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Adam Wittek[a][b] & Janusz Kajzer[c]
[a] Chalmers University of Technology, Sweden
[b] Central Institute for Labour Protection, Poland
[c] Nagoya University, Japan
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Mathematical Modelling of Muscle Effect on the Kinematics of the Head-Neck Complex in a Frontal Car Collision: A Parameter Study

Adam Wittek

Chalmers University of Technology, Sweden
Central Institute for Labour Protection, Poland

Janusz Kajzer

Nagoya University, Japan

A 2-dimensional multibody model of the head-neck complex with muscle elements was developed to estimate the influence of muscles on the kinematics of the head-neck complex in a frontal car collision. With this model the authors evaluated how strongly the calculated influence of muscles depends on 3 important factors: (a) impact severity, (b) reflex time, and (c) parameters that determine characteristics of different components of the muscle model. When muscles were triggered at the beginning of impact, the maximum angle of the head flexion was decreased by the muscles by 40% in a frontal collision with an acceleration of 15 g. The influence of muscles was significant for reflex times lower than 60 (80) ms. The calculated influence of muscles was not sensitive to most parameters of the muscle model.

frontal car collision head-neck complex kinematics muscle effect Hill-type muscle models mathematical modelling

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Correspondence and requests for reprints should be sent to Janusz Kajzer, Department of Mechanical Engineering, Graduate School of Engineering, Nagoya University, Furo-cho, Chikusa-ku, Nagoya, 464-01, Japan. E-mail: <kajzer@mech.nagoya-u.ac.jp>.

1. INTRODUCTION

Muscles are seldom taken into account in the analysis of the biodynamic response of the human body to transient loads associated with car collisions. The question is whether it is always appropriate to disregard muscles in the analysis of injuries that occur at low impact speeds. The answer to this question requires primarily to analyse the degree to which muscles affect kinematics and kinetics of different segments of the human body under transient loads. In this study, the head-neck complex in a frontal impact was selected as an example for the investigation of the muscle effect in a car collision. There are two reasons for this selection. First, frontal car collisions are the most frequent type of car crash. Second, several studies have shown that muscles can significantly affect the kinematics of the head-neck complex when a crash is not so severe.

For instance, Mertz and Patrick (1967, 1971) analysed the biodynamic response of the head-neck complex in rear-end collisions with acceleration up to 6.6 g[1] and speed up to 37 km/h. They found that the maximum head angle was about 50% lower when a participant tensed neck muscles, than when the muscles were relaxed. Indirect evidence to confirm the hypothesis that muscles can significantly influence the flexion/extension angle of the head has been reported by Bosio and Bowman (1986). They identified two modes of the head extension about the occipital condyles in frontal impacts: (a) extension with rebounding after reaching a given peak of extension angle and (b) extension without rebounding after the first peak. The extension without rebounding can be related to significant activity of the neck extensors. The hypothesis that muscle tension can reduce the maximum angle of head flexion can be also confirmed with the results of Wismans, Philippens, Oorschot, Kallieris, and Mattern (1987). They found that in frontal impact with acceleration of 15 g and speed of 50–60 km/h, the peak angle of the head flexion in cadaver tests was greater than the peak angle in volunteer tests. A possible explanation would be that muscle tension restrains the motion of the head of volunteers.

The studies just described have an important limitation; muscle tension was only roughly controlled in all of them. For example, in the experiments by Mertz and Patrick (1967, 1971), a participant was simply

[1] g is the gravity acceleration

asked to relax or to contract muscles. Muscle tension was more accurately controlled in the study by Verriest, Onser, and Viviani (1975), who investigated the response of the head-neck complex of baboons in frontal impacts. Subjects were anesthetised to keep muscles in the relaxed state, and electric stimulation was used to activate muscles. The results of Verriest et al. (1975) indicated that muscle tension can reduce maximum angular acceleration of the head by about 40% in frontal impact with acceleration of 20 g. Measurement of muscle force on humans subjected to transient loads is greatly limited for ethical reasons. An alternative solution is to use mathematical modelling to calculate muscle force.

Muscle force can be predicted with various kinds of mathematical models, which differ in their complexity, for example, phenomenologically-based model by Hill (1938), the cross-bridge model by H. Huxley and Hanson (1954) and A.F. Huxley and Simmons (1971), and the distribution-moment model by Zahalak (1986). The concepts of Hill (1938) make it possible to describe the muscle behaviour in terms of mechanics. For this reason Hill-type models have been widely used in impact biomechanics. For instance, the Hill-type model was used by Pontius and Liu (1976) in their study on the kinematics of the human cervical spine during whiplash, and in the analysis of the muscle effect on the kinematics of the head-neck complex in frontal impacts by Happee and Thunnissen (1994).

The model by Hill (1938) does not have a direct connection with real muscle structure. The structure and parameters of this model can be identified in different ways. The question is how strongly does identification of parameters of the Hill-type model for a given muscle influence the calculation of the muscle effect in a car collision.

Modelling of muscle effect in impacts requires data on the reflex time, that is, the time that is necessary for the nervous system to trigger the muscles. Unfortunately, how the nervous system controls the muscles in impacts remains unclear. So far the stretch and visual reflexes have been the main consideration in the literature (Pontius & Liu, 1976; Happee & Thunnissen, 1994). On the other hand, Szabo and Welcher (1996) suggested that in a car collision muscles may be triggered by the centrally generated response.

The present study attempts to answer the following questions:

- How much do muscles affect the kinematics of the head-neck complex at different impact severity?

- How dependent is the calculated effect of muscles on the reflex time?
- Does the calculated effect of muscles depend on parameters of the muscle model?

A parameter study of a simplified model of the head-neck complex with muscle elements is proposed here as a method to answer these questions.

2. METHODS

2.1. Model of Head-Neck Complex

The current model of the head-neck complex consists of two rigid links: the head link and the neck link. The links are connected by two hinge joints: the neck-torso joint and the head-neck joint (Figure 1). Rotation of the first thoracic vertebra T_1 and the neck link deformation during impact are disregarded. The bases for modelling of the head-neck complex as a system of two rigid links were formulated by Wismans and Spenny (1984), Wismans, Oorschot, and Woltring (1986), and Wismans et al. (1987).

In the current model, the complex system of the head-neck muscles was simplified and represented with three groups of flexors and three

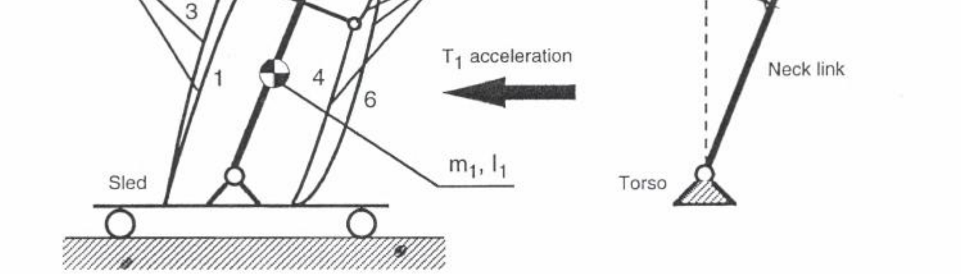

Figure 1. (a) The current model of the head-neck complex with muscle elements (curved lines with numbers); (b) Definition of flexion angles. m_1 and m_2 are the lumped masses of the neck and head, respectively. I_1 and I_2 are the mass moments of inertia of the neck and head, respectively. T_1 is the first thoracic vertebra.

groups of extensors (Figure 1). The influence of muscles on joint reaction forces was disregarded. The muscle effect was represented with torques generated by muscles about the neck-torso and head-neck joints.

Maximum isometric torque of extensors about the neck-torso joint was assumed to be 65 Nm, which is an estimation based on the data by Mertz and Patrick (1971), and Mayoux-Benhamou, Wybier, and Revel (1989). Maximum isometric torque generated by flexors was assumed to be 40% lower than the maximum static torque generated by extensors (Mertz & Patrick, 1971). Passive stiffness of the neck-torso and the head-neck joints (Figure 2) is based on the data by Bowman, Schneider, Lustick, Anderson, and Thomas (1984), and Wismans and Spenny (1984).

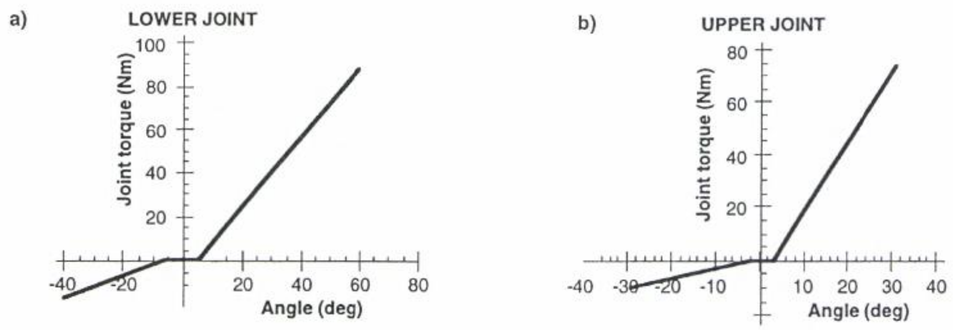

Figure 2. Passive resistive joint torques. (a) Torque about the neck-torso joint; (b) Torque about the head-neck joint. Positive angle is flexion; negative one is extension.

2.2. Initial Position of Head-Neck Complex

Initial values of angles θ_1 and θ_2 strongly influence the dynamic response of the head-neck complex. In this study the position of the head-neck complex prior to impact was treated as constant. Initial values of θ_1 and θ_2 were selected to be 18° and $-16°$, respectively. The basis for this selection is that these values were identified by Wismans et al. (1986) as the average initial angles in the Naval Biodynamics Laboratory (NBDL) frontal impact tests.

2.3. Impact Pulses

Horizontal acceleration of the first thoracic vertebra T_1 was used here as a loading pulse of the head-neck complex. The assumption that the T_1 acceleration can be treated as a load of the head-neck system has been widely used in the literature, for example, Bowman et al. (1984), Bosio and Bowman (1986), and Wismans et al. (1986). T_1 acceleration-time histories used in this study are based on published results of frontal crash tests conducted on volunteers at the Naval Biodynamics Laboratory (NBDL). In the NBDL tests participants were seated in an upright position on a sled accelerator and exposed to short duration accelerations simulating frontal, oblique, and lateral impacts. The resulting motions of the volunteer's head and T_1 were monitored by accelerometers and photographic targets.

Three impact pulses were used to analyse the influence of muscles under different impact severity (Table 1). Pulses *T12* and *T30* correspond to mean values of the horizontal T_1 acceleration-time histories in the NBDL frontal impact tests with sled acceleration of 6 g and 15 g, respectively. Pulse *T70* is based on an upper bound of T_1 horizontal acceleration in the NBDL frontal impacts with acceleration of 15 g. This pulse was used to simulate a very severe impact.

TABLE 1. Characteristics of Impact Pulses Used in This Study

Peak Sled Acceleration (g)	Peak T_1 Acceleration (g)	Symbol	Description	References
6	12	*T12*	Mean value from volunteer tests	Bosio & Bowman (1986; Figure 4, p. 349)
15	30	*T30*	Mean value from the most severe volunteer tests	Wismans, Janssen, Beusenberg, Koppens, & Lupker, (1994; Figure 5.13, p. 93)
15	70	*T70*	Envelope of volunteer tests	Wismans, Philippens, Oorschot, Kallieris, & Mattern, (1987; Figure 4, p. 5)

Notes. T_1—first first thoracic vertebra.

2.4. Reflex Time and Muscle Active State

In this study the reflex time T_{reflex} was defined as the time lag between the start of T_1 acceleration and the initiation of the neuromuscular reaction. It was assumed that the muscle active state equals a constant value A_{min} when the time does not exceed T_{reflex}. For time values greater than T_{reflex}, dynamics of the muscle active state was calculated with a first-order ordinary differential equation of Winters and Stark (1985, 1988). The typical active state-time history calculated with this equation is shown in Figure 3.

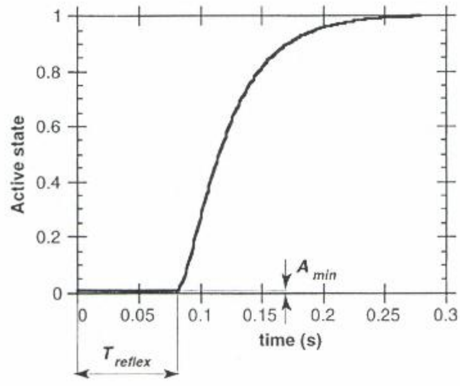

Figure 3. Muscle active state-time history calculated with the differential equation of Winters and Stark (1985, 1988).

Reflex times used in the current study ranged from 0 to 0.2 s. Selection of values for the reflex time was based on the previous review of the literature (Wittek & Kajzer, 1995). The reflex time 0 s corresponds to the situation when muscles start to generate force immediately after the start of impact. A value of 0.06 s can be regarded as the average reflex time of the neck extensors in young participants (Foust, Chaffin, Snyder, & Baum, 1973).

2.5. Muscle Model and Its Parameters

In this study the muscles were simulated by the Hill-type model in the interpretation by Winters and Stark (1985, 1988). The model consists of a contractile element *CE*, a parallel element *PE*, and a series elastic element *SE* (Figure 4). The series elastic element accounts for the series elasticity of both the tendon and the muscle. Dynamics of the current muscle model is described with a first-order ordinary differential equation that relates the time rate of change of the muscle force F_{Mus} to the muscle length l and velocity v, and the active muscle state $A(t)$

$$\frac{dF_{Mus}}{dt} = f[f_{Mus}, \ l(\theta), \ v(\mathring{\theta}), \ A(t)]$$

where θ and $\mathring{\theta}$ are joint angle and joint angular velocity, respectively. Details of this equation are given in the Appendix.

Parameters of mathematical formulae that determine behaviour of the muscle model are based on a previous review of the literature (Wittek & Kajzer, 1995). The following parameters were taken into account in the analysis of the influence of the muscle model parameters on the calculated muscle effect: (a) shape parameter of force-elongation characteristic of the series elastic element C_{SE}, (b) elongation of the parallel elastic element at the maximum isometric force PE_{max}, (c) maximum shortening velocity of the contractile element v_{max}, and (d) the ratio of the force during active lengthening to the isometric force MV_{ml}.

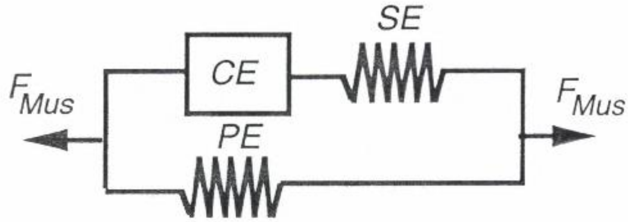

Figure 4. Hill-type model used in the present study. Based on Winters and Stark (1988).

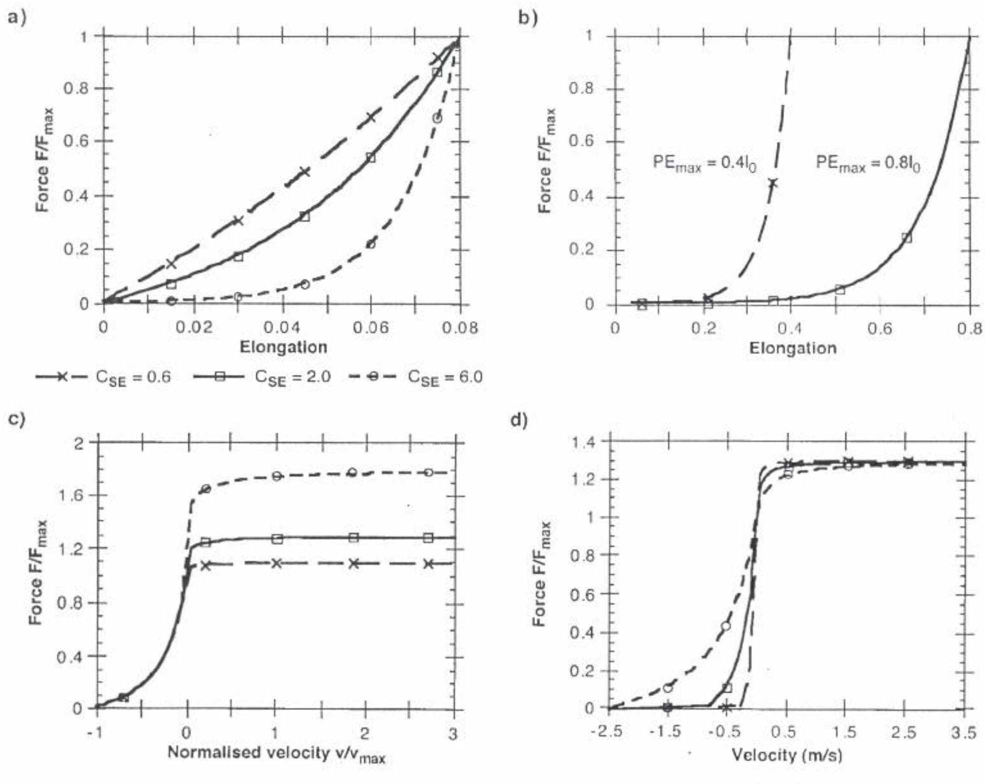

Figure 5. Muscle force for different values of the Hill-type model parameters. (a) *SE* force for different values of C_{SE}; (b) *PE* force for different values of PE_{max}; (c) *CE* force-velocity characteristic for different values of MV_{ml}, and (d) *CE* force-velocity characteristic for different values of v_{max}. F_{max} is the maximum isometric force and l_o is the optimum muscle length.

In this study the elongation of the parallel elastic element was calculated in reference to the optimum muscle length. This length is defined as the length at which generation of the active muscle force is the most efficient. Some basic effects of the analysed parameters of the muscle model on the calculated muscle force are shown in Figure 5. Values for the parameters are given in Table 2.

TABLE 2. Test Matrix for Analysis of Influence of Parameters of the Muscle Model

Parameter	Lower Bound	Reference Value	Upper Bound
v_{max}	0.3 · (reference value)	0.8 m/s	3.0 · (reference value)
C_{SE}	0.3 · (reference value)	2.0	3.0 · (reference value)
PE_{max}	0.3 · (reference value)	0.8 of the optimum length of muscle	(reference value)
MV_{ml}	1.1	1.3	1.8

Notes. v_{max} is the maximum shortening velocity of the contractile element, C_{SE} is the shape parameter of force-elongation characteristic of the series elastic element, PE_{max} is the elongation of the parallel elastic element at the maximum isometric force, MV_{ml} is the ratio of the force during active lengthening to the isometric force.

2.6. Validation of Head-Neck Complex Model

Validation of the kinematics of the head-neck complex model was done by comparison of the calculated time histories of the head angle and the head angular acceleration with the envelopes of the NBDL experimental results reported by Wismans et al. (1986, 1987). The results reported by Wismans et al. (1986, 1987) were obtained in frontal impact tests with peak sled acceleration of 15 g.

Direct validation of the calculation of the muscle force was not possible because of lack of the relevant experimental data on the muscle tension in impacts.

2.7. Programming and Numerical Methods

Programming was done with *Mathematica* 2.2.2 software (Wolfram, 1993). Equations of motion of the head-neck model and dynamic equations of the muscle model were solved with standard *NDSolve* procedure from the *Mathematica* software (Keiper, 1992). *NDSolve* uses Adams predictor-corrector method to solve non-stiff systems of ordinary differential equations, and Gear's method for stiff problems. Computation was done on a *SUN SPARC* 20 workstation.

3. RESULTS

3.1. Influence of Muscles at Different Impact Severity

The influence of muscles on the head flexion angle greatly decreased when the impact severity increased. The maximum angle of the head flexion was reduced by up to 65% at the impact pulse *T12*, and only by about 20% at the impact pulse *T70* (Figure 6).

The pulse *T70* corresponds to the upper bound of the NBDL frontal impact tests with peak sled acceleration of 15 g. It is reasonable to expect that the T_1 acceleration can reach values higher than the pulse *T70* when the sled acceleration is greater than 15 g. This, in turn, suggests that the muscle effect is insignificant in frontal impacts which are more severe than 15 g.

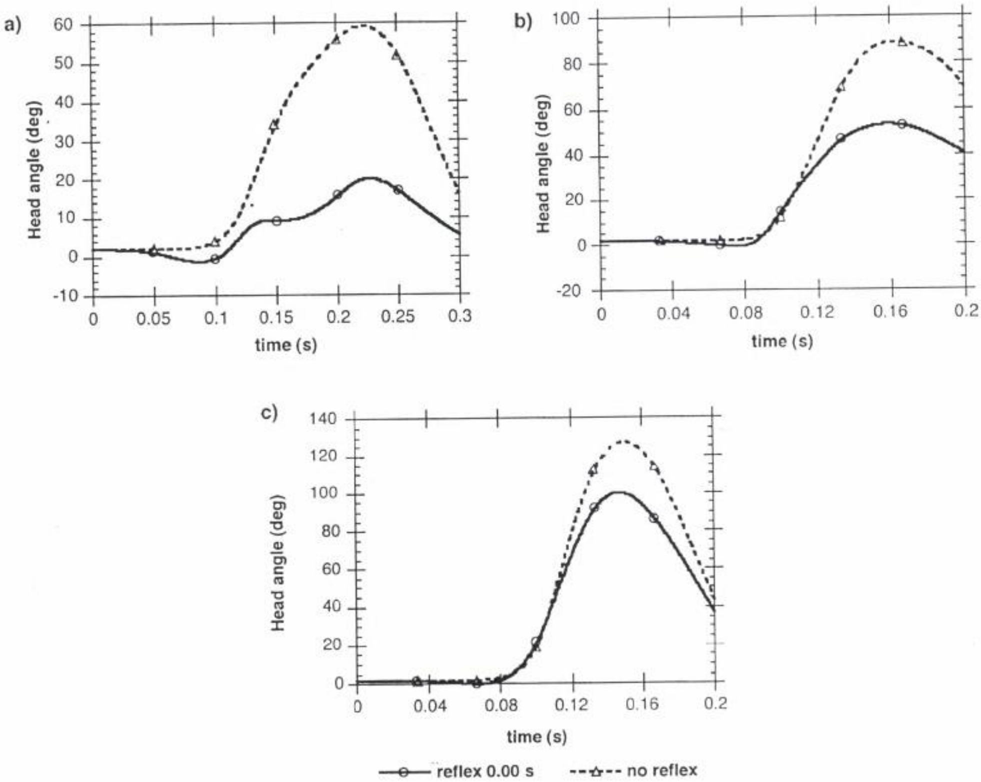

Figure 6. Head flexion angle-time histories at different impact severity for activated (reflex 0.00 s) and inactivated (no reflex) muscles. (a) Results for pulse *T12*; (b) Results for pulse *T30*; (c) Results for pulse *T70*.

3.2. Influence of Reflex Time

When the reflex time was lower than 0.04 s, muscles decreased the maximum angle of the head flexion by about 40% at the impact pulse *T30* (Figure 7 and 8a). However, the maximum angular acceleration of the head was reduced by muscle tension only by about 10% (Figure 8b). Thus, the peak value of the head angular acceleration was probably more affected by the characteristics of an impact pulse itself and the passive properties of joints than by the forces generated by muscles.

For the reflex time greater than 0.10 s the maximum force in extensors was calculated to be lower than 0.8 F_{max}. Furthermore, the force in extensors quickly dropped after its first peak (Figure 9). In consequence the relative influence of muscles on the maximum angle of the head flexion was lower than 20% for long reflex times.

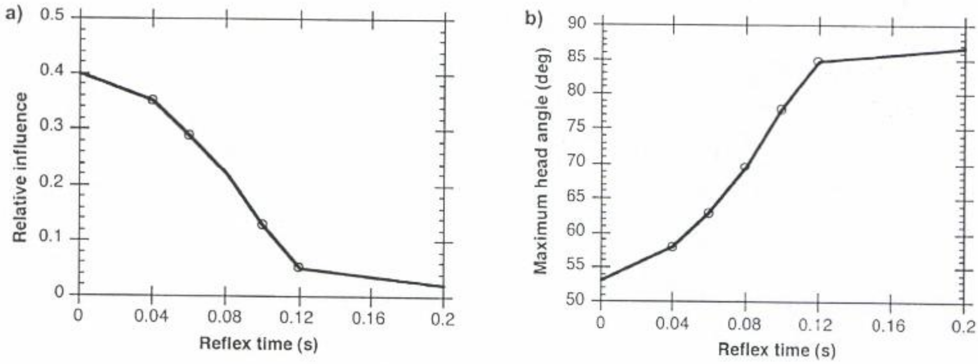

Figure 7. Influence of muscles on the head flexion angle as a function of the reflex time at pulse *T30*. (a) Relative changes of the maximum angle of head flexion; (b) Maximum angle of head flexion.

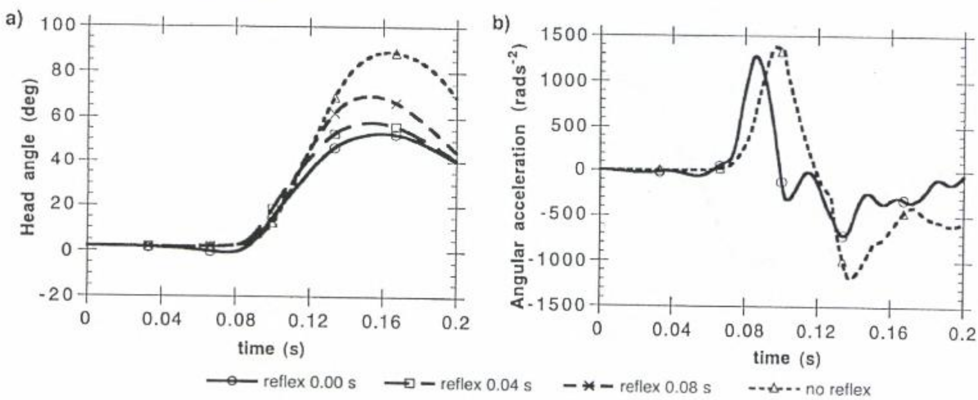

Figure 8. Results for impact pulse *T30* for different reflex times. (a) Angle of head flexion; (b) Angular acceleration of the head.

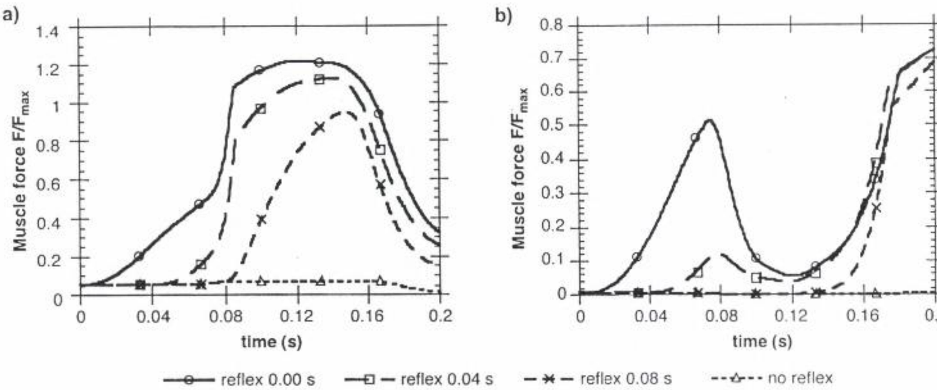

Figure 9. Muscle-force time histories for different reflex times at impact pulse *T30*. (a) Muscle 1 (extensor); (b) Muscle 4 (flexor).

3.3. Influence of Muscle Model Parameters

Analysis of the influence of muscle model parameters indicates that the muscle-force time histories slightly shift towards the right on the time-axis when C_{SE} decreases (Figure 10). The reason for this shift is that the stiffness of series elastic element greatly decreases for low values of C_{SE} (Figure 5). As a muscle elongation is the sum of the elongations of the series element and the contractile element, the elongation of the contractile element decreases when the stiffness of the series elastic element is low. In general, the head angle-time histories were not sensitive to C_{SE}. Variation of C_{SE} by 10 times resulted only in a 3% difference in the maximum angle of head flexion (Figure 10).

The current results show that the maximum shortening velocity v_{max}

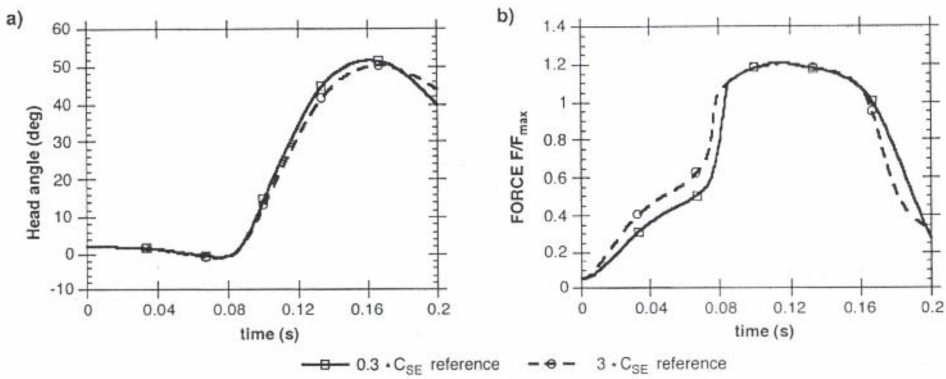

Figure 10. (a) Head flexion angle-time histories and (b) muscle force-time histories for different values of C_{SE}.

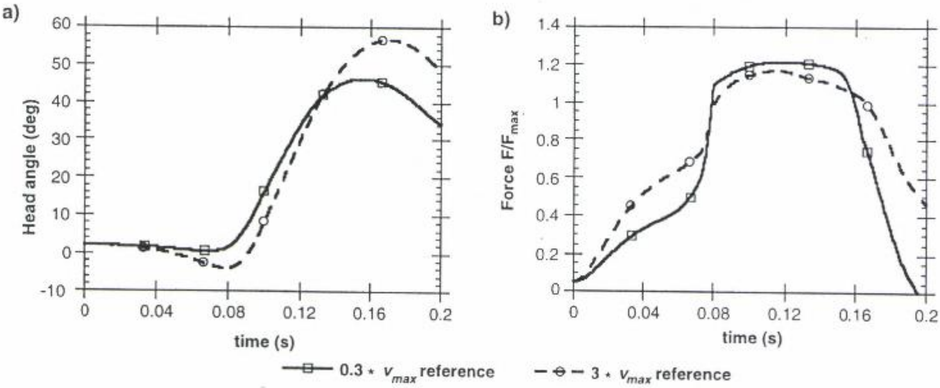

Figure 11. (a) Head flexion angle-time histories and (b) muscle force-time histories for different values of v_{max}.

can relatively strongly affect muscle force-time histories. The influence of v_{max} was the most evident in the initial phase of impact (Figure 11). The explanation is that v_{max} significantly affects the force-velocity characteristic when the muscle performs concentric work. Such concentric work can be performed by extensors in the initial phase of impact when the impact pulse *T30* does not reach high values. As the calculated peak value of muscle force only slightly changes with v_{max}, variation of v_{max} by 10 times exerted only a 20% influence on the maximum angle of the head flexion.

Parameter MV_{ml} proportionally affects the peak value of force generated by the muscle during its active lengthening. The eccentric work dominates the behaviour of neck extensors for the impact pulses considered in the current analysis. Thus, the maximum angle of head flexion significantly decreased when MV_{ml} increased (Figure 12).

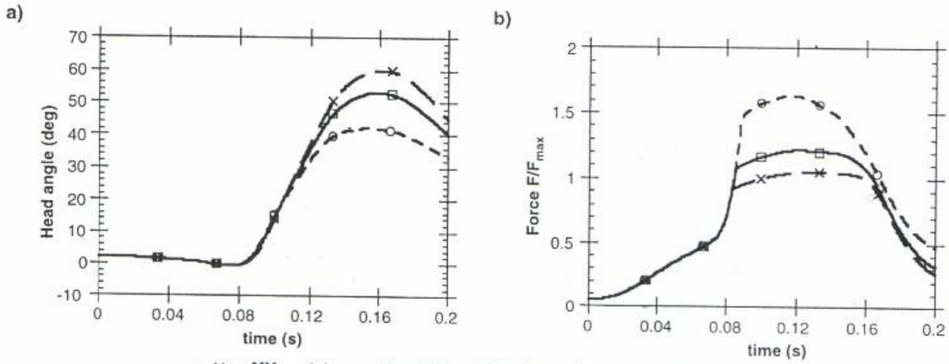

Figure 12. (a) Head flexion angle-time histories and (b) muscle force-time histories for different values of MV_{ml}.

For low values of PE_{max}, the passive force reaches high values at low muscle elongation (Figure 5). In this study the peak value of the muscle elongation was about 0.5 of the optimum muscle length. At this level of elongation the muscle force reached unrealistically high values when the assumed PE_{max} was less than 0.3 (0.35) of the optimum muscle length (Figure 13).

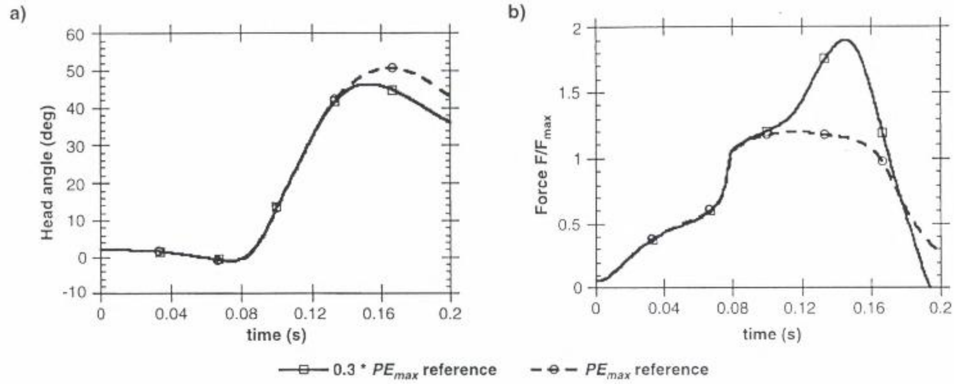

Figure 13. (a) Head flexion angle-time histories and (b) muscle force-time histories for different values of PE_{max}.

3.4. Results of Validation

The envelope of the head flexion angle-time histories calculated in this study study well correlates with the NBDL experimental results by Wismans et al. (1986, 1987; Figure 14). The current model of the head-neck complex well predicts the peak angle of the head flexion. Peak angles of the head flexion were calculated here to be in a range of 52–100°. The corresponding experimental results reported by Wismans et al. (1986, 1987) are 68–95°. Differences between the current results and the data by Wismans et al. (1986, 1987) are related to four important simplifications of the current model of the head-neck complex. First, the trunk and rotation of the first thoracic vertebra were neglected. Second, the complex structure of the neck was modelled as a single rigid link, which neglects neck deformation. Third, the head-neck model has only rotational degrees of freedom. Fourth, characteristics of loading pulses, mass properties of the head-neck model, characteristics of the passive joint torques, and initial position of the head-neck complex were estimated here as the average values of the literature data. Such an estimation is deficient in predicting the whole envelope of biodynamic responses of the participants.

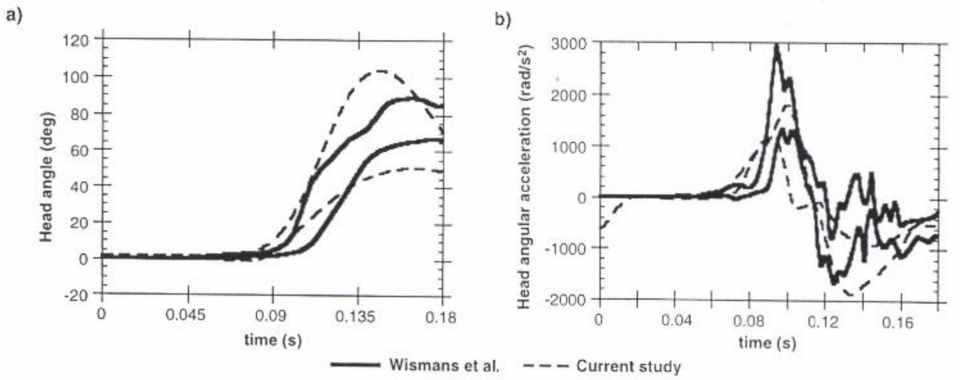

Figure 14. Envelopes of the current results and the experimental results by Wismans et al. (1986, 1987). (a) Angle of head flexion; (b) Angular acceleration of the head.

4. DISCUSSION

Results of this study indicate that muscles can significantly affect kinematics of the head-neck complex in frontal impacts when the following conditions are satisfied simultaneously:

- Horizontal acceleration of a car during a crash is not greater than 15 g,
- Reflex time is less than 60 (80) ms.

When these conditions were satisfied, the maximum angle of the head flexion was decreased by muscle tension by up to 65% and 40% in frontal collisions with the peak car acceleration of 6 g and 15 g, respectively.

In the field of impact biomechanics, injury tolerances to the neck in a frontal car collision are expressed in terms of bending torque and forces developed at the occipital condyles (Wismans, Janssen, Beusenberg, Koppens, & Lupker, 1994). The torque about the occipital condyles is proportional to the head flexion angle (Figure 2). The current results indicated that muscle action can reduce this angle, which provides support for the hypothesis that muscles may exert some protective effect on the neck in a frontal car collision. It should be noted here that the human neck is a complex structure for which a number of different injury mechanisms can take place. Moreover, existing injury criteria to the neck are a function of the duration of the loading (Wismans et al., 1994). Analysis of muscle effect on the magnitude and duration of loading on the head-neck complex requires a mathematical model more advanced than the current one. Therefore, further studies are needed to investigate and quantify the hypothetical protective effect of muscles on the neck injuries.

Current results suggest that determining the parameters of the Hill-type muscle model is not the crucial point in the analysis of the muscle effect on the biodynamic response of the head-neck complex in a car collision. Only the ratio of force during active lengthening to the isometric force was identified here as the parameter crucially affecting both kinematics of the head-neck complex and the peak value of muscle force. The shape parameter of force-elongation characteristic of the series elastic element C_{SE} exerted only a minor influence on the muscle force-time histories. Thus, the authors conclude that this parameter is irrelevant in the analysis of the Hill-type muscle model response to transient loads. The structural response of the head-neck model does not strongly depend on the maximum shortening velocity of the contractile element v_{max}. Therefore, variation of this parameter resulted only in about a 20% difference in the maximum angle of head flexion. As v_{max} affects muscle force-time histories, its influence would probably increase at low impact severity when the effect of the contraction force is stronger. Therefore, the authors suggest that the muscle force-velocity relation may be relevant in the analysis of the head-neck complex response to transient loads. Similar findings have been presented by Winters and Stark (1985) and Winters, Stark, and Seif-Naraghi (1988) in the mathematical modelling analysis of response of the elbow system to transient loads.

The tendency of the current results well agrees with the experimental and simulation results reported in the literature. Head flexion angle-time histories calculated with the present model of the head-neck complex exhibit a strong correlation with the NBDL data of Wismans et al. (1986, 1987; Figure 14). The level of muscle influence calculated here is close to the experimental results of Mertz and Patrick (1967, 1971) and to the results of mathematical modelling by Pontius and Liu (1976) and Happee and Thunnissen (1994). On the other hand, the current study shows that muscles do not significantly decrease maximum angular acceleration of the head, which is contrary to the experimental data by Verriest et al. (1975), who found that muscle force can reduce the peak value of head angular acceleration by about 40% in frontal impact with acceleration of 20 g in baboons. However, their results cannot be directly extrapolated to humans.

A key limitation of the present study is that only a simplified model of the head-neck complex with muscles was used. The complex structure of the neck was represented with a rigid link, and the system of neck muscles was simplified with three flexors and three extensors. Thus, our analysis cannot be regarded as a complete assessment of the muscle influence on the biodynamic response of the head-neck complex. Despite the limitation just described, the present model of the head-neck complex facilitates prediction of the muscle effect on the general kinematics of the head-neck complex in frontal impacts.

5. SUMMARY

This study indicates that muscle effect on the kinematics of the head-neck complex may be important at impact pulses with a peak acceleration lower than 15 g, and for reflex times lower than 60 (80) ms. The calculated effect of muscles was not sensitive to most parameters of the muscle model. The authors found that only the parameters that determine the muscle force-velocity characteristics may be relevant in the analysis of the head-neck complex response to transient loads.

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APPENDIX

Nomenclature

x_{Mus} — muscle elongation
x_{SE} — SE elongation
x_{CE} — CE elongation
v_{Mus} — velocity of muscle elongation/shortening
v_{CE} — velocity of CE elongation/shortening
v_{SE} — velocity of SE elongation/shortening
k_{SE} — SE stiffness
k_{PE} — PE stiffness
F_{Mus} — total muscle force
F_{CE} — force in the contractile element CE, that is, force generated in contraction process
F_{PE} — force in the parallel element PE, that is, passive force
F_{SE} — force in the series elastic element SE
F_{max} — maximum (tetanic) isometric force
C_{SE} — shape parameter of the force-elongation characteristic of SE
SE_{max} — elongation of SE element at F_{max}
C_{PE} — shape parameter of the force-elongation characteristic of PE
PE_{max} — elongation of PE element at F_{max}

Dynamics of muscle model

For the model shown in Figure 4, muscle force is the sum of the contraction force F_{CE} and passive force F_{PE}:

$$F_{Mus} = F_{CE} + F_{PE} \tag{A1}$$

Force in the series elastic element equals contraction force:

$$F_{CE}(x_{CE}, v_{CE}, t) = F_{SE}(x_{SE}). \tag{A2}$$

Contraction force can be described with the following formula:

$$F_{CE}(x_{CE}, v_{CE}, t) = A(t)F_l(x_{CE})F_v(v_{CE}), \tag{A3}$$

where F_l and F_v are muscle force-length and muscle force-velocity characteristics, respectively.

Based on Equations A1 and A2, the first-order time derivative of the muscle force can be expressed as

$$\frac{dF_{Mus}}{dt} = \frac{dF_{SE}}{dt} + \frac{dF_{PE}}{dt} = k_{SE}v_{SE} + k_{PE}\, v_{Mus}. \tag{A4}$$

Stiffness of soft connective tissues is often assumed to be a linear function of force, for example, Winters and Stark (1988) and Fung (1993). This assumption yields the following formulation for the stiffness of the series and parallel elements:

$$k_{SE}(F_{SE}) = \left(\frac{C_{SE}}{SE_{max}}\right)F_{SE} + F_{\max}\frac{C_{SE}/SE_{max}}{e^{C_{SE}}-1} \text{ and} \tag{A5}$$

$$k_{PE}(F_{PE}) = \left(\frac{C_{PE}}{PE_{max}}\right)F_{PE} + F_{\max}\frac{C_{PE}/PE_{max}}{e^{C_{PE}}-1}. \tag{A6}$$

Thus, Equation A4 can be expressed as

$$\frac{dF_{Mus}}{dt} = v_{SE}k_{SE}(F_{SE}) + v_{Mus}k_{PE}(F_{PE}). \tag{A7}$$

Muscle elongation x_{Mus} is the sum of the elongations of the series elastic element x_{SE} and the contractile element x_{CE}, which yields

$$x_{Mus} = x_{SE} + x_{CE} \tag{A8}$$

$$v_{Mus} = v_{SE} + v_{CE}, \text{ and} \tag{A9}$$

$$v_{SE} = v_{Mus} - v_{CE}. \tag{A10}$$

Velocity of the contractile element is obtained with the following formulae:

$$F_v(v_{CE}) = \frac{F_{CE}(x_{CE}, v_{CE}, t)}{A(t)F_l(x_{CE})} = \frac{F_{SE}(x_{SE})}{A(t)F_l(x_{CE})} \text{ and} \tag{A11}$$

$$v_{CE} = F_v^{-1}(v_{CE}). \tag{A12}$$

The final form of the dynamic equation of the current muscle model is

$$\frac{dF_{Mus}}{dt} = [v_{Mus} - F_v^{-1}(v_{CE})]\, k_{SE}(F_{SE}) + v_{Mus}k_{PE}(F_{PE}). \tag{A13}$$