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Functional anatomy of the equine temporomandibular joint: Collagen fiber texture of the articular surfaces



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ABSTRACT

In the last decade, the equine masticatory apparatus has received much attention. Numerous studies have emphasized the importance of the temporomandibular joint (TMJ) in the functional process of mastication. However, ultrastructural and histological data providing a basis for biomechanical and histopathological considerations are not available. The aim of the present study was to analyze the architecture of the collagen fiber apparatus in the articular surfaces of the equine TMJ to reveal typical morphological features indicating biomechanical adaptations. Therefore, the collagen fiber alignment was visualized using the split-line technique in 16 adult warmblood horses without any history of TMJ disorders.

Within the central two-thirds of the articular surfaces of the articular tubercle, the articular disc and the mandibular head, split-lines ran in a correspondent rostrocaudal direction. In the lateral and medial aspects of these articular surfaces, the split-line pattern varied, displaying curved arrangements in the articular disc and punctual split-lines in the bony components. Mediolateral orientated split-lines were found in the rostral and caudal border of the articular disc and in the mandibular fossa. The complex movements during the equine chewing cycle are likely assigned to different areas of the TMJ. The split-line pattern of the equine TMJ is indicative of a relative movement of the joint components in a preferential rostrocaudal direction which is consigned to the central aspects of the TMJ. The lateral and medial aspects of the articular surfaces provide split-line patterns that indicate movements particularly around a dorsoventral axis.

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Introduction

The equine temporomandibular joint (TMJ) lacks in-depth objective clinical studies and studies investigating its role in pathological conditions (Carmalt, 2014; Witte, 2015).

To allow a precise diagnosis of pathological changes within the structures of the equine TMJ, the gross anatomical features of this complex joint have been described in detail by anatomical dissections (Rodríguez et al., 2006). Concomitantly, several studies have been performed to evaluate the suitability and potential relevance of advanced imaging techniques, i.e. radiography (Ebling et al., 2009), computed tomography (Rodríguez et al., 2008; Carmalt et al., 2016), ultrasonography (Rodríguez et al., 2007), magnetic resonance imaging (Rodríguez et al., 2010) and TMJ-arthroscopy (May et al., 2001; Weller et al., 2002). Besides these diagnostic and gross anatomical investigations, functional examinations of the equine masticatory movements have been performed. The initial tests utilized a mograph (Leue, 1941), while more recent research has used

video analysis (Collinson, 1994). Similar to other herbivorous mammals (Hiemae, 1978) the equine chewing cycle has been described as consisting of an opening stroke, a closing stroke and a power stroke (Collinson, 1994; Baker and Easley, 1999; Baker, 2002). The power stroke in equids is described generally as unimodal and mediolateral movements of the mandible (Fortelius, 1985; Kaiser, 2002; Williams et al., 2007). Using optical tracking systems, the detailed 3-D kinematics of the TMJ have been described in each phase of the strokes considering a lateroventral movement of the working side during the opening stroke and a marked mediodorsal movement of the working side during the power stroke (Collinson, 1994; Bonin et al., 2006; Staszuk et al., 2006). Both the direction and the range of rotational and translational movements have been quantified (Bonin et al., 2006). This technique also enabled examinations focused on the influence of different feeds (Bonin et al., 2007), dental corrections (Simhofer et al., 2011) and the effect of acute unilateral TMJ inflammation (Smyth et al., 2015b) on the kinematics of the TMJ. Additionally, masticatory forces have been estimated by placing force sensors on the second and third premolars (Staszuk et al., 2006).

Although a case report has demonstrated histopathological changes in the equine TMJ (Smyth and Carmalt, 2015a), the normal microscopical anatomy of the equine TMJ remains widely

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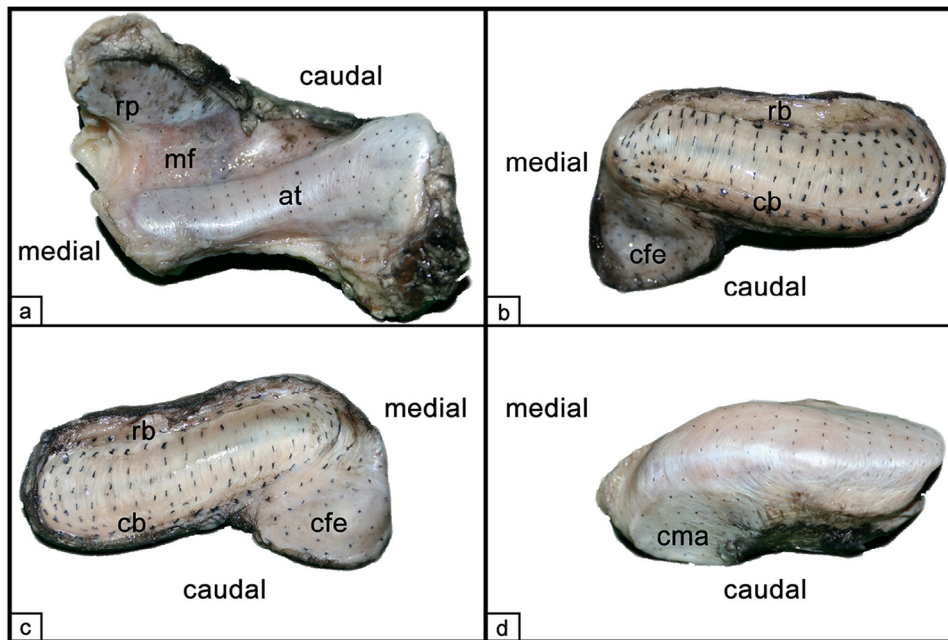


Fig. 1. Articular surfaces obtained from a right temporomandibular joint of a horse demonstrating the split-lines. (a) Temporal components of the TMJ. Rp, retroarticular process; mf, mandibular fossa; at, articular tubercle. (b) Articular disc, dorsal side. rb, rostral border; cb, caudal border; cfe, caudomedial fibrous expansion. (c) Articular disc, ventral side. rb, rostral border; cb, caudal border; cfe, caudomedial fibrous expansion. (d) Mandibular head. cma, caudomedial aspect.

undescribed (Ramzan, 2006). However, ultrastructural features may be important for the understanding of TMJ pathologies, regenerative capabilities and biomechanical considerations.

Therefore, the aim of the present study was to visualize and analyze the architecture of the collagen fiber apparatus in the articular surfaces of the healthy equine TMJ to reveal typical morphological features indicating biomechanical adaptations.

Material and methods

Sixteen adult warmblood horses without any history of TMJ disorders or dental diseases were included. The horses were euthanized for reasons not related to this study and the left and right TMJ were dissected. The articular surface bearing components of the temporal bone (articular tubercle, mandibular fossa and retroarticular process), the condylar process of the mandible (mandibular head, caudomedial aspect of the mandibular head) and the articular disc were removed. The dissected TMJs were examined for signs of degenerative joint disease (chondral lesions, ulcerations, hyperplasia, pannus, osteophytes) by gross inspection. Only joints free of all signs of degenerative joint disease were further evaluated.

The collagen fiber alignment in the articular surfaces was visualized using the split-line technique (Below et al., 2002). This involves the following procedure: a dissecting needle was dipped in commercial grade India ink (Pelikan, Scribto) and inserted into the joint surfaces of the mandibular head, the dorsal and ventral side of the articular disc, the articular tubercle, the mandibular fossa and the retroarticular process of the temporal bone. The depth of penetration on the ventral and dorsal side of the articular disc was about 3 mm. In the mandibular and temporal components of the TMJ, a dissecting needle was inserted into the joint cartilage until the level of subchondral bone was reached. This procedure was repeated in a grid pattern at intervals of 5 mm until the articular surfaces were completely pricked. Each penetration was performed perpendicularly to the articular surface and resulted in a colored line, enabling visualization of the main orientation of the collagen network. This pattern of lines – termed 'split-lines' – arose on each articular surface. Articular surfaces were photographed (Nikon SB-29S, Macro Speedlight) and the split-line patterns were recorded on a schematic map. Subsequently, the split-lines were evaluated according to two parameters: length and orientation (Fig. 1).

The length was assigned to one of three categories: punctiforme (<2 mm), medium (from 2 mm to <4 mm) or large (≥ 4 mm). The orientation was assigned to one of four categories: rostrocaudal, mediolateral, oblique or diffuse (no clear orientation visible).

Additionally, the orientation, presence and length of the split-lines and the general split-line patterns of the articular surfaces of the temporal bone, the mandibular head and the articular disc (dorsal and ventral surface) were compared.

Statistical analyses were performed using the data analysis software GraphPad Prism (v. 6.07; GraphPad Software) and BiAS (v. 9.08; Ackermann, 2010). The split-

line patterns of the central aspects of the articular surfaces were divided into 'rostrocaudal' and 'non-rostrocaudal'. On the medial and lateral aspects of the articular surfaces, the split-line patterns were classified into 'curved' and 'non curved' in case of the articular disc, and into 'punctiforme' and 'non punctiforme' in case of the articular tubercle and mandibular head. To test the relationship between the aspects of the articular surfaces examined and the split-line pattern, the Pearson Chi-Square-test for contingency tables was applied. Initially, the global comparison of all split-line patterns was performed. In case of global statistically significant differences, pair-wise comparisons were performed with the central aspects, controlling the type I error rate using the Bonferroni–Holm-procedure. *P* values of less than or equal to 0.05 were assumed to express statistical significance.

Results

The most constant alignment of split-lines was present in the central two-thirds of the articular surfaces of the articular tubercle, the articular disc and the mandibular head. In these areas, medium sized (articular tubercle and mandibular head) or large sized (articular disc) split-lines were arranged most frequently in rostrocaudal direction ($P < 0.001$; Figs. 2–4). Variations in length and orientation were obtained in the peripheral (lateral and medial) areas of the articular tubercle, the articular disc and the mandibular head and in the mandibular fossa, the retroarticular process and at the caudomedial aspect of the mandibular head (Tables 1 and 2).

Articular tubercle

The orientation of split-lines in the central and medial aspects of articular tubercle was consistent for all specimens. In the centre, medium-sized split-lines were most frequently oriented in a rostrocaudal direction ($P < 0.001$). Towards the medial margin, punctiforme split-lines were identified most commonly ($P < 0.001$). In contrast, the lateral part of the articular surface demonstrated three different arrangements of split-lines. In 14 of 32 specimens, a combination of oblique orientated and punctiforme split-lines was noted (Fig. 3; Table 1). Punctiforme split-lines became visible in 13 of 32 specimens ($P < 0.001$; Fig. 3; Table 1). Finally, a diffuse design was shown in five of 32 specimens (Fig. 2; Table 1).

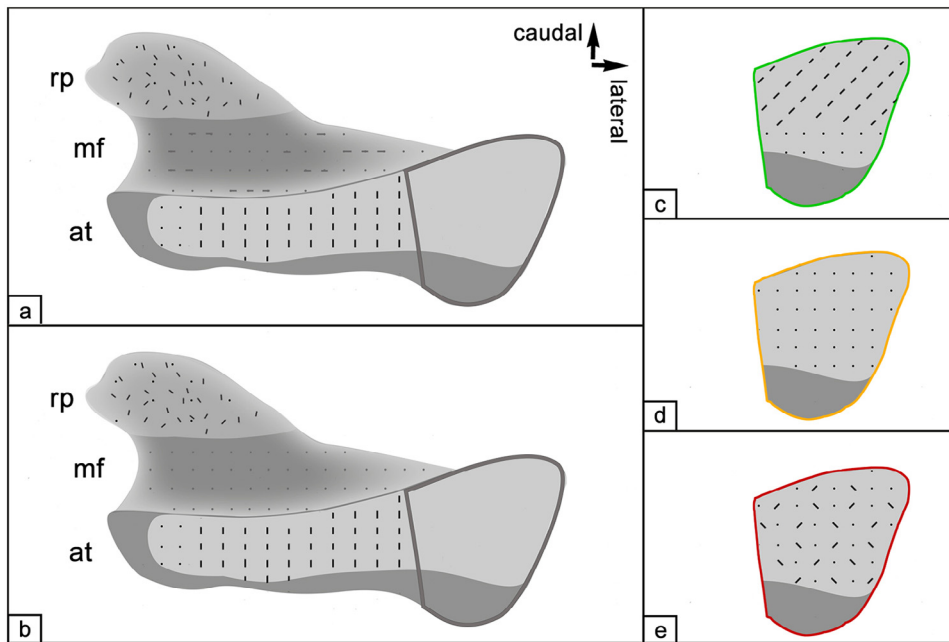


Fig. 2. Split-line patterns of the temporal components of the TMJ. The retroarticular process (rp) and the central and medial aspects of the articular tubercle (at) showed constant split-line arrangements. The mandibular fossa (mf) showed only weak split-line staining and two alternative split-line patterns (a and b). The lateral aspect of the articular tubercle showed three alternative split-line patterns: (c) 14 of 32 specimens; (d) 13 of 32 specimens; (e) five of 32 specimens.

Mandibular fossa

The fibrocartilage covering the mandibular fossa was very thin, hampering adequate insertion of the dissecting needle. However, 20 investigated specimens were suitable to determine a split-line pattern. In seven of the 20 specimens, the mandibular fossa revealed a punctiform split-line pattern (Fig. 2, Table 1). In 13 of 20 specimens, punctiform split-lines were combined with mediolateral orientated split-lines (Fig. 2, Table 1). Remarkably, in six of 20

specimens, the fibro-cartilage of the mandibular fossa was overlaid by a thin membranous tissue resembling a synovial membrane.

Retroarticular process

The retroarticular process exposed a diffuse pattern with no distinct orientation of the split-lines in all 32 investigated specimens (Fig. 2; Table 1).

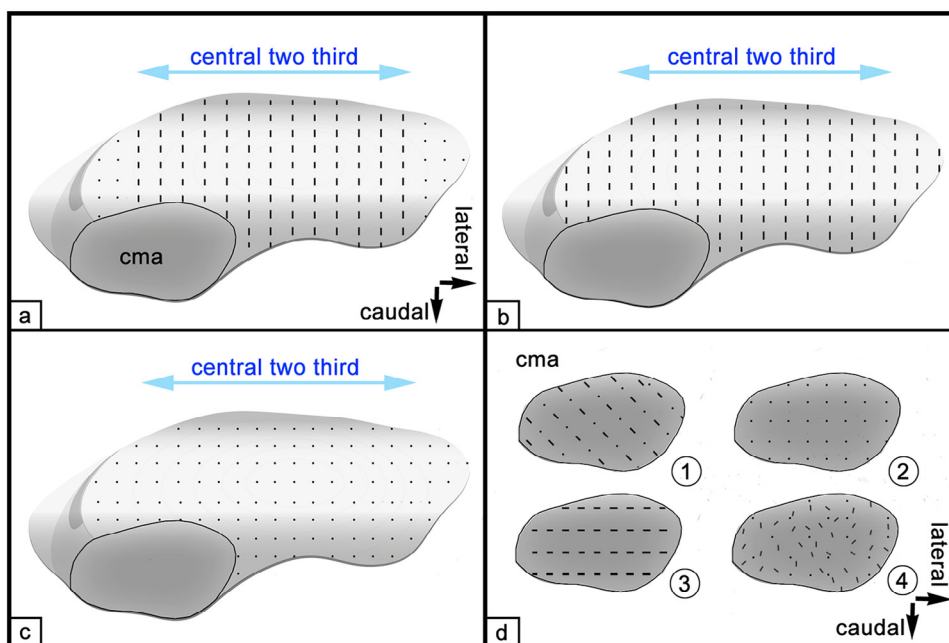


Fig. 3. Split-line patterns of the mandibular head. In 30 of 32 specimens, the central two thirds contained a constant pattern of medium-sized split-lines running in rostrocaudal direction (a and b). In 24 of 32 specimens, the medial and lateral regions contained punctiform split-lines (a). In six of 32 specimens there was rostrocaudal alignment of medium-sized split-lines on the entire articular surface (b). In two of 32 specimens only punctiform split-lines were observed (c). On the caudomedial aspect (cma) of the mandibular head four varying patterns of split-lines were documented (d, 1–4).

Table 1

Side- and site-dependent occurrence of split-line patterns in the temporal part and in the mandibular head of the equine TMJ.

Site	Right	Left	Bilateral
Temporal part of the TMJ			
Medial aspect of the articular tubercle			
Punctiforme	16	16	16
Central aspect of the articular tubercle			
Rostrocaudal	16	16	16
Lateral aspect of the articular tubercle			
Oblique + punctiforme	8	6	4
Punctiforme	6	7	5
Diffuse	2	3	0
Mandibular fossa			
Mediolateral + punctiforme	7	6	4
Punctiforme	3	4	1
Retroarticular process			
Diffuse	16	16	16
Mandibular head			
Central aspect			
Rostrocaudal	16	14	14
Punctiforme	0	2	0
Medial and lateral aspects			
Punctiforme	13	13	10
Rostrocaudal	3	3	2
Caudomedial aspect			
Oblique	15	9	9
Punctiforme	0	3	0
Mediolateral	1	2	1
Diffuse	0	2	0

Mandibular head including its caudomedial aspect

In 30 of 32 specimens, the central two-thirds of the articular surfaces demonstrated a rostrocaudal alignment of medium-sized split-lines ($P < 0.001$; Table 1). Variations were observed in the medial and lateral aspects. In 24 of 32 specimens, the medial and lateral regions contained punctiforme split-lines ($P < 0.001$; Fig. 3; Table 1). Six of 32 specimens also demonstrated a rostrocaudal alignment of medium-sized split-lines on the entire articular surface (Fig. 3; Table 1). Two of 32 specimens showed punctiforme split-lines all over the articular surface (Fig. 3; Table 1).

The caudomedial process of the mandibular head displayed four split-line patterns. An oblique orientation combined with punctiforme split-lines was found in 24 of 32 specimens (Fig. 3; Table 1). In three of 32 cases, there were punctiforme split-lines, and in three of 32 cases a mediolateral alignment of split-lines was observed (Fig. 3; Table 1). In two of 32 specimens the split-lines showed a diffuse alignment, varying in length and orientation (Fig. 3; Table 1).

Articular disc

The dorsal and ventral aspects of the articular disc showed similar arrangements of split-lines. In the central two-thirds, large-sized split-lines most frequently ran in a rostrocaudal direction ($P < 0.001$; Table 2). Towards the medial and lateral border, split-lines most commonly followed a curved path, resembling so-called attractive singular points ($P < 0.001$; Werner et al., 1991). The mediocaudal fibrous expansion of the articular disc revealed a diffuse arrangement of split-lines.

Differences in the orientation of split-lines were present in the prominent rostral and caudal borders of the articular disc (Fig. 4; Table 2). The rostral and caudal borders expressed three different alignments (Fig. 4; Table 2).

A mediolateral and an alternating alignment on the rostral border of the ventral surface were noted in 14 of 32 specimens. A rostrocaudal configuration was found in four of 32 specimens (Table 2). On the caudal border an alternating pattern between

Table 2

Side- and site-dependent occurrence of split-line patterns in the articular disc of the equine TMJ.

Site	Right	Left	Bilateral
Articular disc, ventral aspect			
Rostral border			
Alternating	7	7	4
Mediolateral	8	6	3
Rostrocaudal	1	3	1
Caudal border			
Alternating	12	13	9
Rostrocaudal	2	2	1
Mediolateral	2	1	0
Central aspect			
Rostrocaudal	16	16	16
Medial and lateral aspects			
Curved	16	16	16
Articular disc, dorsal aspect			
Rostral border			
Alternating	9	8	6
Rostrocaudal	5	5	3
Mediolateral	2	3	0
Caudal border			
Alternating	12	13	10
Mediolateral	3	1	1
Rostrocaudal	1	2	1
Central aspect			
Rostrocaudal	16	16	16
Medial and lateral aspect			
Curved	16	16	16

rostrocaudal and mediolateral split-lines was found in 25 of 32 specimens (Table 2). A continuous rostro-caudal orientation was expressed in four of 32 specimens and a continuous mediolateral orientation in three of 32 specimens (Fig. 4; Table 2).

On the rostral border of the dorsal surface, an alternating pattern was found in 17 specimens, a rostrocaudal in 10 specimens and a mediolateral in five of 32 specimens (Table 2). On the caudal border, the alternating pattern was expressed in 25 of 32 specimens (Table 2). In four of 32 specimens, there was a mediolateral orientation and in three of 32 specimens, a rostrocaudal orientation was observed (Fig. 4; Table 2).

Discussion

The split-line technique allowed reliable identification of superficial collagen fiber bundles (Petersen and Tillmann, 1998a) and illustrated biomechanical adaptations in joint compression and motion (Below et al., 2002). The correlation between split-lines and collagen fiber orientation has been validated by polarization microscopy (Ortmann, 1975) and by scanning electron microscopy (Petersen and Tillmann, 1998a). Besides these ultrastructural examinations, functional examinations of the collagen fiber apparatus have been performed using the split-line technique. The latter included mechanical tests (Woo et al., 1976; Roth and Mow, 1980) and computational modeling and finite element simulations (Li et al., 2009; Mononen et al., 2012), demonstrating that the direction of the split-lines is associated with biomechanical properties (Mononen et al., 2012). Furthermore, it is assumed that the main directions of joint movements are reflected by the split-line orientation (Bullough and Goodfellow, 1968; Goodwin et al., 2004; Leo et al., 2004; Böttcher et al., 2009).

Although some areas in the equine TMJ presented varying split-line patterns (caudal and rostral border of the articular disc, lateral zone of the articular tubercle, retroarticular process and caudomedial process of the mandibular head), most articular surfaces demonstrated consistent split-line patterns. There was high similarity between left and right TMJ within each horse and between horses

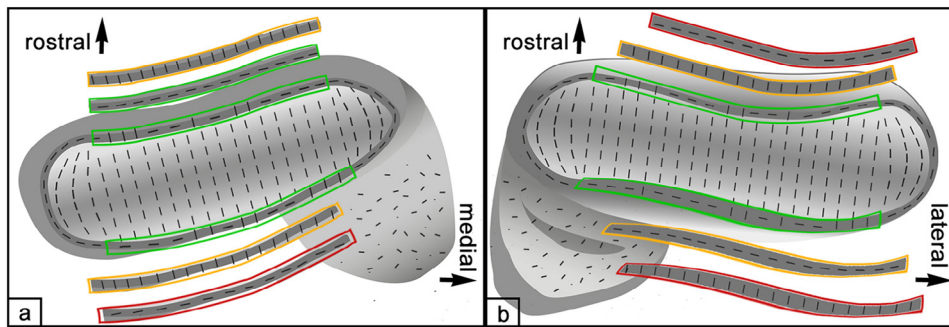


Fig. 4. Split-line patterns in the articular disc. The ventral (a) and dorsal (b) sides of the articular disc showed a constant pattern of large-sized rostrocaudal split-lines in the central aspect. At the lateral and medial sides, curved split-lines indicated the presences of attractive singular points. The colored boxes display alternative split-line arrangements at the rostral and caudal border of the articular disc, with green, yellow and red boxes in descending order of frequency.

in the sampled group, indicating that the masticatory movement was very uniform in the group of horses sampled.

The central two-thirds of the opposing articular surfaces of the articular tubercle, the articular disc and the mandibular head exhibited a homogenous rostrocaudal alignment. Due to this large portion of rostrocaudal split-lines, it is assumed that the central zone of the equine TMJ is preferentially designed for relative movements in a rostrocaudal course. Such a relative movement can result in a rotational movement of the mandible around a horizontal axis (opening and closing of the mouth) or in a rostrocaudal translation of the mandible along a rostrocaudal axis. These assumptions are in accordance with results from kinematic measurements of mandibular motion (Bonin et al., 2006). Unfortunately, the results presented in this study do not allow assigning rotational and translational movements to either the dorsal or the ventral joint compartment. Such an asymmetric location of movements has been found in the human TMJ (Perry, 2001). Furthermore, a deeper knowledge of normal TMJ biomechanics and mastication has assisted the detection of functional disturbances in humans (Okeson, 2013). This might be relevant for prospective diagnostic approaches in equine medicine.

A marked rostrocaudal mobility of the equine mandible of approximately 10 mm (Carmalt et al., 2003; Bonin et al., 2006) has been previously shown to play an important role during ingestion (Rucker, 2004). In order to achieve complete occlusion of the incisors while the horse is lowering his head for food intake, the mandible has to be able to move in rostral direction and to move back caudally by raising the head (Rucker, 2004). Considering that horses spend up to 17 h per day for food intake (McGreevy, 2012), the orientation of the collagen fiber apparatus reflects these functional requirements.

Previous split-line studies have shown that portions of articular surfaces that show consistent split-line patterns are exposed to significant loads (Below et al., 2002). Thus, the central zone of the equine TMJ appears subject to high biomechanical stress and relative movements in a rostrocaudal direction. This observation automatically implies that other movements in the equine TMJ are related to other areas than the central aspects.

According to the kinematic analysis of Bonin et al. (2006), minor translational motions in mediolateral and dorsoventral direction are observed and roll and yaw characteristics of rotational movements. Detailed coordination of such movements in an asymmetric left–right pattern are necessary to facilitate the complex equine chewing cycle (Collinson, 1994; Bonin et al., 2006; Staszuk et al., 2006).

Based on results from previous biomechanical studies using the split-line method (Werner et al., 1991; Lieser, 2003) and on the discovered split-line patterns in the present study, we conclude that the rotational movements are presumably located in the lateral and medial aspects of the articular surfaces, as the collagen fiber patterns indicate predominant movements around a dorsoventral axis.

Zones of major and minor stress can be detected by the path of split-lines. The appearance of attractive singular points, around which split-lines take a hairpin-like or curved course, suggest great stress (Werner et al., 1991; Lieser, 2003). Investigations of the functional anatomy of the human TMJ have demonstrated the appearance of load-bearing attractive singular points in the lateral aspect of the joint in all articular surfaces (i.e. the mandibular head and the articular tubercle and the articular disc; Werner et al., 1991). Remarkably, these regions are predominantly affected in degenerative TMJ diseases (Werner et al., 1991). In contrast to the human TMJ, no attractive singular points were observed on the articular surfaces covering the bony aspects of the equine TMJ. In contrast, attractive singular points were present in the equine articular disc, featuring curved courses of split-lines at its medial and lateral border. Corresponding zones of the mandibular head and the articular tubercle mainly presented punctiforme split-lines. Such split-lines reveal an intersection of collagen fibers at an angle of approximately 90° (Petersen and Tillmann, 1998a), indicating a local compressive strain rather than a dragging strain (Lieser, 2003). The observed combination of attractive singular points in the peripheral zones of the equine articular disc, with punctiforme split-lines in the corresponding zones of the articular tubercle and the mandibular head, suggests that rotational movements around a dorsoventral axis occur in these zones.

The presence of attractive singular points in the lateral and medial zones of the equine articular disc suggests that particular biomechanical strains act on these areas. A recent study analyzing more than 1000 equine TMJ by computed tomography has demonstrated a region of discrete linear mineralization in the articular disc (Carmalt et al., 2016), which closely resembles the lateral attractive singular point determined in the present study. Carmalt et al. (2016) demonstrated that the appearance of this hyperdense zone is related to increasing age. It is likely that this age-dependent occurrence reflects the accumulation of ongoing mechanical stress, as previously demonstrated in the human TMJ (Jibiki et al., 1999). However, no corresponding CT hyperdensity was detected close to the medial attractive singular point, which also presumably receives high biomechanical forces. However, to elucidate ultrastructural changes due to functional adaptations or pathological processes, histological investigations are required. Besides the previously mentioned load-dependent explanation of the curved path of split-lines, there might also be an explanation based on the morphology of the articular disc. The latter structure causes a change of axial forces in tangential forces resulting in circular tensile load, and hence, a curved path of split-lines (Petersen and Tillmann, 1998b). To limit potential movements in mediolateral direction, fixation of the articular disc is required, similar to the menisci of the human knee. To the authors' knowledge, there is no study

describing the mobility of the equine articular disc, and it is generally accepted that the articular disc is attached to the TMJ joint capsule in its entire circumference (Rodríguez et al., 2006).

The minor translational movements of the mandible in mediolateral direction (Bonin et al., 2006) may be particularly reflected in the rostral and caudal border of the articular disc, because in these parts of the TMJ, mediolateral orientated split-lines were found. These zones showed multiple variations, indicating that the movements and forces in these regions were very variable between horses. Similar conclusions could be proposed for the articular surfaces of the retroarticular process. The mandibular fossa showed an inconsistent pattern of split-lines and presented a relatively thin layer of fibrous cartilage. These features suggest that the mandibular fossa was occupied by the mandibular head during phases of mandibular rest rather than during mandibular movements.

Conclusions

This study reports the preferred movement directions and the distribution of biomechanical stresses in different regions of the equine TMJ. The results are in accordance with previous results from kinematic studies, and could provide a substantial basis for further studies focusing on histological and pathohistological changes within the equine TMJ.

Conflict of interest statement

None of the authors of this paper has a financial or personal relationship with other people or organizations that could inappropriately influence or bias the content of the paper.

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