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Dynamic Spatial Tuning of Cervical Muscle Reflexes to Multidirectional Seated Perturbations

Jóna Marín Ólafsdóttir, MSc,* Karin Brodin, PhD,* Jean-Sébastien Blouin, PhD,† and Gunter P. Siegmund, PhD‡

Study Design. Human volunteers were exposed experimentally to multidirectional seated perturbations.

Objective. To determine the activation patterns, spatial distribution and preferred directions of reflexively activated cervical muscles for human model development and validation.

Summary of Background Data. Models of the human head and neck are used to predict occupant kinematics and injuries in motor vehicle collisions. Because of a dearth of relevant experimental data, few models use activation schemes based on *in vivo* recordings of muscle activation and instead assume uniform activation levels for all muscles within presumed agonist or antagonist groups. Data recorded from individual cervical muscles are needed to validate or refute this assumption.

Methods. Eight subjects (6 males, 2 females) were exposed to seated perturbations in 8 directions. Electromyography was measured with wire electrodes inserted into the sternocleidomastoid, trapezius, levator scapulae, splenius capitis, semispinalis capitis, semispinalis cervicis, and multifidus muscles. Surface electrodes were used to measure sternohyoid activity. Muscle activity evoked by the perturbations was normalized with recordings from maximum voluntary contractions.

Results. The multidirectional perturbations produced activation patterns that varied with direction within and between muscles. Sternocleidomastoid and sternohyoid activated similarly in forward and forward oblique directions. The semispinalis capitis, semispinalis cervicis, and multifidus exhibited similar spatial patterns and preferred directions, but varied in activation levels. Levator scapulae and trapezius activity generally remained low, and splenius capitis activity varied widely between subjects.

Conclusion. All muscles showed muscle- and direction-specific contraction levels. Models should implement muscle- and direction-specific activation schemes during simulations of the head and neck responses to omnidirectional horizontal perturbations where muscle forces influence kinematics, such as during emergency maneuvers and low-severity crashes.

Key words: impact biomechanics, cervical muscles, reflex, EMG, spatial tuning patterns, multidirectional perturbations, numerical model validation.

Level of Evidence: N/A

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From the *Department of Applied Mechanics, Chalmers University of Technology, Gothenburg, Sweden; †School of Kinesiology, University of British Columbia, Vancouver, British Columbia, Canada; and ‡MEA Forensic Engineers & Scientists, Richmond, British Columbia, Canada.

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Address correspondence and reprint requests to Gunter P. Siegmund, PhD, MEA Forensic Engineers & Scientists, 11-11151 Horseshoe Way, Richmond, British Columbia, Canada, V7A 4S5; E-mail: gunter.siegmund@meaforensic.com

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Human head and neck models for predicting occupant kinematics and injuries in motor vehicle collisions have increasingly included active cervical musculature in an effort to improve model biofidelity.¹⁻⁸ Various techniques have been used to simulate the active muscle response in the past, including predetermined activation curves^{3,4,6-8} and minimizing muscle force or fatigue during postural control under gravity loading.^{2,5} More recent methods have optimized activation levels to fit the model's kinematic responses to volunteer corridors¹ and implemented feedback control that regulates muscle activation to simulate the central nervous system.^{9,10} Despite the increasing complexity of these muscle recruitment schemes, most models assumed equal activation levels for all muscles within presumed agonist or antagonist groups. To overcome this limitation, a controller capable of simulating individual muscle activation has been developed.¹¹

Despite these various efforts to model active cervical muscle responses, few of the proposed activation schemes are based on or compared with experimental data from *in vivo* recordings of muscle activation before and during loading. The main reason for this shortcoming is a dearth of relevant

experimental data.^{1,2,11,12} Electromyographic (EMG) activity in the cervical muscles of volunteers has been recorded during low-velocity impacts or perturbations, however most of these studies are confined to sagittal plane loading^{13–29} with fewer studies assessing lateral or oblique loading.^{30–34} More importantly, most of these studies have used surface EMG electrodes that capture superficial neck muscles but not deep muscles. One study, however, used a combination of surface and indwelling electrodes to study reflex muscle activation patterns in 9 superficial and deep muscles in subjects exposed to a forward low-speed perturbation while seated on a sled-mounted car seat.³⁵ Despite being limited to 3 male subjects and a single forward perturbation, this study showed that activation levels were not uniform within the agonist and antagonist muscle groups; instead each muscle exhibited its own distinct activation pattern.³⁵ These findings highlight the importance of *in vivo* data for the development and validation of numerical neck muscle models.

The pattern of cervical muscle activation varies with the direction of the intended or imposed head motion. Spatial tuning curves developed from various isometric tasks have shown that each neck muscle has its own preferred activation direction.^{36–39} To date, however, the spatial tuning patterns and preferred directions of cervical muscles have not been quantified for reflex activations during seated perturbations, although this information is key for developing and validating omnidirectional neck muscle models. Thus, the objectives of this study were to determine the activation patterns, spatial distribution and preferred directions of cervical muscles that were reflexively activated by seated perturbations in the horizontal plane.

MATERIALS AND METHODS

Nine subjects participated in the experiment, but data from only 8 subjects (6 males and 2 females, 31 ± 6 yr, 175 ± 7 cm, 77 ± 6 kg) were included in the analysis. Data from 1 subject were removed because of substantial motion and electrical artifacts. All subjects were without history of neck/back pain or injury and provided informed consent. The UBC Clinical Research Ethics Board approved the study. Data from the same group of subjects exposed to different experimental conditions have been published previously,^{35,36,40} and a small subset of the current data (5 subjects, 3 perturbation directions) have appeared in a prior model validation study.¹²

EMG activity was measured with wire electrodes (Stablohm 800A; California Fine Wire, Grover Beach, CA) inserted under ultrasound guidance (Sonos 5500; Agilent Technologies, Andover, MA) into the left sternocleidomastoid (SCM), trapezius (Trap), levator scapulae (LS), splenius capitis (SPL), semispinalis capitis (SCap), semispinalis cervicis (SCerv), and cervical multifidus (CM) muscles (Figure 1).^{35,36} All wires were inserted at the C4–C5 level with an additional CM insertion at C6–C7. Left sternohyoid (STH) muscle activity was measured with surface electrodes (H69P; Kendall-LTP, Huntington Beach, CA). Wire signals were amplified and band-pass filtered (30–1000 Hz) using a Neurolog system (Digitimer Ltd., Welwyn Garden City, United Kingdom) and surface signals were amplified and band-pass filtered (10–1000 Hz)

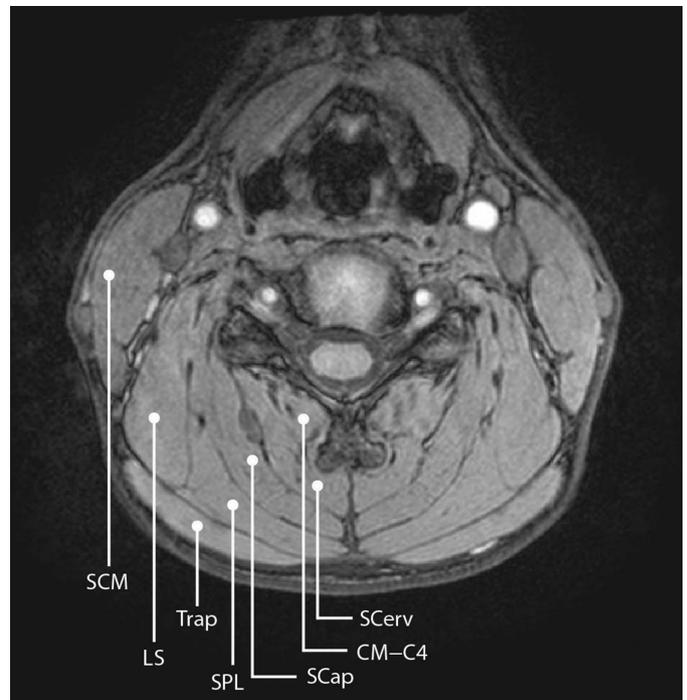


Figure 1. Magnetic resonance image taken at the C4 level illustrating the location of the wire electrodes inserted into the left cervical muscles. Left sternohyoid activity was measured with surface electrodes. SCM indicates sternocleidomastoid; LS, levator scapulae; Trap, trapezius; SPL, splenius capitis; SCap, semispinalis capitis; SCerv, semispinalis cervicis; CM-C4, cervical multifidus C4–C5 level.

using a Myosystem 1400 (Noraxon, Scottsdale, AZ) before being acquired at 2 kHz.

Subjects were seated unrestrained in a sled-mounted car seat (seatback angle = 27° rearward of vertical) without a head restraint, depicted in Figure 2. They were instructed to face forward, rest their arms on their lap, and relax their face and neck muscles. Subjects experienced 3 perturbations ($a_{\max} = 1.55g$, $\Delta v = 0.50$ m/s) in each of 8 directions

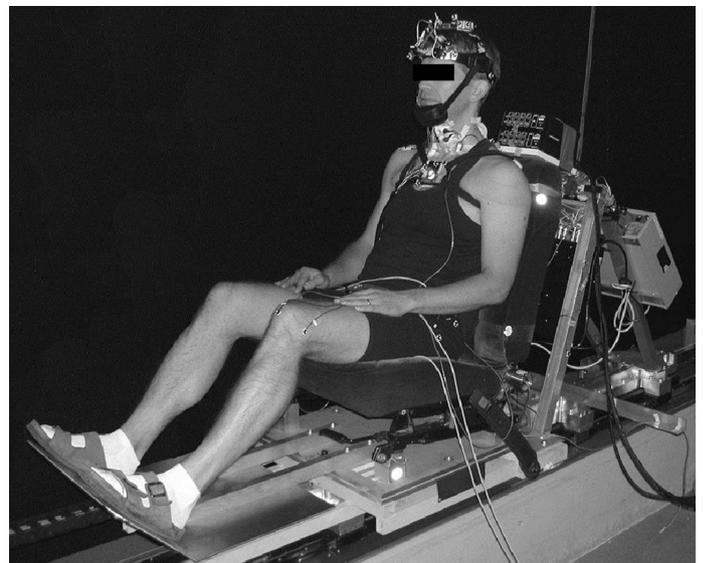


Figure 2. Experimental sled configuration.

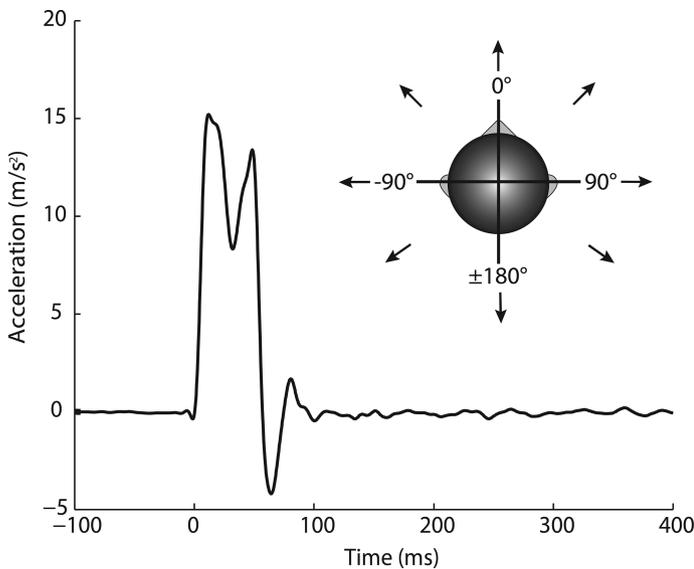


Figure 3. Sled acceleration and perturbation directions. Same acceleration pulse was applied in all perturbation directions.

in intervals of 45° from forward, which was defined as 0° (Figure 3). Perturbations were presented without warning in 4 randomized blocks of 6 trials with opposite directions (*e.g.*, 0° and 180° , or 90° and -90°) presented pseudorandomly within each block. Before the perturbation tests, subjects performed isometric maximum voluntary contractions (MVCs) in the 8 corresponding directions. To ensure a habituated, startle-free response, subjects experienced 16 forward perturbations of the same intensity prior to the multidirectional perturbations.^{25,26}

All EMG data were high-pass filtered (wire, 50 Hz³⁵; surface, 20 Hz⁴¹) to remove motion artifacts before calculating their root-mean-square (20-ms window). Perturbation EMG data were normalized with the maximum 1-second moving average root-mean-square EMG observed for each muscle across all 8 MVC directions. The following missing or contaminated data were excluded: all SPL data from 1 subject, all STH data from another subject, 1 right lateral (90°) trial from a third subject, and 2 forward right ($+45^\circ$) trials from a fourth subject.

To concentrate our analysis on reflex muscle activity and minimize contribution from voluntary muscle activity,^{42,43} we examined the first burst of activity (80–140 ms) after the perturbation. To examine each muscle's dynamic spatial tuning pattern, the median normalized root-mean-square activity (20-ms window) for each muscle across all subjects in each perturbation direction was extracted at 90, 110, and 130 milliseconds (covering 80–100 ms, 100–120 ms, and 120–140 ms, respectively). To study the difference in directional tuning between muscles the orientation, referred to as the preferred direction, of each spatial tuning pattern was determined. The preferred direction was defined as the mean vector direction of the tuning pattern. The preferred direction for the MVCs was calculated similarly and was based on the median maximum 1-second moving average activity of each

muscle. Subject-specific preferred directions were determined from the vector sum of the median EMG from the 3 repeated trials in each direction. The significance of the population's mean preferred direction was tested using a Rayleigh test, where significance indicated a nonuniform distribution of preferred directions.⁴⁴ Focus, which quantifies the variability about each preferred direction, was computed by dividing the vector sum of the 8 direction-specific EMG values by its arithmetic sum. Focus approaches zero when a muscle is equally active in all directions or symmetrically active and 1 when a muscle is primarily active in 1 direction.

RESULTS

Before perturbation onset, median activation levels were between 0.6% and 3.7% MVC when averaged over 500 milliseconds. During the perturbation, activation patterns varied with direction within and between muscles (Figures 4, 5). Anterior muscles (SCM and STH) were most active during forward (0°) and forward oblique ($\pm 45^\circ$) perturbations whereas posterior muscles, aside from SPL, were most active during rearward (180°) and rearward oblique ($\pm 135^\circ$) perturbations. A combination of anterior and posterior muscles was active during lateral ($\pm 90^\circ$) perturbations.

Because similar spatial patterns of muscle activation were observed in most muscles at all 3 time points (Figure 5; Table 1), the results presented here concentrated on the 110-millisecond time point. At this time, the resultant head rotation, excluding axial rotation, remained small ($1.0^\circ \pm 0.6^\circ$) compared with its maximum ($15.1^\circ \pm 5.2^\circ$). Axial head rotation also remained small ($0.3^\circ \pm 0.2^\circ$) compared with its maximum ($5.1^\circ \pm 3.0^\circ$). SCM and STH had similarly high maximum activation levels (61% MVC and 63% MVC, respectively; Figure 5) and similar preferred directions (Tables 1, 2). SCM remained active in all but 2 perturbation directions ($+135^\circ$ and 180°), whereas STH was primarily active only between $\pm 45^\circ$ and thus had a higher focus (Table 3). The SCap, SCerv, and CM-C6 exhibited similar spatial patterns, preferred directions (-158° to -172°), and focus values, but maximum activation levels varied between these 3 muscles (36%–89% MVC; Figure 5). CM-C4 activation levels were low except in rearward perturbations, and were more bilaterally symmetrical than other posterior muscles. LS and TRAP remained below 8% MVC in all perturbation directions except for TRAP in the -90° and -135° directions (10% MVC and 16% MVC, respectively).

Despite its posterior anatomical location, median activation levels for SPL were between 19% and 27% MVC during forward (0°), forward oblique ($\pm 45^\circ$), and lateral ($\pm 90^\circ$) perturbations, but below 15% MVC in rearward (180°) and rearward oblique ($\pm 135^\circ$) directions (Figure 5). Although SPL's preferred direction was generally anterolateral, this varied between the 3 time points by 106° (Table 1), which was considerably larger than the 27° range for other muscles recruited more than 20% MVC. SPL also had the largest range of subject-specific preferred directions and was without a significant common mean (Table 2). Four subjects had an ipsilateral anterolateral preference (focus, 0.07–0.51)

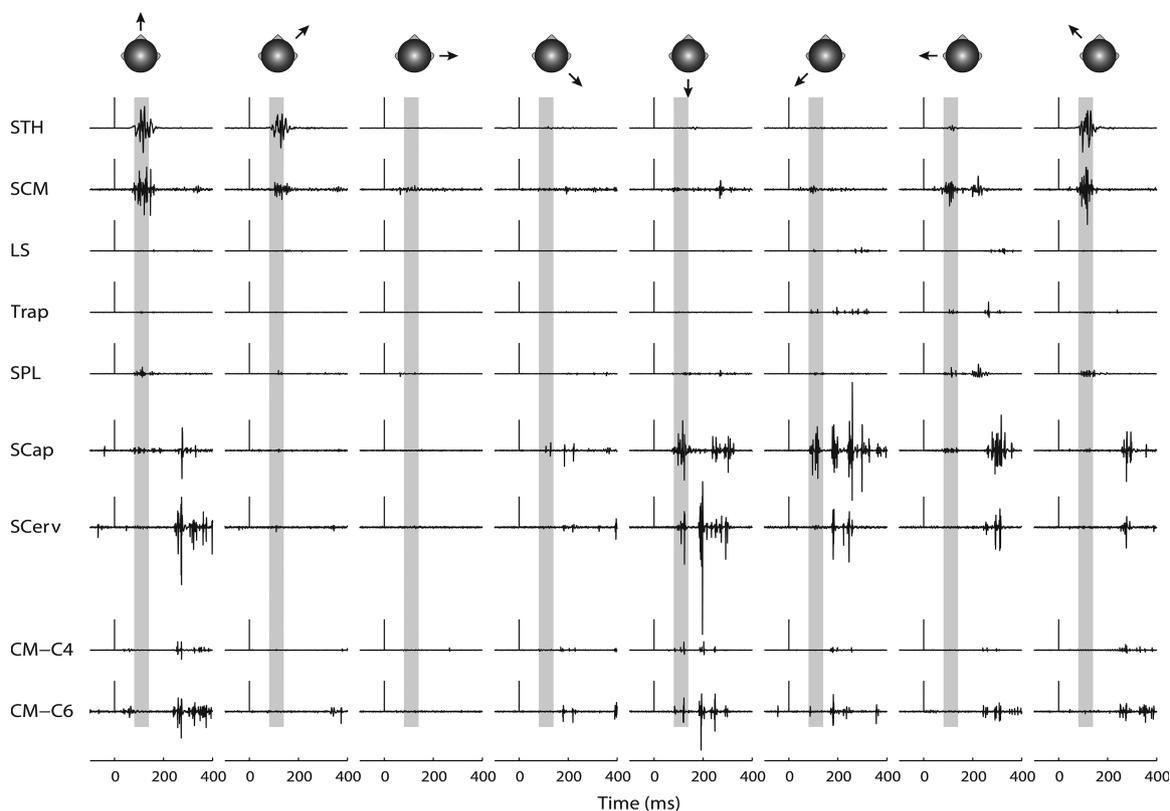


Figure 4. Exemplar raw EMG for a single subject during each perturbation direction (acceleration direction indicated by arrow). The vertical lines indicate $t = 0$ ms, and the shaded areas from 80 to 140 ms highlight the investigated intervals of 90, 110, and 130 ms. SCM indicates sternocleidomastoid; STH, sternohyoid; LS, levator scapulae; Trap, trapezius; SPL, splenius capitis; SCap, semispinalis capitis; SCerv, semispinalis cervicis; CM-C4, cervical multifidus C4–C5 level; CM-C6, cervical multifidus C6–C7 level; EMG, electromyography.

and 3 subjects had a contralateral posterolateral preference (focus, 0.13–0.66; perimeter tick marks in Figure 5). A similar bimodal pattern was present in SPL's spatial focus (Table 3), but involved different subjects. SPL exhibited the largest difference (72°) in its median preferred directions between the isometric (MVCs) and dynamic (110 ms) conditions, whereas this difference remained within 18° for all other muscles (Table 1).

DISCUSSION

On the basis of neck muscle reflexes evoked in seated volunteers accelerated in multiple horizontal directions, we developed dynamic spatial tuning curves that showed variable activation amplitudes and preferred directions for 9 superficial and deep neck muscles. These direction- and muscle-specific contraction levels highlight the importance of modeling individual muscles rather than groups of anatomically adjacent muscles during simulations of the head and neck responses to omnidirectional horizontal perturbations where muscle forces matter, such as emergency maneuvers and low-severity crashes. Therefore, this study provides muscle activation data relevant to numerical models used for low g -level scenarios and for the onset of crash simulations, before voluntary bracing or extensive head rotation develops.

Our acceleration pulse ($a_{\max} = 1.55g$, $\Delta v = 0.50$ m/s) was less severe than many low-speed crashes, but more severe,

albeit of shorter duration, than emergency braking events. Although muscle responses have been shown to scale with both pulse acceleration and speed change,^{18,23,28} these prior data were acquired using surface electrodes and thus it remains unclear whether similar scaling occurs in deep neck muscles. The muscles studied here form a large proportion of the total muscle area at the C4–C5 level, however the dynamic spatial response of the remaining cervical muscles remains unknown. Although our subject group included both female and male volunteers, we did not have sufficient subjects to assess gender differences. Qualitatively, however, the female preferred direction data (highlighted by perimeter plus signs in Figure 5) were similar to the male data for all muscles. Only 1 initial posture was tested here, and the potential influence of different postures, such as the arms raised and grasping a steering wheel, remains to be investigated.

From a clinical perspective, our findings reveal that large and spatially varying levels of reflex muscle activity can be evoked by low-speed collisions from different directions. Even at the low-speed changes applied here, some subjects exhibited contraction levels above 100% MVC. At increased speed changes, it is possible that even higher contractions levels could be reached.^{18,23,28} Because the supramaximal contractions were direction-specific, clinicians need to consider impact direction when assessing neck muscles in patients. Moreover, the SCM, STH, and SCap muscles exhibited the

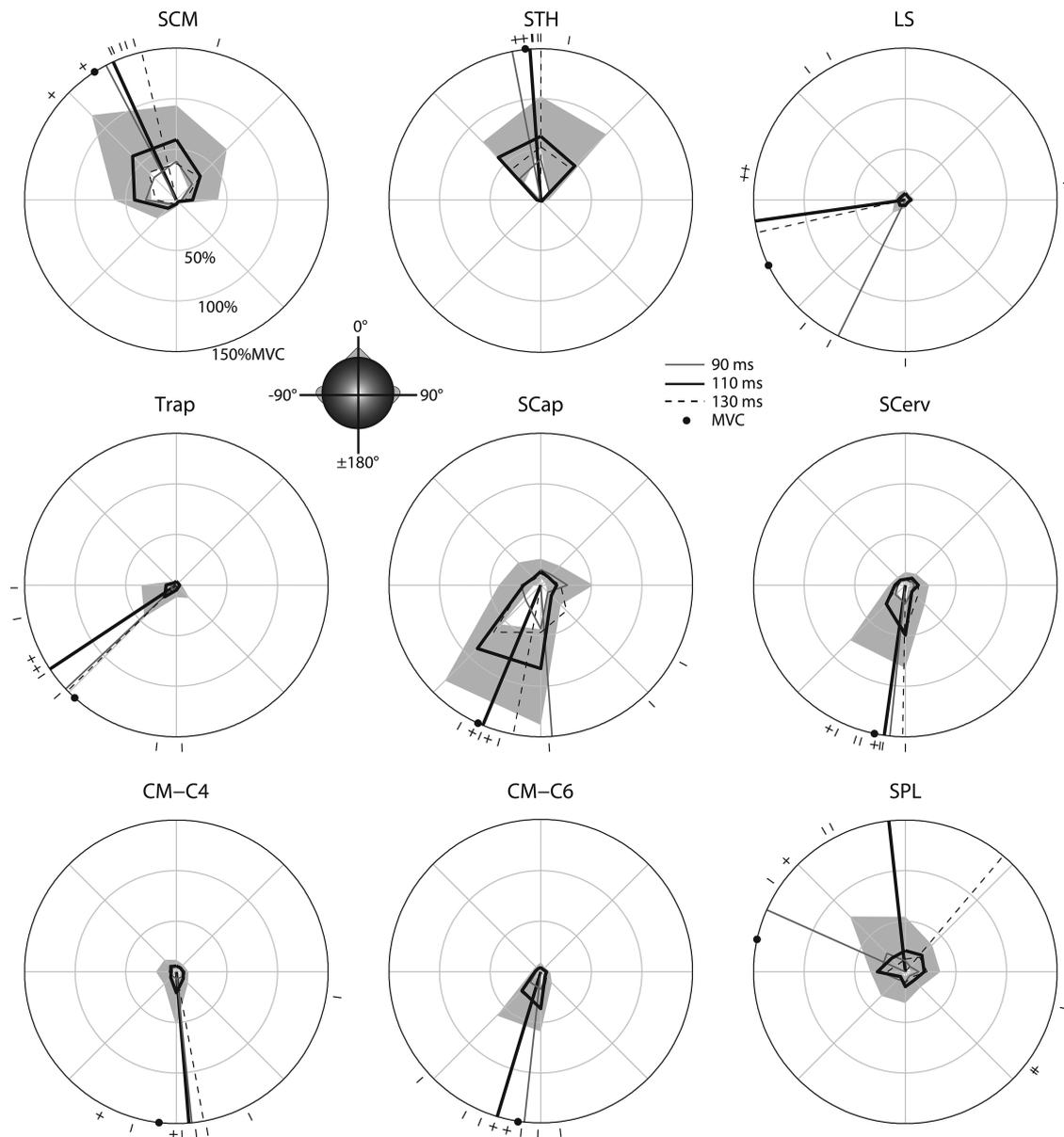


Figure 5. Group median muscle-specific preferred directions and dynamic spatial tuning patterns of the normalized (%MVC) muscle activation levels at 90, 110, and 130 ms. The shaded areas represent the interquartile range (25th–75th percentile) of activation levels at 110 ms. Preferred directions for the dynamic responses at all 3 time points are shown by the radial lines and for MVCs by the perimeter black dots. Subject-specific preferred directions at 110 ms are shown as perimeter tick marks (line for males, plus for females). SCM indicates sternocleidomastoid; STH, sternohyoid; LS, levator scapulae; Trap, trapezius; SPL, splenius capitis; SCap, semispinalis capitis; SCerv, semispinalis cervicis; CM–C4, cervical multifidus C4–C5 level; CM–C6, cervical multifidus C6–C7 level; MVC, maximum voluntary contraction.

highest activation levels and therefore may be most susceptible to eccentric contraction injury.

Most muscles we measured showed dynamic spatial patterns consistent with their anatomical location and presumed function. LS and Trap activity generally remained low, consistent with previous observations during voluntary cervical motion.^{38,45,46} These findings indicate that LS and Trap play a limited role in head stabilization during both voluntary and externally induced movements. In contrast, the 2 anterior muscles (STH and SCM) activated strongly in perturbation directions with a forward component. Although STH's main function is reportedly to depress the hyoid bone,⁴⁷ its

consistent activation here and in prior studies²² suggests that it also plays a role in head stabilization during forward and forward-oblique ($\pm 45^\circ$) perturbations. This role is supported by modeling work showing that the relatively large moment arm of the infrahyoid muscles allow them to contribute about one-quarter of the total flexor moment of the cervical spine.^{5,48} The dynamic directional preference we observed for SCM activation was consistent with prior isometric data,^{36–39} which included low activity in extension and posterolateral extension to the contralateral side.

The posterior muscles SCap, SCerv, and CM generated similar dynamic spatial patterns, preferred directions and

TABLE 1. Preferred Directions (°) of the Median Spatial Tuning Patterns for Each Muscle During the MVC Task and Perturbation (Black Perimeter Dot and Radial Lines Depicted in Figure 5, Respectively)

Muscles	Perturbation			
	MVC	90 ms	110 ms	130 ms
	(°)	(°)	(°)	(°)
SCM	-33	-28	-25	-13
STH	-6	-10	-4	0
LS	-116	-154	-98	-102
Trap	-138	-133	-124	-134
SCap	-156	176	-158	-170
SCerv	-168	-174	-172	-179
CM-C4	-173	174	175	170
CM-C6	-171	-174	-163	-163
SPL	-78	-66	-6	40
Angular difference from 110-ms time point*				
Mean	9	14	...	7
SD	6	19	...	4

*Absolute difference. SPL was excluded from the calculation.
 SCM indicates sternocleidomastoid; STH, sternohyoid; LS, levator scapulae; Trap, trapezius; SCap, semispinalis capitis; SCerv, semispinalis cervicis; CM-C4, cervical multifidus C4-C5 level; CM-C6, cervical multifidus C6-C7 level; SPL, splenius capitis; MVC, maximum voluntary contraction.

spatial foci (except CM-C4) that were also similar to those reported previously for isometric tasks.³⁶⁻³⁹ Despite the similarities, the levels of activation varied considerably between these 3 muscles, with SCap having the highest activity and CM the lowest activity. This activation pattern is perhaps morphologically and mechanically logical given SCap's large physiological cross-sectional area, large moment arm,⁴⁹⁻⁵¹ and therefore its high moment-generating capacity. Greater activity in CM at the C6 level than at the C4 level might similarly be explained by the larger moment generating capacity at the lower level.⁵¹ These activation patterns suggest that the central nervous system recruits the posterior muscles, and perhaps even different segments of these muscles, on the basis of their mechanical advantage to resist motion in specific directions. This proposition is supported by other isometric data³⁶ (from the same group of subjects) showing that, as the exerted force increased, the central nervous system switched from evenly distributing muscle recruitment to recruiting muscles that from an anatomical perspective could contribute more strongly to the force being generated. Recruitment based on mechanical advantage has also been observed in other muscle systems, such as the deep trunk muscles in anticipatory postural adjustments⁵² and intercostal muscles during respiration.⁵³ Nonetheless, others have pointed out that mechanical advantage may not be the only factor that determines cervical muscle recruitment,³⁸ and further work is needed to examine the dynamic spatial tuning patterns in the context of 3-dimensional head and neck mechanics.³⁸

Unlike the other muscles tested here, SPL's preferred directions for the median dynamic response, subject-specific dynamic responses, and median MVC response did not match its posterolateral anatomical location. Instead, we found that

TABLE 2. Preferred Directions (°) of the Spatial Tuning Patterns for Each Muscle and Subject During Perturbation (110 ms, Perimeter Tick Marks Depicted in Figure 5) and the Group Mean ± AD

Muscles	Subjects								
	S01	S02	S03	S04	S05	S06	S07	S08	Mean ± AD
	(°)	(°)	(°)	(°)	(°)	(°)	(°)	(°)	(°)
SCM	-15	-18	-35	-23	-20	-50	15	-24	-20* ± 17
STH	10	...	-6	-1	0	-9	-3	-3	-2* ± 6
LS	-152	84	-82	-37	-141	-79	±180	-28	-100 ± 63
Trap	-173	-133	-121	-124	178	-117	-91	-102	-130* ± 29
SCap	-165	137	-161	-150	119	-155	177	-158	-178* ± 31
SCerv	-172	-162	-152	-171	-164	-169	-155	±180	-166* ± 9
C4	169	153	-152	178	173	-179	-164	99	171* ± 29
C6	-173	-179	-168	173	-152	-163	-158	-132	-164* ± 16
SPL	...	-30	-47	128	-56	127	103	-27	2 ± 71

*Significant mean preferred direction (P < 0.05).

SCM indicates sternocleidomastoid; STH, sternohyoid; LS, levator scapulae; Trap, trapezius; SCap, semispinalis capitis; SCerv, semispinalis cervicis; CM-C4, cervical multifidus C4-C5 level; CM-C6, cervical multifidus C6-C7 level; SPL, splenius capitis; AD, angular deviation.

TABLE 3. Focus of Subject-Specific Spatial Tuning Patterns for Each Muscle at the 110-ms Time Point, and the Group Mean \pm SD

Muscles	Subjects								Mean \pm SD
	S01	S02	S03	S04	S05	S06	S07	S08	
SCM	0.53	0.51	0.64	0.62	0.25	0.26	0.35	0.55	0.46 \pm 0.16
STH	0.76	...	0.73	0.78	0.78	0.69	0.56	0.76	0.72 \pm 0.08
LS	0.18	0.43	0.42	0.12	0.67	0.24	0.21	0.31	0.32 \pm 0.18
Trap	0.74	0.16	0.57	0.57	0.60	0.70	0.32	0.47	0.52 \pm 0.20
SCap	0.40	0.36	0.46	0.45	0.31	0.69	0.51	0.63	0.48 \pm 0.13
SCerv	0.73	0.35	0.40	0.37	0.33	0.56	0.54	0.19	0.43 \pm 0.17
C4	0.24	0.23	0.22	0.52	0.61	0.29	0.42	0.04	0.32 \pm 0.19
C6	0.52	0.26	0.72	0.53	0.63	0.69	0.57	0.09	0.50 \pm 0.22
SPL	...	0.51	0.51	0.13	0.07	0.14	0.66	0.43	0.35 \pm 0.23

Focus varies from 0 (activation level the same in all directions) to 1 (activation occurs in 1 direction only).

SCM indicates sternocleidomastoid; STH, sternohyoid; LS, levator scapulae; Trap, trapezius; SCap, semispinalis capitis; SCerv, semispinalis cervicis; CM-C4, cervical multifidus C4-C5 level; CM-C6, cervical multifidus C6-C7 level; SPL, splenius capitis; SD, standard deviation.

SPL's preferred direction was generally anterolateral, with 3 subjects exhibiting a posterolateral preference, but to the contralateral side. These contralateral findings were not explained by low-spatial focus; indeed one of these subjects had the highest spatial focus observed in SPL. Similar inter-subject variability for the SPL muscle has been reported in the same subjects performing different isometric tasks^{35,36} and in different subjects performing a similar isometric task.^{39,45} In contrast, other researchers have observed lateral and posterolateral preferred directions that suggest the expected behavior for SPL during isometric contractions.^{37,38} The reason for these differences between studies remains unclear. Recording from different functional compartments within SPL in different subjects was proposed as one possible explanation³⁶; however, subsequent work suggests that this explanation is incorrect.⁵⁴ Another possible explanation is that SPL acts primarily as an axial rotator rather than extensor,⁵⁴ which may suggest that some subjects were reflexively stabilizing against perturbation-induced axial head rotation. Nevertheless, the role of SPL during multidirectional dynamic loading is not fully understood and therefore its activation patterns should be treated cautiously until additional information is available.

Numerical models with active muscles should account for the distribution of activity between the different cervical muscles observed here to predict head-neck motion for different impact directions. In the past, most models have assumed uniform muscle activity within each of the presumed agonist and antagonist muscle groups for simulated impacts in the sagittal plane.^{1,3,4,6-9} On the basis of the current work, this assumption might be appropriate for muscles such as the STH and SCM, but it is an oversimplification when applied to posterior muscles. Moreover, this simplifying assumption becomes even less tenable, even for the anterior muscles, when considering

other impact directions. On the basis of this study, numerical models that include a representation of the neuromuscular control of cervical muscles through feedback need to employ strategies that can account for the directional preferences of these muscles. For posterior muscles, except SPL, the same directional strategy could be used for the different muscles, but with the level of activation related to the mechanical advantage of each muscle. This proposed control approach integrates the sensory feedback mechanism of the central nervous system with the biomechanical constraints of the head-neck structure and might be an advantageous method for simulating the control of individual cervical muscles in different motion planes.

CONCLUSION

Most of the cervical muscles studied here showed a directional preference during multidirectional perturbations. Different neck muscles responded with different levels of activation that seemed to be related to their mechanical advantage. The data can be used to improve, tune or validate current and future numerical models that aim to predict head-neck motion and/or the influence of muscle tension on injury mechanisms in various loading scenarios. On the basis of our findings, neck models should implement muscle- and direction-specific activation schemes to more faithfully mimic the actual human responses to seated perturbations.

➤ Key Points

- ❑ Cervical muscles generate dynamic spatial patterns with distinct preferred directions during multidirectional perturbations.

- ❑ Individual muscles belonging to the same agonist or antagonist group exhibit different activation levels for some perturbation directions. Simulating muscle groups with uniform activity levels is an oversimplification.
- ❑ The sternohyoid muscle contributes to head stabilization during forward and forward oblique perturbations, whereas the levator scapulae and trapezius muscles have a limited role in all directions.

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