Published in final edited form as:

Hum Mov Sci. 2010 April ; 29(2): 243–258. doi:10.1016/j.humov.2010.02.003.

KINEMATIC SYNERGIES DURING SACCADDES INVOLVING WHOLE-BODY ROTATION: A STUDY BASED ON THE UNCONTROLLED MANIFOLD HYPOTHESIS

Adriana M. Degani¹, Alessandro Danna-Dos-Santos², Thomas Robert³, and Mark L. Latash¹

¹ Department of Kinesiology, The Pennsylvania State University, University Park, PA 16802 USA

² NSA-Fisioterapia, Londrina, PR 85010-530, Brazil

³ LBMC, INRETS, Université Claude Bernard Lyon 1, F-69675, Bron, France

Abstract

We used the framework of the uncontrolled manifold hypothesis to study the coordination of body segments and eye movements in standing persons during the task of shifting the gaze to a target positioned behind the body. The task was performed at a comfortable speed and fast. Multi-segment and head-eye synergies were quantified as co-varied changes in elemental variables (body segment rotations and eye rotation) that stabilized (reduced the across trials variability) of head rotation in space and gaze trajectory. Head position in space was stabilized by co-varied rotations of body segments prior to the action, during its later stages, and after its completion. The synergy index showed a drop that started prior to the action initiation (anticipatory synergy adjustment) and continued during the phase of quick head rotation. Gaze direction was stabilized only at the movement completion and immediately after the saccade at movement initiation under the “fast” instruction. The study documents for the first time anticipatory synergy adjustments during whole-body actions. It shows multi-joint synergies stabilizing head trajectory in space. In contrast, there was no synergy between head and eye rotations during saccades that would achieve a relatively invariant gaze trajectory.

Keywords

kinematics; synergy; eye movements; vertical posture

Introduction

An operational definition for the notion of motor synergy has been introduced based on the principle of motor abundance (Gelfand & Latash 1998; reviewed in Latash, Scholz & Schöner 2002, 2007). This principle suggests that, when the central nervous system has to coordinate a large set of elements to satisfy a few task constraints (known as the problem of motor redundancy, Bernstein 1967), it does not select a single optimal solution but rather facilitates

Address for correspondence: Mark Latash, Department of Kinesiology, Rec.Hall-267, The Pennsylvania State University, University Park, PA 16802, USA, tel: (814) 863-5374, fax: (814) 863-4424, mll11@psu.edu.

Publisher's Disclaimer: This is a PDF file of an unedited manuscript that has been accepted for publication. As a service to our customers we are providing this early version of the manuscript. The manuscript will undergo copyediting, typesetting, and review of the resulting proof before it is published in its final citable form. Please note that during the production process errors may be discovered which could affect the content, and all legal disclaimers that apply to the journal pertain.

families of solutions that are equally capable of solving the task. For the task of performing an accurate movement with a kinematically redundant effector, this principle predicts trial-to-trial co-varied changes in the involvement of the elements (joints) that would keep important characteristics of the task (for example, the endpoint trajectory) relatively invariant across repetitive trials. Correspondingly, a kinematic synergy may be defined and quantitatively estimated as task-specific co-variation of the involvement of the elements.

Several studies have documented co-varied changes in joint angles that stabilize important features of performance in a variety of tasks including sit-to-stand, pointing, Frisbee throwing, body swaying, and quick-draw shooting (Scholz & Schöner 1999; Scholz, Schöner & Latash 2000; Domkin Laczko, Jaric, Johansson & Latash 2002; Freitas, Duarte & Latash 2006; Yang & Scholz 2005; Yang, Scholz & Latash 2007). In this study, we explore the action of turning and looking at a target (for example, turning and looking at a car that has beeped behind one's back). This action is kinematically redundant, and it allows to explore kinematic synergies at two levels, at the level of body segment rotations that could stabilize head trajectory in space and at the level of head and eye rotations that could stabilize gaze trajectory in space.

We performed analysis of kinematic synergies using the computational approach associated with the uncontrolled manifold (UCM) hypothesis (Scholz & Schöner 1999; reviewed in Latash et al. 2002, 2007). This hypothesis assumes that the controller acts within a space of elemental variables and organizes within that space a sub-space (UCM) corresponding to a desired value of a potentially important performance variable. Further, the controller limits variance in directions orthogonal to the UCM while allowing relatively large variance within the UCM. According to the introduced definition of a kinematic synergy, a set of elemental kinematic variables (α_i) forms a synergy stabilizing a performance variable PV, if variance across repetitive trials mostly lies within the null-space of a matrix (Jacobian) that maps small changes in α_i onto changes in PV. This matrix is a linear approximation of the UCM. This definition of a synergy relies on the relative amounts of variance within the two sub-spaces (the UCM and the orthogonal sub-space), not on their absolute magnitudes. That is why, in many studies, an index of synergy (ΔV) was used reflecting the relative difference between the amounts of variance per dimension in the two sub-spaces.

Based on the mentioned studies that have documented kinematic synergies, we did expect to see a multi-joint synergy stabilizing head trajectory in space. The situation with the eye-head synergy was much less obvious. On the one hand, the well-known mechanism of the vestibulo-ocular reflex (VOR) produces co-varied head and eye rotations that stabilize gaze direction in space. However, the VOR is effective during target fixation and tracking, while its gain have been reported to drop during saccades that occur simultaneously with head movement (Jürgens, Becker & Reiger 1981; Lauritis & Robinson 1986; Pelisson, Prablanc & Urquizar 1988; Tomlinson 1990; Galiana & Guitton 1992; Tabak, Smeets & Collewyn 1996; reviewed in Freedman 2008). Will the amplitude of the initial saccade covary with the amplitude of the first phase of head rotation in space across trials such that the gaze trajectory is relatively invariant? Can the CNS organize a synergy between two effectors that are so different in their mechanical properties and neurophysiological mechanisms? Several earlier studies have suggested some kind of head-eye coordination during large-amplitude gaze shifts (Guitton & Volle 1987; Misslisch, Tweed & Vilis 1998; Freedman & Sparks 2000; Stahl 2001; Cinelli, Patla & Stuart 2007; McCluskey & Cullen 2007). A hypothesis has been offered on a feed-forward coordination of eye and head movements (Freedman 2001). However, none of those studies used the operational definition of synergies mentioned earlier and the associated analysis based on the UCM hypothesis to quantify head-eye synergies.

In addition to these main questions, we also explored characteristics of the time profiles of the involved kinematic synergies, in particular their possible changes in preparation to action

(anticipatory synergy adjustments, Olafsdottir, Yoshida, Zatsiorsky & Latash 2005; Shim, Olafsdottir, Zatsiorsky & Latash 2005) and their dependence on the speed of action. Based on the mentioned studies, we hypothesized that gaze shifts will be associated with anticipatory synergy adjustments and that synergy indices will show a drop during phases of quick gaze shift.

Methods

Ethical approval

All participants in the reported studies gave written consent according to the procedures approved by the Office for Research Protection of the Pennsylvania State University in compliance with the Helsinki Declaration.

Participants

Eight healthy adults (four males and four females), mean age 27.1 years (1.4 SE), mean height 1.72 m (0.02 SE), and mean mass 69.5 kg (6.5 SE) participated in the study. The participants were healthy, without any known neurological, muscular, or ocular disorders (normal vision without glasses).

Apparatus

Two kinematic tracking systems were used on the present study. A ProReflex motion analysis system with four cameras (Qualysis Track Manager version 1.7.187 – Qualysis Medical) was used to capture the coordinates of nine passive markers at 240 Hz and an Eyelink-II System (version 2.11.) was used to track the eye coordinates with respect to the head reference frame at a frequency of 500 Hz by using a headband with mounted cameras (headset mass of 420 g). An external trigger was used to synchronize the initiation of the data collection for the two systems.

Procedures

Four segments were considered in this study: three body segments (lower body, trunk, and head) and the eyes (see the rigid body model in Figure 1C). Three custom made rigid clusters of reflective markers were used to measure the segments kinematics (one cluster per segment). Each cluster was composed of a rigid tripod with the base fixed on bony parts of the body segments in order to limit artifacts due to soft tissue motion. The branches of the cluster was composed of three orthogonal 15-cm-long wooden rods with reflective markers on the top of each rod (1.5 cm diameter each). The first cluster was mounted on the top of the Eyelink helmet fixed on the skull, the second cluster was mounted on the right shoulder (acromion), and the third cluster was mounted on the right pelvis (anterior superior iliac spine). It allowed the computation of the orientation of three nominal segments representing the lower body, trunk, and head in space. A schematic representation of the clusters is shown in Figure 1A and the kinematic rigid body model used in this experiment is illustrated in Figure 1C. Note that, further in the text, we use “lower body”, “trunk”, and “head” to refer to the assumed rigid segments, not to actual anatomical body structures.

The experiment started with a single trial, which was used to compute the maximum gaze shift amplitude for each participant. This test was performed to ensure that the main trials were not affected by a ceiling effect. Participants were instructed to stand comfortably barefoot on the platform (0.5 m wide and 0.47 m long) with the arms crossed on the chest. The feet were placed apart at the shoulder width, parallel to each other, with the body weight distributed equally between the two feet. Each participant was instructed to look forward at a target (diameter 0.005 m) placed 0.8 m in front of the participant on a blackboard (0.5 m × 0.5 m) at the eye

level. Then, the participant was asked to rotate the body to the right (clockwise when watched from above) without moving the feet and shift the gaze to look as far as possible behind the body.

After this initial trial, a second target with the diameter of 0.02 m was placed 1.8 m behind the participant (resulting in an angular size of 0.64°) at the eye level and at 160° to the right with respect to the original gaze direction. The main task of the experiment was to perform a self-paced whole-body smooth rotation about the vertical axis and look at this visual target placed behind the body without moving the feet. The participants were asked to shift the gaze to the target and not to correct their final body and eye position once they reached the target. Prior to each trial, the participants were asked to occupy the same initial posture and to look at the target described in the previous paragraph. The initial state was visually controlled by two experimenters to ensure that the initial posture (including the head position) was reproducible across trials. The participant's feet were in the same place across all trials. Figure 1 (panels A and B) illustrates the experimental setup.

Each participant performed series of trials under two different instructions: a) at a natural comfortable speed (CSP, comfortable self-paced) and b) as quickly as possible (FSP, fast self-paced). The two velocities were used because earlier studies showed that indices of synergies were highly sensitive to the rate of change of the elemental variables (Latash, Scholz, Danion & Schöner 2002; Shim et al. 2005). A familiarization period was given to each participant prior to data collection. On average, it took 3 to 5 practice trials for the participants to feel comfortable with the task. A total of 25 trials were performed under each instruction (CSP and FSP, balanced across participants). The initial body position was the same as described for the single trial performed at the beginning of the experiment. The position of the feet was marked and reproduced over all the trials. A 5-s time interval between two successive trials was used to perform drift corrections of the Eyelink-II system. Drift correction was performed prior to each trial according to the Eyelink-II system specifications. Also, a 30-s break was taken after every 10 trials to perform calibration of the Eyelink-II system. Participants were asked not to blink during the movements. The experiment took about 60 minutes.

Data Processing

All the signals were processed off-line using Matlab 6.5 software package. Only those trials where all the body markers were recognized by the ProReflex system during the entire action were submitted to further analyses. We also rejected trials with blinks during the motion. A total of twelve trials per condition (CSP and FSP) were selected randomly from all the accepted trials for further analysis for each condition and each participant. Twelve was the lowest number of acceptable trials per condition across all conditions and participants.

Signals from the ProReflex system were re-sampled at 500 Hz and filtered with a 50 Hz low-pass, second order, zero-lag Butterworth filter. The clusters placed on the head, shoulder, and pelvis were used to compute the orientation of three rigid bodies defined previously (Figure 1, panel C). Unfiltered signals from the Eyelink-II system were used to allow better detection of the eye motion.

Rotations of the nominal body segments (lower body, trunk and head) in space were computed in 3D from the marker trajectories using a classical Euler's angle procedure. Only rotations about the vertical axis were analyzed in this study. Rotations about other axes, orthogonal to the vertical axis, were found to be negligible.

The Eyelink II System recorded the movement of both right and left eyes; however, only the right eye rotation about the vertical axis was analyzed in this study (pilot analysis of the left eye rotation showed qualitatively similar results). The output from the system was the eye

rotation within the head reference frame. The gaze rotation (direction of line of vision in space) was computed as the sum of the head rotation in space and the eye rotation within the head reference frame.

The rotation of each body segment in space (lower body, trunk, head, and eye, Figure 1, panel C) will be referred to as θ_{LEG} , θ_{TRUNK} , θ_{HEAD} , and θ_{GAZE} , respectively. The relative angle between successive rigid bodies was computed as the difference between their rotations in space. These rotations will be referred to as α_{LEG} (lower body in space), α_{TRUNK} (trunk with respect to the lower body), α_{HEAD} (head with respect to the trunk), and α_{EYE} (eye with respect to the head). Note that $\alpha_{\text{LEG}} = \theta_{\text{LEG}}$. Angular velocities were computed by numerical derivation (third-order finite difference method) from the angular displacements.

The following computations were performed using individual trials. Each trial was aligned by the initiation of the first large-amplitude saccade defined as the time when the angular velocity of the eye with respect to the head (α'_{EYE}) reached 5% of its peak value in that particular trial. This moment will be referred to as the time of movement initiation (t_0). The time profile of the angular velocity of the head in space (θ'_{HEAD}) was used to determine the end of the movement (t_{END}) as the moment when the angular velocity of the head dropped to 5% of its peak value observed in that particular trial. Movement time (MT) was computed as: $\text{MT} = t_{\text{END}} - t_0$. The trials were aligned according to t_0 ; the purpose of the trial alignment was to ensure that analysis of variance was performed across trials at comparable phases of the action. Figure 2 illustrates how the movement initiation and movement termination times were defined.

We tried different methods of alignment during the pilot stages of analysis including, in particular, alignment by gaze shift initiation and termination. Other methods resulted in very large spreads of movement time values across trial by the same subject. This led to misalignment of such phases of the movement as the saccade and the VOR. Our method gave the most consistent movement time values and the best alignment of identifiable movement phases.

The peak amplitude of each body segment rotation was computed as the difference between its maximum and initial angle, over the period from t_0 and t_{END} . The final amplitude of each body segment rotation was defined as the difference between final angle (at t_{END}) and initial angle (at t_0). Note that for some measures such as θ_{HEAD} , peak and final amplitudes are very similar. In contrast, for the eye, counter-rotation toward the end of the saccade renders final amplitude considerably smaller than peak amplitude.

Two types of analyses were employed on this study. Our first analysis focused on data series around the moment of movement initiation. More precisely, 200 ms time windows were selected before and after the beginning of the first large-amplitude saccade (t_0). In this analysis, all the data were analyzed in real time (seconds) to avoid distorting the trajectory of the saccade by time normalization. The second analysis used the data obtained for the whole movement. These time series were time normalized to 100% covering the interval $\{t_0, t_{\text{END}}\}$ to make the data comparable across trials and participants.

Analysis of kinematic synergies

The framework of the uncontrolled manifold (UCM) hypothesis was used for quantitative analysis of kinematic synergies. As mentioned in the Introduction, the UCM hypothesis is based on an assumption that the controller acts in the space of elemental variables and selects within that space a sub-space (UCM) corresponding to a desired value of a performance variable. Then the controller tries to limit the variability of the elemental variables to the UCM (Scholz & Schöner 1999; Latash et al. 2002, 2007). Within this analysis, hypotheses are being tested on whether particular performance variables are stabilized by co-varied across trials

adjustments in elemental variables. One of the advantages of the analysis is the possibility to analyze one and the same data set with respect to different performance variables (test different hypotheses). To estimate variance within the UCM and orthogonal to the UCM (V_{UCM} and V_{ORT}), relations between small changes in the elemental variables and in the performance variable are commonly considered in a linear approximation. The UCM is approximated by the null-space of a corresponding Jacobian matrix ($\mathbf{J}$). By definition, the null-space of $\mathbf{J}$ is a set of all vector solutions $\mathbf{x}$ of the equation $\mathbf{J}\mathbf{x} = \mathbf{0}$. To justify the assumption of linearity, analysis of variance is typically performed across deviations of the variables recorded at comparable phases of the action across trials from the averaged across trials values (reviewed in detail in Latash et al. 2007). If the dimensionality of the original space of elemental variables is n , and the performance variable is uni-dimensional (as in all the analyses presented in this study), the UCM has the dimensionality of $(n-1)$.

Average trajectories of the elemental variables, such as rotations of the lower body (α_{LEG}), trunk (α_{TRUNK}), head (α_{HEAD}), eye (α_{EYE}), and head in space (θ_{HEAD}), were computed across trials for each participant and each condition separately. Further, the average trajectories were subtracted from the trajectories in each individual trial, and the deviations were projected onto the UCM computed for the corresponding performance variable and onto its orthogonal complement (for more details on these steps see Scholz et al. 2000; Domkin et al. 2003). Both amounts of variance per degree of freedom (V_{UCM} and V_{ORT}) were computed across trials. V_{UCM} and V_{ORT} correspond to the variability that does not affect the performance variable (V_{UCM}) and the variability that does (V_{ORT}).

Finally, the difference between V_{UCM} and V_{ORT} was estimated using an index of synergy (ΔV), where $\Delta V = (V_{\text{UCM}} - V_{\text{ORT}})/V_{\text{TOTAL}}$, where all variance indices were computed per degree-of-freedom and V_{TOTAL} means total variance. The normalization by V_{TOTAL} was done to allow comparison across participants and across action phases. Note that $\Delta V > 0$ correspond to proportionally more variance within the UCM; such values were interpreted as a synergy in the space of elemental variables stabilizing the performance variable. Higher positive values of the index of synergy are interpreted as stronger kinematic synergies. When $\Delta V = 0$, the amount of variance per dimension is the same in directions that correspond to a change in the performance variable and along directions that keep the performance variable unchanged. Negative indices of synergy may be interpreted as a reflection of a predominantly positive co-variation of elemental variables contributing to a change in the performance variable or destabilizing it. Recall that the terms stabilizing and destabilizing are used not in the meaning of mechanical or dynamic stability but to imply lower and higher variability of performance variables as compared to what could be expected if all the elemental variables varied across trials independently.

We performed three separate UCM analyses based on the following equations:

$$\begin{aligned}\theta_{\text{HEAD}} &= \alpha_{\text{LEG}} + \alpha_{\text{TRUNK}} + \alpha_{\text{HEAD}}, \\ \theta_{\text{GAZE-A}} &= \theta_{\text{HEAD}} + \alpha_{\text{EYE}}, \text{ and} \\ \theta_{\text{GAZE-B}} &= \alpha_{\text{LEG}} + \alpha_{\text{TRUNK}} + \alpha_{\text{HEAD}} + \alpha_{\text{EYE}}.\end{aligned}$$

The first approach considered co-variations across-trials of α_{LEG} , α_{TRUNK} and α_{HEAD} related to stabilization of the head trajectory in space (θ_{HEAD}). The second approach considered co-variations across trials of α_{EYE} and θ_{HEAD} related to stabilization of gaze trajectory ($\theta_{\text{GAZE-A}}$). And the third approach considered co-variation across trials of α_{EYE} , α_{HEAD} , α_{TRUNK} , and α_{LEG} related to stabilization of gaze trajectory ($\theta_{\text{GAZE-B}}$). Note an important difference between the second and third analysis: They involve different sets of elemental variables and, hence, are performed in spaces of different dimensionalities.

Since angular rotations in the same plane are additive, the Jacobian matrices were $\mathbf{J}_1 = [1 \ 1 \ 1]^T$, $\mathbf{J}_2 = [1 \ 1]^T$, and $\mathbf{J}_3 = [1 \ 1 \ 1 \ 1]^T$ for the three mentioned analyses, respectively. The dimensionality of the orthogonal complement was always unity for all three analyses, while the dimensionality of the UCM was 2, 1, and 3 respectively. As a result, depending on the type of analysis, ΔV data were within the following ranges, $[+1.5; -3]$, $[+2, -2]$, and $[+1.33; -4]$. Prior to applying parametric statistics, these data were z-transformed, taking into account the actual limits of the index of synergy (see Robert, Zatsiorsky & Latash 2008).

Subsequently, variance indices (V_{UCM} and V_{ORT}) and indices of synergy for all three analyses described (ΔV_{HEAD} , ΔV_{GAZE-A} , and ΔV_{GAZE-B}) were computed for both real-time series in the interval ± 200 ms about the time of movement initiation (t_0) and for the normalized-time data over the whole action.

Steady-state indices of synergy before the action were computed for both ΔV_{HEAD} and ΔV_{GAZE-B} as averages over the time interval from -0.2 to -0.1 s prior to t_0 . We noticed that the index of synergy could start to drop before movement initiation, a phenomenon described earlier for quick force production tasks and termed anticipatory synergy adjustment (ASA, Shim et al. 2005; Olafsdottir et al. 2005). Hence, we computed the average index of synergy and its standard deviation during the steady-state and defined the time when the index of synergy before movement initiation dropped under this value by more than twice its standard deviation.

Steady-state values of the index of synergy after the action were also computed. In this case, normalized-time data were used and the index of synergy data were averaged between 100% and 125% after t_{END} .

Indices of variance (before, during, and after the action) from the time-normalized data were averaged over 10% time windows ($MT = 100\%$). Based on visual analysis of the patterns of the index of synergy, we selected four time windows, the time prior to movement initiation (T1, from -20% to -10% prior to t_0), the time interval after the saccade (T2, from 40% to 50% of MT), the time interval when most participants showed a late eye rotation during the fast condition (T3, from 60% to 70% of MT), and the steady-state after the movement (T4, from 110% to 120% of MT , after t_{END}).

Standard methods of descriptive and non-parametric statistics (Kruskal-Wallis test) were used to analyze kinematic and synergy indices. Post-hoc tests (Mann-Whitney test) were used to further analyze significant effects. The main factors were *Condition* (initial trial, CSP and FSP), *Speed* (CSP and FSP), *Amplitude* (maximal amplitude and final amplitude), *Body-segment* (levels depended on particular comparisons), *Variance-index* (V_{UCM} and V_{ORT}), *Performance-variable* (θ_{HEAD} , θ_{GAZE-A} , and θ_{GAZE-B}), and *Time-window* (T1, T2, T3, and T4). The level of significance was set at $p = 0.05$.

Results

General behavior

The task was very natural and easy for the participants except for the no-blinking instruction. The smallest number of acceptable trials per condition per subject was 12; for consistency, we accepted exactly 12 trials for each participant and each condition. On average, the movement time for the comfortable speed condition was 1.12 s (± 0.13 s), and for the fast condition it was 0.55 s (± 0.02 s).

Typically, the eyes started to move before the head did under both comfortable and fast speed conditions. The initial phase of eye motion was characterized by a large-amplitude saccade

that lasted for about 0.2 s. The body segments started to move during the saccade and continued their motion after the saccade terminated. After the saccade, the eyes typically rotated in the opposite direction, towards the center of the orbit. We instructed the participants not to perform conscious corrections of movements. This instruction was used to reduce the occurrence of idiosyncratic changes in control signals that would complicate interpretation of the analysis of synergies. However, corrective head movements could be seen at the end of the task, particularly under the fast instruction. The participants were unaware of those corrections.

The average final angular gaze shift in the horizontal plane under the comfortable speed condition was $161^\circ (\pm 2^\circ)$, while under the fast condition it was $168^\circ (\pm 8^\circ)$, both with respect to the original position. As a result, participants showed a tendency towards overshooting the target under the fast condition but not under the comfortable speed condition. The off-plane rotations (the angular deviations in the participant's sagittal and frontal planes) were relatively minor (note that the sagittal plane rotated with the action). In particular, by the end of the movement, participants showed negligible head rotation in space in both sagittal ($0.9^\circ \pm 0.6^\circ$ and $2.1^\circ \pm 0.9^\circ$ for the comfortable and fast speed conditions respectively) and frontal ($1.0^\circ \pm 0.2^\circ$ and $1.7^\circ \pm 0.3^\circ$ for the comfortable and fast speed conditions respectively) planes. Figure 3 shows typical time profiles of the leg, trunk, head, and eye rotations for five individual trials performed by a typical participant under the comfortable and fast speed conditions. In this illustration, the initial angular variables were set to zero for each trial.

During the initial trial (shifting the gaze by as much as possible, see Methods), the maximal gaze shift amplitude with respect to the original position was $201^\circ (\pm 5^\circ)$. The gaze shift amplitude during the main experimental trials was significantly smaller. Hence, there was no ceiling effect associated with the task.

Kinematic characteristics

The peak amplitude of the saccade (α_{EYE}) was similar under both comfortable and fast speed conditions ($43^\circ \pm 2^\circ$ and $44^\circ \pm 2^\circ$, respectively). The peak amplitude of the movement throughout the action of all segments analyzed (α_{LEG} , α_{TRUNK} , and α_{HEAD}) was also similar between the comfortable and fast speed conditions (Kruskal-Wallis' tests with *Speed* as the factor; $p > 0.1$ for all tests). Figure 4A shows the average peak amplitude of the eye and body segment rotations under the comfortable and fast speed conditions.

During the last portion of the action, the head continued to rotate in space up to an average amplitude of $140^\circ (\pm 5^\circ)$ for the comfortable speed condition and $153^\circ (\pm 4^\circ)$ for the fast condition, while the eyes counter-rotated under the influence of the vestibulo-ocular reflex. No correlation between the peak amplitude of the saccade (α_{EYE}) and the peak amplitude of the head rotation in space (θ_{HEAD}) over the whole action was found. R-values averaged -0.12 (ranging from -0.54 to 0.19) and -0.05 (ranging from -0.54 to 0.67), for the comfortable and fast speed conditions, respectively.

Figure 4B shows the peak amplitude and final angular position of the eye rotation (α_{EYE}) under the comfortable and fast speed conditions. Note that the eye showed larger angular displacement during the movement but then moved back such that its final deviation from the initial position was much smaller than its maximal deviation, $21^\circ (\pm 3^\circ)$ and $43^\circ (\pm 2^\circ)$ under the comfortable speed condition and $15^\circ (\pm 4^\circ)$ and $44^\circ (\pm 2^\circ)$ under the fast condition, respectively. These findings were confirmed by Kruskal-Wallis' tests (*Amplitude* as factor, $p < 0.01$ for both conditions).

Analysis of kinematic synergies

Further, we used the framework of the UCM hypothesis to analyze whether covariation of elementary rotations across trials stabilized performance variables such as head rotation in space and gaze direction (see Methods). In particular, we investigated whether α_{LEG} , α_{TRUNK} , and α_{HEAD} co-varied to stabilize the head trajectory in space (α_{HEAD}), whether α_{EYE} and θ_{HEAD} co-varied to stabilize the gaze trajectory ($\theta_{\text{GAZE,A}}$), and whether all four elementary rotations (α_{LEG} , α_{TRUNK} , α_{HEAD} , and α_{EYE}) co-varied to stabilize the gaze trajectory ($\theta_{\text{GAZE,B}}$). The index of synergy (ΔV) was computed within the framework of the UCM hypothesis, as described in the Methods section, for all three analyses (ΔV_{HEAD} , $\Delta V_{\text{GAZE-A}}$, and $\Delta V_{\text{GAZE-B}}$). These analyses were run for the real-time data within the time interval ± 200 ms about the movement initiation time (t_0) and for the time-normalized data over the whole movement duration (from t_0 to t_{END}).

Figure 5 (panels A, B, and C) shows the angular displacements of the lower body (α_{LEG}), trunk (α_{TRUNK}), head (α_{HEAD}), eye (α_{EYE}), head in space (θ_{HEAD}), and gaze (θ_{GAZE}) about the time of movement initiation averaged across the participants. The initial angular variables averaged across trials within each participant were set to zero. Note that this had no effect on the computed variance indices across trials. The other three panels of Figure 5 (D, E, and F) shows the index of synergy for the three analyses (ΔV_{HEAD} , $\Delta V_{\text{GAZE-A}}$, and $\Delta V_{\text{GAZE-B}}$) for the comfortable and fast speed conditions (averaged across the participants).

Before movement initiation, small rotations of the lower body, trunk, and head covaried across trials to stabilize head orientation in space as reflected by the positive indices of synergy prior to t_0 (Figure 5D). In this Figure (and also in Figures 6 and 7), mean across subjects values of ΔV indices are presented with error bars that were computed in the following way. The ΔV indices were z-transformed as mentioned in the Methods. Standard errors of the mean were computed. Then, the standard error values were un-log-transformed, and those values were plotted on the graphs. The average ΔV_{HEAD} values over the time interval from -0.2 to -0.1 s prior to t_0 were similar for the comfortable and fast speed conditions ($\Delta V_{\text{HEAD}} = 0.98$ ranging from 0.72 to 1.28, and $\Delta V_{\text{HEAD}} = 0.84$, ranging from -0.06 to 1.24, respectively, both significantly positive, $p < 0.01$, Wilcoxon's signed-rank test). Similar findings were obtained for the analysis of a system of four rotations (α_{LEG} , α_{TRUNK} , α_{HEAD} , and α_{EYE}) contributing to the gaze direction ($\Delta V_{\text{GAZE-B}}$): Prior to movement initiation, leg, trunk, head, and eye orientations co-varied across trials to stabilize gaze direction (Figure 5F). The averaged $\Delta V_{\text{GAZE-B}}$ indices were similar for the comfortable and fast speed conditions ($\Delta V_{\text{GAZE-B}} = 0.67$, ranging from 0.12 to 1.04, and $\Delta V_{\text{GAZE-B}} = 0.62$, ranging from -0.17 to 1.25, respectively, both significantly positive, $p < 0.01$). Kruskal-Wallis test showed no effect of *Speed* on the indices of synergy. In contrast, UCM analysis of the co-variation of α_{EYE} and θ_{HEAD} prior to t_0 showed highly variable $\Delta V_{\text{GAZE-A}}$ indices that were not different from zero or negative for both comfortable and fast speed conditions (Figure 5E).

The ΔV_{HEAD} and $\Delta V_{\text{GAZE-B}}$ indices showed a trend to fall just prior to movement initiation under both comfortable and fast speed conditions (Figures 5D and 5F). In particular, ΔV_{HEAD} started to drop 0.04 s (± 0.03 s) and 0.02 s (± 0.03 s) before t_0 under the comfortable and fast speed conditions. The $\Delta V_{\text{GAZE-B}}$ index showed an earlier drop under the comfortable speed condition (0.09 s ± 0.02 s before t_0) as compared to the fast condition (0.04 s ± 0.02 s before t_0). Kruskal-Wallis' tests showed no effect of *Speed* (comfortable and fast speed) for the time ΔV_{HEAD} started to drop ($p > 0.1$), and an effect of *Speed* for the time $\Delta V_{\text{GAZE-B}}$ started to drop ($p < 0.05$). After the movement initiation (t_0), both indices of synergy dropped to zero or to negative values and stayed non-positive over the first 0.20 s of the movement (Figure 5, panels D and F).

Figure 6 (panels A, B, and C) shows the time normalized profiles of the angular displacement of the lower body (α_{LEG}), trunk (α_{TRUNK}), head (α_{HEAD}), eye (α_{EYE}), head in space (θ_{HEAD}), and gaze (θ_{GAZE}) for both comfortable and fast speed conditions. The other three panels of Figure 6(D, E, and F) shows synergy indices (ΔV_{HEAD} , $\Delta V_{\text{GAZE-A}}$, and $\Delta V_{\text{GAZE-B}}$, respectively) averaged across participants.

The pre-movement positive indices of synergy and their early drop can also be seen in Figure 6 (panels D and F). After the saccade, ΔV_{HEAD} showed a gradual recovery into positive values under both comfortable and fast speed conditions (Figure 6D). After the movement termination, ΔV_{HEAD} achieved similar positive steady-state values under both comfortable and fast speed conditions ($\Delta V_{\text{HEAD}} = 0.53$, ranging from -0.18 to 1.29, and $\Delta V_{\text{HEAD}} = 0.78$, ranging from 0.26 to 1.35, respectively, both positive, $p < 0.05$). The index $\Delta V_{\text{GAZE-B}}$ achieved higher steady-state values under the comfortable speed condition as compared to the fast condition ($\Delta V_{\text{GAZE-B}} = 1.08$, ranging from 0.18 to 1.28, and $\Delta V_{\text{GAZE-B}} = 0.77$, ranging from -0.05 to 1.21, respectively, both positive, $p < 0.05$). Kruskal-Wallis tests confirmed no effect of *Speed* for ΔV_{HEAD} after movement termination ($p > 0.30$) and an effect of *Speed* for $\Delta V_{\text{GAZE-B}}$ ($p < 0.05$).

Analysis of gaze direction as the sum of two rotations (α_{EYE} and θ_{HEAD}) showed complex time profiles that varied significantly across participants (Figure 6E), likely because of the variability in the timing and magnitude of eye counter-rotations following the saccade. For statistical analysis, we averaged $\Delta V_{\text{GAZE-A}}$ values over 10% time windows. Figure 7 shows the results of this procedure (only the averages are shown to make the figure readable). We selected four time windows (T1, T2, T3, and T4) reflecting specific phases of the action that were reproducible across participants (see Methods).

Before movement initiation (t_0), there was a mixture of negative and low-positive $\Delta V_{\text{GAZE-A}}$ indices under both conditions. Under the comfortable speed condition, $\Delta V_{\text{GAZE-A}}$ was negative before movement initiation ($\Delta V_{\text{T1}} = -0.59$, ranging from -1.34 to -0.14) and it increased during the movement to significantly positive values. Kruskal-Wallis test showed an effect of *Time-window* (T1, T2, T3, and T4) on $\Delta V_{\text{GAZE-A}}$ for the comfortable speed condition ($p < 0.001$). Post-hoc analyzes (Mann-Whitney) for the data in the comfortable speed condition confirmed an effect of *Time-window* (smaller index of synergy at T1 than at T2, T3, and T4, $p < 0.05$; higher index of synergy at T4 than at T1, T2, and T3, $p < 0.01$; and higher index of synergy at T3 than at T2, $p < 0.05$). For the fast condition, the trend of $\Delta V_{\text{GAZE-A}}$ was under the significance level.

Discussion

Our experiments provided answers to the main questions formulated in the Introduction. We did observe a multi-joint synergy stabilizing the head trajectory in space, and the synergy index showed reproducible across participants modulation over the movement time. In contrast, we saw no signs of a head-eye synergy that would stabilize the gaze trajectory during saccades, while a head-eye synergy stabilized gaze direction in space during steady-states and toward the end of the action, when the head movement has slowed down. The following discussion focuses on issues of head and gaze stabilizing synergies and feed-forward (anticipatory) changes in such synergies.

Multi-joint synergies stabilizing head trajectory

Several earlier studies have shown that during whole-body movements, such as sit-to-stand and both spontaneous and voluntary sway, individual joint rotations co-vary across repetitive trials such that certain potentially important kinematic variables show lower variability than what could have been expected from independent variation of joint angles (Scholz & Schöner

1999; Reisman, Scholz & Schöner 2002; Freitas et al. 2006; Hsu, Scholz, Schöner, Jeka & Kiemel 2007). The list of kinematic variables stabilized by such multi-joint synergies included coordinates of the center of mass in both vertical and anterior-posterior directions, trunk orientation with respect to the vertical, and head coordinate in the anterior-posterior direction. Our study explored a different kinematic variable that seemed most salient to the task of gaze shift, namely head orientation with respect to the initial position. The results have shown that, during steady-states and phases of slow head rotation, the three segment rotations (α_{LEG} , α_{TRUNK} , and α_{HEAD}) co-varied such that the head trajectory in space remained relatively invariant. Hence, we can conclude that head trajectory in space is indeed an important variable stabilized by coordinated rotation of the body segments.

Several studies have suggested that head movements may be organized to optimize eye rotation such that the eyes remain in an optimal range within the orbit (Stahl 2001; Hollands, Zivara & Bronstein 2004; Solomon, Kumar, Jenkins & Jewell 2006; McCluskey & Cullen 2007). Since in our experiments the location of the target remained the same, an optimal head trajectory was likely selected by the participants and stabilized across trials by the three-joint synergy after a few practice trials. Note that several earlier studies have documented the emergence and strengthening of synergies in relatively easy tasks following a short practice session (Latash, Yarrow & Rothwell. 2003; Kang, Shinohara, Zatsiorsky & Latash 2004). The overall pattern of joint rotation in our study was similar to those described earlier (Solomon et al. 2006).

It is generally agreed that, during large-amplitude gaze shifts, a command for the head motion is generated in preparation to and largely independent of the eye movement initiation (Zangemeister & Stark 1982; Phillips et al. 1996; Freedman 2001; Corneil, Olivier & Munoz 2002; Corneil & Elsley 2004). Our observations support this idea by showing early changes in the index of head-stabilizing synergy (ΔV_{HEAD}) that were observed 40–100 ms prior to the initiation of the saccade. These changes belong to the group of anticipatory synergy adjustments (ASAs), that consist of an early drop in the synergy index prior to a quick change of the corresponding performance variable (see also Corneil, Munoz & Olivier 2007). ASAs have until now been reported only for tasks of quick multi-digit force production; in those studies, ASAs represented a drop in the index of synergy of multi-finger synergies stabilizing total force produced by a set of fingers 100–150 ms prior to a quick voluntary change in the total force (Olafsdottir et al. 2005; Shim et al. 2005; Shim, Park, Zatsiorsky & Latash 2006). ASA involved a drop in V_{UCM} that could be accompanied by an increase in V_{ORT} . To our knowledge, this study is the first to report ASAs for multi-joint kinematic synergies.

ASAs have been assumed to reflect feed-forward changes in (weakening of) the multi-element synergy stabilizing a performance variable in preparation to its quick change to make sure that the controller does not have to fight its own pre-existent synergy (Goodman & Latash 2006). Immediately following ASAs, a further drop in the synergy index is typically observed (Olafsdottir et al. 2005), similar to our observations (Fig. 6D). This drop may be related to two processes, continuation of the ASA and effects of timing errors that are amplified during quick actions (Latash, Shim & Zatsiorsky 2004; Goodman, Shim, Zatsiorsky & Latash 2005). The synergy recovers with a drop in the rate of change of the performance variable, head angular position in space, such that, by the new steady-state, the index of head-stabilizing synergy is as high as prior to the action initiation.

Note that our method of index of synergy computation makes $\Delta V > 0$ associated with a head stabilizing synergy, and the highest theoretical index of synergy is +1.5. This value means that all the variability at the level of rotations is perfectly intercompensated such that the head trajectory in space shows no variability across trials. The indices of synergy observed in our study were very high, close to +1 at steady-states. So, we can claim that the controller did care

about ensuring a reproducible head position (trajectory), possibly to be able to plan eye movements in a reproducibly moving reference frame (cf. McCluskey & Cullen 2007).

Coordination of head and eye rotations

In our experiments, the participants could not see the target before movement initiation but they had had sufficient experience of shifting the gaze to that target. It is reasonable to assume, therefore, that an internal representation of a remembered target played an important role in the generation of the saccade and the first phase of quick head movement (see Flanagan, Terao & Johansson 2008).

As in earlier studies of large-amplitude gaze shifts, our participants performed a combination of a quick large-amplitude head rotation in space and a series of eye movements that ultimately limited the final eye movement amplitude to about 20° (Freedman & Sparks 1997; Stahl 1999; Cinelli et al. 2007; McCluskey & Cullen 2007; Anastasopoulos, Ziavra, Hollands & Bronstein 2009). Note that the saccade at movement initiation was typically of a larger amplitude leading to peak amplitude of eye rotation of over 40°. Its peak velocity was relatively low corresponding to earlier reports of a drop in saccade peak velocity with large head involvement in the gaze shift (Freedman & Sparks 1997). Later eye movements (see Figure 3) could be observed in the opposite direction thus bringing the eye into a more central position within the orbit. These observations are different from a classical complex “single saccade plus single saccade-like head movement” described for both cats and humans (Guitton, Douglas & Volle 1984; Guitton & Volle 1987). During the latest part of the movement, the head continued to move while the gaze direction was kept nearly stationary, likely helped by the mechanism of the vestibulo-ocular reflex (cf. Tomlinson 1990).

We would like to make a comment here related to the use of angular variables in our analyses rather than angular velocity variables that may be more adequate for the vestibulo-ocular reflex action. Our choice of variables was dictated by the fact that the task was formulated using an angular variable, that is gaze direction. There is no simple way of creating a Jacobian that would link rotational velocities to gaze direction. We admit that the choice of variables in our analyses could be suboptimal for addressing the vestibulo-ocular reflex action, but at this time, this problem does not seem to be easily solvable.

The vestibulo-ocular reflex could be expected to result in a strong gaze-stabilizing synergy in the initial steady-state. However, this was not the case as reflected by the non-positive values of the index of synergy. Before t_0 , a mixture of negative and low-positive $\Delta V_{\text{GAZE-A}}$ indices seems to be due to micro-saccades during fixating the initial target. Another possible reason is variations in the gaze direction across trials compatible with the target size and minimal variations in the head position (given that the subjects were strongly encouraged to occupy the same posture across trials).

The synergy index, $\Delta V_{\text{GAZE-A}}$ was non-positive over the first part of the movement, and it became positive only during later intervals (intervals T2 and T3 in Figure 8) and at the steady-state after the movement termination. During fast eye movements, such as the initial saccade during both comfortable and fast speed conditions and later fast eye rotations during the fast condition, the index of synergy dropped, while it could be relatively high ($\Delta V > 0$) in other movement phases. These observations are similar to the reported loss of synergies during fast actions (Latash, Scholz, Danion & Schöner 2002; Olafsdottir et al. 2005).

Overall, our experiments have shown that the central nervous system organizes synergies of body rotations to stabilize head trajectory in space. However, it fails to organize a similar synergy between the saccade (the same seems to be true for later fast eye rotations) and head-

in-space rotation. There may be several, mutually non-exclusive, reasons for the lack of a gaze-stabilizing eye-head synergy.

First, gaze shift during saccades is very quick. As shown in several earlier studies, a quick, discrete shift of a performance variable frequently leads to destruction of synergies stabilizing this variable even if such synergies are present during slower shifts of the same performance variable (Latash et al. 2002a; Shim et al. 2005), likely due to the timing errors (Goodman et al. 2005; Friedman, SKM, Zatsiorsky & Latash 2009). So, it is possible that the lack of a gaze stabilizing synergy originated from the high speed of the action.

Second, the inertial properties of the head and eye ball are so dramatically different that this, by itself, could make any attempts at stabilizing a variable that they produce together futile.

Third, the neurophysiological mechanisms involved in the saccade generation differ rather significantly from those involved in the control of whole-body voluntary movements (for reviews see Orban de Xivry & Lefèvre 2007; Freedman 2008). Both systems rely on such major structures as the basal ganglia and cerebral cortices, but the saccade generation seems to be more heavily dependent on processes in the brain stem and midbrain structures. The current finding of the lack of synergies between head and eye movements during saccades may be revealing of certain limitations in the ability of the neural controller to organize actions towards a common goal when different neurophysiological structures are involved.

We would like to acknowledge several limitations of the study. First, we studied an action of turning around without moving one's feet. Although such actions happen in everyday life, one may question whether our results and conclusions can be generalized for any gaze shifts involving body rotation. Without more studies, we cannot speculate on generalization of our findings to other types of saccadic gaze shifts. Second, our method of analysis of synergies is based on several assumptions, in particular on an assumption that variations in elemental variables across trials at comparable phases of the movement were small. This might be true for body segment rotations, but the eye saccades could have led to large differences across trials leading to distorted indices of synergy. We hope that development of the method for analysis of single trials (across time samples) would allow to overcome the latter problem and validate our conclusions.

The analyses of variance across trials are very sensitive to the employed trial alignment procedures. To study the first phase of the movement, we tried two types of alignment, by head motion initiation and by eye saccade initiation. The alignment by the head movement initiation grossly distorted the saccade data because the saccades became misaligned, and the averaged across trials data produced unreasonably long "saccades". The unavoidable misalignment of the head movement data when the trials were aligned by the saccade initiation produced much less dramatic effects of the head kinematic data. We have to admit, however, that the choice of the alignment method could have an effect on the results.

Acknowledgments

The study was in part supported by an NIH grant NS-035032.

References

- Anastasopoulos D, Ziavra N, Hollands M, Bronstein A. Gaze displacement and inter-segmental coordination during large whole body voluntary rotations. *Experimental Brain Research* 2009;193:323–336.
- Barborica A, Ferrera VP. Modification of saccades evoked by stimulation of frontal eye field during invisible target tracking. *Journal of Neuroscience* 2004;24:3260–3267. [PubMed: 15056705]

- Bernstein, NA. On the Construction of Movements. Medgiz; Moscow: 1947. (in Russian)
- Cinelli M, Patla A, Stuart B. Involvement of the head and trunk during gaze reorientation during standing and treadmill walking. *Experimental Brain Research* 2007;181:183–191.
- Corneil BD, Elsley JK. Countermanding eye-head gaze shifts in humans: marching orders are delivered to the head first. *Journal of Neurophysiology* 2005;94:883–895. [PubMed: 15728762]
- Corneil BD, Munoz DP, Olivier E. Priming of head premotor circuits during oculomotor preparation. *Journal of Neurophysiology* 2007;97:701–714. [PubMed: 17079344]
- Corneil BD, Olivier E, Munoz DP. Neck muscle responses to stimulation of monkey superior colliculus. II. Gaze shift initiation and volitional head movements. *Journal of Neurophysiology* 2002;88:2000–2018. [PubMed: 12364524]
- Crawford JD, Ceylan MZ, Klier EM, Guitton D. Three-dimensional eye-head coordination during gaze saccades in the primate. *Journal of Neurophysiology* 1999;81:1760–1782. [PubMed: 10200211]
- Crawford JD, Guitton D. Visual-motor transformations required for accurate and kinematically correct saccades. *Journal of Neurophysiology* 1997;78:1447–1467. [PubMed: 9310435]
- Crawford JD, Vilis T. Axes of eye rotation and Listing's law during rotations of the head. *Journal of Neurophysiology* 1991;65:407–423. [PubMed: 2051188]
- Domkin D, Laczko J, Jaric S, Johansson H, Latash ML. Structure of joint variability in bimanual pointing tasks. *Experimental Brain Research* 2002;143:11–23.
- Flanagan JR, Terao Y, Johansson RS. Gaze behavior when reaching to remembered targets. *Journal of Neurophysiology* 2008;100:1533–1543. [PubMed: 18632880]
- Freedman EG. Interactions between eye and head control signals can account for movement kinematics. *Biological Cybernetics* 2001;84:453–462. [PubMed: 11417057]
- Freedman EG. Coordination of the eyes and head during visual orienting. *Experimental Brain Research* 2008;190:369–387.
- Freedman EG, Sparks DL. Eye-head coordination during head-unrestrained gaze shifts in rhesus monkeys. *Journal of Neurophysiology* 1997;77:2328–2348. [PubMed: 9163361]
- Freitas SMSF, Duarte M, Latash ML. Two kinematic synergies in voluntary whole-body movements during standing. *Journal of Neurophysiology* 2006;95:636–645. [PubMed: 16267118]
- Friedman J, SKM V, Zatsiorsky VM, Latash ML. The sources of two components of variance: An example of multifinger cyclic force production tasks at different frequencies. *Experimental Brain Research* 2009;196:263–277.
- Galiana HL, Guitton D. Central organization and modeling of eye-head coordination during orienting gaze shifts. *Annals of the New York Academy of Sciences* 1992;656:452–471. [PubMed: 1599162]
- Gelfand IM, Latash ML. On the problem of adequate language in movement science. *Motor Control* 1998;2:306–313. [PubMed: 9758883]
- Glenn B, Vilis T. Violations of Listing's law after large eye and head gaze shifts. *Journal of Neurophysiology* 1992;68:309–318. [PubMed: 1517824]
- Goodman SR, Shim JK, Zatsiorsky VM, Latash ML. Motor variability within a multi-effector system: Experimental and analytical studies of multi-finger production of quick force pulses. *Experimental Brain Research* 2005;163:75–85.
- Guitton D, Douglas RM, Volle M. Eye-head coordination in cats. *Journal of Neurophysiology* 1984;52:1030–1050. [PubMed: 6335170]
- Guitton D, Volle M. Gaze control in humans: eye-head coordination during orienting movements to targets within and beyond the oculomotor range. *Journal of Neurophysiology* 1987;58:427–459. [PubMed: 3655876]
- Heremans E, Helsen WF, Feys P. The eyes as a mirror of our thoughts: quantification of motor imagery of goal-directed movements through eye movement registration. *Behavioral and Brain Research* 2008;187:351–360.
- Hollands MA, Zivara NV, Bronstein AM. A new paradigm to investigate the roles of head and eye movements in the coordination of whole-body movements. *Experimental Brain Research* 2004;154:261–266.
- Hollands MA, Marple-Horvat DE. Coordination of eye and leg movements during visually guided stepping. *Journal of Motor Behavior* 2001;33:205–216. [PubMed: 11404215]

- Hsu WL, Scholz JP, Schöner G, Jeka JJ, Kiemel T. Control and estimation of posture during quiet stance depends on multijoint coordination. *Journal of Neurophysiology* 2007;97:3024–3035. [PubMed: 17314243]
- Jürgens, R.; Becker, W.; Reiger, P. Different effects involved in the interactions of saccades and the vestibulo-ocular reflex. In: Cohen, B., editor. *Vestibular and oculomotor physiology*. Vol. 374. NY Acad Sci; New York, NY: 1981. p. 744-754.
- Kang N, Shinohara M, Zatsiorsky VM, Latash ML. Learning multi-finger synergies: An uncontrolled manifold analysis. *Experimental Brain Research* 2004;157:336–350.
- Klier EM, Wang H, Crawford JD. Three-dimensional eye-head coordination is implemented downstream from the superior colliculus. *Journal of Neurophysiology* 2003;89:2839–2853. [PubMed: 12740415]
- Latash, ML. *Synergy*. Oxford University Press; New York: 2008.
- Latash ML, Scholz JF, Danion F, Schöner G. Finger coordination during discrete and oscillatory force production tasks. *Experimental Brain Research* 2002a;146:412–432.
- Latash ML, Scholz JP, Schöner G. Motor control strategies revealed in the structure of motor variability. *Exercise and Sport Science Reviews* 2002b;30:26–31.
- Latash ML, Scholz JP, Schöner G. Toward a new theory of motor synergies. *Motor Control* 2007;11:275–307.
- Latash ML, Shim JK, Zatsiorsky VM. Is there a timing synergy during multi-finger production of quick force pulses? *Experimental Brain Research* 2004;159:65–71.
- Latash ML, Yarrow K, Rothwell JC. Changes in finger coordination and responses to single pulse TMS of motor cortex during practice of a multi-finger force production task. *Experimental Brain Research* 2003;151:60–71.
- Lauritis VP, Robinson DA. The vestibulo-ocular reflex during human saccadic eye movements. *Journal of Physiology* 1986;373:209–233. [PubMed: 3489091]
- McCluskey MK, Cullen KE. Eye, head, and body coordination during large gaze shifts in rhesus monkeys: Movement kinematics and the influence of posture. *Journal of Neurophysiology* 2007;97:2976–2991. [PubMed: 17229827]
- Misslisch H, Tweed D, Vilis T. Neural constraints on eye motion in human eye-head saccades. *Journal of Neurophysiology* 1998;79:859–869. [PubMed: 9463447]
- Olafsdottir H, Yoshida N, Zatsiorsky VM, Latash ML. Anticipatory covariation of finger forces during self-paced and reaction time force production. *Neuroscience Letters* 2005;381:92–96. [PubMed: 15882796]
- Orban de Xivry JJ, Lefèvre P. Saccades and pursuit: two outcomes of a single sensorimotor process. *Journal of Physiology* 2007;584:11–23. [PubMed: 17690138]
- Pelisson D, Prablanc C, Urquizar C. Vestibuloocular reflex inhibition and gaze saccade control characteristics during eye-head orientation in humans. *Journal of Neurophysiology* 1988;59:997–1013. [PubMed: 3367207]
- Phillips JO, Ling I, Siebold C, Fuchs AF. Behavior of primate vestibulo-ocular reflex neurons and vestibular neurons during head-free gaze shifts. *Annals of the New York Academy of Sciences* 1996;781:276–291. [PubMed: 8694420]
- Reisman DS, Scholz JP, Schöner G. Differential joint coordination in the tasks of standing up and sitting down. *Journal of Electromyography and Kinesiology* 2002;12:493–505. [PubMed: 12435546]
- Robert T, Zatsiorsky VM, Latash ML. Multi-muscle synergies in an unusual postural task: Quick shear force production. *Experimental Brain Research* 2008;187:237–253.
- Scholz JP, Schöner G. The uncontrolled manifold concept: Identifying control variables for a functional task. *Experimental Brain Research* 1999;126:289–306.
- Scholz JP, Schöner G, Latash ML. Identifying the control structure of multijoint coordination during pistol shooting. *Experimental Brain Research* 2000;135:382–404.
- Shim JK, Olafsdottir H, Zatsiorsky VM, Latash ML. The emergence and disappearance of multi-digit synergies during force production tasks. *Experimental Brain Research* 2005;164:260–270.
- Shim JK, Park J, Zatsiorsky VM, Latash ML. Adjustments of prehension synergies in response to self-triggered and experimenter-triggered load and torque perturbations. *Experimental Brain Research* 2006;175:641–653.

- Solomon D, Kumar V, Jenkins RA, Jewell J. Head control strategies during whole-body turns. *Experimental Brain Research* 2006;173:475–486.
- Stahl JS. Eye-head coordination and the variation of eye-movement accuracy with orbital eccentricity. *Experimental Brain Research* 2001;136:200–210.
- Tabak S, Smeets JB, Collewyn H. Modulation of the human vestibuloocular reflex during saccades: probing by high-frequency oscillation and torque pulses of the head. *Journal of Neurophysiology* 1996;76:3249–3263. [PubMed: 8930270]
- Takahashi M, Uemura T, Fujishiro T. Studies of the vestibulo-ocular reflex and visual-vestibular interactions during active head movements. *Acta Otolaryngology* 1980;90:115–124.
- Tomlinson RD. Combined eye-head gaze shifts in the primate. III. Contributions to the accuracy of gaze saccades. *Journal of Neurophysiology* 1990;64:1873–1891. [PubMed: 2074470]
- Xiao Q, Barborica A, Ferrera VP. Modulation of visual responses in macaque frontal eye field during covert tracking of invisible targets. *Cerebral Cortex* 2007;17:918–928. [PubMed: 16723405]
- Yang JF, Scholz JP. Learning a throwing task is associated with differential changes in the use of motor abundance. *Experimental Brain Research* 2005;163:137–158.
- Yang JF, Scholz JP, Latash ML. The role of kinematic redundancy in adaptation of reaching. *Experimental Brain Research* 2007;176:54–69.
- Zangemeister WH, Stark L. Gaze latency: variable interactions of head and eye latency. *Experimental Neurology* 1982;75:389–406. [PubMed: 7106221]

Figure 1. An illustration of the lateral (panel A) and superior (panel B) perspectives of the experimental design with nine passive markers and the headband with its cameras. Panel C shows the kinematic model of human body used in this study. The angular motion around the vertical axis of three rigid bodies (lower body, trunk, and head) and both eyes were included in the model.

Figure 2.

An illustration of how movement initiation (t_0), movement termination (t_{END}) and movement time (MT) were defined from 5% of the peak velocity of eye rotation to 5% of the peak velocity of the head rotation in space. Time profiles of angular displacement and velocity of eye rotation (α_{EYE} and α'_{EYE} , respectively) and head rotation in space (θ_{HEAD} and θ'_{HEAD} , respectively) of a single trial.

Figure 3. Time profile of five typical trials under the comfortable self-paced (CSP) and fast self-paced (FSP) conditions by a typical participant (# 7). The angular displacement of the lower body (α_{LEG}), trunk (α_{TRUNK}), head (α_{HEAD}), and eye (α_{EYE}), and the rotations of the head in space (θ_{HEAD}) and gaze (θ_{GAZE}) are shown in real time. The initial angular variables in all trials were set to zero for this particular illustration.

Figure 4.

A: Peak amplitude of the lower body (α_{LEG}), trunk (α_{TRUNK}), head (α_{HEAD}), eye (α_{EYE}), head in space (θ_{HEAD}), and gaze (θ_{GAZE}) under the comfortable self-paced (CSP) and fast self-paced (FSP) conditions. Averages across participants with standard error bars are shown. B: Peak amplitude (maximal angular deviation from the original orientation) and final eye position (α_{EYE}) under both comfortable self-paced (CSP) and fast self-paced (FSP) conditions. Averages across participants with standard error bars are shown. Note: * means significant difference ($p < 0.05$).

Figure 5.

Angular trajectories (the left panels) and the indices of synergy (ΔV , the right panels) for both comfortable self-paced (CSP) and fast self-paced (FSP) conditions in the vicinity of the saccade. Trajectories of the lower body (α_{LEG}), trunk (α_{TRUNK}), head (α_{HEAD}), and eye (α_{EYE}) in real time are shown in panels A and B, while trajectories of the head in space (θ_{HEAD}) and gaze (θ_{GAZE}) in real time are shown in panel C. Indices of synergy are shown for head in space (ΔV_{HEAD} , panel D) and gaze ($\Delta V_{\text{GAZE-A}}$ and $\Delta V_{\text{GAZE-B}}$ in panels E and F, respectively) trajectory stabilization under the CSP and FSP conditions. Averages across participants are shown. Standard errors of the mean were computed using z-transformed ΔV values; the graphs show those SEM values after an un-log-transformation.

Figure 6.

Angular displacements (the left panels) and the indices of synergy (ΔV , the right panels) for both comfortable self-paced (CSP) and fast self-paced (FSP) conditions during the entire movement. Angular displacement of the lower body (α_{LEG}), trunk (α_{TRUNK}), head (α_{HEAD}), and eye (α_{EYE}) in normalized time are shown in panels A and B, while trajectories of the head in space (θ_{HEAD}) and gaze (θ_{GAZE}) in normalized time are shown in panel C. Indices of synergy are shown for head in space (ΔV_{HEAD} on panel D) and gaze (ΔV_{GAZE-A} and ΔV_{GAZE-B} on panels E and F, respectively) trajectory stabilization analyses under both conditions. Averages across participants are shown. Standard errors of the mean were computed using z-transformed ΔV values; the graphs show those SEM values after an un-log-transformation.

Figure 7.

The index of synergy between eye rotation and head rotation in space computed for gaze trajectory stabilization ($\Delta V_{\text{GAZE-A}}$) under the comfortable self-paced (CSP) and fast self-paced (FSP) conditions. Averages across participants are shown over 10% movement time intervals. Note: Only time windows T1 (from -20% to -10%), T2 (from 40% to 50%), T3 (from 60% to 70%), and T4 (from 110% to 120%) were subjected to statistical assessment. Standard errors of the mean were computed using z-transformed ΔV values; the graphs show those SEM values after an un-log-transformation.