Exp Brain Res (2006) 173: 153–158
DOI 10.1007/s00221-006-0375-0

RESEARCH ARTICLE

Susan E. Coulson · Nicholas J. O'Dwyer
Roger D. Adams · Glen R. Croxson

Bilateral conjugacy of movement initiation is retained at the eye but not at the mouth following long-term unilateral facial nerve palsy

Received: 26 August 2005 / Accepted: 17 January 2006 / Published online: 8 March 2006

Abstract Voluntary eyelid closure and smiling were studied in 11 normal subjects and 11 patients with long-term unilateral facial nerve palsy (FNP). The conjugacy of eyelid movements shown previously for blinks was maintained for voluntary eye closures in normal subjects, with movement onset being synchronous in both eyes. Bilateral onset synchrony of the sides of the mouth was also observed in smiling movements in normal subjects. In FNP patients, initiation of movement of the paretic and non-paretic eyelids was also synchronous, but markedly delayed relative to normal (by 136 ms = 32%). The initiation of bilateral movements at the mouth was similarly delayed, but in contrast to the eyes, it was not synchronous. Central neural processing in the FNP subjects was normal, however, since unilateral movements at the mouth were not delayed. The delays therefore point to considerable additional information processing needed for initiating bilateral facial movements after FNP. The maintenance of bilateral onset synchrony in eyelid closure and its loss in smiling following FNP is an important difference in the neural control of these facial regions. Bilateral conjugacy of eyelid movements is probably crucial for coordinating visual input and was achieved apparently without conscious effort on the part of the patients. Bilateral conjugacy of movements at the sides of the mouth may be less critical for normal function, although patients would very much like to achieve it in order to improve the appearance of their smile. Since the everyday frequency of eyelid movements is considerably greater than that of smiling, it is possible that the preserved eyelid conjugacy in these patients with long-term FNP is merely a product of greater experience. However, if synchrony of movement onset is found to be preserved in patients with acute FNP, then it would suggest that eyelid conjugacy has a privileged status in the neural organisation of the face.

Keywords Facial paralysis · Facial expression · Reaction time · Neuronal plasticity · Eyelids

S. E. Coulson (✉) · R. D. Adams
School of Physiotherapy, The University of Sydney,
PO Box 170, 1825 Lidcombe, NSW, Australia
E-mail: s.coulson@fhs.usyd.edu.au
Tel.: +61-2-93519416
Fax: +61-2-93519278

N. J. O'Dwyer
School of Exercise and Sport Science,
The University of Sydney, Sydney, Australia

G. R. Croxson
VMO, Royal Prince Alfred Hospital, Sydney, Australia

Introduction

The face plays a major role in interpersonal communication. In patients with unilateral facial nerve palsy (FNP), reduced control of facial movements, such as marked asymmetry of smiling, can lead to difficulties in the expression of emotion that adversely affect quality of life (Coulson et al. 2004). The eyes are also affected and paresis of the eyelid on the affected side can result in inadequate corneal coverage. Problems arising thereafter can range from slight ocular irritation to corneal ulceration, perforation and blindness (May and Schaitkin 2000). Such difficulties at the eyes and mouth are most frequently the reason that patients present for facial rehabilitation following FNP and the present findings emerged from a clinical trial of such rehabilitation. Voluntary eye closure and smiling were studied. Previous research studies examining eyelid movements following FNP have focused on blinks. There has been little study of voluntary reaction times (RTs) for eyelid movements or smiling following FNP.

Normal eyelid movements are highly conjugate in nature. During blinks the movements of both eyelids are tightly controlled with respect to their onset time, offset time, amplitude, peak velocity and duration (Stava et al. 1994). Without such closely conjugate movements, the evolutionary advantage of binocular summation and fusion, and of the retrieval of depth information from binocular disparity (McNeill 2003; Barton 2004), would be significantly reduced. Other factors in evolution favouring conjugacy in eyelid movements may have been the need to mediate the brief suppression of vision in both eyes during blinks and saccades (Chekaluk and Llewellyn 1992), and, because of their proximity, the need for both eyes to be simultaneously protected when physically threatened. Eyelid movements are also highly adaptive in that the nervous system can modify the inherent relation between the magnitude of a blink-evoking stimulus and the magnitude of the reflex response in order to compensate for internally or externally imposed perturbations (Evinger and Manning 1988). Modification of neurons in longer latency, polysynaptic reflex pathways appears to underlie these adaptive processes.

Adaptive changes in control of blinks are of particular interest in patients with FNP. Following damage to the facial nerve, there is a reduction in the magnitude of orbicularis oculi contraction and a decrease in blink amplitude, with slowing of the peak closing velocity, producing a lag of the paretic eyelid (Sibony et al. 1991; Huffman et al. 1996). However, kinematic changes occur bilaterally, so that the non-paretic eyelid is also affected. Bilateral increases in main sequence slope (the linear relationship of blink velocity vs. amplitude) suggest that the drive to both orbicularis oculi muscles is increased to compensate for weakening of the affected eyelid (Sibony et al. 1991; Huffman et al. 1996). These bilateral changes are thought to represent an expression of Hering's law of equal innervation (Hering 1942) as it pertains to orbicularis oculi (Sibony et al. 1991) and levator palpebrae superioris (Gay et al. 1967). Importantly, compensatory changes following FNP are correlated with the level of paresis and are reversed with recovery of strength (Huffman et al. 1996; Syed et al. 1999), suggesting the continuous operation of adaptive control systems that adjust motor output to muscle response. The neural substrate for this adaptation is thought to be altered synaptic efficacy of interneurons in brainstem pathways (Nacimiento et al. 1992; Huffman et al. 1996; Syed et al. 1999).

The present study reports data from digital video recordings made in a clinical setting (Coulson et al. 2006a, b), where the magnitude of most effects observed greatly exceeded the temporal resolution of the video measurements (40 ms). The RTs for voluntary initiation of bilateral eyelid and mouth movements were found to be markedly delayed in FNP patients relative to normal subjects. The preparation of these voluntary movements therefore required time-consuming processing, which points to extensive central neural re-organisation following the peripheral lesion. Whereas, the onset of movement was ostensibly concurrent on the paretic and non-paretic sides at the eyes, however, this was not so at the mouth. Consequently, conjugacy was found to be preserved in the initiation of eyelid but not mouth movements, showing that the imperatives of neural re-organisation differ significantly for these two areas of the face.

Method

Eleven subjects with FNP greater than 1 year post onset (mean 8.5 years) and 11 age- and sex-matched controls (mean age 48.5 years, 3 males, 8 females) participated in the study. The aetiologies of FNP were Bell's Palsy (2), surgical removal of vestibular schwannoma (8) and facial nerve neuroma (1). The most widely used system for grading patients after facial nerve paralysis is the House Brackmann Facial Grading System, which categorises patients into six grades according to the severity of facial deficit (House and Brackmann 1985). The House Brackmann grades for the subjects in the present study were Grade II (one patient), Grade III (five patients) and Grade IV (five patients). These grades represent a range from mild to moderately severe dysfunction. All procedures were approved by The University of Sydney Human Ethics Committee and conformed to the Declaration of Helsinki.

The focus of the clinical trial for which these data were collected was the asymmetry of smiling following FNP, since this asymmetry was of particular concern to the patients. Eyelid movements were included for comparison with movements at the mouth. Three movements were studied: voluntary bilateral eye closure, a bilateral smile and a unilateral smile. The smile was naturally bilateral in the control subjects, but it was asymmetrical and largely unilateral in FNP subjects, due to their unilateral paresis. Therefore, in order to obtain both a bilateral and unilateral smile from each group, the FNP subjects also produced an attempt at a symmetrical, bilateral smile; while for comparison, the control subjects also produced an asymmetrical, unilateral smile. The bilateral smile by the FNP subjects constituted baseline performance of a symmetrical smile which was to be improved in the clinical trial. Standard instructions for clinical assessment were employed for eyelid closure: "close your eyes, do not close them tightly, simply close them"; and for the smile: "smile". The instructions for the bilateral smile in the FNP subjects were: "smile evenly on both sides of your mouth"; while the instructions for the unilateral smile in the control subjects were: "smile on one side of your mouth only". The side chosen for each control subject was the same as the affected side of the FNP subject with whom they were matched.

A digital video camera (Canon MVX150i) was mounted on a tripod, with a panel containing a red, a green and a blue light attached near the lens. The subjects were seated facing the camera and next to a mirror, so that the coloured lights were reflected and recorded on the videotape. Each of the facial movements was allocated to a light colour, the allocation being randomly-determined and also randomised across the subjects, who had been screened for compromised colour vision prior to the study. The subjects were then asked to immediately produce the designated facial movement in response to illumination of the lights. The movements were thus produced as a three-choice RT task in both groups. The order of movements was randomised for each subject. Following practice trials with each light colour/movement combination, five trials of each movement were collected. To test for repeatability of the measures, data collection was repeated under identical conditions 2 weeks after the first session.

Data were captured at 25 frames per second. The magnitude of the most important experimental effects observed was several multiples of the resulting 40 ms temporal resolution. The hardware (Matrox Millennium P650 Display adapter, Matrox RT.X100 Xtreme video capture and edit card) and software (Adobe Premiere Pro v7.0 video capture and edit software) for the digital video analysis provided clear and stable images without blurring, the ability to freeze a single frame for indefinite intervals, and simple forward and backward frame transitions. RTs from onset of coloured light to onset of movement were measured separately for each eyelid and each corner of the mouth. The onset of movement was defined as the first video frame in which a change from the previous frame was detected at each location. Movement time (MT) from onset to completion was also measured for the eyelids only, in order to document the lag of the paretic eyelid. The completion of movement was defined as the first video frame in which no change from the previous frame was detected. All measurements were made by a single experimenter (SEC).

Analyses of variance (ANOVAs), with one group factor and four repeated measures factors, were employed to compare the RTs for eye closure and smiles and MTs for eye closure between the FNP and control groups. The respective factors in the 2×3×2×2×5 ANOVA of RTs were group (control, FNP), movement task (bilateral eye closure, bilateral smile, unilateral smile), side (left and right in control group; non-paretic and paretic in FNP group), data collection session (1, 2) and trial (1, 2, 3, 4, 5). Since no significant differences were found between sessions or trials, only the results for groups, movement tasks and sides are presented. Between or within subjects contrasts were employed as appropriate to assess differences between levels of individual factors.

Results

Comparison between the two eyes in each subject showed no differences in RTs in either group, within the temporal resolution of measurement (Fig. 1: bilateral eye closure). In fact, for both eyes in both groups, the initiation of eyelid movement always occurred in the same video frame, with not a single exception out of 110 trials per group. However, the RT was prolonged in the FNP group by 136 ms ($F_{1,20} = 18.1$, $P < 0.001$)—a 32% increase.

The initiation of movement at both sides of the mouth in the bilateral smile also always occurred in the same video frame in control subjects, but not in the FNP subjects. The RT was again prolonged in FNP subjects ($F_{1,20} = 10.2$, $P < 0.01$), by 165 ms on the non-paretic

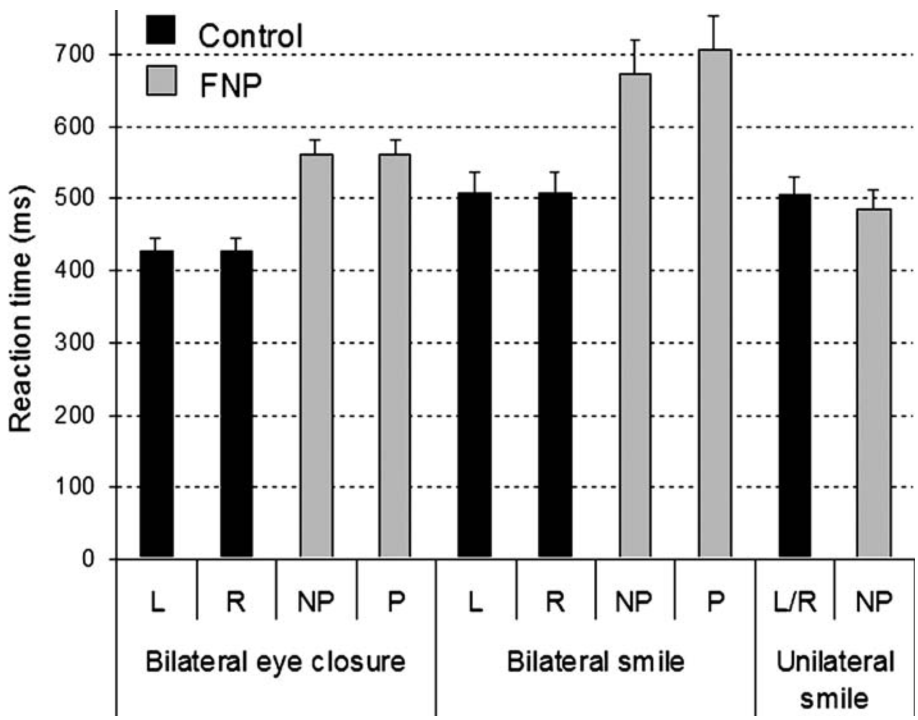

Fig. 1 Mean RTs (±SE) for all facial movements in both groups. *L* left, *R* right, *NP* non-paretic side, *P* paretic side

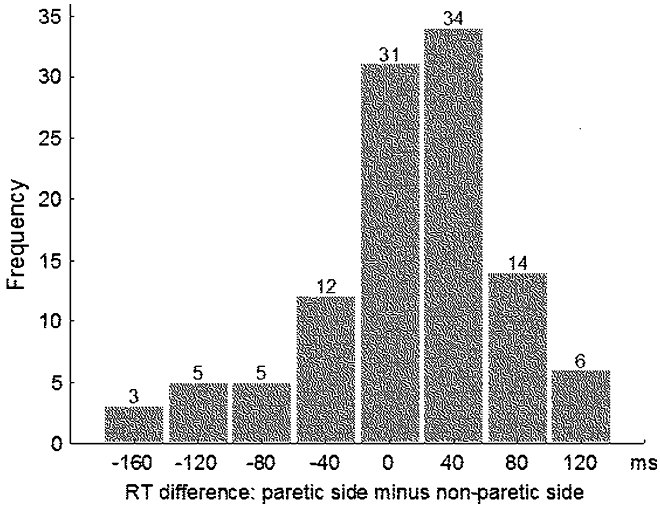

Fig. 2 Distribution of RT differences between paretic and non-paretic side during a bilateral smile in FNP subjects. A positive difference means a longer RT on the paretic side

side and by 199 ms on the paretic side—a mean 36% increase (Fig. 1: bilateral smile).

The small difference (mean 34 ms) between the sides of the mouth in initiation of the bilateral smile in the FNP subjects ($F_{1,10}=13.2$, $P<0.01$) was less than one video frame on average (Fig. 1). The distribution of these differences in RT between the paretic and non-paretic sides was examined (11 subjects×2 data collection sessions×5 trials = 110 trials). The RTs were longer on the paretic side in 54 trials, about the same (i.e., in the same video frame) in 31 trials, and shorter on the paretic side in only 25 trials (Fig. 2). Thus, the non-paretic side generally led in attempts to produce symmetrical onsets.

The initiation of a unilateral smile revealed no difference in RTs between control and FNP subjects ($F_{1,20}=0.33$, $P=0.57$). This confirms that central neural processing was unaffected in the FNP subjects (Fig. 1: unilateral smile).

As can be seen in Fig. 1, in the control group, the RT was shorter at the eyes (mean 425 ms) than for bilateral or unilateral smiles ($F_{1,10}=13.4$, $P<0.01$), which had similar latencies (means 507 and 504 ms). In the FNP group, the RT was also shorter at the eyes than for the bilateral smile (means 561 vs. 689 ms, respectively; $F_{1,10}=9.5$, $P<0.01$); but in contrast to the control group, the RT was longer at the eyes than for the unilateral smile (means 561 vs. 483 ms, respectively; $F_{1,10}=10.6$, $P<0.01$).

Lastly, examination of eyelid MTs revealed no differences between eyes in the control group. In the FNP group, however, downward MT of the eyelid on the paretic side took over four times longer than the non-paretic side (means 815 vs. 197 ms; $F_{1,10}=61.2$, $P<0.0001$).

Discussion

Markedly delayed but synchronous initiation of movement of both the paretic and non-paretic eyelids was observed in a group of patients with long-term FNP. In contrast, the initiation of bilateral movements at the mouth was not synchronous across sides, although the movements were similarly delayed. Bilateral conjugacy of eyelid movements is likely to be crucial for coordinating visual input, but may be less critical for function at the mouth, although patients would very much like to achieve it in order to improve the appearance of their smile. The patients in this study were entering treatment to gain a more symmetrical smile, but they had received no treatment to achieve eyelid synchrony.

Most research on eyelid movements has focused on blinks. There have been few studies of the less automatic, more consciously controlled, voluntary movements of the eyelids and apparently no reports of voluntary RTs for eyelid movements. In normal subjects in this study, it was found that the conjugacy of eyelid movements shown previously for blinks (Stava et al. 1994) and lid saccades (Wouters et al. 1995) is maintained in voluntary eyelid movements. Within the temporal resolution of measurement, both the onset times and duration of eyelid movements were found to be synchronous in both eyes.

Previous studies of eyelid movements following FNP also have focused on blinks. Even in severely affected cases, conjugacy was found to be preserved in the initiation of spontaneous and voluntary blinks (Huffman et al. 1996). Both closing and opening phases began concurrently, although the closing phase terminated earlier on the paretic side. In our patient group, while voluntary closure was found to begin concurrently in both eyelids, we had not set out to collect data on blinks. Therefore, we re-examined the video tape recordings and identified ten spontaneous blinks during the data collection sessions in every FNP and control subject. In every case without exception, the onset of movement of both eyelids occurred in the same video frame. Therefore, the conjugacy in initiation of movement appeared to apply equally to spontaneous blinks and voluntary eyelid movements. The duration of voluntary eyelid movement, however, continued for much longer on the paretic than the non-paretic side, as the patients strove to complete the closure. Hence, conjugacy was preserved in the onset but clearly not in the duration of eyelid closure in FNP patients.

A major finding in the present study was the one-third increase in the time to initiation of bilateral eyelid and mouth movements in FNP patients. The non-paretic and paretic eyelids were equally delayed (136 ms), thus reinforcing the inherent conjugacy of the movements; whereas the paretic side of the mouth (199 ms) was more delayed than the non-paretic (165 ms), thus reflecting the failure of conjugacy of these movements. There was no delay for the same subjects when initiating unilateral movements at the mouth. Not surprisingly, therefore, it was only with bilateral movements that the difficulty arose in these patients. The magnitude of these RT delays for bilateral movements, however, is not readily explained. The mean RTs recorded in the control group were 425 ms for eye closure and 507 ms for the bilateral smile. These are typical of values expected for a three-choice RT task (Hyman 1953) in accord with Hick's (1952) law, which states that the RT increases with the number of stimulus-response alternatives. The additional delays in the FNP group would themselves constitute fast, simple RTs (i.e., a RT to only one stimulus-response alternative). Hence, many synapses and substantial information processing would be interposed in that interval. It is not clear why this amount of additional processing is required.

Since synchronous bilateral movements are more difficult to accomplish following FNP, an increase in the RT could be expected because more difficult movements entail additional information processing and hence require more time for their preparation (Henry and Rogers 1960). It is unlikely, however, that the prolonged RTs observed are under deliberate, conscious control. It is well established that a motor response and a conscious response are two very different things (Jensen 1979; Castiello et al. 1991). Jensen (1979) asked subjects to attempt to gradually lengthen their RT and found that they could not do so. Instead their RTs jumped from minimum values (~250 ms in his study) to much higher values, in the range from 500 to 1,000 ms. Therefore, it does not seem plausible that, following FNP, patients are consciously controlling the response onsets of the paretic and non-paretic side to ensure that they occur synchronously.

It is more likely that the movements of both sides are controlled as a synergy or coordinative structure (Turvey 1977). Bimanual movements also can be initiated synchronously and this synchrony is thought to be produced via central programming of functional groupings of muscles (coordinative structures) that are constrained to act as a single unit (Kelso et al. 1979). Evidence has been presented that homologous lower limb joints may also be controlled by common motor programs (Gauffin et al. 1988; Tropp et al. 1995; Waddington and Adams 1999). If the movements of both sides are programmed together, then the additional RT delay could be due to preparation for the increased MT. In the case of the eyelids, for example, the MT of 815 ms for eyelid closure on the paretic side was markedly increased compared with 169 ms in the control group. RTs are known to be greatly increased for movements of longer duration (Klapp and Erwin 1976), due to the time necessary to prepare the movement (Schmidt and Lee 1999).

The additional preparation time apparently required to achieve bilateral synchrony of movement may arise from the central neural reorganisation that occurs following FNP, which is likely to depend on cortical as well as brainstem pathways. Synaptic reorganisation of the facial nucleus leading to functional changes in crossed trigemino-facial brainstem reflex pathways has been implicated in the central reorganisation of reflex blinks following FNP (Nacimiento et al. 1992), while the cerebellum has been implicated in adaptive gain changes of eyelid movements (Evinger et al. 1989). Unilateral facial nerve transection in adult rats has been shown to produce representational changes in ipsilateral (Toldi et al. 1999) as well as contralateral motor cortex (Toldi et al. 1996). Therefore, functional reorganisation of voluntary facial movements following FNP is likely to involve changes in synaptic effectiveness and representational maps (Buonomano and Merzenich 1998) not only in brainstem pathways but also in the motor cortex bilaterally.

The maintenance of bilateral onset synchrony in eyelid closure and its loss in smiling, despite similarly delayed movement onsets relative to normal (Fig. 1), is an important difference in the neural control of these two facial regions. The conjugacy in the initiation of eyelid movements was maintained apparently without conscious effort on the part of the patients. In contrast, there was a struggle to achieve bilateral conjugacy during smiling, as evidenced by the differences between RTs for both sides of the mouth (Fig. 2). In no subject were these inter-side differences consistent across trials. However, since the average frequency of normal blinking is ~1,000 h^{-1} (Huffman et al. 1996), these patients with long-term FNP would have experienced considerably more 'trials' of eyelid movements than of smiling. Consequently, it will be of interest to determine (with finer temporal resolution of measurement) whether such conjugacy is also present in patients with acute FNP. If eyelid conjugacy takes time to develop following FNP, then it might be considered a routine product of learning and adaptation. However, if eyelid conjugacy is preserved early following FNP, then it suggests that it has a privileged status in the neural organisation of the face. This would be further evidence of the highly adaptive nature of eyelid movements and prompt the question of the neural locus of the adaptation.

References

Barton RA (2004) Binocularity and brain evolution in primates. Proc Natl Acad Sci USA 101(27):10113–10115

Buonomano DV, Merzenich MM (1998) Cortical plasticity: from synapses to maps. Annu Rev Neurosci 21:149–186

Castiello U, Paulignan Y, Jeannerod M (1991) Temporal dissociation of motor responses and subjective awareness. Brain 114:2639–2655

Chekaluk E, Llewellyn K (1992) Saccadic suppression: a functional viewpoint. In: Chekaluk E, Llewellyn K (eds) The role of eye movements in perceptual processes. Advances in Psychology, 88. Oxford, North-Holland, pp. 171–198

Coulson SE, O'Dwyer NJ, Adams RD, Croxson GR (2004) Expression of emotion and quality of life after facial nerve paralysis. Otol Neurotol 25:1014–1019

Coulson SE, Adams R, O'Dwyer N, Croxson GR (2006a) Physiotherapy rehabilitation of the smile after long term facial nerve palsy using video self-modeling and implementation intentions. Otolaryngol Head Neck Surg 134:48–55

Coulson SE, Adams R, O'Dwyer N, Croxson GR (2006b) Use of video self-modeling and implementation intentions following facial nerve paralysis. Int J Ther Rehabil 13(1) (in press)

Evinger C, Manning KA (1988) A model system for motor learning: adaptive gain control of the blink reflex. Exp Brain Res 70:527–538

Evinger C, Pellegrini JJ, Manning KA (1989) Adaptive gain modification of the blink reflex. Ann NY Acad Sci 563:87–100

Gauffin H, Tropp H, Odenrick P (1988) Effect of ankle disc training on postural control in patients with functional instability of the ankle joint. Int J Sports Med 9:141–144

Gay A, Salmon ML, Windsor CE (1967) Hering's Law, the levators and their relationship in disease states. Arch Opthalmol 77:157–161

Henry F, Rogers DE (1960) Increased response latency for complicated movements and the 'memory drum' theory of neuromuscular reaction. Res Q 31:448–458

Hering E (1942) Spatial sense and movements of the eye. The American Academy of Optometry, Baltimore, pp 152–161

Hick WE (1952) On the rate of gain of information. Q J Exp Psychol 4:11–26

House JW, Brackmann DE (1985) Facial nerve grading system. Otolaryngol Head Neck Surg 93:146–147

Huffman M, Baker RS, Stava MW, Chuke JC, Rouholiman BR, Porter JD (1996) Kinematic analysis of eyelid movements in patients recovering from unilateral facial nerve palsy. Neurology 46:1079–1085

Hyman R (1953) Stimulus information as a determinant of reaction time. J Exp Psychol 45:188–196

Jensen AR (1979) g: Outmoded theory or unconquered frontier? Creat Sci Technol 2:16–29. Cited in Wegner D, The Illusion of Conscious Will, 2002. MIT Press, Cambridge, MA, p 56

Kelso J, Southard DL, Goodman D (1979) On the coordination of two-handed movements. J Exp Psychol Hum Percept Perform 5:229–238

Klapp ST, Erwin CI (1976) Relation between programming time and duration of the response being programmed. J Exp Psychol Hum Percept Perform 2:591–598

May M, Levine R, Bhupendra C, Patel R, Anderson M (2000). Eye reanimation techniques. In: May M, Schaitkin BM (eds) The facial nerve. Theime, New York, pp 677–773

McNeill WH (2003) The biological basis of human history. Perspectives in Biology and Medicine, 2003, The John Hopkins University Press, 46(3):371–382

Nacimiento W, Podoll K, Graeber MB, Topper R, Mobius E, Ostermann H, Noth J, Kreutzberg GW (1992) Contralateral early blink reflex in patients with facial nerve palsy: indication for synaptic reorganization in the facial nucleus during regeration. J Neuro Sci 109:30–35

Schmidt RA, Lee TD (1999) Motor control and learning A. Behavioral emphasis, 3rd edn. Human Kinetics, Champaign, IL

Sibony P, Evinger C, Manning KA (1991) Eyelid movements in facial paralysis. Arch Opthalmol 109:1555–1561

Stava MW, Huffman MD, Baker RS, Epstein AD, Porter JD (1994) Conjugacy of spontaneous blinks in man: eyelid kinematics exhibit bilateral symmetry. Invest Ophthalmol Vis Sci 35:3966–3971

Syed N, Delgado A, Sandbrink F, Schulman AE, Hallett M, Floeter MK (1999) Blink reflex recovery in facial weakness: an electrophysiologic study of adaptive changes. Neurology 52:834–838

Toldi J, Laskawi R, Landgrebe, Wolff JR (1996) Biphasic reorganization of somatotopy in the primary motor cortex follows facial nerve lesions in adult rats. Neurosci Lett 203:179–182

Toldi J, Farkas T, Perge J, Wolff J-R (1999) Facial nerve injury produces a latent somatosensory input through recruitment of the motor cortex in the rat. Neuroreport 10:2143–2147

Tropp H, Odenrick P, Gillquist M (1995) Stabilometry recordings in functional and mechanical instability of the ankle joint. Int J Sports Med 6:180–182

Turvey MT (1977) Preliminaries to a theory of action with reference to vision. In: Shaw R, Bransford J (eds) Perceiving, acting, and knowing. Erlbaum, Hillsdale, NJ, pp 211–265

Waddington G, Adams R (1999) Ability to discriminate movements at the ankle and knee is joint specific. Percept Mot Skills 89:1037–1041

Wouters RJ, van den Bosch WA, Stijnen T, Bubberman AC (1995) Conjugacy of eyelid movements in vertical eye saccades. Invest Ophthalmol Vis Sci 36:2686–2694