

Vestibular contributions to cycling balance across different speeds

Master's thesis

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Vestibular contributions to cycling balance across different speeds

How does vestibular perturbation affect upper-body muscle activity and balance-related kinematics during seated cycling and is this balance-related effect modulated by speed?

By

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Abstract

Balance control relies on the integration of visual, proprioceptive and vestibular information, with the relative contribution of these sensory signals depending on task demands. Although vestibular contributions to standing and walking have been extensively investigated, their role in cycling balance remains largely unknown. This study used electrical vestibular stimulation (EVS) to introduce a vestibular-driven error signal and investigate how vestibular perturbations influence balance-related kinematics and upper-body muscle activity during seated cycling and whether these responses are modulated by cycling speed. Sixteen healthy young adults performed non-peddalling treadmill cycling trials at 5, 10 and 18 km/h under both non-EVS and stochastic EVS conditions. Steer and roll kinematics and activity of six upper-body muscles involved in steering and postural stabilization were recorded. Time-domain measures quantified changes in response magnitude, while gain and coherence between EVS and steering rate, roll rate and muscle activity were calculated in the frequency domain to characterize vestibular coupling. EVS significantly increased root mean square (RMS) steering rate and RMS roll rate and increased mean activity in all investigated muscles except the erector spinae. RMS steering rate and EVS-steering gain decreased significantly with increasing cycling speed, whereas RMS roll rate and EVS-roll gain were not significantly affected by speed. Significant EVS coupling was observed with steering rate over approximately 0.5-8 Hz and roll rate over 0.5-4 Hz. Vestibular coupling with muscle activity was generally low and muscle-specific, with coherence observed over 0.5-3 Hz for flexor digitorum, 0.5-6 Hz for biceps brachii and erector spinae and 0.5-8 Hz for triceps brachii, deltoid anterior and deltoid posterior. Muscle response gain decreased significantly with increasing cycling speed for all investigated muscles, while coherence was largely maintained across speeds. Together, these findings demonstrate that vestibular perturbations systematically influence cycling balance through steer and roll kinematics and coordinated upper-body muscle responses. Greater steering and muscular response gains at lower cycling speeds, despite largely preserved coherence, suggest that vestibular input remains coupled to balance control across speeds while the magnitude of the resulting motor responses is modulated according to the dynamic stabilization demands of the bicycle-rider system.

Preface

This thesis marks the end of my graduation project and the closing chapter of my studies. I would like to thank Jason and Patrick for trusting me with this project and for their guidance throughout the process and also Matto for joining our (almost) weekly meetings in which I could ask questions, discuss ideas and was challenged to think further. I would also like to thank Martin, Matto and Patrick for helping me during the experiments. I really appreciated having an extra pair of hands and someone to think along with me whenever things did not go as planned. A special thanks to Martin for helping me get started with the data analysis after the pilot measurements, when I was feeling a bit overwhelmed by how to approach everything and to Jason and Benjamin for helping me with the more technical aspects of the OptiTrack system and treadmill. And thanks to Mark for taking the time to join my graduation committee.

Thank you to all participants who took part in the experiments for their time and patience, especially when the equipment did not always cooperate. Furthermore, thanks to everyone in the Bicycle lab for always being available to discuss ideas or problems and to 'the writing club' for making the process of getting that first version of my thesis on paper a little easier. A special thanks to Dana, with whom I could also share the more personal ride of the past three quarters of a year. It was really nice to have such a friend close by.

Finally, I would like to thank my parents and boyfriend for always being there to listen and support me when needed. Looking back, I am proud of what I have accomplished and of the thesis that I have put together. Although it was my own journey, I am very grateful to everyone who contributed to it in their own way.

1 Introduction

Human balance control relies on the integration of visual, proprioceptive and vestibular information to maintain stability during movement [1,2]. The relative contribution of these sensory systems is task dependent and adapts according to changes in biomechanical constraints and stabilization demands [1]. Among these sensory modalities, vestibular information provides feedback on linear and rotational head motion relative to Earth's gravitational field and contributes to postural regulation through vestibulospinal pathways that influence muscle activity and body kinematics [2]. While vestibular contributions to balance control have been extensively investigated during standing and walking, far less is known about their role during cycling, where balance control is speed dependent [3-5].

Electrical vestibular stimulation (EVS) is commonly used to investigate vestibular contributions to balance control by introducing a controlled perturbation of vestibular afferent signals [2]. By relating the EVS input to body motion and muscle activity, gain and coherence analyses can be used to characterize the magnitude and frequency characteristics of vestibular contributions to balance control. Coupling between the EVS input and a measured output indicates that the output systematically responds to the vestibular perturbation, providing evidence of a vestibular contribution to that response [6]. Studies employing EVS during standing and walking have shown that vestibular responses vary between muscles and depend on stimulus frequency and movement phase. Furthermore, these responses are modulated by the stabilization demands of the task, being strongest when active balance control is required and reduced when external support decreases the need for active stabilization [6,7].

Compared with standing and walking, cycling provides a distinct balance task in which the rider and bicycle form a dynamically coupled bicycle-rider system [5]. Lateral stability is maintained primarily by steering into an emerging roll, while coordinated trunk and limb movements provide additional contributions to balance control [3,4,8]. Upper-body muscles contribute to this control by supporting the rider and generating forces at the handlebars to control steering movements [9]. Although bicycles are statically unstable, they can exhibit intrinsic self-stable behaviour within specific speed ranges due to their mechanical and inertial properties [4,5]. This speed dependence suggests that maintaining balance at lower speeds may require greater active sensorimotor control, whereas at higher speeds the intrinsic dynamics of the bicycle-rider system may reduce the demands on active stabilization [3-5]. Cycling speed therefore provides a means to vary the dynamics of the bicycle-rider system and investigate whether vestibular contributions to balance control change accordingly.

The present study aimed to determine how vestibular perturbation affects upper-body muscle activity and balance-related kinematics during cycling and whether these responses are modulated by cycling speed. To address this question, participants cycled at three different speeds with and without stochastic EVS, while steering behaviour, roll motion and upper-body muscle activity were recorded. The effects of vestibular perturbation on these measures were assessed by comparing cycling with and without EVS, while vestibular contributions were quantified by examining the coupling between the EVS stimulus and steering behaviour, roll motion and upper-body muscle activity across cycling speeds. We hypothesized that EVS would induce a vestibular

balance perturbation requiring compensatory steering and postural responses, resulting in increased steer and roll activity and increased activation of upper-body muscles involved in steering and postural stabilization. In addition, we expected EVS to couple with steering behaviour, roll motion and upper-body muscle activity, indicating a vestibular contribution to these balance-related responses. Finally, based on the greater expected reliance on active sensorimotor stabilization at lower cycling speeds, we hypothesized that vestibular-evoked response gain would be greatest at the lowest cycling speed and decrease with increasing speed.

2 Methods

2.1 Subjects

Eighteen healthy adults (8 male and 10 female, mass 70.1 ± 13.2 kg, height 177.9 ± 11.0 cm) between 20 and 27 years volunteered to participate in this study. Participants had no known neurological, vestibular or musculoskeletal disorders or a history of epilepsy. One participant voluntarily withdrew from the study before completing the experimental protocol and data from one participant were excluded due to equipment malfunction during data collection, resulting in incomplete measurements. Hence, data from sixteen participants were included in the final analysis. Before the experiment, each subject received information about the design and purpose of the study and gave written informed consent. The ethical committee of the faculty Mechanical Engineering at TU Delft approved the project (Letter of Approval #6672).

2.2 Experimental setup

2.2.1 Bicycle-treadmill

All trials were performed on a treadmill in the Bicycle Lab at TU Delft. The treadmill is capable of speeds between 0.5 and 18 km/h and is equipped with a 2.6 m $\times$ 1.13 m (L $\times$ W) belt. Participants rode a 2008 Batavus Browser city bicycle that was secured to the front of the treadmill using a rope and pulley system that allowed the bicycle to freely transverse the treadmill width. To ensure participant safety, they wore a full-body harness attached to an overhead support structure and a helmet throughout all trials. In addition, safety railings were positioned on both sides of the treadmill that served as external support for the participants when needed. An overview of the complete experimental setup is shown in Figure 1, with additional rear and side-view photographs provided in Appendix A (Figure A1).

2.2.2 Electrical vestibular stimulation

EVS was used to evoke controlled vestibular perturbations during cycling. During EVS, a low-amplitude electrical current is applied, modulating the firing rate of vestibular afferents and generating a virtual vestibular error signal that evokes the sensation of head motion without mechanically perturbing the participant [2]. EVS was delivered to participants using carbon rubber electrodes (9 cm²) coated with conductive electrode gel (Spectra Gel 360, Parker, Fairfield, NJ, USA). Electrodes were positioned bilaterally over the mastoid processes and secured using adhesive tape and an elastic headband (Elastofix, C-25m stretched, BSN Medical, Hamburg, Germany). Participants were stimulated using a stochastic white-noise current signal (peak amplitude 4 mA, RMS 1.18 mA) delivered at 200 Hz, generated on a computer using LabView 2019b software (National Instruments, Austin, TX, USA) and delivered with a constant current isolated stimulator STMISOLA (Biopac Systems Inc., Goleta, CA, United States). Stochastic stimulation was selected because it provides broadband vestibular excitation with a favourable signal-to-noise ratio [11]. The stimulus amplitude was selected based on pilot measurements to evoke robust vestibular responses without inducing participant discomfort and was in accordance with previous stochastic EVS studies investigating standing balance [10,11].

A specific head orientation was maintained throughout all trials to ensure consistent alignment of the vestibular perturbation, using a laser pointer mounted on the participant's helmet that projected onto a visual target positioned in front of the treadmill. Before the experimental trials, the target position was individually adjusted with the participant's head positioned 19° nose-up, as determined using a level aligned between the inferior orbital margin and the auditory meatus. This head orientation has been shown to align the virtual vestibular error signal with the earth-horizontal plane and maximize roll-related postural responses evoked by binaural bipolar EVS [2,12].

2.2.3 Motion capture system

An OptiTrack Motion Capture system (Natural Point Inc., Corvallis, OR, USA) was used to record the motion of the bicycle and rider during the trials. The system consisted of eight infrared cameras which simultaneously detected reflective markers attached to the bicycle and rider, allowing reconstruction of their three-dimensional positions within a calibrated measurement volume. The capture volume was calibrated prior to the measurement sessions according to the manufacturer's guidelines [13]. A total of eleven markers were attached to the bicycle to capture bicycle kinematics, while four markers were placed on the rider at anatomical landmarks on the shoulders (acromion processes) and knees (most lateral inferior aspect of the lateral femoral epicondyles) to capture rider motion. The motion capture marker locations are shown in Figure 1. Marker trajectories were recorded at a sampling frequency of 120 Hz.

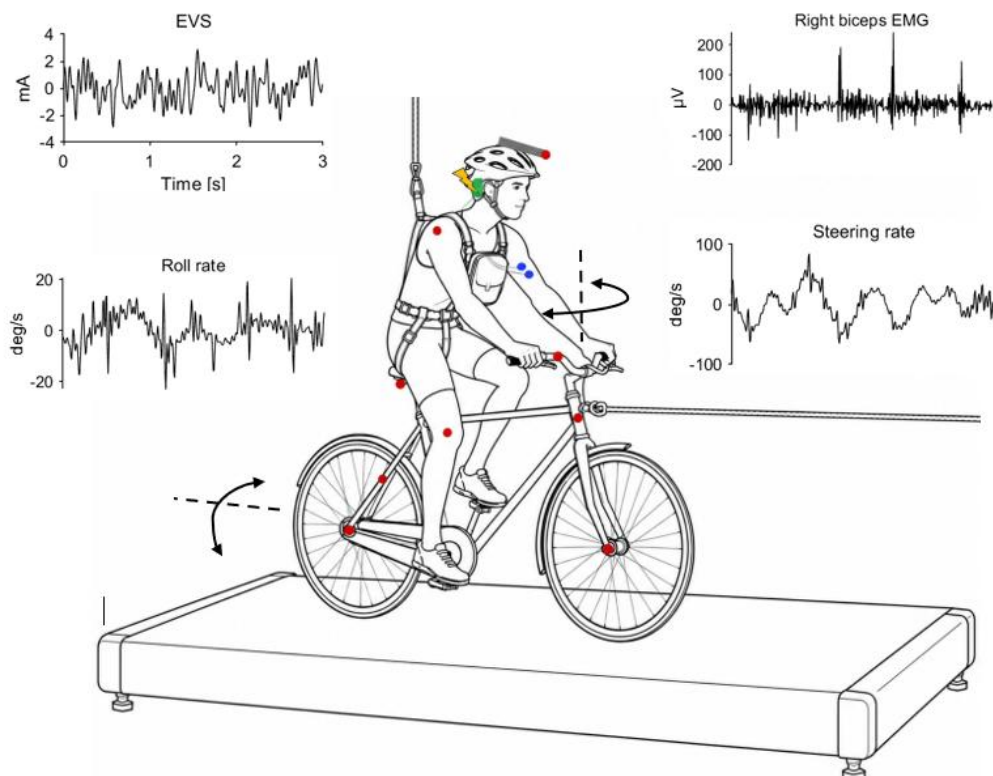


Figure 1. Overview of the experimental setup showing the bicycle-treadmill configuration. Red circles indicate the motion capture marker locations (shown on one side of the rider only), the green electrode behind the ear indicates the EVS electrode position and the bag at the front of the participant contained the wireless EMG amplifier. Only one EMG electrode pair (blue circles) is shown for clarity; all recorded muscle locations are described in section 2.2.4. Example EVS, EMG, steering rate and roll rate signals are shown. The side safety railings are omitted for clarity.

2.2.4 Electromyography system

Muscle activity was recorded using surface electromyography (EMG) with a Porti7-32 ET biosignal acquisition system (TMSi, Oldenzaal, the Netherlands). Surface EMG signals were acquired using bipolar Ag/AgCl electrodes (Kendall H124SG, Cardinal Health 200, LLC, Waukegan, IL, USA) connected to the Porti7-32 ET amplifier. The amplifier differentially amplified the EMG signals, converted the analog signals to digital data and streamed them to a laptop computer for real-time monitoring and storage using a custom MATLAB interface. EMG signals were recorded at a sampling frequency of 2000 Hz.

Prior to electrode placement, the skin was prepared by cleaning the electrode sites with an alcohol wipe and NuPrep Skin Gel (Weaver and Company, Aurora, CO, USA) to reduce electrode-skin impedance. A ground electrode was placed over the medial bony part of the right wrist (ulnar styloid process) and bipolar surface electrodes were placed over the muscle bellies of selected upper-body muscles according to SENIAM recommendations where applicable [14].

EMG activity was recorded from selected upper-body muscles based on their functional roles in bicycle stabilization and control. Previous studies have identified the erector spinae (ES) as an important trunk stabilizer and deltoid anterior (DA), deltoid posterior (DP), biceps brachii (BB) and triceps brachii (TB) as key contributors to steering and handlebar stabilization under varying cycling conditions [9,15-20]. The flexor digitorum (FD) was included as a representative forearm muscle to quantify muscle activity associated with maintaining grip on the handlebars during cycling [16]. Together, these muscles represent the relevant upper-body muscle groups involved in bicycle stabilization and control and were therefore selected. Bilateral EMG recordings were obtained from FD, BB and TB to assess potential left-right asymmetries in vestibular-evoked responses. DA, DP and ES were recorded on the right side only. The recorded muscles and corresponding electrode locations are illustrated in Figure 2.

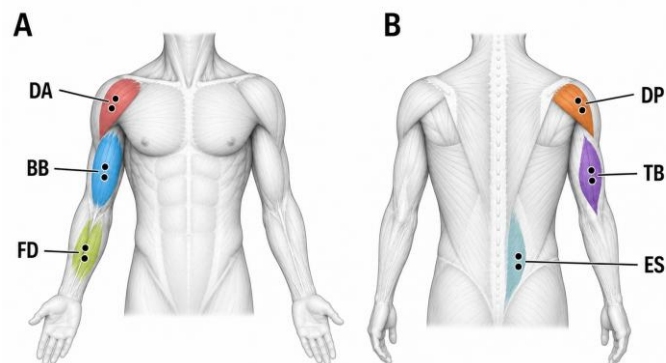


Figure 2. Surface EMG electrode placement for the recorded upper-body muscles. (A) anterior view and (B) posterior view. Black circles indicate bipolar electrode locations.

2.3 Protocol

2.3.1 Preparation and familiarisation

When participants arrived, their weight and height were measured and they were asked to report their hand dominance. Before the start of the experimental trials, participants underwent an EVS familiarisation procedure to ensure that the stimulation was well tolerated before cycling. During this procedure, participants were first exposed to a 1-minute stochastic white-noise signal with a peak amplitude of 1 mA while seated. After the first 30 seconds, participants were asked to stand while the stimulation continued, unless they reported discomfort. The stimulation signal was subsequently increased in 1 mA steps to a maximum peak amplitude of 4 mA, corresponding to the amplitude used during the experimental trials on the bicycle. The same 1-minute procedure was repeated after each increase in stimulation amplitude. Participants were constantly monitored for discomfort and instructed to immediately report any sense of nausea. The rubber electrodes were repositioned when participants reported any stinging sensation to limit the influence of uneven current distributions.

Following EVS familiarisation, EMG electrodes were placed on the selected muscles and maximum voluntary contraction (MVC) tests were performed to obtain reference values for subsequent EMG normalization. Participants were seated on a chair next to the vertical safety railing and grasped the railing with the test arm, while the contralateral arm could be used for support on the horizontal part of the railing. The elbow of the test arm was maintained at approximately 90° of flexion and the shoulder was aligned with the vertical side rail, allowing the pushing and pulling forces to be applied perpendicular to the railing. For each arm, participants performed three 3-second maximal pushing contractions followed by three 3-second maximal pulling contractions against the railing. The procedure was first completed for the right side and repeated for the left side.

2.3.2 Experimental trials

Each participant completed six cycling trials: a 2-minute trial without EVS and a 5-minute trial with EVS at each of three cycling speeds (5, 10 and 18 km/h). The three cycling speeds were selected based on the predicted dynamic stability characteristics of the 2008 Batavus Browser bicycle. According to the linearized bicycle-rider model described by Meijaard et al. [4], the dynamic behaviour of a bicycle can be described by several characteristic motion modes, each characterized by an eigenvalue whose real part determines whether the corresponding mode is stable or unstable. The corresponding eigenvalues of the 2008 Batavus Browser bicycle are shown as a function of forward speed in Figure 3.

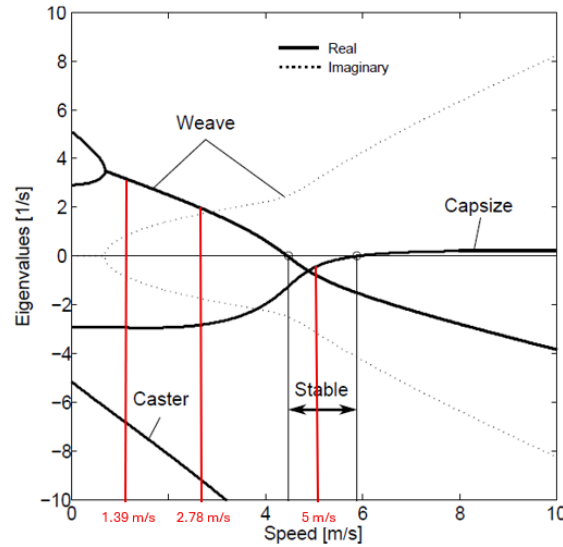


Figure 3. Eigenvalues of the 2008 Batavus Browser bicycle as a function of forward speed. The selected cycling speeds (5, 10, 18 km/h) are indicated by red vertical lines [21].

At 5 km/h (1.39 m/s) and 10 km/h (2.78 m/s), the real part of the weave eigenvalue is positive, indicating an unstable weave mode that requires stabilization through the rider's control actions, whereas the remaining modes are stable in this speed range. The positive real part is larger at 5 km/h than at 10 km/h, indicating that perturbations associated with the weave mode grow more rapidly at 5 km/h and are therefore expected to be more difficult for the rider to stabilize. At 18 km/h (5 m/s), the real part of the weave eigenvalue is negative, indicating a stable weave mode in which perturbations decay over time. These differences in dynamic stability formed the basis for selecting the three cycling speeds used in this study.

Before beginning the experimental trials at each speed, participants completed a 2-5 minute familiarisation period to adapt to cycling on the treadmill at the corresponding speed. The order of the speed blocks and the EVS conditions within each block was randomized across participants. However, the two trials at each speed were always performed consecutively to maintain familiarity with that speed. Throughout each trial, participants were instructed to remain seated without pedalling and to keep the helmet-mounted laser aligned with a target located on a wall approximately 2 meters in front of them. For one participant, the laser was not functioning and the participant was therefore instructed to maintain the required head position without visual feedback. Rest periods were provided between trials according to participant preference.

2.4 Data analysis

2.4.1 Kinematic analysis

OptiTrack motion capture data were exported from Motive (v. 2.3.7, Natural Point Inc., Corvallis, OR, USA) and processed in MATLAB R2023b (MathWorks, Natick, MA, USA). Marker trajectories were used to calculate steering angle and roll angle following the method described by Moore et al. [8]. Non-finite angle samples resulting from missing marker data were replaced using linear interpolation. To remove minor constant offsets resulting from small inaccuracies in marker placement, the calculated angle signals were mean-centred prior to further processing. The mean-centred angle signals were subsequently low-pass filtered using a 4th order zero-phase

Butterworth filter with a cut-off frequency of 30 Hz. Steering rate and roll rate were then obtained by numerically differentiating the filtered angle signals using the numerical gradient operator implemented in MATLAB. For one participant, one trial was excluded because no motion capture data were recorded due to a Motive malfunction.

To ensure a consistent comparison between the EVS and non-EVS conditions, root mean square (RMS) values of steering rate and roll rate were calculated over 120 seconds of valid data. For the non-EVS condition, the analysis started at the beginning of the trial, whereas for the EVS condition, the analysis started at the onset of the synchronised stimulation signal. Samples collected during periods of safety railing contact were excluded from the analysis. Railing contact was identified based on the relative position of the hand markers with respect to the handlebar markers. In trials without hand markers, railing contact was identified by visual inspection of the motion capture data. Following exclusion of railing-contact samples, subsequent valid samples were included until a total of 120 seconds of valid data had been obtained.

2.4.2 EMG analysis

Raw EMG signals were processed in MATLAB following standard EMG signal processing procedures described by Winter [22]. Bipolar EMG signals were high-pass filtered (4th order zero-phase Butterworth, cut-off frequency 40 Hz), full-wave rectified and low-pass filtered (4th order zero-phase Butterworth, cut-off frequency 100 Hz). Mean muscle activity was subsequently calculated for each muscle over the same 120-second analysis window used for the kinematics analysis, with safety railing contact samples excluded. For one subject two trials were excluded from the EMG analysis due to poor signal quality.

The EMG signals recorded during the MVC trials were processed separately using the same high-pass filtering and full-wave rectification steps, after which the rectified signals were low-pass filtered (4th order zero-phase Butterworth, cut-off frequency 20 Hz) to obtain a smoothed linear envelope. The MVC value for each muscle was defined as the maximum amplitude of this envelope over the complete MVC recording and was used to normalize mean EMG amplitudes, which were expressed as a percentage of MVC (%MVC) [23].

2.4.3 Frequency domain analysis

Gain, phase and coherence spectra between the EVS input signal and steering rate, roll rate and muscle activity were calculated to quantify changes in the vestibular coupling across frequencies. As a supplementary analysis, EVS coupling with lateral shoulder displacement was examined to assess whether vestibular-evoked upper-body motion showed similar frequency characteristics to steering and upper-body muscle responses. Lateral shoulder displacement was calculated as the medio-lateral displacement of the midpoint between the left and right shoulder markers relative to the bicycle centreline. Spectral estimates were obtained by applying a Fourier transform to 2-second Hanning windowed segments with 50% overlap. The Hanning window reduced spectral leakage, whereas the overlap increased the number of available segments for spectral estimation [24]. Windows containing samples associated with safety railing contact were excluded from the spectral analysis. Consequently, the number of valid windows differed between trials depending on the amount of railing contact.

Coherence quantifies the linear relationship between the EVS input and each output signal as a function of frequency and was calculated as:

$$C_{xy}(f) = \frac{|S_{xy}(f)|^2}{S_{xx}(f)S_{yy}(f)} \quad (1)$$

where S_{xy} denotes the cross-spectrum between the EVS input (x) and output signal (y), and S_{xx} and S_{yy} represent the corresponding auto-spectra. Coherence ranges from 0 to 1, with higher values indicating stronger linear coupling between the EVS input and output signal and a value of 1 representing a perfect linear, noise-free input-output relationship [25].

Gain and phase were calculated from the frequency-response function between the EVS input and each output signal:

$$H_{xy}(f) = \frac{S_{xy}(f)}{S_{xx}(f)} \quad (2)$$

Gain was obtained as $|H_{xy}(f)|$ and represents the magnitude of the output response relative to the EVS input. Phase represents the phase relationship between the input and output signals and was obtained from the unwrapped phase angle of $H_{xy}(f)$ [25].

A 95% confidence limit (CL) was calculated for the coherence spectra to test the null hypothesis of no linear coupling between the EVS input and the output signal at each frequency. Coherence exceeding the 95% CL was interpreted as evidence of a statistically detectable linear relationship with the EVS input, but did not necessarily indicate strong coupling, since the magnitude of coherence was considered separately [26]. The 95% CL was calculated as:

$$CL = 1 - 0.05^{1/(L-1)} \quad (3)$$

where L represents the number of segments used to estimate coherence. Since consecutive Hanning windows overlapped by 50%, an effective number of segments (L_{eff}) was estimated to account for the dependence introduced by the overlap and used as L in the calculation of the 95% CL. L_{eff} was estimated from the number of valid 2-second segments by correcting for the squared normalized correlation between overlapping Hanning-windowed segments. Since the number of valid windows differed between trials, the most conservative 95% CL, corresponding to the smallest L_{eff} , was displayed in all coherence spectra.

2.4.4 Model-based roll prediction

A model-based roll prediction was performed to investigate whether the measured EVS-induced roll responses could be explained by the mechanical coupling between steering and roll motion predicted by bicycle dynamics. The model-based roll rate was predicted from the measured steering rate using a steering-to-roll transfer function derived from the simplified linear bicycle model described by Karnopp [27]. Bicycle-specific model parameters were derived from the physical properties of the 2008 Batavus Browser bicycle-rider system reported by Moore et al. [21]. The derivation of the transfer function and the adopted model parameters are provided in Appendix B.

The measured steering rate signal was transformed to the frequency domain using a Fourier-transform procedure in MATLAB. To apply the Laplace-domain transfer function $G(s)$ to the frequency-domain data, the transfer function was evaluated at $s = j2\pi f$ where f is the frequency in Hz. The predicted roll-rate spectrum was then calculated as:

$$\dot{\theta}_{pred}(f) = G(j2\pi f)\dot{\Delta}_{meas}(f) \quad (4)$$

where $\dot{\Delta}_{meas}(f)$ and $\dot{\theta}_{pred}(f)$ denote the measured steering-rate and predicted roll-rate spectra respectively. Gain, phase and coherence between the EVS input and predicted roll rate were then calculated using the same procedure described in Section 2.4.3.

2.5 Statistical analysis

Statistical analyses were performed in IBM SPSS Statistics (IBM Corp., Armonk, NY, USA). Data from 16 participants and six trials per participant were included, corresponding to 96 planned observations. Following the trial exclusions described in Sections 2.4.1 and 2.4.2, 95 observations were available for the kinematic analyses and 94 observations for the EMG analyses. To account for repeated measurements within participants while retaining all available observations in the presence of missing data, linear mixed-effects models (LMMs) were used for the statistical analysis [28].

For the time-domain analyses, separate LMMs were fitted to assess the effects of EVS condition (non-EVS, EVS), cycling speed (5, 10, 18 km/h) and their interaction on eight dependent variables: RMS steering rate, RMS roll rate and mean muscle activity (%MVC) of each of the six investigated muscles. Cycling speed was entered as a continuous predictor and participant as a random intercept. The model was specified as:

$$Y_{ij} = \beta_0 + \beta_1 EVS_{ij} + \beta_2 Speed_{ij} + \beta_3 (EVS_{ij} \times Speed_{ij}) + u_i + \varepsilon_{ij} \quad (5)$$

where Y_{ij} represents the dependent variable for participant i in trial j , β_0 the fixed intercept, u_i represents the subject-specific random intercept and ε_{ij} represents the residual error.

For the frequency-domain analyses, mean gain and mean coherence were calculated from the gain and coherence spectra described in Section 2.4.3. Output-specific frequency ranges were defined based on the bandwidth over which consistent EVS-output coherence was observed at group level. This ensured that mean gain was calculated only over frequencies showing significant EVS-output coupling, as gain estimates outside this bandwidth cannot be reliably interpreted and should therefore not be used in mean calculations. The resulting frequency ranges were 0.5-8 Hz for steering rate and 0.5-4 Hz for roll rate. For muscle activity, mean gain and coherence were calculated over 0.5-3 Hz for FD, 0.5-6 Hz for BB and ES and 0.5-8 Hz for TB, DA and DP. This yielded one mean gain and one mean coherence value per participant and cycling speed.

Separate LMMs were fitted to assess the effect of cycling speed on mean coherence and mean gain for steering rate, roll rate and each of the six investigated muscles. Mean coherence and mean gain were analysed separately for each of these eight output signals, resulting in sixteen separate models. Only EVS trials were included, with cycling speed entered as a continuous fixed effect and participant as a random intercept:

$$Y_{ij} = \beta_0 + \beta_1 Speed_{ij} + u_i + \varepsilon_{ij} \quad (6)$$

Phase was evaluated descriptively and was not included in the statistical analyses. As a supplementary analysis, mean gain and mean coherence of lateral shoulder displacement were calculated over 0.5-8 Hz and analysed separately using the same LMM specification.

Bonferroni correction was applied across the eight dependent variables to account for multiple comparisons. For the time-domain analyses, the correction was applied separately to the EVS, speed and EVS $\times$ speed effects. For the frequency-domain analyses, it was applied separately to mean gain and mean coherence. This resulted in eight comparisons within each family and therefore the significance threshold of $p = 0.05/8 = 0.00625$. As lateral shoulder displacement was a supplementary analysis, it was not included in the Bonferroni correction and was evaluated at $p = 0.05$.

3 Results

Participants completed seated, non-peddalling cycling trials at 5, 10 and 18 km/h, both with and without EVS. All sixteen participants were able to maintain balance and complete the trials at each speed, although three participants briefly contacted the safety railing on one or more occasions. To illustrate the measured signals, representative time series from an EVS trial are shown in Figure 4.

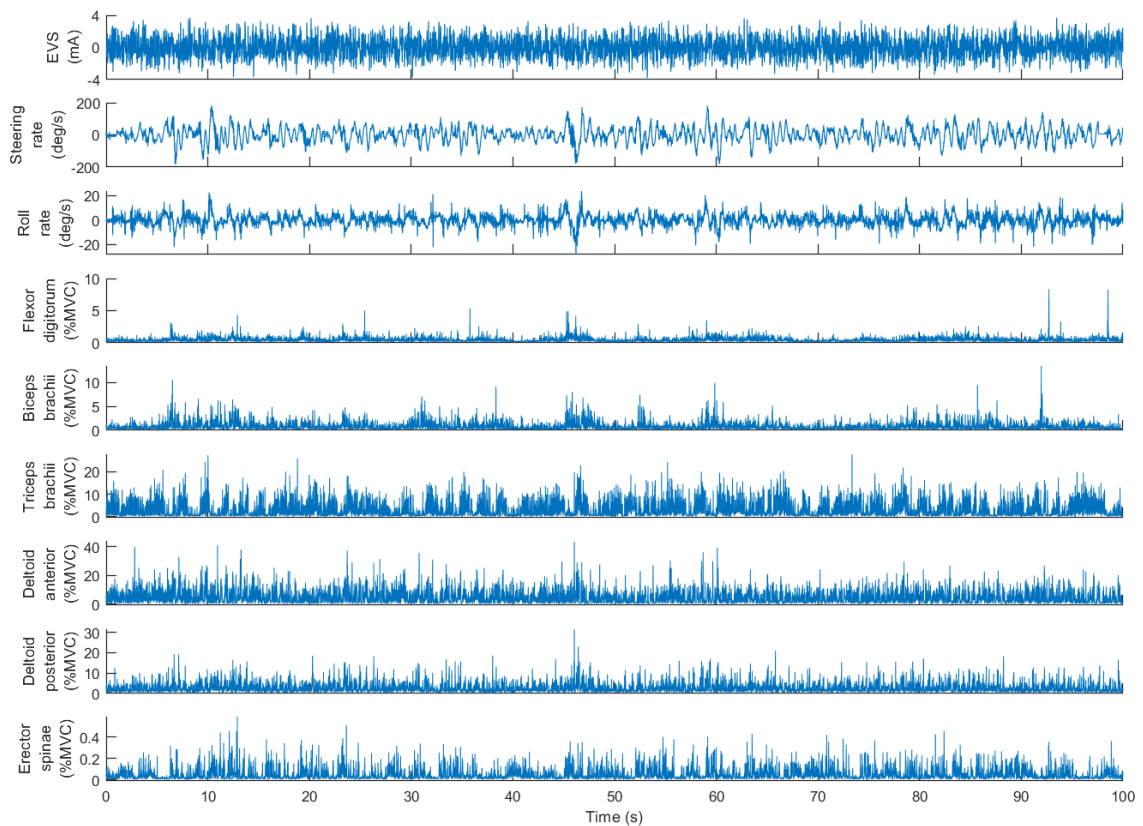


Figure 4. Representative time series from one participant during an EVS trial at 5 km/h. The EVS signal, steering rate, roll rate and muscle activity of the six investigated muscles are shown for the first 100 s following stimulus onset. Differences are visible between the kinematic signals, with more pronounced fluctuations in steering rate than in roll rate. Differences in muscle activity are also visible across the recorded muscles, with relatively pronounced activity in triceps brachii, deltoid anterior and deltoid posterior.

3.1 Kinematic responses

As shown in Figure 5A, RMS steering rate was elevated by EVS at all three speeds and decreased progressively with increasing cycling speed (mean and SD values are reported in Table 1A). These patterns were supported by the statistical model, which revealed significant effects of cycling speed and EVS, as well as a significant EVS $\times$ speed interaction (all $p < 0.001$; Appendix C, Table C1). RMS roll rate was also consistently elevated during EVS trials, but varied little across

cycling speeds (Figure 5A). Accordingly, the statistical model revealed a significant effect of EVS ($p < 0.001$), but no significant effect of cycling speed ($p = 0.930$) or EVS $\times$ speed interaction ($p = 0.267$; Appendix C, Table C1).

3.2 Muscle activity

As shown in Figure 5B, mean muscle activity (%MVC) was generally higher during EVS than during non-EVS trials, although the magnitude of this difference varied across muscles (mean and SD values are reported in Table 1B). When comparing EVS with the corresponding non-EVS condition at each cycling speed, relative increases ranged from 102-144% for BB at 5 and 10 km/h and from 76-126% for DP across all three speeds, while increases of 40-87% were observed for DA, 40-85% for FD and 10-32% for TB. These patterns were supported by significant effects of EVS for FD ($p = 0.006$), BB ($p = 0.002$), TB, DA and DP (all $p < 0.001$), whereas the effect for ES was not significant ($p = 0.009$; Appendix C, Table C1).

For all muscles, mean muscle activity generally decreased with increasing cycling speed during EVS trials, whereas little variation across speeds was observed during non-EVS trials (Figure 5B). Significant effects of cycling speed were observed for DA and DP (both $p = 0.002$) and ES ($p = 0.005$), whereas no significant effects were observed for FD ($p = 0.017$), BB ($p = 0.039$) or TB ($p = 0.022$). No EVS $\times$ speed interactions reached the corrected significance threshold (all $p \geq 0.014$; Appendix C, Table C1).

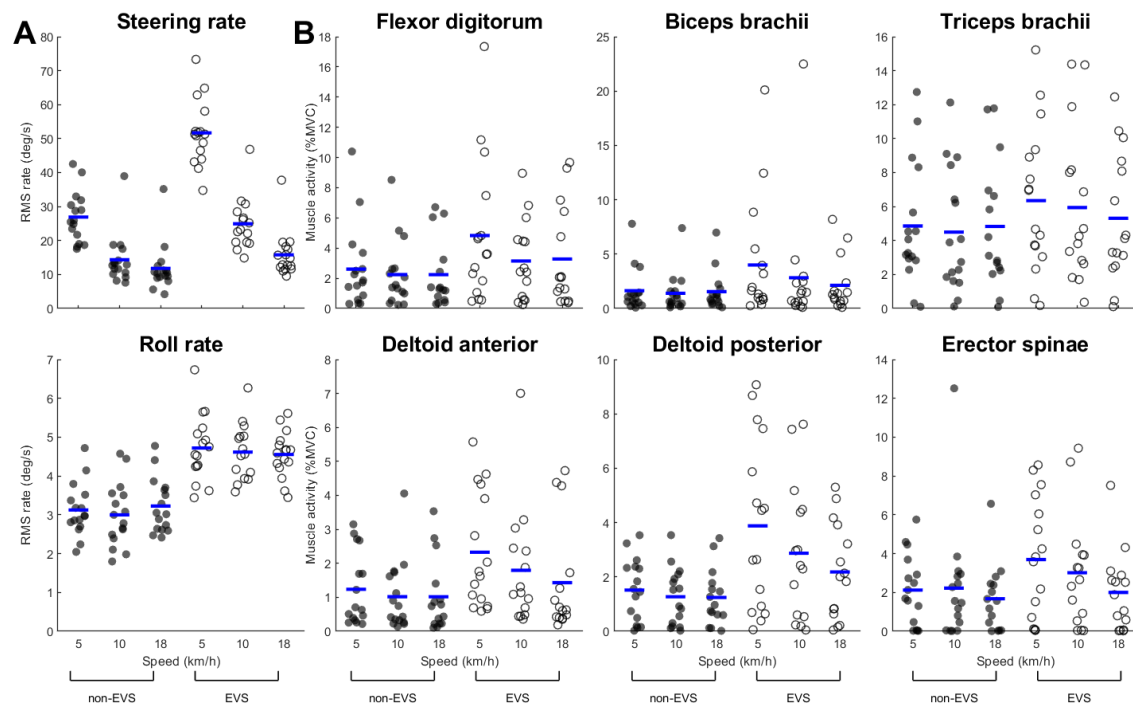


Figure 5. Kinematic and muscle activity results. (A) RMS steering rate and RMS roll rate for each experimental condition. (B) Mean muscle activity (%MVC) for each experimental condition. Filled and open black dots represent individual participants during non-EVS and EVS trials, respectively. Blue horizontal lines indicate the group mean.

Table 1. Mean $\pm$ SD values of RMS steering rate, RMS roll rate and mean muscle activity (%MVC) for each experimental condition

Outcome	Non-EVS			EVS		
	5 km/h	10 km/h	18 km/h	5 km/h	10 km/h	18 km/h
A. RMS kinematics (deg/s)						
Steering rate	26.90 $\pm$ 7.48	14.34 $\pm$ 7.38	11.80 $\pm$ 6.98	51.69 $\pm$ 9.56	24.92 $\pm$ 7.77	15.80 $\pm$ 6.63
Roll rate	3.12 $\pm$ 0.68	3.00 $\pm$ 0.82	3.23 $\pm$ 0.70	4.72 $\pm$ 0.85	4.62 $\pm$ 0.73	4.56 $\pm$ 0.59
B. Mean muscle activity (%MVC)						
Flexor digitorum	2.61 $\pm$ 2.72	2.24 $\pm$ 2.22	2.24 $\pm$ 2.27	4.83 $\pm$ 4.67	3.14 $\pm$ 2.66	3.28 $\pm$ 3.30
Biceps brachii	1.64 $\pm$ 2.01	1.40 $\pm$ 1.78	1.55 $\pm$ 1.81	4.00 $\pm$ 5.47	2.83 $\pm$ 5.57	2.13 $\pm$ 2.45
Triceps brachii	4.86 $\pm$ 3.62	4.49 $\pm$ 3.6	4.83 $\pm$ 3.78	6.35 $\pm$ 4.33	5.94 $\pm$ 4.55	5.31 $\pm$ 3.80
Deltoid anterior	1.24 $\pm$ 1.07	1.02 $\pm$ 1.03	1.02 $\pm$ 1.07	2.32 $\pm$ 1.70	1.79 $\pm$ 1.74	1.43 $\pm$ 1.62
Deltoid posterior	1.52 $\pm$ 1.15	1.27 $\pm$ 1.04	1.24 $\pm$ 1.04	3.14 $\pm$ 3.14	2.87 $\pm$ 2.51	2.18 $\pm$ 1.77
Erector spinae	2.12 $\pm$ 1.82	2.22 $\pm$ 3.01	1.67 $\pm$ 1.73	3.70 $\pm$ 3.13	3.01 $\pm$ 2.90	2.00 $\pm$ 2.04

3.3 EVS-kinematics coupling

Coherent responses to EVS were observed for both steering rate and roll rate across a range of frequencies (Figure 6A). Steering rate coherence exceeded the 95% CL (0.023) over approximately 0.5-8 Hz, with peak coherence values of approximately 0.20-0.25 around 3-4 Hz. Roll rate coherence exceeded the 95% CL over a narrower frequency range of 0.5-4 Hz, with values of approximately 0.15-0.17. Gain and phase were plotted only at frequencies where coherence exceeded the 95% CL.

Steering rate gain was highest at lower frequencies and showed a clear speed-dependent effect, where gain was highest at 5 km/h and decreased with increasing cycling speed. This pattern was supported by the statistical analysis, which revealed a significant effect of cycling speed on mean steering rate gain ($p < 0.001$), whereas mean steering rate coherence was not affected by cycling speed ($p = 0.933$; Appendix C, Table C2). Steering rate phase became increasingly negative with frequency, indicating an increasing phase lag relative to the EVS input.

Roll rate gain similarly decreased with increasing frequency but showed little variation across cycling speeds. Consistent with this observation, the statistical model showed no significant effect of speed on mean roll rate gain ($p = 0.223$) or mean roll rate coherence ($p = 0.706$; Appendix C, Table C2). Roll rate phase also became increasingly negative with frequency. Mean gain and coherence values for steering rate and roll rate at each cycling speed are shown in the insets of Figure 6A.

The predicted roll rate (Figure 6B) exhibited a gain pattern similar to the measured roll rate, with comparable gain magnitudes and a similar decrease with increasing frequency. EVS-predicted roll rate coherence showed a similar pattern to EVS-steering rate coherence. Predicted roll rate was used as a model-based comparison and was therefore not subjected to statistical analysis.

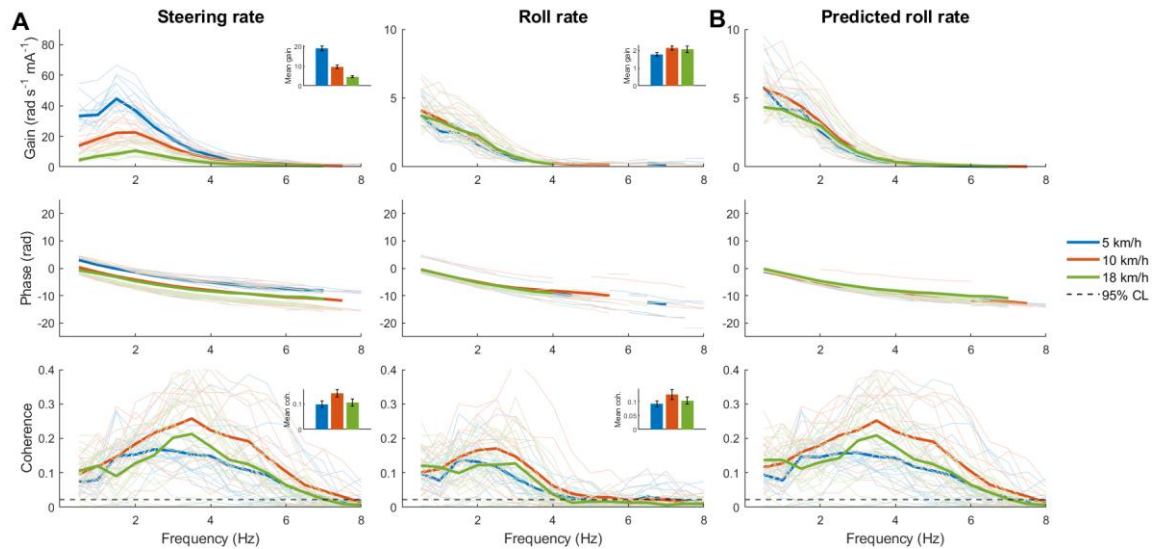


Figure 6. Gain, phase and coherence spectra between the EVS input signal and (A) steering rate, roll rate and (B) predicted roll rate. Light-coloured lines represent individual participants, while thick-coloured lines represent the group mean for each cycling speed. The dashed horizontal line indicates the 95% CL (0.023). Inset bar plots summarize the mean gain and coherence for each cycling speed, with error bars representing the SEM across participants.

3.4 EVS-muscle activity coupling

EVS-muscle coupling varied across the investigated muscles, with generally low coherence and a clear decrease in gain with increasing speed (Figures 7 and 8). Gain, phase and coherence spectra are presented separately for arm muscles (FD, BB and TB; Figure 7) and shoulder and trunk muscles (DA, DP and ES; Figure 8). Gain and phase were plotted only at frequencies where coherence exceeded the 95% CL. For the arm muscles, FD and BB showed low coherence, with values exceeding the 95% CL over approximately 0.5-3 Hz and 0.5-6 Hz respectively. TB showed somewhat higher coherence, with values above the 95% CL over a broader frequency range of approximately 0.5-12 Hz, with the highest values occurring below 8 Hz. For the shoulder and trunk muscles coherence was generally higher than for the arm muscles and was primarily above the 95% CL between approximately 0.5 and 8 Hz. DA showed the most pronounced frequency-dependent pattern, with a peak around 2-4 Hz, whereas coherence for DP and ES remained low with less pronounced frequency-dependent variation.

For all muscles, gain spectra showed a consistent speed-dependent pattern (Figures 7 and 8). Gain was highest at 5 km/h and decreased progressively with increasing cycling speed across the investigated frequency range. Phase generally became slightly more negative with increasing frequency, with similar trends across the arm, shoulder and trunk muscles.

Mean gain and mean coherence values used for statistical analyses are shown in the insets of Figures 7 and 8. Consistent with the observed gain spectra, cycling speed had a significant effect

on mean gain for all investigated muscles (DA $p = 0.002$, all other $p < 0.001$; Appendix C, Table C2). In contrast, a significant effect of cycling speed on mean coherence was only observed for ES ($p = 0.004$; Appendix C, Table C2). No significant effect was found for FD ($p = 0.098$), BB ($p = 0.981$), TB ($p = 0.448$), DA ($p = 0.486$), or DP ($p = 0.480$).

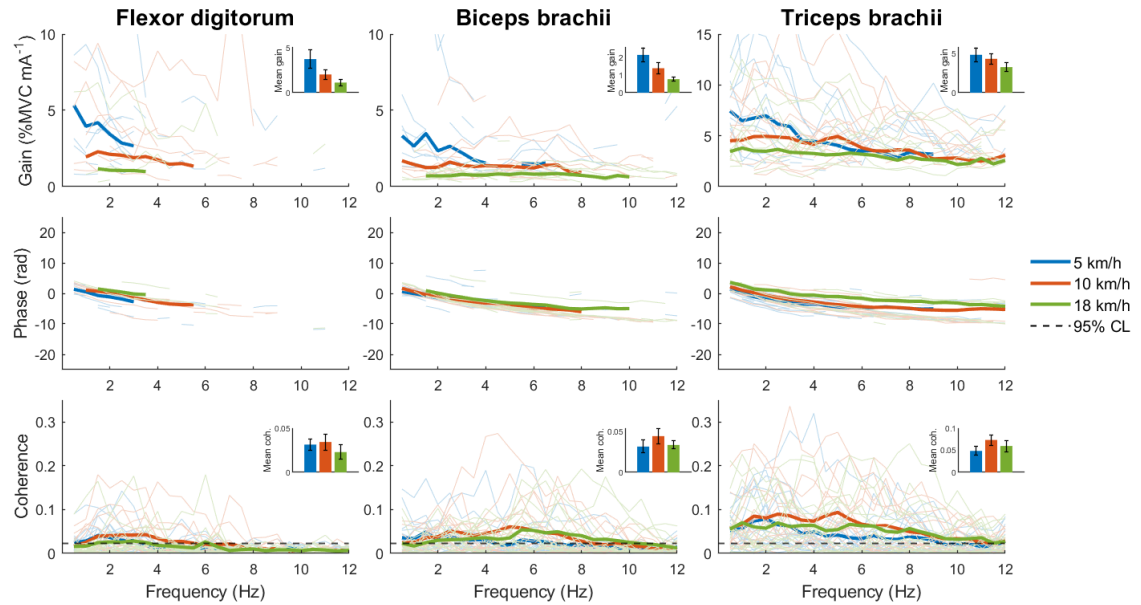


Figure 7. Gain, phase and coherence spectra between the EVS input signal and the arm muscles (flexor digitorum, biceps brachii, triceps brachii). Light-coloured lines represent individual participants, while thick-coloured lines represent the group mean for each cycling speed. The dashed horizontal line indicates the 95% CL (0.023). Inset bar plots summarize the mean gain and mean coherence for each cycling speed, with error bars representing the SEM across participants.

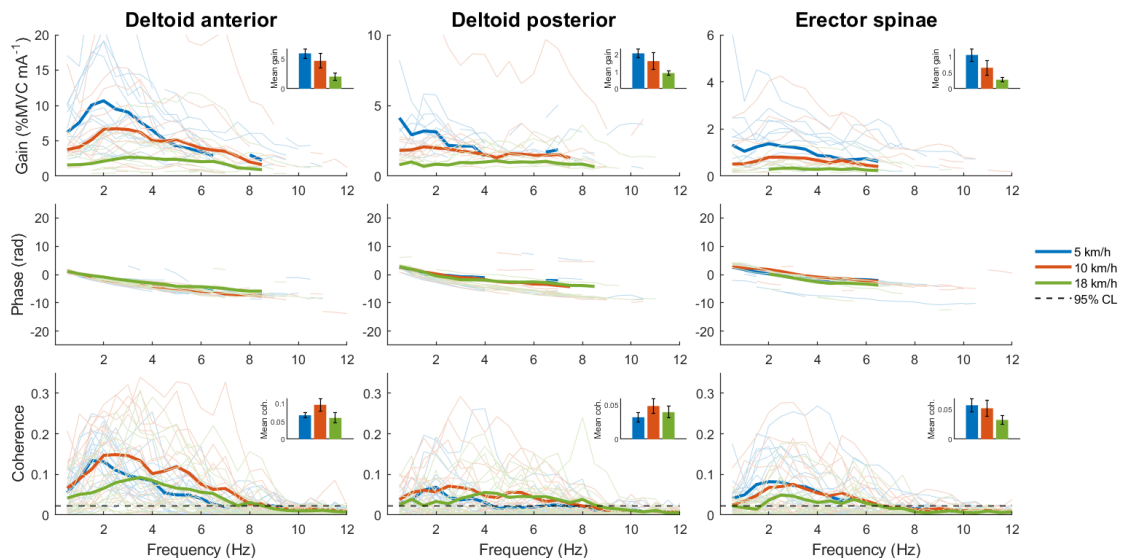


Figure 8. Gain, phase and coherence spectra between the EVS input signal and the shoulder and trunk muscles (deltoid anterior, deltoid posterior, erector spinae). Light-coloured lines represent individual participants, while thick-coloured lines represent the group mean for each cycling speed. The dashed horizontal line indicates the 95% CL (0.023). Inset bar plots summarize the mean gain and mean coherence for each cycling speed, with error bars representing the SEM across participants.

Qualitatively EVS-muscle coupling patterns were observed for the contralateral arm muscles, for which gain, phase and coherence spectra are presented in Appendix D (Figure D1). These spectra exhibited similar coherence magnitudes, frequency bandwidths and speed-dependent behaviour in the gain spectra as the corresponding ipsilateral arm muscles.

Gain, phase and coherence spectra of lateral shoulder displacement are presented in Appendix D (Figure D2). Coherence between EVS and shoulder displacement exceeded the 95% CL over a broad frequency range of 0.5-8 Hz, similar to steering rate and the shoulder muscles (DA and DP). Shoulder displacement gain showed a clear speed dependence, with higher gain at lower cycling speeds, resembling the pattern observed for steering rate, DA and DP. This pattern was supported by a significant effect of cycling speed on mean gain ($p < 0.001$), whereas mean coherence was not significantly affected by speed ($p = 0.855$).

4 Discussion

4.1 Vestibular perturbations and bicycle dynamics

EVS significantly increased both RMS steering rate and RMS roll rate, demonstrating an effect of the vestibular perturbation on bicycle motion. In the frequency domain, significant coherence was observed between EVS and both steering and roll rate, indicating systematic coupling of vestibular input to both kinematic components. The broader and descriptively higher coherence with steering suggests that vestibular perturbations were more consistently expressed in steering motion. This is consistent with steering being the primary control mechanism for maintaining lateral balance, as steering directly shifts the wheel contact points to control balance, whereas roll motion is strongly shaped by the resulting mechanical dynamics of the bicycle-rider system [3,8].

The magnitude of the vestibular-evoked steering response was strongly dependent on cycling speed. RMS steering rate and EVS-steering gain decreased significantly with increasing speed, whereas EVS-steering coherence was not significantly affected by cycling speed. The reduction in gain indicates that a given vestibular perturbation resulted in smaller steering responses at higher cycling speeds. This is consistent with the greater reliance on active steering corrections when the stabilizing contribution of the bicycle dynamics is reduced at lower cycling speeds [3]. The preserved coherence despite the reduction in gain suggests that the vestibular-steering response was rescaled rather than disengaged as the bicycle dynamics became more stabilizing.

Despite the pronounced speed dependence of EVS-steering gain, EVS-roll gain remained relatively constant across speeds, with no significant effect of cycling speed. This contrasting response is notable and suggests that changes in vestibular-evoked steering are not proportionally reflected in roll motion. The model-predicted roll, which was calculated from the measured steering response using the bicycle dynamics, showed a similar gain pattern across cycling speeds to the measured roll response. This agreement suggests that the relatively constant EVS-roll gain may partly be explained by the speed-dependent mechanical relationship between steering and roll. Thus, bicycle dynamics may transform changes in steering response magnitude such that they are less apparent in the resulting roll motion. However, the extent to which these dynamics explain the different speed dependence of steering and roll gain remains unclear.

4.2 Upper-body stabilization during cycling

Although EVS significantly increased mean muscle activity in all upper-body muscles except for ES, the frequency-domain analyses indicate that vestibular input was expressed differently across muscles. Broader coherence bandwidths were observed for TB, DA, DP and ES than for FD and BB. Although statistically detectable EVS-muscle coupling was observed, coherence magnitudes were generally lower compared with the kinematic responses. Interestingly, the muscles showing the largest increases in mean activity from the non-EVS to the EVS condition at the same cycling speed were not necessarily those exhibiting the strongest vestibular coupling. Although BB activity increased up to 144% following EVS at 10 km/h, coherence remained low across the frequency spectrum, whereas DA and DP combined large increases in activity with broad coherence

bandwidths. This is consistent with previous studies showing that vestibular responses depend primarily on the functional role of individual muscles in maintaining balance rather than on their level of background activity [6,29]. This indicates that increased muscle activation alone does not necessarily reflect a direct vestibular contribution, but may also represent a generalized increase in upper-body stiffness or co-contraction in response to the perturbation.

Vestibular-evoked muscle responses also showed a clear speed dependence. EVS-muscle gain decreased significantly with increasing cycling speed for all investigated muscles, whereas EVS-muscle coherence was generally unaffected by speed, except for erector spinae, which showed a significant speed effect. The similar speed dependence of muscle and steering gain, together with the role of the upper-body muscles in bicycle stabilization [30], suggests that larger vestibular-evoked muscle responses at lower cycling speeds may be related to the greater steering corrections required for balance. The observed vestibular coupling with shoulder displacement further supports the involvement of the upper body in the vestibular response, as vestibular input was coupled not only to shoulder muscle activity but also to shoulder movement, with both showing similar speed-dependent modulation.

Previous studies similarly support a role of upper-body muscle recruitment in rider stabilization. Duc et al. [15] demonstrated that constraining lateral bicycle sway reduced global upper-body muscle activity, indicating that these muscles contribute to controlling lateral bicycle sway and maintaining upper-body stability. Similarly, Turpin et al. [16] identified functional muscle synergies in which the ES and shoulder muscles were primarily associated with upper-body stabilization during cycling. Although participants in the present study did not pedal, bicycle balance still required continuous stabilization of the upper body while responding to vestibular perturbations. The broader coherence bandwidths observed for TB, DA, DP and ES are therefore consistent with the role of these muscles in rider stabilization. In particular, the observed EVS-ES coupling suggests that vestibular-evoked muscle responses were not restricted to muscles involved in steering, as ES contributes to trunk stabilization without directly generating forces at the handlebars. Together, these findings suggest that vestibular perturbations evoke coordinated upper-body muscle responses in both steering control and postural stabilization.

4.3 Vestibular responses in standing and walking

The vestibular coupling observed during cycling is consistent with previous findings during standing and walking, where stochastic EVS produced significant coupling with postural sway and balance-related muscle activity [31,32]. Importantly, these responses are modulated according to the demands of the balance task. During standing, vestibular responses are substantially reduced when external support minimizes the need for active balance control [31,33], while vestibular responses during walking vary with locomotor conditions and the phase of the gait cycle [32,34,35].

The speed-dependent modulation of vestibular responses appears to differ between walking and cycling. In the present cycling study, steering and upper-body muscle gain decreased with increasing speed, but coherence was largely preserved. During walking, in contrast, both vestibular gain and coherence decrease with increasing locomotor velocity [32,34], suggesting a reduced contribution of vestibular feedback at higher speeds. This may be related to the shorter time available for feedback corrections, as increasing walking speed shortens the stance period,

together with the strong phase dependence of vestibulomuscular coupling across the gait cycle [34,35]. During cycling, increasing speed makes the bicycle dynamics more stabilizing, reducing the magnitude of active steering corrections required for lateral balance [3]. Faster cycling may therefore reduce the magnitude of the motor output required in response to vestibular input while vestibular coupling remains preserved. Thus, whereas faster walking may reduce the relative contribution of vestibular feedback to locomotor control, faster cycling appears to reduce the motor response through speed-dependent bicycle dynamics without diminishing the underlying vestibular coupling.

4.4 Limitations and future perspectives

Several methodological considerations should be taken into account when interpreting the present findings. First, all experiments were performed during treadmill cycling, providing a controlled environment for standardized vestibular stimulation and accurate motion capture measurements. However, treadmill cycling may not fully represent balance control during overground cycling, as the rider remains relatively stationary on the treadmill, altering the visual flow associated with forward movement and eliminating variations in terrain that may affect balance during natural cycling. Participants were also instructed not to pedal, simplifying the interpretation of the vestibular responses but excluding cyclic lower-limb forces and additional sensory feedback associated with pedalling, which may alter the mechanical interaction between the rider and bicycle and affect how balance corrections are generated. Future studies should therefore investigate the effects of EVS during overground cycling and under pedalling conditions to determine whether the observed vestibular responses generalize to more natural cycling conditions.

Only selected upper-body muscles were investigated, chosen based on previous literature and their expected involvement in steering and upper-body stabilization. Although this targeted the muscles most relevant to the present research questions, cycling balance involves coordinated whole-body control. The present measurements therefore provide only a partial representation of the whole-body responses involved in cycling balance and could not determine how vestibular responses are distributed across the body. Future studies should therefore incorporate more comprehensive whole-body kinematics together with upper- and lower-body muscle activity to further clarify how vestibular feedback contributes to coordinated balance control during cycling.

The present study included only healthy young adults, limiting the generalizability of the findings to other populations. Vestibular function and postural control are known to decline with ageing [36], suggesting that the vestibular contributions to cycling balance observed in the present study may differ in older adults. Moreover, older adults who regularly cycle have been reported to show better postural stability than non-cycling older adults [37]. Investigating vestibular contributions to cycling in older adults may therefore provide insight into age-related changes in balance control and the potential role of cycling in maintaining safe mobility.

Finally, only stochastic EVS was applied in the present study, enabling characterization of vestibular contributions across a broad range of frequencies. However, this stimulation paradigm is primarily suited to look into frequency-domain characteristics of vestibular control. Previous studies in standing and walking have shown that different vestibular stimulation paradigms probe

complementary aspects of vestibular function, with transient or pulse-based perturbations providing insight into response latencies and discrete corrective balance responses [2]. Future studies could therefore investigate whether different EVS paradigms evoke distinct motor strategies or reveal additional aspects of vestibular control during cycling.

5 Conclusion

The aim of this study was to investigate vestibular contributions to balance control during cycling and how these are modulated by cycling speed. The findings demonstrate that vestibular feedback contributes systematically to cycling balance. EVS increased steer and roll motion and generally increased upper-body muscle activity, supporting the hypothesis that vestibular perturbations evoke compensatory kinematic and muscular responses. Furthermore, significant coupling between EVS and steering rate, roll rate and upper-body muscle activity confirmed that vestibular input systematically contributes to these balance-related responses.

The hypothesis that vestibular-evoked response gain would be greatest at lower cycling speeds was largely supported. Steering and muscle response gains decreased with increasing cycling speed, whereas roll response gain remained relatively constant across speeds. The similarity between measured and model-predicted roll responses suggests that this contrasting behaviour may partly be explained by the mechanical coupling between steering and roll within the bicycle-rider system. Coherence was generally maintained across cycling speeds, suggesting that vestibular input remained coupled to balance control while the magnitude of the resulting steering and muscular responses was reduced at higher speeds. Furthermore, vestibular coupling differed between muscles, supporting a functional role of vestibular feedback in coordinated upper-body stabilization.

Taken together, vestibular perturbations affect cycling balance through coordinated kinematic and muscular responses, with their expression depending on cycling speed and the dynamics of the bicycle-rider system. This study provides new insight into the sensorimotor mechanisms underlying cycling balance and highlights the task-dependent nature of vestibular control during cycling.

Use of AI tools

ChatGPT (OpenAI) was used only to improve language, grammar and readability of text written by the author. It was not used to generate scientific content, analyse data or interpret results. Figure 1 was generated using ChatGPT as the basis for the cyclist and treadmill illustration. All experimental details, annotations and graphical elements were manually added by the author.

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Appendix A. Experimental setup

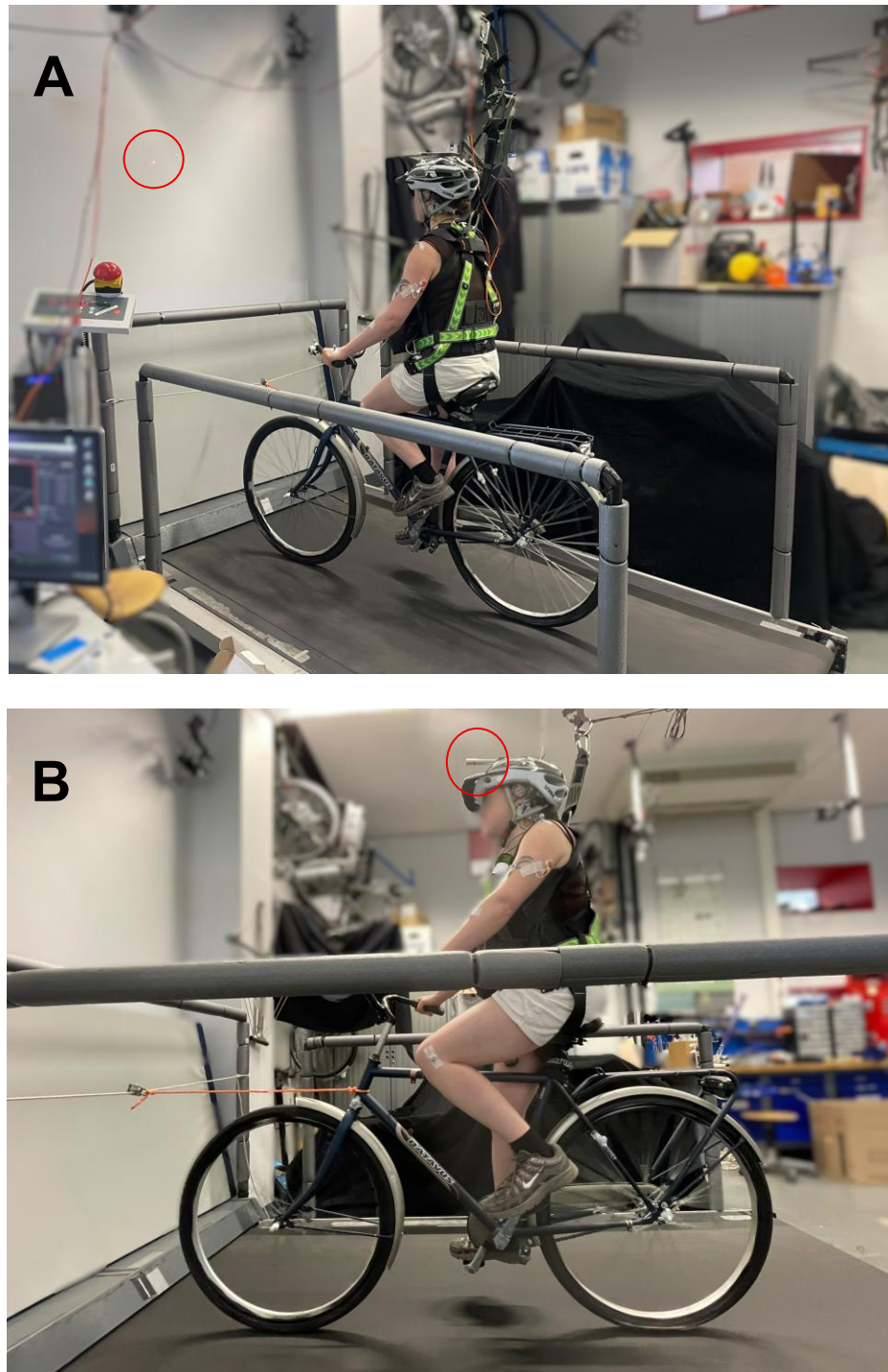


Figure A1. Photographs of the experimental bicycle-treadmill setup. (A) Rear view of the participant seated on the bicycle on the treadmill, showing the safety railings and the full-body harness attached to an overhead support structure. The red circle indicates the laser projection on the wall. (B) Side view of the experimental setup, providing a closer view of the rope and pulley attachment used to secure the bicycle and the helmet-mounted laser, indicated by the red circle.

Appendix B. Derivation of the steering-to-roll transfer function

Following the simplified linear bicycle model described by Karnopp [27], the relationship between steering and roll motion is governed by

$$(I_1 + mh^2)\ddot{\theta} - mgh\theta = -\frac{mh}{a+b}(bU\dot{\delta} + U^2\delta) \quad (B1)$$

where θ is the bicycle roll angle, δ is the steering angle, U is the forward velocity, m is the combined bicycle-rider mass, h is the height of the combined centre of mass above the ground, I_1 is the roll moment of inertia about the combined centre of mass and a and b are the longitudinal distances from the combined centre of mass to the rear- and front-wheel contact points, respectively.

Applying the Laplace transform to Equation B1 gives

$$(I_1 + mh^2)s^2\Theta(s) - mgh\Theta(s) = -\frac{mh}{a+b}[bUs\Delta(s) + U^2\Delta(s)] \quad (B2)$$

where $\Theta(s)$ and $\Delta(s)$ denote the Laplace transforms of the roll angle and steering angle respectively. Collecting terms gives:

$$[(I_1 + mh^2)s^2 - mgh]\Theta(s) = -\frac{mh}{a+b}(bUs + U^2)\Delta(s) \quad (B3)$$

Rearranging Equation B3 results in the steering-to-roll transfer function

$$G(s) = \frac{\Theta(s)}{\Delta(s)} = -\frac{\frac{mh}{a+b}(bUs + U^2)}{(I_1 + mh^2)s^2 - mgh} \quad (B4)$$

Assuming zero initial conditions, the Laplace transforms of roll rate and steering rate are given by

$$\dot{\Theta}(s) = s\Theta(s) \quad (B5)$$

and

$$\dot{\Delta}(s) = s\Delta(s) \quad (B6)$$

the transfer function relating steering rate to roll rate is identical to Equation B4:

$$\frac{\dot{\Theta}(s)}{\dot{\Delta}(s)} = \frac{s\Theta(s)}{s\Delta(s)} = \frac{\Theta(s)}{\Delta(s)} = G(s) \quad (B7)$$

Model parameters

The parameters required for the simplified Karnopp model were derived from the physical properties of the 2008 Batavus Browser bicycle-rider system reported by Moore et al. [21]. In this paper, the bicycle-rider system was represented as the combined rear body and rider (B), handlebar/fork assembly (H), rear wheel (R) and front wheel (F). The masses, center-of-mass locations and moments of inertia of these bodies were taken from Table 12 of Moore et al. [21].

The total system mass was obtained by summing the masses of the four bodies:

$$m = m_B + m_H + m_R + m_F = 86 + 4.35 + 3.12 + 2.02 = 95.49 \text{ kg} \quad (\text{B8})$$

The location of the combined centre of mass was calculated as the mass-weighted average of the individual centre-of-mass locations:

$$x_{COM} = \frac{\sum_i m_i x_i}{m} = 0.316 \text{ m}, \quad z_{COM} = \frac{\sum_i m_i z_i}{m} = -0.982 \text{ m} \quad (\text{B9})$$

In the coordinate system used by Moore et al [21], the vertical z -axis points downward, such that points above the ground plane have a negative z -coordinate. Therefore, the height of the combined centre of mass above the ground was

$$h = -z_{COM} = 0.982 \text{ m} \quad (\text{B10})$$

Since the origin of the coordinate system is located at the rear-wheel contact point, the longitudinal distance from the combined centre of mass to the rear-wheel contact point is $a = x_{COM}$. Using the wheelbase $w = 1.120 \text{ m}$, the corresponding distance to the front-wheel contact point was calculated as

$$b = w - a = 1.120 - 0.316 = 0.804 \text{ m} \quad (\text{B11})$$

Finally, the roll moment of inertia of the complete bicycle-rider system about its combined centre of mass was obtained by shifting the roll inertia of each rigid body to the combined centre of mass using the parallel-axis theorem and summing the individual contributions:

$$I = \sum_i [I_{xx,i} + m_i(z_i - z_c)^2] = 14.88 \text{ kg m}^2 \quad (\text{B12})$$

The resulting parameters used in the simplified Karnopp model were therefore

$$m = 95.49 \text{ kg}, \quad h = 0.982 \text{ m}, \quad I = 14.88 \text{ kg m}^2, \quad a = 0.316 \text{ m}, \quad b = 0.804 \text{ m}$$

Appendix C. Statistical analysis results

Table C1. Statistical analysis results for the effects of cycling speed, EVS and the EVS × speed interaction on RMS steering rate, roll rate and mean muscle activity (%MVC)

Outcome	EVS	Speed	EVS x Speed
Steering rate	$F(1, 76.08) = 87.57, p < 0.001$	$F(1, 76.06) = 198.76, p < 0.001$	$F(1, 76.56) = 34.04, p < 0.001$
Roll rate	$F(1, 75.99) = 50.87, p < 0.001$	$F(1, 75.97) = 0.01, p = 0.930$	$F(1, 75.97) = 1.25, p = 0.267$
Flexor digitorum	$F(1, 74.02) = 8.10, p = 0.006$	$F(1, 74.26) = 5.93, p = 0.017$	$F(1, 74.01) = 1.55, p = 0.218$
Biceps brachii	$F(1, 74.06) = 9.82, p = 0.002$	$F(1, 74.32) = 4.42, p = 0.039$	$F(1, 74.05) = 2.97, p = 0.089$
Triceps brachii	$F(1, 74.01) = 13.08, p < 0.001$	$F(1, 74.06) = 5.49, p = 0.022$	$F(1, 74.00) = 3.26, p = 0.075$
Deltoid anterior	$F(1, 74.07) = 19.60, p < 0.001$	$F(1, 74.22) = 9.98, p = 0.002$	$F(1, 74.06) = 4.37, p = 0.040$
Deltoid posterior	$F(1, 74.08) = 29.09, p < 0.001$	$F(1, 74.34) = 10.85, p = 0.002$	$F(1, 74.07) = 6.27, p = 0.014$
Erector spinae	$F(1, 74.08) = 7.14, p = 0.009$	$F(1, 74.37) = 8.30, p = 0.005$	$F(1, 74.07) = 2.53, p = 0.116$

Table C2. Statistical analysis results for the effect of cycling speed on mean gain and coherence of the EVS-kinematic, EVS-muscle and EVS-lateral shoulder displacement coupling

Outcome	Mean coherence	Mean gain
Steering rate	$F(1, 30.03) = 0.01, p = 0.933$	$F(1, 30.46) = 92.94, p < 0.001$
Roll rate	$F(1, 30.31) = 0.15, p = 0.706$	$F(1, 30.25) = 1.55, p = 0.223$
Flexor digitorum	$F(1, 29.35) = 2.93, p = 0.098$	$F(1, 29.35) = 18.26, p < 0.001$
Biceps brachii	$F(1, 30.26) = 0.00, p = 0.981$	$F(1, 29.20) = 18.29, p < 0.001$
Triceps brachii	$F(1, 29.26) = 0.59, p = 0.448$	$F(1, 29.06) = 16.20, p < 0.001$
Deltoid anterior	$F(1, 30.00) = 0.50, p = 0.486$	$F(1, 31.37) = 16.83, p < 0.001$
Deltoid posterior	$F(1, 29.619) = 0.51, p = 0.480$	$F(1, 31.39) = 11.70, p = 0.002$
Erector spinae	$F(1, 29.27) = 9.51, p = 0.004$	$F(1, 29.22) = 28.30, p < 0.001$
Lateral shoulder displacement	$F(1, 30.03) = 0.03, p = 0.855$	$F(1, 30.06) = 19.75, p < 0.001$

Appendix D. Additional gain, phase and coherence spectra

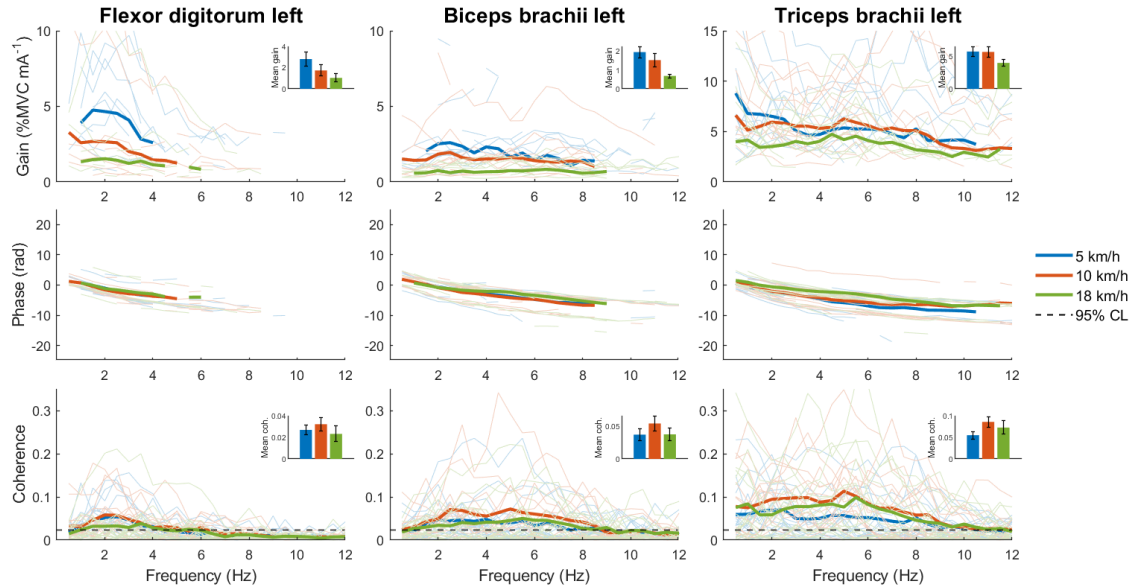


Figure D1. Gain, phase and coherence spectra between the EVS input signal and the contralateral arm muscles (flexor digitorum, biceps brachii, triceps brachii). Light-coloured lines represent individual participants, while thick-coloured lines represent the group mean for each cycling speed. The dashed horizontal line indicates the 95% CL (0.023). Inset bar plots summarize the mean gain and mean coherence for each cycling speed, with error bars representing the SEM across participants.

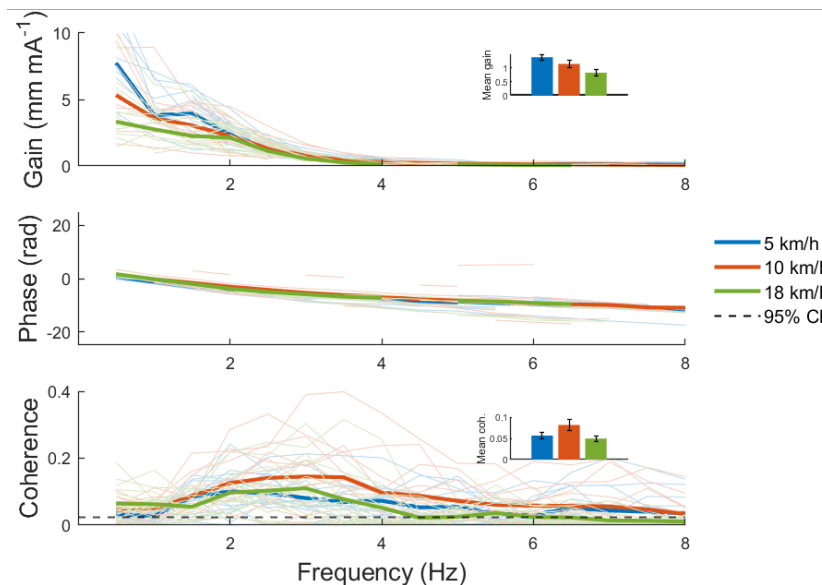


Figure D2. Gain, phase and coherence spectra between the EVS input signal and the lateral displacement of the shoulder centre relative to the bicycle frame. Light-coloured lines represent individual participants, while thick-coloured lines represent the group mean for each cycling speed. The dashed horizontal line indicates the 95% CL (0.023). Inset bar plots summarize the mean gain and mean coherence for each cycling speed, with error bars representing the SEM across participants.

