muscles in Humans and Chimpanzees: Duchenne Revisited and Extended

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Abstract

The pioneering work of Duchenne (1862/1990) was replicated in humans using intramuscular electrical stimulation and extended to another species (*Pan troglodytes*: chimpanzees) to facilitate comparative facial expression research. Intramuscular electrical stimulation, in contrast to the original surface stimulation, offers the opportunity to activate individual muscles as opposed to groups of muscles. In humans, stimulation resulted in appearance changes in line with Facial Action Coding System (FACS) action units (AUs), and chimpanzee facial musculature displayed functional similarity to human facial musculature. The present results provide objective identification of the muscle substrate of human and chimpanzee facial expressions—data that will be useful in providing a common language to compare the units of human and chimpanzee facial expression.

Keywords

facial muscles; intramuscular electrical stimulation; primates; Duchenne

Evolutionary and comparative facial expression research requires a translatable common language to compare human facial expressions to the facial displays of other primate species. Comparison of facial expressions with other primate species is essential to fully understand the adaptive function of facial communication in human society, and unless we endeavor to seek comparisons on more than one level (emotion, appearance, social function, muscular basis, and neural correlates), we may never build the complete picture. The Facial Action Coding System (FACS; Ekman & Friesen, 1978; Ekman, Friesen, & Hager, 2002a) is widely used in human facial expression research and is set apart from other facial expression coding schemes as it is anatomically based. FACS is partially informed by the seminal work of Duchenne (1862/1990), who electrically stimulated human facial muscles to understand how facial landmarks are fashioned into facial expressions and is thus premised on a correspondence between observable facial movements and the contraction of individual facial muscles. As a result, not only is the system translatable between individuals, but it also has the potential to be comparable between species. A necessary first step for the development of an equivalent coding system for use in other primates is to establish the correspondence between the activity of facial muscles and the resulting facial movements in both species.

Many investigations—spanning various disciplines—rely on an understanding of facial muscle location and the muscular basis of facial movements: electromyographic recording of facial movement (e.g., Soussignan, Ehrle, Henry, Schall, & Bakchine, 2005; Stark, Walter, Schienle, & Vaitl, 2005), assessment of facial muscle strength (Neely & Pomerantz, 2002), treatment of facial palsy (e.g., Shrode, 1993) and neural control of facial muscles (Root and Stephens, 2003; Sherwood et al., 2005) are all premised on the assumption that we know which facial muscles are acting when we observe/record surface movement. Surprisingly, despite advances in electrical stimulation techniques, the original work of Duchenne has not been replicated to better inform our understanding of the appearance of individual facial muscle movements (Ekman & Friesen, 1978, conducted stimulation studies in the development of FACS, but the details have not been given in any publication). The large surface electrodes used in Duchenne's studies would have produced a diffuse electrical current, possibly activating numerous muscles (and/or nerve structures) in any one trial. For example, some stimulations of zygomatic major include activations of orbicularis oculi (Duchenne, 1862: plate 35). The electrode is placed only in the region of zygomatic major, so in this case it seems likely that nerves supplying the orbicularis oculi have been stimulated in addition to the target muscle. Intramuscular electrical stimulation techniques, on the other hand, can deliver the stimulation current directly to the target muscle via microelectrodes inserted into the muscle (Keen & Fuglevand, 2003; Seifert & Fuglevand, 2002), allowing much greater control over the resulting muscle activation. In addition, Duchenne framed his work within an emotional context—in contrast to the objective nature of FACS. His aim was to recreate the expression of emotion on the face, and, to achieve this, he often combined muscle stimulation with voluntary movement by his participants. As a result, the specific movement associated with individual muscles is sometimes ambiguous.

FACS, built upon the work of Hjortso (1970), relates action units (AUs) to individual muscle movements. Other assessment tools have been developed to study facial expression, for example the Maximally Discriminative Facial Movement Coding System (Izard, 1979), but these have focused more on the emotional significance of movement and less on the movement itself. An AU is defined as a movement that can be performed by the human face independently of other actions and can be detected by trained human observers. Some muscles, however, are thought to be involved in more than one AU or may consistently contract in association with another muscle. There are 33 AUs that relate directly to the craniofacial musculature (e.g., cheek raise, AU6; lip raiser, AU10) and an additional 25 AUs that relate to head and eye movements and miscellaneous movements (e.g., tongue show, AU19; eyes down, AU64). This system is widely used in facial expression research and has helped to standardize descriptions and measurements of facial movement within and between studies. Configurations of facial

movements (expressions) can be easily identified and processed, but details of facial movement are not detected as readily. Identifying the subtle facial movements of FACS (AUs) requires extensive training, as coders need to direct attention away from the facial expression and focus on individual movement components of the face. While this may not sound difficult, because humans process facial expressions holistically, it is often difficult to ignore the global configuration of the face and its expression, rather than focus on individual features (Calder, Young, Keane, & Dean, 2000).

At present, nonhuman primate facial expression research does not have a similar standardized system of facial measurement. Despite excellent ethograms of chimpanzee facial expressions (e.g., Chevalier-Skolnikoff, 1973; van Hooff, 1973; van Lawick-Goodall, 1968; Parr, Cohen, & de Waal, 2005), chimpanzee facial expressions are referred to by different categorical names and using different terminology, making it very difficult to compare similar expressions in the same species across studies (let alone across different species). It has long been noted that primate species have physically similar facial displays (Darwin, 1872/1998), yet despite some evolutionary and comparative studies that have considered homology and phylogenetic relationships in terms of appearance (Andrew, 1963; Chevalier-Skolnikoff, 1973; van Hooff, 1972; Ladygina-Kohts, 1935; Preuschoft, 1995; Redican, 1982; Waller & Dunbar, 2005) and some seminal early studies (Huber, 1931), similarity has not been assessed in relation to the facial musculature. Identification of the underlying musculature of facial displays allows us to distinguish between those displays that look similar (but have different muscular bases), those displays that look different (but have similar muscular bases), and those that are similar on both levels. Facial expressions are inextricably linked to facial muscle movements, and so similarity of the muscular basis cannot be ignored when investigating phylogenetic relationships between species. Thus, having a reliable system for assessing appearance but also one that additionally verifies the underlying musculature is critical for studies of primate facial communication and comparisons with human facial expression.

Several studies to date have understood these problems and have applied FACS techniques to help standardize the identification and comparison of primate facial expressions. Steiner, Glaser, Hawilo, & Berridge (2001), for example, applied elements of FACS to analyze nonhuman primates' affective reactions to taste, and Preuschoft & van Hooff (1995) used FACS to describe primate silent bared-teeth displays. Despite the importance of these initial efforts, FACS has, as yet, only been fully developed for use with human subjects. Analysis of the muscular basis and corresponding movement in the target species are essential to apply the system to another primate. In contrast to the literature describing the appearance of primate facial displays (e.g., Andrew, 1963; Bard, 1998; Chevalier-Skolnikoff, 1973; van Hooff, 1972, 1973; Ladygina-Kohts, 1935; Redican, 1982; Preuschoft & van Hooff, 1992; Preuschoft, 1995; Parr et al., 2005; Waller & Dunbar, 2005), the literature describing and comparing the facial muscles of primate species is surprisingly sparse (but see Huber, 1931). Despite some excellent anatomical descriptions with extrapolated function (*Otolemur*; Burrows & Smith, 2003), to date functional facial movement has not been demonstrated in primate species'. Chimpanzees (*Pan troglodytes*) live in complex social groups, display a rich communicative repertoire (Chevalier-Skolnikoff, 1973; van Hooff, 1973; van Lawick-Goodall, 1968), are a phylogenetically close species to humans, and are an ideal species with which to begin comparative facial expression analyses. The studies reported here are a critically important step in the development and design of the chimpanzee FACS (Vick, Waller, Parr, Smith Pasqualini, & Bard, in press).

The replication of Duchenne's work is essential both to confirm the correspondence between muscle movements and facial appearance changes, and to reinforce the assumptions of FACS. Additionally, the extension to chimpanzees is vital to apply the same rigorous observational techniques to another species. The aims of the current study were: a) to replicate Duchenne

(1862/1990) and test the assumed correspondence between muscle contraction and FACS AUs, b) to use the same stimulation techniques to identify the appearance of facial muscle action in chimpanzees, and c) to compare muscle movements between the two species in order to build a chimpanzee FACS.

Methods

Human Participants

Weak electrical stimulations of individual facial muscles were performed on six healthy human volunteers (four female, two male, ages 22–46 yr) at the University of Arizona. All subjects gave informed consent to participate in the study, and all experimental procedures were approved by the Human Investigation Committee of the University of Arizona.

Chimpanzee Subjects

Weak electrical stimulations of individual facial muscles were performed on two adult male chimpanzees (ages 14 and 17 years) from Yerkes National Primate Research Center, Emory University. To minimize unnecessary anesthesia, animals due for annual veterinary survey were used. The testing sessions lasted approximately 40 min. All anesthetics (Telazol and Propofol) were administered by veterinarians in accordance with approved Institutional Animal Care and Use Committees (IACUC) and veterinary procedures. As these subjects were part of a group used for cognition studies, they had been trained to present voluntarily for initial injections (with positive reinforcement training).

Procedures

An extensive review of the human and chimpanzee facial musculature was conducted to inform electrode placement, although the literature concerning chimpanzee facial muscles was surprisingly sparse. A comparison of dissected human and chimpanzee facial muscles are depicted in Figure 1.

The procedures involving human and chimpanzee subjects were the same, except where noted. Human subjects were seated upright in a dental chair. The chimpanzee subjects were positioned prone on a testing table, and the head was propped up to an angle of approximately 30° with respect to horizontal. The skin sites overlying various muscles were identified and cleansed with alcohol (see Figure 1 for location of facial muscles). Electrical stimulation was then applied to individual facial muscles in turn (in most cases right side of the face only)—see Figure 2 for an example of electrode placement. A sterilized tungsten microelectrode (250 μm shaft diameter, ~2 μm tip diameter) was inserted through the skin and directed toward the target muscle. The microelectrode served as the active (cathode) electrode and a surface electrode served as the return (anode) electrode. In human subjects, the surface electrode (silver silver-chloride, 4 mm diameter) was fixed near the superior-lateral margin of the forehead whereas in the chimpanzee subjects, the surface electrode (silver silver-chloride, 1 cm diameter, disposable EKG electrode) was taped to the skin on the chest.

Initially, low-intensity (1–4 mA) constant current pulses (0.5 ms in duration) were delivered by a stimulator and optically isolated constant current unit (Grass Instruments S88—West Warwick, Rhode Island) at a rate of 1 pulse/s. The position of the microelectrode was manually adjusted until a site was found that evoked motor responses in the target muscle. The muscle was then activated using a 2-s train of stimulus pulses at 30 pulses/s in order to evoke a sustained contraction of the target muscle. On repeated trials, the magnitude of the stimulus pulses was progressively increased from a level that barely elicited movement (<1 mA) up through levels that evoked strong muscular contractions. In human subjects, the upper limit of stimulus current was often also dictated by the level of discomfort associated with high stimulus

intensities that could be tolerated by a subject (usually < 8 mA). Typically, the type of movement was similar across stimulus intensities at a given location. On occasion, however, when using larger stimulus pulses (> ~6 mA), the form of the movement altered, perhaps due to the activation of muscles near to the target muscle.

Three to five trials of sustained stimulation were elicited (duration of peak movement < 3 s) for a stimulus intensity that appeared to activate the muscle in isolation. If several attempts failed in stimulating movement in that area, the microelectrode was withdrawn and reinserted into a new site to test a different muscle. Not all muscles were tested in all subjects due to various constraints—time (chimpanzees: maximum 40 min duration of anesthetic; humans: maximum 120 min testing period per participant), discomfort, or a lack of anatomical information in the literature. Where information (from the literature) was lacking or a muscle was believed to be very small, we conducted thorough exploration through repeated insertions in the area.

Two digital video cameras were positioned at frontal and profile angles to capture the change in the shape of the face in response to the stimulations for subsequent analysis. Video cameras were set to record once a successful stimulation was achieved and repeated.

Analysis

Human stimulation footage was observed and coded by three certified human FACS coders; two were present during the stimulation study (BW and SJV) and one was fully independent of the design, execution, and objectives of the study (MM). In the first instance, an example of a successful stimulation for each muscle was extracted by BW and sent to the additional coders (SJV and MM). Additional coders were not told, at this stage, which muscle was being attempted. SJV was present during the experiment, but sound had been removed and the clips reordered. All coders were asked to watch each clip (approximately 2–5s in duration) and decide which AU(s) were present at peak movement (peak movement as identified by each coder). Coding agreement for human stimulation is shown in the results (Table 1). All chimpanzee footage was described (initially) by BW, and exemplar clips were extracted and sent to SJV for any additional descriptions. Given that the chimpanzee stimulations represent part of the ChimpFACS development process, ascribing ChimpFACS codes at this stage was deemed circular, and so detailed discussions were conducted to reach unanimous agreement on appropriate descriptions.

Results and Discussion

The following section combines the results and discussions of both studies, so that the findings for each muscle can be compared to Duchenne's original observations, the FACS AUs, and between the two species. Grouped by the emotional terms ascribed by Duchenne, we first present background information for each muscle: gross anatomical structure in both species (see Figure 1), using Gray 1918/1995 for human muscles unless otherwise stated (see text for specific chimpanzee references); assumed correspondence with FACS AUs; and human facial expressions reported to contain this movement (Table 10–1: Emotion predictions, from Ekman, Friesen, & Hager, 2002b). We then report and discuss appearance change on stimulation in both species. Table 1 details the comparisons between human muscles described in Duchenne, FACS, and the current study (detailing coding agreement), and Table 2 summarizes similarities and differences between human and chimpanzee stimulated muscle movements. In addition, Table 3 summarizes the human muscles found in this study in comparison to previous studies.

'The Muscle of Attention'

Medial frontalis and lateral frontalis—The human frontalis muscle has no bony attachments and originates from the anterior margin of the galea aponeurotica (see Figure 1). Medial fibers are continuous with the procerus and are believed to underlie AU1 (inner brow raiser); lateral fibers of the frontalis blend with orbicularis oculi and are believed to underlie AU2 (outer brow raiser): both AUs form part of surprise and fear expressions (all prototypes), and AU1 is also associated with 2 of 3 sadness prototypes. Duchenne illustrated stimulation of the lateral section only, to illustrate attention, and also included frontalis stimulation in the muscles complementary to surprise. The chimpanzee frontalis has the same origin, but is reported to mingle with the auricularis superior et anterior (muscle associated with ear movement, not shown in Figure 1) more so than in man (Huber, 1931); lateral and medial sections are not referred to in the anatomical literature.

Human stimulation: Stimulation of the medial section of the frontalis was attempted in five participants and achieved in three. When the muscle was stimulated, the skin of the medial forehead was pushed superiorly causing horizontal wrinkles to form and the medial portion of the eyebrow to elevate (see <http://www.apa.org/suppl 01a>). In some participants, these wrinkles were curved upwards. These appearance changes were qualitatively similar to AU1 and sufficient to code AU1. Stimulation of the lateral section was attempted and achieved in all six participants. Figure 2 (and <http://www.apa.org/suppl 02a>) shows the resulting appearance change when the muscle was stimulated. When the muscle was stimulated, the lateral portion of the eyebrow was pulled upwards causing an arched shape to the eyebrow. The lateral portion of the eye cover fold was stretched upwards. Horizontal wrinkles formed above the lateral portion of the eyebrow. These appearance changes are similar to those demonstrated by Duchenne, although, as aforementioned, he considered this movement to be the whole frontalis muscle. These movements were equivalent to AU2 and sufficient to code AU2. The appearance changes associated with medial frontalis contraction were not seen, and so we concluded that the two portions of frontalis can be mechanically distinct.

Chimpanzee stimulation: Medial (superior to glabella) and lateral (superior to mid-brow) sections were stimulated separately, which led to elevation of the medial and mid to lateral portions of the brow, respectively (see Figure 2 and <http://www.apa.org/suppl 01b> and [02b](http://www.apa.org/suppl 02b)). Both sites of stimulation resulted in small transverse wrinkles on the forehead. Huber (1931) viewed the connection of the frontalis with auricularis superior et anterior as a more primitive condition and suggested that differentiation between these muscles in humans has occurred due to both growth of the cranial vault and greater selection for facial movement over ear movement. Rinn (1984) suggested that brow movements in humans are vestiges of ear perking in lower mammals, given that the brows and ears had former connection. Some mammals move their ears when orienting attention (Andrew, 1963), and interestingly, brow movements in humans can be conversational signals of emphasis and attention (Ekman, 1979). We did not, however, see any evidence of ear movement during frontalis contraction in chimpanzees, indicating that functional differentiation has also occurred in chimpanzees.

'The Muscle of Reflection'

Depressor supercilli—Duchenne did not discuss this muscle specifically, but depressor supercilli action seems to be involved in Duchenne's orbicularis oculi stimulation (referred to as the muscle of reflection) - depressor supercilli is sometimes considered to be part of the orbicularis oculi. When considered structurally distinct, it is described as originating from the nasion and inserting onto the medial part of the superciliary arch (eyebrow). FACS does not identify isolated movement of this muscle, but considers contraction to underlie AU4 (brow lowerer) along with procerus and corrugator supercilli, and individual movement is extrapolated from this combined action (inner brow lowerer; AU42). In FACS emotion

predictions, AU4 is associated with facial expressions of fear (all prototypes), sadness (2 of 3 prototypes), and anger (all prototypes). Huber (1931) stated that the depressor supercilli is present in some primates and controls the eyebrow whiskers, although it is unclear to which species he was referring, and this muscle is not mentioned specifically in relation to the chimpanzee.

Human stimulation: Stimulation was attempted and achieved in five participants (see Figure 3 and <http://www.apa.org/suppl 03>). The medial corner of the eyebrow was lowered and depressions and bulging were produced at the root of the nose. These features are consistent with the FACS descriptions of AU42, but, in addition, oblique glabella depressions were observed. These depressions are likely to form wrinkles at strong contraction, and so we conclude that glabella frown-wrinkles (characteristic of AU4) are more likely to be the result of depressor supercilli and not, in fact, corrugator supercilli.

Chimpanzee stimulation: Repeated stimulation at various positions in both subjects failed to achieve action that could have resulted from depressor supercilli (although see orbicularis oculi stimulation for brow lowering action; <http://www.apa.org/suppl 07c>).

'The Muscle of Aggression'

Procerus—Procerus arises by tendinous fibers from the superficial fascia covering the lower part of the nasal bone and upper part of the lateral nasal cartilage. It then fans superiorly and inserts onto the skin of the lower forehead between the brows, where the fibers mingle with frontalis. According to FACS, this muscle usually acts in concert with corrugator supercilli and depressor supercilli (brow lowerer; AU4) and levator labii superioris (nose wrinkler; AU9) and is associated with facial expressions of fear, sadness, anger, and disgust (as noted above). Independent action is rare, but described as AU41 (glabella lowerer). Duchenne described this muscle as the muscle of aggression, and his observations concur with FACS descriptions. The drawings of both Huber (1931) and Pellatt (1979b) suggest that procerus is less differentiated from frontalis and levator labii superioris alaeque nasi in the chimpanzee than in humans.

Human stimulation: Stimulation was attempted and achieved in five participants (see Figure 3 and <http://www.apa.org/suppl 04a>). The skin of the glabella was pulled down, forming bulges and pouches and producing horizontal wrinkles at the root of the nose. These appearance changes are consistent with both the observations of Duchenne and the appearance changes of AU41 (glabella lowerer).

Chimpanzee stimulation: Contraction caused the medial portion of the brows to depress (see <http://www.apa.org/suppl 4b>) and wrinkles to form in the glabella region superior to the nose. Strong contraction resulted in depression of the lateral portions of the brow and wrinkling of the skin lateral to the nose. This latter movement may have been due to stimulation of fibers of levator labii superioris alaeque nasi, indicating undifferentiation.

'The Muscle of Pain'

Corrugator supercilli—The corrugator supercilli originates from the medial portion of the superciliary arch (superior to depressor supercilli) and inserts onto the deep surface of the skin above the mid-portion of the orbital arch. Together with procerus and depressor supercilli, this muscle is believed to depress and draw together the brows (as a frown) when contracted (brow lowerer; AU4), contributing to facial expressions of fear, sadness and anger (as noted above). Isolated movement is not commonly coded using the FACS system, but Ekman et al. (2002a) described independent action as AU44 (eyebrow gatherer), where the brows are drawn together. Interestingly, Duchenne attributed a different movement to this muscle action (coded as AU1, inner brow raiser, + AU4, brow lowerer, in FACS) and described the effect of

stimulation as a look of profound suffering, with resignation; he labeled the corrugator the muscle of pain. Given small sample size, possible individual variation, and inconsistent reports (see Huber, 1931; Pellatt, 1979b), it is unclear whether the corrugator is always present in the chimpanzee (although recent dissections have found a distinct corrugator: Burrows, Waller, Parr & Bonar, 2006).

Human stimulation: Stimulation was attempted and achieved in four participants (see Figure 3 and <http://www.apa.org/suppl/05a>). The skin above the eyebrow did gather medially, but, instead of lowering or pushing the medial brow corners closer together, the medial gathering was accompanied by a medial brow elevation and twisting movement. As a result, the appearance change was qualitatively similar to AU1 + AU4 and not AU4 or AU44. Note that the appearance changes associated with stimulation of medial frontalis (inner brow raiser; AU1) did not include the gathering movement, so the two stimulations, although similar, had important qualitative differences. Interestingly, these observations are compatible with current anatomical research, which has revised understanding of the fine structure of this muscle (Isse & Elahi, 2001). In agreement with Duchenne, we conclude that, when corrugator supercilli is acting in isolation, it produces AU1 + AU4 and does not produce vertical glabellar frown lines. Given the gathering movement above the brows, this muscle is still likely to contribute to AU4, but any medial brow elevation is likely to be antagonistic to procerus when acting in this combination.

Chimpanzee stimulation: Repeated stimulation at various positions in both subjects failed to achieve action that could have resulted from corrugator supercilli. The controversy over presence of the chimpanzee corrugator is of particular interest considering that the chimpanzee has been described as showing a well-developed frown (Ladygina-Kohts, 1935; Pellatt, 1979b). In contrast, Parr, Preuschoft, & de Waal (2002) reported that the frown is an uncommon action. Given that we were unable to locate and stimulate any musculature to draw the brows together, it may be that fixed vertical furrows between the chimpanzee brows give the impression of a frown, even if facial muscles are not contracting.

'The Muscles of Joy and Benevolence'

Zygomatic major—The zygomatic major in humans originates in the zygomatic arch and inserts onto the modiolus (muscular node at the corner of the mouth). Contraction is thought to elevate the lip corners superolaterally (lip corner puller, AU12) and is associated with facial expressions of happiness (all prototypes). Duchenne labeled this muscle (along with the inferior part of orbicularis oculi, which circles the eye) the muscle of joy and benevolence and demonstrated contraction similar to AU12. This muscle is present in the chimpanzee, and, although some strands still connect to the ear, many fibers are attached to the zygomatic arch (Bolwig, 1964; Huber, 1931; Pellatt, 1979b).

Human stimulation: Stimulation was attempted and achieved in four participants (see Figure 4 and <http://www.apa.org/suppl/06a>). The lip corner was pulled superolaterally toward the ear (AU12).

Chimpanzee stimulation: Initial attempts to stimulate this muscle (superior and lateral to modiolus) caused global activation of many muscles, probably due to stimulation of the temperofacial branch of the facial nerve (Duchenne caused the same effect when first attempting to locate the zygomatic major in humans, plate 6). Isolated contraction elevated the lip corners, retracting the modiolus superolaterally (see Figure 4 and <http://www.apa.org/suppl/6b>) and caused transverse wrinkles to form lateral to the modiolus (characteristic of AU12). AU12 is commonly perceived as a smile expression in humans, and so the finding that the same action results from the same muscle in chimpanzees is of

considerable significance. This action is likely to be involved in the silent bared-teeth display in chimpanzees, which has been proposed as a homologue of the human smile (van Hooff, 1972).

Orbicularis oculi—Orbicularis oculi is the sphincter muscle that orbits the eye and in humans two portions can be distinguished. The palpebral portion arises from the bifurcation of the medial palpebral ligament forming a series of concentric curves and inserts onto the lateral palpebral raphé (small fibrous band between eyelids). When contracted, this portion is thought to tighten the eyelids (lid tightener, AU7). The fibers of the orbital portion arise from the nasal part of the frontal bone and frontal process of the maxilla, forming a complete ellipse, and the upper fibers blend with frontalis and corrugator supercilli. Contraction of this orbital portion is thought to elevate the infraorbital triangle (cheek raiser, AU6) and is associated with happiness facial expressions (1 of 2 prototypes). Duchenne did not comment on these separate inner and outer sections, but instead considered the inferior and superior sections of orbicularis oculi to be functionally distinct. While he did not report or illustrate independent contraction of the inferior section, he did refer to this section as the muscle of joy and benevolence (along with zygomatic major) leading Ekman, Friesen, and Davidson (1990) to later term this “genuine” smile, the Duchenne smile. The dissection drawings of the chimpanzee seem to distinguish the palpebral and orbital portions of orbicularis oculi (Huber, 1931; Pellatt, 1979b; Swindler & Wood, 1973; see Fig. 1), but these portions are not referred to directly. In addition, Pellatt (1979b) observed in the chimpanzee a small band of fibers extending from the orbital portion of orbicularis oculi to join the levator labii superioris above the lip; he suggested this may be an incipient zygomatic minor (see Fig. 1), the muscle that deepens the nasolabial furrow (AU11) in humans.

Human stimulation: Stimulation of the palpebral fibers was not attempted directly due to close proximity to the eye. Stimulation of the orbital portion was attempted in three participants and achieved in two (see Figure 4 and <http://www.apa.org/suppl 07a>). The skin inferior and lateral to the eye was pushed medially and superiorly, causing the skin below the eye to bag and wrinkle (characteristic of AU6), although not all appearance changes of AU6 were observed (i.e., crow’s feet wrinkles). There was some lowering of the upper lid, but no tightening, so it is possible that the palpebral portion contracted in addition (MM coded AU7: lid tightener, which is a subtly different action also caused by orbicularis contraction).

Chimpanzee stimulation: Stimulation of the orbital portion (inferior and lateral to eye) of orbicularis oculi elevated the cheek superomedially, pushing the skin towards the eye (as in human AU6; see Figure 4 and <http://www.apa.org/suppl 07b>). The strands connecting orbicularis oculi to the upper lip were visible on strong contraction, but did not elevate the upper lip. In addition, strong contraction depressed the brow. When the stimulation site was repositioned superior to the eye (on the brow), this depression was stronger, but may have been due to activation of depressor supercilli. Again, we did not attempt to stimulate the palpebral portion of orbicularis oculi due to thinness of the skin and proximity to the eye.

‘The Muscle of Lasciviousness’

Nasalis—According to FACS, nasalis controls dilation and contraction of the nostril wings (nostril dilate, AU38; nostril compress, AU39). Nasalis pars alaris (dilator naris) arises from the maxilla (lateral to the nose near the canine tooth) and attaches to the alar cartilage (nostril wing). Nasalis pars transversa (compressor naris) arises from the maxilla (lateral to the nose near the canine tooth) and passes superomedially to meet the opposite muscle at the bridge of the nose. Interestingly, Duchenne ascribed a different function to nasalis (labeled the muscle of lasciviousness) and described the alar of the nose moving obliquely and superiorly (much like part of the nose wrinkle, AU9).

Human stimulation: We did not attempt to stimulate this muscle directly, but during levator labii superioris alaeque nasi trials we found a movement that bore resemblance to the nasalis stimulation of Duchenne (Duchenne 1862/1990, plate 38), see <http://www.apa.org/suppl 8>. The skin of the bridge of the nose is wrinkled and contracted as if pinched, one of the movements seen in AU9 (nose wrinkle). We conclude, therefore, that a portion of nasalis is acting in association with levator superioris labii alaeque nasi in AU9.

Chimpanzee stimulation: We did not attempt to locate and stimulate this muscle due to small size.

'The Muscle of Sadness'

Triangularis—In humans, the triangularis (depressor anguli oris) has a long, linear origin in the mandible, continues lateral to the depressor labii inferioris, and inserts onto the modiolus, mingling with the risorius and orbicularis oris. Thought to cause lip corner depression according to both FACS (lip corner depressor, AU15) and Duchenne, it has been labeled the muscle of sadness and disgust (Duchenne) and has since been associated with sadness (all prototypes) and disgust facial expressions (1 of 6 prototypes). Pellatt (1979b) noted that it has the same general arrangement in the chimpanzee, although is strongly interlaced with the platysma (neck tightener, AU21).

Human stimulation: Stimulation was attempted and achieved in two participants (see <http://www.apa.org/suppl 09a>). The lip corners were pulled inferiorly, and the minimum criteria necessary to code AU15 were displayed.

Chimpanzee stimulation: We were able to stimulate the triangularis at a position inferior to the lip corner (see <http://www.apa.org/suppl 09b>). Contraction caused the lip corners to depress (similar to AU15). No evidence of movement was found in the skin of the neck, suggesting that this muscle is also mechanically distinct from the platysma in chimpanzees.

'The Muscles of Weeping and Whimpering'

Zygomatic minor—Originating from the lateral surface of the zygomatic arch and inserting medially on the upper lip, the zygomatic minor is thought to elevate the upper lip superolaterally and deepen the nasolabial furrow when contracted (nasolabial furrow deepener, AU11). To Duchenne, this muscle expressed weeping, whimpering, and tears of pity, although the plates depicting contraction (plate 46) seem to involve more AUs than AU11 alone, so may not illustrate independent action of this muscle. FACS associates AU11 with sadness (1 of 3 prototypes), although contribution to expressive movement may be rare: it was found in only 36% of individuals (racial origins not stated) in a study of 50 cadavers (Pessa, Zadoo, Adrian, Yuan, & Garza, 1998), yet an earlier study of 620 Kyushu-Japanese cadavers (Sato, 1968) found incidence of 94% (females) and 97% (males). Swindler and Wood (1973) show the zygomatic minor in the chimpanzee, and, although Burrows et al. (2006) found this muscle in recent dissections, it has not been described in other sources of facial dissection.

Human stimulation: Exploration in the area did not result in any movement likely to result from zygomatic minor.

Chimpanzee stimulation: Although we did not achieve isolated stimulation of this muscle, we noticed some tightening of muscle strands attached to orbicularis oculi (considered to be an incipient zygomatic minor; Pellatt 1979b), on stimulation of orbicularis oculi.

Levator labii superioris—In humans, levator labii superioris originates from the maxilla and zygomatic arch above the infraorbital foramen and inserts onto muscles of the upper lip at

the nasolabial furrow; in the chimpanzee, this muscle is well differentiated and wider than in humans (Pellatt, 1979b). This muscle is thought to elevate the upper lip (upper lip raiser, AU10) in humans. Duchenne labeled this muscle (along with zygomatic minor) the muscle of weeping and sadness, yet, although some of the features of AU10 are present in his demonstrations (deepening of the nasolabial furrow), upper lip raising is not. Within FACS, AU10 is a component of disgust (3 of 6 prototypes) and anger (2 of 7 prototypes).

Human stimulation: Stimulation was attempted in two participants, but we were unable to achieve muscle contraction. Participants found electrode insertion too uncomfortable in this area, and so attempts were discontinued.

Chimpanzee stimulation: Stimulation superior to the lateral portion of the upper lip (inferior and lateral to nose) caused the upper lip to elevate (see <http://www.apa.org/suppl 10>). The upper lip fattened, causing the skin to tighten and vertical wrinkles to reduce. Given the greater degree of prognathism in chimpanzees, this muscle may be wider to enable the longer upper lip to be elevated when baring the teeth.

Levator labii superioris alaeque nasi—In humans, the levator labii superioris alaeque nasi arises from the upper part of the frontal part of the maxilla and divides into lateral and medial strips. The medial strip inserts onto the skin and alar cartilage (laterally) and the lateral strip inserts into the upper lip. According to FACS contraction elevates the upper lip and wrinkles the nose (nose wrinkler, AU9). Duchenne illustrated contraction of this muscle (similar to AU9) and believed this muscle to express discontent and bad humor: FACS associates AU9 with disgust (3 of 6 prototypes). In the chimpanzee, levator labii superioris alaeque nasi appears to mingle with procerus to a greater extent than in humans (Huber, 1931; Pellatt, 1979b).

Human stimulation: Stimulation was attempted in two participants and achieved in one (see Figure 5 and <http://www.apa.org/suppl 11a>). The skin alongside the nose was pulled upwards causing wrinkling, although the wrinkling of the skin on the bridge of the nose was absent (see nasalis stimulation). In addition, the glabella region lowered and protruded, indicating that procerus was recruited during stimulation of this muscle—perhaps due to intermingling fibers.

Chimpanzee stimulation: Stimulation of levator labii superioris alaeque nasi (immediately lateral to the alar cartilage) resulted in wrinkling of the skin lateral and superior to the nose, moving the skin superiorly and elevating the upper lip very slightly (see Figure 5 and <http://www.apa.org/suppl 11b>). Strong contraction caused the brows to depress with marked wrinkles superior to the nose, indicating that procerus may have been recruited (these muscles may be somewhat intermingled).

‘The Muscle of Fright, of Terror’

Platysma—In humans, the platysma is a broad sheet arising from the fascia covering the upper parts of the pectoralis major and deltoideus. Some fibers insert onto the mandible and others into the skin and subcutaneous tissue of the lower face. When contracted, the skin of the neck is tightened (neck tightener, AU21) depressing the skin and causing bulges and wrinkles in the skin of the neck; and, although Duchenne labeled the platysma as the muscle of fright and terror and demonstrated stimulation of this muscle, it is not associated with any of the prototypical expression or their major variants within FACS. Similar to the human platysma, the chimpanzee platysma has retained little or none of the nuchal portion (Pellatt, 1979b; Swindler & Wood, 1973), which is present in *Papio ursinus*, for example (Pellatt, 1979a). Also, the chimpanzee platysma inserts onto the lower lip (skin and subcutaneous tissue) and slightly into the bone of the mandible.

Human stimulation: We did not attempt to stimulate this muscle in humans due to anticipated discomfort—the neck region seemed to be particularly uncomfortable.

Chimpanzee stimulation: Stimulation of the platysma caused the skin inferior to the lower lip to depress and tighten and elevated the skin of the nuchal region (not shown in Figure 3a due to angle of the image).

Additional Muscles

Caninus—The caninus (levator anguli oris) arises from the canine fossa of the maxilla and inserts at the modiolus in humans. When contracted it elevates the lips corners and puffs the cheeks (FACS: cheek puffer, AU13), although this action is uncommon. Duchenne does not discuss this muscle and it is not associated with any main FACS expression configurations. Huber (1931) stated that the caninus is less differentiated in the chimpanzee and Pellatt (1979b) described it as poorly developed.

Human stimulation: Stimulation was attempted and achieved in two participants (see <http://www.apa.org/suppl 12>). The lip corner was pulled superiorly, but with no lateral pull as in AU12. Appearance changes were equivalent to the minimum criteria associated with AU13.

Chimpanzee stimulation: We were unable to locate and stimulate the caninus.

Risorius—Originally thought to control smiling and laughing (risor [Latin]—a laughter), the risorius has been considered unique to humans (Huber, 1931). The risorius arises below the zygomatic arch and inserts at the modiolus, but is known to exhibit high individual variability: Pessa et al. (1998) found the risorius in only 6% of human specimens examined, but Sato (1968) found the muscle in 86% (females) and 89% (males) of Kyushu-Japanese cadavers. FACS attributes lateral mouth corner retraction to the risorius (lip stretch, AU20), although it often works in concert with the platysma (neck tightener, AU21): within FACS emotion predictors, AU20 is associated with fear expressions (1 of 2 prototypes). Duchenne did not demonstrate isolated contraction of the risorius, but showed the platysma stimulations (labeled the muscle of fright and terror), which may also involve risorius action. Although not often referred to directly in the chimpanzee, the dissection drawings of both Pellatt (1979b) and Huber (1931) show a bundle of fibers from the platysma crossing the triangularis and inserting onto the modiolus in the chimpanzee, and recent dissections have also located a risorius (Burrows et al., 2006).

Human stimulation: Stimulation was attempted and achieved in one participant (see <http://www.apa.org/suppl 13>). The mouth corner was retracted laterally (and not superiorly) and displayed the minimum criteria necessary to code AU20. However, due to the subtlety of the movement there was some disagreement among coders over ascribing AU20, lip stretch (BW and SJV) or AU14, dimpler (MM). Both action units lead to the lateral pull of the mouth corners and presence of electrode might have lead to the appearance of dimpling which is a key indicator of AU14.

Chimpanzee stimulation: We were unable to locate and stimulate movement from this muscle.

Mentalis—The mentalis muscle arises from incisive fossa of the mandible and descends to insert onto the skin of the chin in humans. During contraction, the skin of the chin boss elevates, causing the lower lip to protrude, and causes wrinkles and dimples to form in the skin of the chin boss (FACS: chin raiser, AU17). Duchenne did not address the function of mentalis, but FACS associates AU17 with disgust (2 of 6 prototypes) and anger (2 of 7 prototypes). Huber

(1931) and Pellatt (1979b) both mentioned the mentalis in the chimpanzee, but Pellatt noted that it is small and distinct.

Human stimulation: Stimulation was attempted and achieved in two participants (see <http://www.apa.org/suppl 14a>). The skin of the chin was pushed superiorly, causing dimples and wrinkles to form over the chin boss (equivalent to AU17), although the movement did not cause the lip to protrude (possible due to the low intensity stimulation).

Chimpanzee stimulation: On stimulation at a position inferior to the medial part of the lower lip, the skin inferior to the mouth (chin region) was pushed superiorly toward the lower lip (see <http://www.apa.org/suppl 14b>). There was no evidence of lower lip protrusion (as seen in human AU17) or characteristic dimpling of the skin—perhaps due to absence of a bony chin boss.

Orbicularis oris—In humans, a number of muscles converge at the corner of the mouth to form a compact fibromuscular mass, the modiolus. Gray (1918/1995) states that there is little value in considering the actions of the individual muscles of the mouth in isolation, as controlled three-dimensional mobility of the modiolus allows integrated activity of the cheeks, lips, and jaws. However, independent movements of the lower face have been distinguished within FACS. In humans, movements attributed to the orbicularis oris have been categorized as funneling the lips (lip funneler, AU22), tightening the lips (lip tightener, AU23), pressing the lips together (lip presser, AU24), and rolling lips between teeth (lip suck, AU28); FACS associates these movements with anger expression configurations (7 of 7 prototypes contain one of these movements). Duchenne did not address the function of this muscle. In the chimpanzee, this muscle is well defined, although marked differences in the shape of the lower face are likely to yield differences in appearance during contraction.

Human stimulation: Stimulation was attempted and achieved in one participant (see <http://www.apa.org/suppl 15a>). We were unable to achieve full orbital movements through stimulation, although localized pursing/tightening movement was seen at the specific site receiving stimulation—similar in appearance to the tightening movement seen in AU23 (lip tightener). Exploration in this area was uncomfortable, and so we did not attempt to stimulate other possible movements from this muscle.

Chimpanzee stimulation: Stimulation at numerous sites surrounding the mouth all resulted in the same function—localized pursing/tightening movement of the lip margin and some funneling of the lips (see <http://www.apa.org/suppl 15b>). Only strong stimulation or simultaneous upper and lower lip stimulation caused the full funnel (lip funneler, AU22), where the lips funneled and protruded.

Buccinator—The buccinator is found at the lining of the buccal wall in humans; it arises from the maxilla and mandible (corresponding to the three molar teeth) and converges toward the modiolus, where the central fibers intersect each other, the inferior fibers being continuous with the upper segment of the orbicularis oris and the superior fibers with the lower segment. The main function seems to be masticatory as it compresses the cheeks to keep food in the mouth (perhaps involved in sucking); but within FACS, cheek dimpling is also attributed to this muscle (dimpler, AU14). Duchenne did not discuss this muscle, and it is not associated with any of the main expression configurations (although recent studies have associated a unilateral AU14 with contempt: Matsumoto & Ekman, 2004). Pellatt (1979b) noted a small buccinator in the chimpanzee (and no buccal pouches as are common in Old World primates).

Human stimulation: Stimulation was attempted in one participant, but was not achieved.

Chimpanzee stimulation: We were unable to locate and stimulate movement from this muscle.

Depressor labii inferioris—In humans, the depressor labii inferioris (quadratus labii inferioris) arises from the mandible and inserts onto the skin of the lower lip, blending with the paired muscle from the other side. Laterally, it is continuous with the platysma. When contracted, the lower lip depresses, displaying the lower teeth (FACS: lower lip depressor, AU16). Duchenne does not discuss this muscle, but FACS associates AU16 with disgust expressions (2 of 6 prototypes). Pellatt (1979b) stated that although present in the chimpanzee, the depressor labii inferioris is not differentiated from the platysma.

Human stimulation: Stimulation was attempted and achieved in two participants (see <http://www.apa.org/suppl 16a>). The electrode was inserted medial and inferior to the lip corner and resulted in a very slight (although codable) movement. Contraction resulted in the lower lip pulling inferiorly and exposing the lower teeth, displaying appearance changes equivalent to AU16.

Chimpanzee stimulation: Stimulation inferior and slightly lateral to the medial portion of the lower lip caused the lower lip to depress inferiorly (see <http://www.apa.org/suppl 16b>). There was an absence of skin movement below the jaw line, thus distinguished from platysma action: we conclude that the depressor labii in chimpanzees is capable of independent movement.

Summary

Figure 6 illustrates the range of facial movements that are possible in the human and the chimpanzee face. There are 20 facial muscles in the human face that are considered to have expressive function. Of these, 10 were stimulated by Duchenne; 19 have been associated with specific facial movements in FACS; and 15 were stimulated using intramuscular electrical stimulation in the current study (Table 3). In addition, of these 20 muscles, 12 were located and stimulated in chimpanzees (Table 2).

General Discussion

In the present study, we have documented facial movements associated with activity in individual muscles in humans and chimpanzees using intramuscular electrical stimulation. We have replicated the main findings of Duchenne (1862/1990) - still cited by both anatomists and psychologists as the main reference documenting facial movement in humans. Furthermore, we have clarified the muscular basis of AUs and set the foundations for developing an anatomically based FACS for use with another species (chimpanzees). These findings allow direct comparison of facial muscle function between the two species and, therefore, provide the basis for examination of evolutionary and functional significance of differences and similarities in facial expression.

The results of the experiments presented here bear similarity to the observations of Duchenne and the muscle/surface movement correspondence presented within FACS. The one finding which contrasts with FACS is, interestingly, in accordance with the findings of Duchenne. The muscles involved in AU4 (corrugator supercilli, depressor supercilli, and procerus) are rarely seen acting in isolation, and so function of each of these muscles has been largely extrapolated from anatomy. Here, however, we succeeded in stimulating each of the three muscles (in apparent isolation) and, thus, can add to current understanding of individual function. Appearance changes resulting from corrugator supercilli stimulation concur with the observations of Duchenne (medial and superior corrugation) and are also confirmed by recent anatomical investigations (Isse & Elahi, 2001).

Although the stimulation methods used here allow muscle structures to be targeted directly (as opposed to Duchenne's original surface stimulation), there are still some limitations. The sample size is small, and it is difficult to fully assess the findings (particularly the absences in the chimpanzee) without more subjects. In addition, despite the precise nature of the stimulation, it is still possible that multiple structures were acting in unison to produce the movements. For example, the current delivered by the micro-electrode may have, in some cases, spread to and activated nearby nerves that innervated muscles other than the target muscle. To limit this possibility, we used the lowest stimulus current that provided a clearly visible motor response, but which appeared to activate the muscle in isolation. Because we are unable to determine the precise location of muscles and nerves under the skin, however, we cannot ensure that in all cases only the target muscle was stimulated. How muscles work together to produce the many expressions of the face is unanswered and extremely important to fully understand the nature of universal facial expression production. Further studies are clearly needed to build on this initial work. The contribution of the current study is to demonstrate that base units of movements can be stimulated (from an understanding of the musculature) that correspond with FACS.

It has been suggested (e.g., Schmidt & Cohn, 2001) that the degree of individual variation of facial muscle structure and configuration found within human populations makes it unlikely that individual muscle movements are linked to specific surface movement. If universal facial expressions can exist without uniform muscle structure, then expressions may be produced by flexible operation of different muscles. However, the particular muscles that have been found to vary most between individuals may not feature in common expressions. For example, the midfacial muscles most instrumental in universal expression production (zygomatic major, levator labii superioris, levator labii superioris alaeque nasi) were found in 100% of individuals examined in one study (Pessa et al., 1998), and 94–98% of individuals examined in another (Sato, 1968). Moreover, the muscles that were found to have the greatest variation (risorius, zygomatic minor) are not common in emotional configurations (2 of 22 prototypes in total Ekman et al., 2002b). It is worthy of note, however, that larger scale surveys are needed to form a wider picture of universal facial muscle variation.

The chimpanzee and human face display a high degree of similarity in terms of muscle movement, but some differences are worthy of note. The upper face of humans appears more specialized for eyebrow movement than in the chimpanzee perhaps due to the increased signal value of the eyebrows (which have retained hair covering on a relatively hairless face). Notably, we did not find evidence of musculature capable of drawing the brows together (knitting/frowning/gathering) in the chimpanzee, although we were able to stimulate brow elevation and depression. It is possible that more than one muscle may need to contract simultaneously to produce this knitting/frowning movement, but we were able to stimulate these muscles individually in humans. Most muscle movements of the lower face were found to be similar between humans and chimpanzees, but qualitative appearance on contraction differed due to additional cheek fat in humans and the prognathism of the chimpanzee face; many lower face movements in humans change appearance of the cheeks and associated furrows and wrinkles.

Lastly, of considerable significance is the finding that the zygomatic major (lip corner puller, AU12; contributes to smile expression in humans) functions similarly to elevate the lip corners in chimpanzees. As no other muscles were demonstrated to have similar function, it is reasonable to conclude that zygomatic major is contracting during the silent bared-teeth display (SBT), in which the lip corners are retracted and elevated (van Hooff, 1973; Parr et al., 2005; Waller & Dunbar, 2005). This suggestion has long been the subject of debate, as the chimpanzee SBT is thought to be homologous with the human smile (van Hooff, 1972). Further studies are needed to identify similarities (and perhaps homologues) with human expressions. In sum, the facial musculature of chimpanzees and humans share many of the same basic

structures, both morphologically and functionally, and, given the close phylogenetic relationship between these two species and common need for socially communicative tools, it is likely that further investigation will reveal similarity in expression configurations as well as the component movements demonstrated here.

Duchenne aimed to create emotional scenes on the human face, assuming that there was a direct relationship between emotion and specific muscle movements. Hence, he labeled the structures with emotional terms ('muscle of joy' etc.). The same assumption has not been made here. The goal was to record muscle movements of the face to facilitate observational methods, and thus stimulate further investigation of how and why faces communicate information. FACS (and the developing ChimpFACS: Vick et al., in press) are objective tools for the measurement of facial movement, and neither system is premised on a particular theoretical perspective.

Conclusions

Duchenne (1862/1990) added to the anatomical knowledge of human facial muscles by defining them functionally and, in so doing, assigned morphological limits to the sheets of facial musculature (Hueston & Cuthbertson, 1978). Here, we have replicated this pioneering work through intramuscular electrical stimulation and expanded the paradigm to another species by locating and electrically stimulated individual muscles in the chimpanzee. The muscle comparison presented here is an essential platform from which to identify and describe movements in the chimpanzee face and to determine the muscular components of facial expression in chimpanzees. Moreover, this approach could be useful if extended to other related species, thus aiding the assessment of continuity and homology of facial displays across primate species. A system built on this information should facilitate development of a common language to record and analyze facial displays within and between species, at the levels of both appearance and underlying musculature. The human FACS has provided such a language with which to observe, record, and analyze human facial expression, and now we have the data to expand this paradigm to another species.

Acknowledgments

This research was supported in part by grant RR-00165 from NIH/NCRR to the Yerkes National Primate Research Center, and NIH R01-MH068791 (to LAP), a Research Interchange grant from The Leverhulme Trust (to KAB) and grant NS-39489 from NIH/NINDS (to AJF) The Yerkes National Primate Research Center is accredited by the American Association for Accreditation of Laboratory Animal Care. We would like to thank the Yerkes Veterinary staff and Lori Panu for their assistance during the procedure. Marc Mehu (MM) at The University of Liverpool provided FACS coding assistance for which we are very grateful. Thanks are also extended to Paul Ekman, Jan van Hooff, Alan Costall and Emily Bethell for helpful comments and to Chester Zoological Gardens (United Kingdom) for allowing us to collect and use images of their chimpanzees, and the Living Links Center, Emory University. Four anonymous reviewers provided constructive feedback and many useful comments.

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Appendix

Glossary of Anatomical Terms

<i>Anterior</i>	At a position towards the front of another structure
<i>Fascia</i>	Fibrous tissue
<i>Glabella</i>	Space between the eyebrows

<i>Inferior</i>	At a position below another structure
<i>Infraorbital furrow</i>	Furrow below eye, from inner eye corner to cheekbone. See FACS
<i>Infraorbital triangle</i>	Area above nasolabial furrow and below infraorbital furrow. See FACS
<i>Lateral</i>	At a position farther from the midline of the body than another structure
<i>Mandible</i>	Lower jaw bone
<i>Maxilla</i>	Upper jaw bone
<i>Medial</i>	At a position closer to the midline of the body than another structure
<i>Modiolus</i>	Muscular node at the corner of the mouth
<i>Nasolabial furrow</i>	Furrow from nostril corner to its termination above, at or below the mouth corner. See FACS
<i>Nuchal</i>	Relating to the back of the neck
<i>Posterior</i>	At a position behind (more dorsal than) another structure
<i>Superciliary arch</i>	Eyebrow
<i>Superior</i>	At a position above another structure
<i>Zygomatic arch</i>	Cheekbone

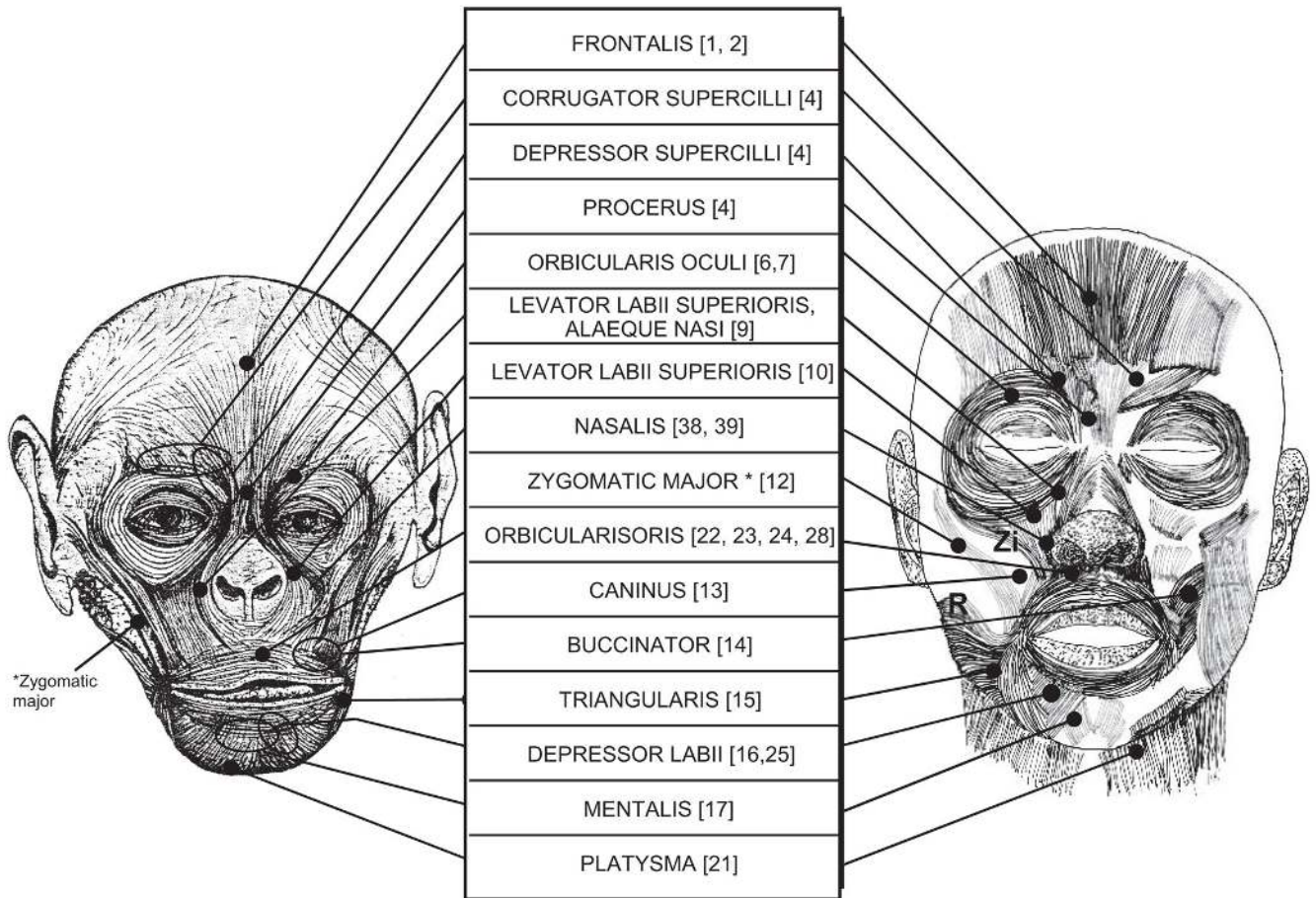


Figure 1. Comparison of the location, structure and relative size of facial muscles in human and chimpanzee. Numbers shown are human FACS action units (Ekman et al., 2002a). Where the specific muscle is not shown, the general area is circled. Muscles not shown in the central table reported only in human, but see Burrows, Waller, Parr and Bonar (2006) (Zi = Zygomatic Minor, R = Risorius). Human diagram adapted from Hager (2000) and chimpanzee dissection diagram adapted from Pellatt (1979b). All images used with permission.

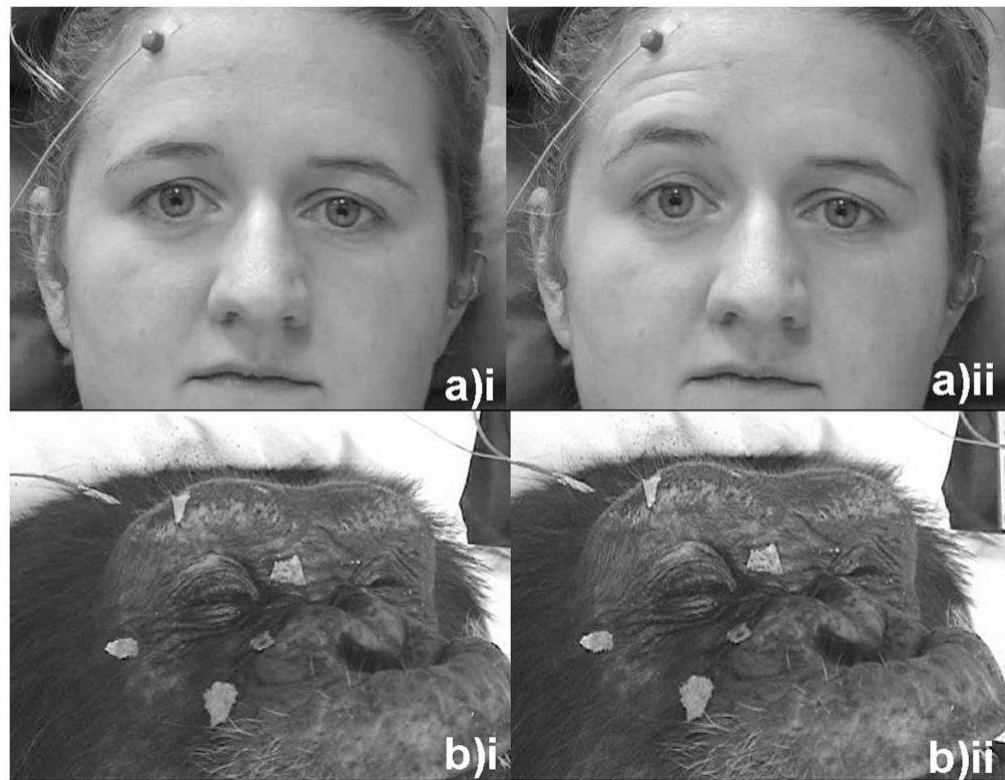


Figure 2. Intramuscular electrical stimulation of lateral frontalis in human (a) and chimpanzee (b), showing muscle at rest (i) and appearance change as muscle contracts on stimulation (ii).



Figure 3. Intramuscular electrical stimulation of the facial muscles involved in FACS AU4 (brow lowerer) in humans—corrugator supercilli (a), procerus (b), and depressor supercilli (c). Muscle is shown at rest (i) and during stimulation (ii).



Figure 4. Intramuscular electrical stimulation of the facial muscles described by Duchenne as the muscles of joy and benevolence: Zygomatic major in human (a) and chimpanzee (b) and orbicularis oculi in human (c) and chimpanzee (d). Muscle is shown at rest (i) and during stimulation (ii).



Figure 5. Intramuscular electrical stimulation of levator labii superioris alaeque nasi in human (a) and chimpanzee (b). Muscle is shown at rest (i) and during stimulation (ii).

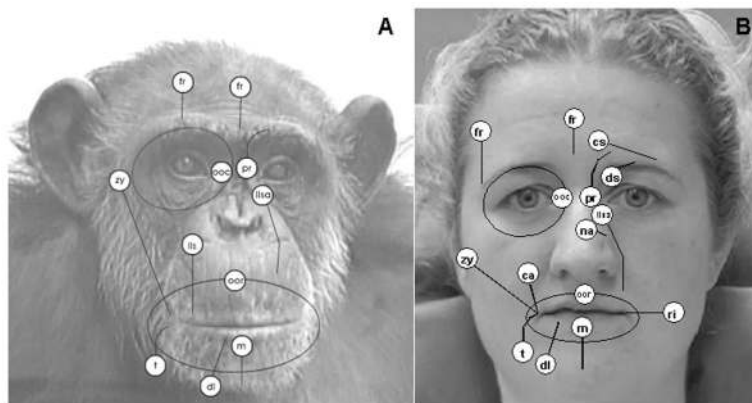


Figure 6.

Direction of movement during intramuscular electrical stimulation of facial muscles in the chimpanzee (A) and human (B). White circles correspond to approximate muscle origins (excepting orbital muscles) and black lines show estimated length/orbit of the muscle. Contraction resulted in movement toward the origin (orbital muscles reduced aperture of orbit). Labels: fr = frontalis (medial and lateral portions), pr = procerus, cs = corrugator supercilli, ds = depressor supercilli, ooc = orbicularis oculi, ilsa = levator labii superioris alaeque nasi, ils = levator labii superioris, na = nasalis, zy = zygomatic major, ca = caninus, ri = risorius, oor = orbicularis oris, t = triangularis, dl = depressor labii, m = mentalis. Platysma action is not shown due to the angle of the image. Chimpanzee image from Yerkes Primate Center, used with permission.

Table 1

Function of the Facial Muscles of Humans According to Duchenne, FACS, and Current Study

Muscle	Duchenne label	FACS AU	Function on stimulation (FACS AU)	FACS Coding agreement
Frontalis, pars medialis	—	AU1 (inner brow raiser)	AU1	3/3
Frontalis, pars lateralis	Muscle of attention/surprise	AU2 (outer brow raiser)	AU2	3/3
Depressor supercilli	—	AU42 (inner brow lowerer)	AU42	3/3
Procerus	Muscle of aggression	AU41 (glabella lowerer)	AU41	3/3
Corrugator supercilli	Muscle of pain	AU44 (eyebrow gatherer)	AU1 3 AU4	3/3
Zygomatic major	Muscle of joy and benevolence	AU12 (lip corner puller)	AU12	3/3
Orbicularis oculi, pars orbitalis	Muscle of joy and benevolence	AU6 (cheek raiser)	AU6	2/3*
Nasalis	Muscle of lasciviousness	—	Wrinkles skin on bridge of nose (part of AU9)	3/3
Triangularis	Muscle of sadness	AU15 (lip corner depressor)	AU15	3/3
Zygomatic minor	Muscle of weeping and whimpering	AU11 (nasolabial furrow deepener)	Not stimulated	—
Levator labii superioris	Muscle of weeping and whimpering	AU10 (upper lip raiser)	Not stimulated	—
Levator labii superioris alaeque nasi	Muscle of weeping and whimpering	AU9 (nose wrinkler)	AU9	3/3
Caninus	—	AU13 (cheek puffer)	AU13	3/3
Risorius	—	AU20 (lip stretch)	AU20	2/3*
Mentalis	—	AU17 (chin raiser)	AU17	3/3
Orbicularis oris	—	AU22 (lip funneler)	AU23 only	3/3
		AU23 (lip tightener)	(Other FACS AUs not stimulated)	
		AU24 (lip presser)		
Buccinator	—	AU14 (dimpler)	Not stimulated	—
Depressor labii	—	AU16 (lower lip depressor)	AU16	3/3

Note. FACS = Facial Action Coding System; AU = action units.

* See text for details of coding disagreement.

Table 2**Observed Function of the Facial Muscles of Humans and Chimpanzees Based on Intramuscular Electrical Stimulation**

Muscle	Stimulated function in human	Stimulated function in chimpanzee
Frontalis, pars medialis	Elevates the medial portion of the brow (AU1: inner brow raiser)	Elevates the medial portion of the brow
Frontalis, pars lateralis	Elevates the lateral portion of the brow (AU2: outer brow raiser)	Elevates mid and lateral portion of the brow
Orbicularis oculi, pars orbitalis	Elevates the infraorbital triangle (cheek) superiorly and medialwards (AU6: cheek raiser)	Inferior portion elevates infraorbital triangle (or equivalent area) superiorly and medialwards. Superior section lowers mid and lateral portion of brows (may be Depressor supercilli, see text)
Orbicularis oculi, pars palpebralis	Not attempted	Not attempted
Corrugator Supercilli	Draws the brow medially and superiorly (AU1 3 AU4: inner brow raiser 3 brow lowerer)	Area explored in detail, but muscle not located
Procerus	Depresses the medial portion of the brow and protrudes the skin of the glabella (part of AU4: brow lowerer)	Depresses the medial portion of the brow
Depressor supercilli	Depresses the medial portion of the brow (part of AU4: brow lowerer)	Area explored in detail, but muscle not located
Zygomatic major	Elevates lip corners superiorly and draws lip corners laterally, increasing angle of the mouth (AU12: lip corner puller)	Elevates lip corners superiorly and draws lip corners laterally, increasing angle of the mouth
Zygomatic minor	Area explored in detail, but muscle not located	Area explored in detail, but muscle not located
Platysma	Not attempted	Elevates the skin of the nuchal region
Caninus	Elevates lip corners sharply (AU13: cheek puffer)	Area explored in detail, but muscle not located
Risorius	Draws lip corners laterally (AU20: lip stretcher)	Area explored, but muscle not located
Levator labii superioris alaeque nasi	Wrinkles the skin alongside the nose (AU9: nose wrinkler)	Wrinkles the skin surrounding the nose
Levator labii superioris	Area explored in detail, but muscle not located	Elevates the upper lip
Nasalis	Wrinkles skin on bridge of nose (part of AU9)	Area explored, but muscle not located
Triangularis	Depresses lip corners (AU15: lip corner depressor)	Depresses lip corners
Mentalis	Pushes skin of the chin boss superiorly (AU17: chin raiser)	Pushes skin of the chin area superiorly
Buccinator	Area explored in detail, but muscle not located	Area explored, but muscle not located
Depressor labii	Depresses medial portion of lower lip (AU16: lower lip depressor)	Depresses medial portion of lower lip
Orbicularis oris	Tightens lip margins (AU23: lip tightener). Other FACS movements not stimulated (AU22: lip funneler, AU24: lip presser; AU28: lip suck)	Reduces lip aperture and funnels/protrudes lips

Note. AU = action units; FACS = Facial Action Coding System.

Table 3

Comparison of Human Facial Muscles Examined by Duchenne, FACS, and Current Intramuscular Electrical Stimulation Study

Facial muscle	Stimulated by Duchenne	Described in FACS	Stimulated in current study
Frontalis, pars medialis		✓	✓(3/5)
Frontalis, pars lateralis	✓	✓	✓(6/6)
Depressor supercilli		✓	✓(5/5)
Procerus	✓	✓	✓(5/5)
Corrugator supercilli	✓	✓	✓(4/4)
Zygomatic major	✓	✓	✓(4/4)
Orbicularis oculi, pars orbitalis	✓	✓	✓(2/3)
Orbicularis oculi, pars palebralis		✓	
Nasalis	✓		✓(1/1)
Triangularis	✓	✓	✓(2/2)
Zygomatic minor	✓	✓	
Levator labii superioris		✓	
Levator labii superioris alaeque nasi	✓	✓	✓(1/2)
Platysma	✓	✓	
Caninus		✓	✓(2/2)
Risorius		✓	✓(1/1)
Mentalis		✓	✓(2/2)
Orbicularis oris		✓	✓(1/1)
Buccinator		✓	
Depressor labii		✓	✓(2/2)
Number of muscles (total)	10/20	19/20	15/20

Note. Proportion of participants successfully stimulated shown in last column. FACS = Facial Action Coding System.