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The Influence of Sensory Information on Two-Component Coordination During Quiet Stance

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Abstract

When standing quietly, human upright stance is typically approximated as a single segment inverted pendulum. In contrast, investigations which perturb upright stance with support surface translations or visual driving stimuli have shown that the body behaves like a two-segment pendulum, displaying both in-phase and anti-phase patterns between the upper and lower body. We have recently shown that these patterns co-exist during quiet stance; in-phase and anti-phase for frequencies below and above 1 Hz respectively. Here we investigated whether the characteristics of these basic patterns were influenced by the addition or removal of sensory information.

Ten healthy young subjects stood upright on a rigid platform with different combinations of sensory information: eyes were open or closed with or without light touch contact (< 1 N) of the right index fingertip with a 5 cm diameter rigid force plate. The in-phase and anti-phase pattern co-exist in both the AP and ML directions of sway. The real part of trunk-leg complex coherence decreased with the addition of vision and light touch, corresponding to a transition from the in-phase to anti-phase pattern at a lower frequency. In the AP direction, the decrease was only observed at frequencies below 1 Hz where the in-phase pattern predominates. Additional sensory information had no observable effect at sway frequencies above 1 Hz, where the anti-phase pattern predominates. Both patterns are clearly the result of a double-linked inverted pendulum dynamics, but the coherence of the in-phase pattern is more susceptible to modulation by sensory information than the anti-phase pattern.

INTRODUCTION

Human upright stance is often approximated as a single-joint inverted pendulum, pivoting around the ankle during quiet stance [1–2]. When perturbed, additional patterns associated with a double-linked pendulum are then observed, such as the anti-phase hip strategy [3]. The generally accepted idea is that these basic patterns are centrally selected from a set of motor programs, arising from high-level neural strategies and implemented by complex sensorimotor control processes to most effectively counteract the physical characteristics of the perturbation [4]. However, recent work has questioned this distinction between quiet and perturbed stance [5]. The same in-phase (i.e., ankle strategy) and anti-phase (i.e., hip strategy) patterns between

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upper and lower body segments observed in response to perturbed stance co-exist at different frequency ranges during quiet unperturbed stance. At frequencies below approximately 1 Hz, coordination between the trunk and legs assumes an in-phase pattern, while above 1 Hz, an anti-phase pattern predominates.

The coexistence of in-phase and anti-phase body sway during quiet, unperturbed stance raises a number of issues regarding how these patterns arise. These two patterns are clearly a result of double-link inverted pendulum dynamics [6], although a neural control system is necessary to maintain upright stability. Thus, even quiet unperturbed stance requires a complex mixture of biomechanical and neural control. In the present study, we investigated how the addition or removal of sensory information influences the co-existing in-phase and anti-phase patterns observed during quiet stance. Are the mechanical characteristics of both in-phase and anti-phase patterns influenced by the addition/removal of sensory information? We also studied the relationship between upper and lower body segments in both the anterior-posterior (AP) and medial-lateral (ML) directions to determine whether the in-phase and anti-phase patterns coexist in both directions of sway.

METHODS

Subjects

Ten individuals participated, three women and seven men, ranging in age from 18 to 31 years (mean age = 23.9, SD = 4.4). All subjects were right-handed, healthy and physically active, with no known musculoskeletal injuries or neurological disorders that might affect their ability to maintain balance. The procedures used in the experiment were approved by the Institutional Review Board at the University of Maryland. Informed written consent was obtained from all participants in the study.

Apparatus

The subjects stood on a rigid platform with their right index finger touching a static touch plate placed in front of the subject's right shoulder. The touch device consisted of a smooth horizontal metal plate (5 cm in diameter) supported by a tripod. The plate was adjusted in height and position to allow subjects to assume a comfortable arm position, typically with ≈ 10 – 15 degrees of elbow flexion. When the subjects applied forces of more than 1 N, an auditory alarm sounded. The visual environment consisted of an array of lab equipment against a wall approximately 3 m away, with normal ambient light levels. Kinematics of the shoulder (the scapula), hip (the greater trochanter), knee (the lateral femoral condyle) and ankle (the lateral malleolus) were measured by attaching four LED markers on the left side of the subject and were sampled at 100 Hz using an Optotrak (Northern Digital, Inc.) system. Three LED markers were put on the force platform aligned with the corner facing the cameras as a reference, so that the data could be rotated from the cameras' own coordinate system into the subject's global coordinate system later in the data analysis. A bank of three cameras was placed to the left front of the subjects to measure the movements of the markers.

Procedures

The subjects stood upright with heels 1 cm apart pointed outward at an angle of 15 degrees between each foot and the midline. The floor was marked with tape so that the same foot position could be repeated on each trial and subject. The experimental trials included two visual conditions, eyes closed or eyes open and two fingertip contact conditions, no contact, or light touch contact, in which the vertical touch force applied on the touch plate by the right index fingertip was limited to 1 N. The four conditions were identified as follows: Neither = eyes closed and no touch contact, Touch = eyes closed and touch contact, Vision = eyes open and no touch contact, Both = eyes open and touch contact.

Subjects began each trial by looking straight ahead at fixation target against a wall approximately 3 m away. In the Touch conditions, subjects were instructed to take as much time as possible to find a comfortable position and keep the fingertip on the same spot on the touch plate throughout the trial. If the alarm sounded, the subjects were told to keep their fingertip in contact with the touch plate while reducing the force at the fingertip. During the no touch trials, the subjects were asked to keep both arms crossed behind their back so that their hands were touching at approximately waist level. This prevented the arms from blocking the markers as subjects faced the camera. Once the subjects felt ready, they said “yes” and the experimenter initiated data acquisition 5 seconds later.

Each condition was run three times for a total of 12 trials for each subject. All trials were 240 seconds, the order of the trials across conditions were randomized for each subject. The subject was asked to sit and rest for two minutes after completing a trial. One trial was discarded due to technical difficulties.

Analysis

Kinematics—The trunk and leg segment were assumed to lie on the line connecting every two adjacent joints with the knee being ignored, which was based on the fact that knee joints remain approximately stationary during AP sway motions [7]. AP/ML trunk and leg angles with respect to vertical were calculated using the AP/ML and vertical positions of the ankle, hip and shoulder markers. All subsequent analysis was applied separately for the AP and ML directions.

Sway Variability—For each segment angle trajectory, a velocity trajectory was calculated using finite differences with a time step of 0.1 s, which was applied to reduce measurement noise for calculation of sway velocity. This was the only filter employed to the data set. *Position variability* and *velocity variability* was computed as the standard deviations of the angle trajectory and its velocity trajectory, respectively, and averaged across trials.

Spectral Analysis—For each trial means were subtracted from the leg and trunk angle trajectories and the power spectral densities (PSDs) of the legs and trunk and cross spectral density (CSD) between the legs and trunk were computed in Matlab using Welch’s method with a 20 second Hanning window and 50% overlap. PSDs and CSDs were averaged across the three trials (one subject had only 2 Touch trials). The 20 second window for spectral analysis produced PSDs and CSDs with a 0.05 Hz frequency step. To increase statistical power, frequency values from 0.05 to 3 Hz were divided into 15 bins (4 values per bin), and the PSDs and CSDs were averaged in each bin.

For each subject and condition, complex coherence c_{12} was computed as

$$c_{12} = \frac{p_{12}}{\sqrt{p_{11}p_{22}}},$$

where p_{12} is CSD between the legs and trunk, and p_{11} and p_{22} are PSDs for the leg and trunk segment, respectively.

Figure 1a shows the trunk-leg complex coherence in the complex plane from a single trial. Each symbol indicates a different frequency in steps of 0.05 Hz. There are two common ways to decompose complex coherence. Figure 1b–c shows a decomposition into real and imaginary parts. Figure 1d–e shows a decomposition into (magnitude-squared) coherence r^2 and cophase θ , where the distance r and angle θ are defined in Figure 1a. A positive cophase indicates that the leg segment led the trunk segment.

The real-imaginary decomposition of complex coherence was used for two reasons. First, the imaginary part of complex coherence was generally small and changes across frequency were primarily due to the real part (see Results). Second, complex coherence was often near the origin of the complex plane at frequencies where the shift from in-phase to anti-phase trunk-leg coordination occurred, leading to highly variable co-phase and complicating its statistical analysis. It will be useful to understand how the real-imaginary and coherence-cophase decompositions of complex coherence are related, since the latter decomposition is often used in the literature [5]. For example, if the imaginary part of complex coherence remains small while the real part goes from positive to negative with increasing frequency (Figure 1b–c), then cophase shows a sudden transition from nearly in-phase (0 deg) to nearly anti-phase (180 deg) accompanied by a drop in coherence at the transition (Figure 1d–e).

Statistics—The log of the position and velocity variability in both directions was analyzed using Condition x Segment repeated-measure ANOVAs with Greenhouse-Geisser adjusted p values. Use of the log transform tends to reduce skewness and deviations from sphericity. Each pair of conditions was tested for a main Condition effect using a mixed model with unstructured covariance, the Tukey-Kramer adjustment for multiple comparisons, and the Kenward-Roger adjustment for reducing small sample bias.

The following statistical analyses were applied separately in the AP and ML directions. The log of the PSDs was analyzed using a Condition x Segment x Frequency repeated-measure ANOVA with Greenhouse-Geisser adjusted p values. Then, the log-PSD was averaged across Condition, and paired t -tests were used to test for a Segment effect at each of the 15 frequency bins, using the method of Benjamini and Hochberg [8] to control the false discovery rate (FDR) at less than 0.05. Because p values at different frequencies are dependent, control of the FDR is approximate. For plotting variability and PSDs we used geometric means to be consistent with our use of the log transform in our statistical analyses: the log of the geometric mean equals the arithmetic mean of the logs.

The real and imaginary parts of complex coherence were analyzed separately. First, for each condition and frequency bin, we tested whether the measure was different from 0 using a t -test, with the FDR controlled at less than 0.05. Then, we performed a Condition x Frequency repeated-measure ANOVA with Greenhouse-Geisser adjusted p values. Every condition pair was tested for a main Condition effect using a mixed model with unstructured covariance and Tukey-Kramer and Kenward-Roger adjustments. In those cases with a significant Condition x Frequency interaction, every condition pair and frequency bin were tested for a Condition effect using paired t -tests, with the FDR controlled at less than 0.05.

RESULTS

Sway Variability

Figure 2 shows the mean position and velocity sway variability in both directions. The variability of the trunk segment was higher than the leg segment, supported by significant main Segment effects ($p < 0.004$). There were highly significant main Condition effects for both AP and ML velocity variability ($p < 0.001$). All conditions were different between each other except for the pairs: Both vs. Touch, Touch vs. Vision for both segments; and Neither vs. Vision for the trunk segment in the AP direction. For the ML direction, Neither was different from the other three conditions in the leg segment and different from the Both condition in the trunk segment. For position variability, the main Condition effect was significant in the AP direction ($p < 0.04$) but not in the ML direction ($p = 0.76$), with differences only between the Vision and Both conditions.

The only significant Condition x Segment interaction was found for AP velocity variability ($p < 0.004$); adding sensory information decreased the log-variability more for the leg segment than for the trunk segment, that is, the percentage decrease in variability was greater for the leg segment. This was supported by the result that the Neither and Vision conditions were significantly different for the leg segment, but not the trunk segment.

Trunk and Legs Segment PSDs

Figure 3a–f shows the mean trunk and leg segment PSDs. Repeated-measure ANOVAs revealed significant Condition x Frequency interactions ($p < 0.005$) and Segment x Frequency interactions ($p < 0.0001$) for both directions. All main effects were also significant ($p < 0.02$); the Condition x Segment and Condition x Segment x Frequency interactions were not significant ($p > 0.05$).

The presence of a Segment x Frequency interaction for the log-PSD indicates that the percentage difference between PSDs was not uniform across frequency. The trunk PSD tended to be greater than the leg PSD, with the largest percentage differences occurring at the higher frequencies (Figure 3). To test for segment effects in more detail, we averaged the log-PSD across condition and tested for a segment effect at each frequency bin. For the AP direction, the log-PSD was greater for the trunk than the legs for all frequency bins ($\text{FDR} < 0.05$; see Methods). For the ML direction, this was true for all frequency bins except for 0.25–0.40 Hz, where we found no significant difference.

Trunk-Leg Coordination

Consistent with a previous study [5], Figure 4 shows the co-existence of trunk-leg in-phase and anti-phase patterns during quiet stance in both directions.

Both sway directions show a similar dependence of complex coherence on frequency. The real part (Fig. 4a,c) begins close to 0.5 at the lowest frequency, rises slightly, decreases, crosses the x-axis to signify a shift from the right side to left side of the complex plane, and eventually decreases to approximately -0.6 . The imaginary part (Fig. 4b,d) was approximately zero across all frequencies in both directions, except for a significant increase in the 0.45–0.60 Hz frequency bin for the Neither condition in the ML direction ($\text{FDR} < 0.05$). Recall that this complex coherence pattern corresponds to a shift in cophase from in-phase to anti-phase accompanied by a decrease in magnitude-squared coherence at the transition (Fig. 1).

Since values of the imaginary part were close to zero, changes in complex coherence across frequency were primarily due to the real part. This was especially true in the AP direction, where the imaginary part did not show any significant dependence on Frequency ($p > 0.35$ for the main Frequency effect and Condition x Frequency interaction). There were significant main Frequency effects for the real part in both directions ($p < 0.0001$) and for the imaginary part in the ML direction ($p = 0.002$).

The real and imaginary parts of complex coherence showed strong Condition effects in both directions. In all cases, there was a significant main Condition effect ($p < 0.005$). The real and imaginary parts tended to decrease significantly ($p < 0.05$) with increasing sensory information (AP real part: Vision & Both < Neither; AP imaginary part: Both < Neither, Touch & Vision; ML real part: Touch, Vision & Both < Neither; ML imaginary part: Both < Vision).

There was a significant Condition x Frequency interaction only for the real part in the AP direction and the imaginary part in the ML direction ($p < 0.004$). Adding vision tended to decrease the real part in the AP direction near the transition from positive to negative ($\text{FDR} < 0.05$: Vision < Neither for 0.45–1.00 Hz; Vision < Touch for 0.45–0.80 Hz). Thus, the transition from in-phase to anti-phase occurred at a lower frequency when visual information was

available. Adding touch tended to decrease the imaginary part in the ML direction, with Condition effects found in isolated frequency bins in the range 0.25–1.20 Hz.

DISCUSSION

The coordination between trunk and leg segment angles during quiet stance was studied to determine how the addition or removal of sensory information influenced their coordinative relationship at different frequencies. We found three main results. First, additional touch or visual information led to a decrease in variability of both the trunk and leg segments. The trunk segment displayed higher variability than the leg segment in all conditions, with the difference in segment variability larger at higher frequencies. Minor differences were observed between the segments due to condition, indicating that additional sensory information led to a similar decrease in segment variability.

Second, co-existing patterns of coordination were found in both directions of sway. At sway frequencies below 1 Hz, the trunk and legs were primarily in-phase in the AP direction. In the ML direction, an increase in imaginary coherence above the horizontal axis (Figure 4d) indicated a trunk-leg pattern that was continually shifting with frequency, traveling above the horizontal axis (Figure 1a). Presently, the mechanism underlying the difference in phase between the ML and AP directions below 1 Hz is unknown. Above 1 Hz, the AP and ML directions both assume an anti-phase pattern.

It has been argued that control of sway in the AP and ML directions are independent, based upon recordings of separate center of pressure profiles under each foot. AP balance is primarily under ankle (plantar/dorsiflexor) control, whereas ML balance is under hip (abductor/adductor) control [9]. Despite different muscular synergies involved in each direction of sway, the present results showing similar patterns of coordination between the trunk and legs suggest that the same control strategy may be realized through different muscular components.

Third, additional touch or visual information decreased the real part of complex coherence, corresponding to a transition from in-phase to anti-phase at a lower frequency. In the AP direction, this decrease depended on frequency and was only observed below 1 Hz, that is, at frequencies near or below the in-phase to anti-phase transition. These condition effects were observed for successive frequency bins, resulting in a relatively wide frequency band of significant differences. In contrast, no effects for the real part of complex coherence were observed above 1 Hz. Above 1 Hz, the phase relationship between the trunk and legs is predominantly anti-phase, suggesting the anti-phase pattern is less influenced by sensory information than the in-phase pattern observed below 1 Hz.

The addition of touch led to an observable decrease in the real part of complex coherence only in the ML direction. This may be related to how the sensory environment is structured. Placement of the touch plate lateral to the body on the right side emphasized touch information in the ML direction. Previous experiments have shown if the touch plate is placed in front of the body with the hand/arm oriented along the midline of the body, light touch effects sway primarily in the AP direction [10]. Similar effects on sway are observed depending on whether the visual display moves in the medial-lateral or anterior-posterior direction [11–12]. Even though the touch and visual information in the present experiment was static, the structure of the touch and visual inputs were such that they influenced sway in a particular direction.

Mechanical vs Neural Control

These results replicate and add to the recent finding of Creath et al [5], who showed co-existing in-phase (ankle strategy) and anti-phase (hip strategy) pattern during quiet stance. Rather than viewed as centrally selected from a set of motor program [4], these patterns can be viewed as

fundamental modes, either of which may become more prevalent if a perturbation or task excites it preferentially [7]. The present results add to this view, showing the in-phase pattern is more sensitive to sensory information than the anti-phase pattern.

There are speculative explanations for these results. One possibility is that the sensitivity of the in-phase pattern to sensory changes pattern reflects a greater degree neural control than the anti-phase pattern, whose underlying basis may be primarily due to the biomechanics of the human body approximated as a double pendulum [6]. Recent experiments provide some support for this view. Biomechanical manipulations such as adding weights to the body have proven to influence coherence at frequencies above 1 Hz, where the anti-phase pattern predominates while having little effect on coherence where the in-phase pattern predominates [13]. Moreover, muscle activity during quiet stance has shown a consistent phase relationship between muscles as well as between muscle activity and limb kinematics at lower frequencies below 1 Hz, but no consistent phase at frequencies above 1 Hz [14]. The lack of coherent muscle activity above 1 Hz suggests a diminished role for active neural control of the anti-phase pattern.

Despite such evidence, it is unknown whether the anti-phase pattern is actively produced by the control system (feedback), or whether it emerges due to musculotendon and body dynamics (the plant). It is also not known whether state estimation takes such multi-joint coordination patterns into account when interpreting sensory information. State estimation for postural control is generally thought to involve an internal model of the body's dynamics [15–18]. Because most of the power of postural sway is at low frequencies, state estimation based on a single-joint (ankle) internal model may be sufficient for postural control during quiet stance. Clearly mechanical processes are important in the control of the in-phase and anti-phase coordination modes observed during quiet stance. However, the degree to which neural processes and state estimation play a role in each pattern may differ substantially.

Another possible explanation is that changes in coherence reflect changes in the sensory noise level as sensory information is added/removed. However, it is unclear why such changes are only observed below 1 Hz where the in-phase pattern predominates. One possibility is that the signal-to-noise ratio is lower at frequencies above 1 Hz, making it difficult to detect changes due to sensory manipulation.

Summary

From the perspective of the current literature, our view is one of a schism between biomechanical and nervous system accounts of human postural control. Certain research groups focus on the complicated biomechanical problem of controlling the multi-joint human body while ignoring how the nervous system solves the problem of estimating the position and velocity of the individual body segments [19–21]. We and other groups have concentrated on the problem of estimating body dynamics using a simplified single-joint (ankle) model of body mechanics [2,17,18,22]. The few multi-joint models that include state estimation require further analysis [15,16,23–24].

The present results emphasize the need to resolve the biomechanical and neural control problem of upright stance. The origin of the in-phase and anti-phase patterns remains controversial [3]. Biomechanical accounts have been offered [6], but such accounts do not satisfy how the two-linked approximation of the human body assumes different patterns depending upon: type of perturbation (mechanically or with sensory information); the presence of neurological deficit; and even cognitive influence [4]. The co-existence of these patterns during quiet stance changes the prevailing view that coordinative patterns are centrally “selected” and suggests

the patterns observed when the body is perturbed reflect an excitation of patterns already present in the unperturbed state.

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Fig 1.

Complex coherence describing the linear relationship between the leg and trunk angles for a single trial in the ML direction. (a) Complex coherence plotted in the complex plane. Each symbol indicates a different frequency in steps of 0.05 Hz. (b–c) Complex coherence decomposed into its real and imaginary parts. (d–e) Complex coherence decomposed into (magnitude-squared) coherence r^2 and cophase θ .

Fig 2. Position viability in the AP (a) and ML (c) directions for each condition. Velocity variability in the AP (b) and ML (d) directions for each condition.

Fig 3. Power spectral density (PSD) of the trunk and leg angle in the (a–c) AP and (d–f) ML directions. PSDs of trunk and leg angle in the (a) & (d) Neither condition. (b–c) & (e–f) in all four conditions.

Fig 4.
The real and imaginary parts of complex coherence plotted separately in the (a–b) AP and (c–d) ML directions.