Is there a timing synergy during multi-finger production of quick force pulses?

Mark L. Latash, Jae Kun Shim, Vladimir M. Zatsiorsky

Department of Kinesiology, Penn State University, University Park, PA 16802, USA

Running title: Multi-finger timing synergies

Key Words: Synergy, finger, force, timing, human

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

Abstract

We studied whether characteristics of individual finger force profiles covaried across repetitions of a quick force pulse production task to stabilize the required magnitude and timing of the peak force. Subjects produced series of quick force pulses by pressing with all four fingers of the right hand on force sensors under the instruction to keep the magnitude of the peak of total force at 15 N and reach the force peaks at prescribed times. Individual finger force pulses were then reshuffled across trials to create a surrogate data set. The surrogate data set showed a lower average peak force with a larger dispersion. This finding has been interpreted as pointing at predominantly negative covariation among finger force pulses in the actual data that stabilized the required magnitude of the total force, a force synergy. The difference between the actual and surrogate data sets was significant early into the pulse time, starting about 40 ms after the pulse initiation. This finding points at a central nature of the negative covariation without a major role played by visual or proprioceptive feedback. In contrast, the surrogate data set showed smaller dispersion of the timing of the total peak force suggesting positive covariation of the timings of individual finger force pulses in the actual data interpreted as the lack of a timing synergy. These results have been confirmed with principal component (PC) analysis. The first PC for the timing of the individual finger peak forces accounted for over 90% of the total variance for the actual data set and for under 40% of the total variance for the surrogate data set. The fourth PC for the magnitudes of the finger forces accounted for under 4% of the total variance for the actual data set and for over 15% of the variance for the surrogate data set. The data are interpreted within the uncontrolled

manifold hypothesis; they support the hierarchical control scheme suggested by Schöner (1995).

Introduction

The famous problem of motor redundancy (Bernstein 1967; Turvey 1990a,b) has been studied using a variety of tasks and multi-effector systems including force production by fingers of the human hand acting in parallel (Li et al. 1998; Latash et al. 2002a). When several fingers produce a time profile of the total force, $F_{TOT}(t)$, that needs to reach a particular magnitude at a particular time, individual finger force profiles, $F_i(t)$, may show different covariation across several trials at the same task.

Imagine that in one trial a finger produces a higher force as compared to its typical average contribution to the total force. By doing this, it introduces an error into $F_{TOT}(t)$. Other fingers may continue producing their typical average forces, or they may also produce higher forces that would amplify the original error in $F_{TOT}(t)$, or they may produce lower forces to compensate for the error introduced by the first finger. In earlier studies, a term *synergy* has been used only with respect to the last case, i.e. when individual fingers show error compensation with respect to a particular performance variable such as $F_{TOT}(t)$ (Latash et al. 2001, 2002a; Scholz et al. 2002).

Imagine now that a finger in one trial produces a force profile, which differs from its typical contribution not in magnitude but in timing, i.e. it happens a bit earlier or a bit later. This timing error may lead to errors in the timing of $F_{TOT}(t)$. Similarly to the earlier example, one may ask a question whether other fingers adjust the timing of their force pulses to (partly) compensate for the effects of the original error on the timing of $F_{TOT}(t)$. In other words, are there *timing synergies* among fingers that stabilize a certain timing feature of $F_{TOT}(t)$, for example the time of its peak value, in addition to synergies in the magnitudes of finger forces?

A number of studies have shown that fingers demonstrate negative force covariation across trials, i.e. synergies with respect to the magnitude of total force, particularly during slow force production tasks and at relatively high forces (Latash et al. 2001, 2002a; Scholz et al. 2002, 2003). During faster tasks and at low forces, finger forces tend to show positive covariation across trials that destabilizes the total force profile. The issue of error compensation in timing has been elusive (e.g., Latash et al. 2002b).

The main purpose of this study has been to analyze error compensation among finger forces with respect to both timing and magnitude in a task when the fingers are instructed to produce quick $F_{TOT}(t)$ pulses such that the peak of each pulse reaches a certain magnitude at a certain time. Unlike many earlier studies (reviewed in Latash et al. 2002a), we have not assumed linear relations between possible small errors in the magnitude and timing of individual finger force pulses and characteristics of $F_{TOT}(t)$. To study effects of possible covariation of the timing and magnitude parameters of $F_i(t)$, we compared characteristics of $F_{TOT}(t)$ profiles for a series of trials by a subject to similar characteristics computed for a surrogate “data” (cf. Kudo et al. 2000; Muller and Sternad 2003) when $F_{TOT}(t)$ was computed as the sum of $F_i(t)$ profiles taken from different trials. Obviously, no covariation among individual force profiles, either in the magnitude or in the time domain, was expected in the surrogate series.

Methods

Subjects: Eight healthy volunteers participated in the experiment, 4 males and 4 females. All subjects were right-handed according to their preferential hand use during writing and eating. The age of the subjects ranged from 22 to 30 years. Their average weight was 65.13 ± 11.54 kg; their average height was 1.72 ± 0.09 m. All subjects gave informed consent according to the procedures approved by the Office for Regulatory Compliance of Penn State University.

Apparatus: A detailed description of the setup can be found in Li et al. (1998). Four piezoelectric sensors (Model 208A03, Piezotronic, Inc.) amplified by AC/DC conditioners (M482M66) were used for force measurement. Cotton covers were attached to the upper surface of the sensors to increase friction and prevent the influence of finger skin temperature on the measurements. The sensors were medio-laterally distributed 30 mm apart. The position of the sensors could be adjusted in the forward-backward direction within 60 mm to fit individual subject's hand anatomy. The sensors were placed inside the groove in the wooden board so that the subject could place his or her fingers comfortably on the sensors.

During the experiment, the subject sat in a chair facing the testing table with his/her right upper arm at approximately 45° of abduction in the frontal plane and 45° of flexion in the sagittal plane, the elbows at approximately 45° of flexion. A wooden board supported the wrist and the forearm. A wooden piece shaped to fit comfortably under the subject's palm helped maintain a constant configuration of the hand and fingers. Metacarpophalangeal joints were all about 20° into flexion and all interphalangeal joints were slightly flexed, so that the hand formed a dome (Figure 1A). The subjects were allowed to select a comfortable position of the thumb. A computer monitor was located about 0.8 m away from the subject. It displayed the task (see later) and also the current actual total force produced by all the fingers. A customized LabVIEW program was used for data acquisition, and a MATLAB program was written for data processing. Force data were sample at 1000 Hz.

<Figure 1 about here>

Procedure: Prior to each trial, the subject sat relaxed with the fingers of the right hand on the sensors. The computer generated two beeps (get ready), and then a cursor showing the total force produced by all four fingers started to move along the screen of the monitor in front of the subject. The monitor also showed a grid of 8 vertical lines spread evenly such that it took the cursor 3 s to cover the distance from one line to the next one. A horizontal line showed the subjects the magnitude of the total force they were supposed to reach during each force pulse. For all subjects this magnitude was selected to be 15 N. This was based on our earlier experience that showed no fatigue during force production with such characteristics, while the range allowed sufficient resolution of force measurement.

The subjects were instructed to produce series of very quick pulses of the total force by pressing naturally with all four fingers such that the peaks of the pulses occurred at the intersections of the horizontal line with the vertical lines. The subjects were reminded to relax the fingers while the cursor moved between the lines. Five practice trials (eight force pulses in each trial) were given to each subject. Then, the data were collected over the next 6 trials, also containing eight force pulses per trial, such that the total number of collected force pulses was 48. No explicit accuracy constraints were imposed, but the subjects were encouraged to produce pulses whose peaks landed as closely as possible to the points of line interaction. Force pulses with the peaks that showed errors of over 15% from the prescribed level (15 N) were discarded during off-line analysis; on average, the number of rejected trials per subject was 4.3. Thirty pulses were randomly selected from the pool of accepted trials and used for analysis for each subject.

Data Analysis: Force pulses $F_{TOT}(t)$ were aligned according to the time (time zero, t_0) of the vertical line about which each pulse had been generated (Figure 1B). The time (t_{PEAK}) and magnitude (F_{PEAK}) of each $F_{TOT}(t)$ were measured. The beginning (t_{START}) of each $F_{TOT}(t)$ was defined as the time when the first derivative $dF_{TOT}(t)/dt$ reached 5% of its peak value during each force pulse. Time to peak (Δt) was defined as the difference between t_{START} and t_{PEAK}.

A surrogate data set was created using random permutations of thirty numbers in MATLAB. Force profiles for each of the four fingers $F_i(t)$ (i = I-index, M-middle, R-ring, and L-little) were randomly selected from different pulses, and aligned according to t_0 and summed up. This procedure was repeated 30 times to create a set of 30 $\Phi_{TOT}(t)$ time series. The surrogate data set was processed in the same way as the original data set to define τ_{PEAK}, Φ_{PEAK}, τ_{START}, and $\Delta\tau$.

The duration from start to peak of each force pulse within both actual and surrogate sets was taken to be 100%. Variances in the total force computed at each 10% of the pulse time were compared across the two data sets.

Principal component analysis (PCA) was used to analyze covariation among the times of individual finger peak forces and among their peak magnitudes for both original and surrogate data sets. This analysis was run for the four timing variables and for the four force magnitude, separately, as well as for all eight variables combined. We also performed single-value decomposition (SVD) analysis of the covariance matrices and compared the results of SVD and PCA. There were only minor differences; hence, in the paper we present the results of the PCA only. The amount of total variance accounted for by individual PCs was defined for each data set and each subject separately.

Statistics: Standard descriptive statistics were run; the data are presented in the text as means and standard deviations. ANOVA was used to compare average characteristics of the force pulses with factors SUBJECT (eight levels), SET (actual and surrogate), and TIME (ten levels). Nonparametric Wilcoxson's signed-rank test was used to compare indices of dispersion between the actual and surrogate sets.

Results

All the subjects were able to produce series of very quick and accurate force pulses. The average time from the beginning of each force pulse to its peak was 165.89 ± 44.55 ms. Their average peak force was 15.03 ± 1.44 N.

Figure 2A illustrates a typical force pulse $F_{TOT}(t)$ and corresponding individual finger force pulses, $F_i(t)$ for a representative subject. Figure 2B shows a typical set of force profiles for a surrogate trial created by selecting at random $F_i(t)$ from different trials. Note the following features of the surrogate $\Phi_{TOT}(t)$: Its peak level of force is smaller, the $\Phi_{TOT}(t)$ starts somewhat earlier than $F_{TOT}(t)$ in Figure 2A, and its peak is closer to the required time t_0 (zero in Figure 2). These features were typical across subjects.

<Figure 2 about here>

Table 1 presents averaged across subjects characteristics of the actual and surrogate sets. Comparisons of the averages were performed using a two-way SUBJECT x SET ANOVA. These comparisons revealed significant differences between the actual and surrogate sets in the peak force ($F_{PEAK} > \Phi_{PEAK}$; $F_{[1,464]} = 136.98$; $p < 0.001$) [$F_{[df,\ Error\ df]}$], in peak force time ($t_{PEAK} > \tau_{PEAK}$; $F_{[1,464]} = 14.60$; $p < 0.001$), in the starting time of the force pulses ($\tau_{START} > t_{START}$; $F_{[1,464]} = 73.97$; $p < 0.001$), and in the time it took the force to reach its peak ($\Delta\tau > \Delta t$; $F_{[1,464]}$ $F_{[1,464]} = 178.85$; $p < 0.001$). Wilcoxon's signed-rank test was used to compare standard deviations across the two sets. It revealed significantly higher magnitudes of the standard deviation for Φ_{PEAK} as compared to F_{PEAK} ($p < 0.001$), for t_{PEAK} as compared to τ_{PEAK} ($p < 0.01$), and for $\Delta\tau$ as compared to Δt ($p < 0.001$).

<Table 1 about here>

To analyze the time course of the difference in the dispersion between $F_{TOT}(t)$ and $\Phi_{TOT}(t)$, variances computed across series of trials for each subject separately were compared between the actual and surrogate sets (VarF vs. VarΦ) at each 10% of the force pulse time. Figure 3A shows the time profile of the difference between the two variances (ΔVar = VarΦ – VarF). Note that ΔVar is positive from the very beginning of the trial. This was confirmed with a SUBJECT x TIME ANOVA ($F_{[1, 464]} = 13.37$; $p < 0.001$). One-way ANOVAs comparing ΔVar to zeros at each TIME level showed that there were significant effects on all TIME levels from 0 to 100% ($F_{[1,14]} > 33.63$; $p < 0.001$). Panel B of Figure 2 shows the ΔVar in dimensionless units computed as the difference between VarΦ and VarF after each of them was divided by the average value of Φ (F) over the same time interval squared. The difference between the normalized indices of variance shows a different behavior. It is negative early in the force pulse and then stabilizes at a positive value that shows minimal fluctuations over most of the force pulse duration.

<Figure 3 about here>

Principal component (PC) analysis of the times of individual finger peak forces for the actual and surrogate data sets has revealed a significant difference between the two sets in the amount of variance accounted for by the first PC. For the actual data sets, in each subject, PC1 accounted for over 90% of the total variance (94.33 ± 3.01%). For the surrogate data set, PC1 accounted for only about 34% of the total variance (34.15 ± 1.17%). These results are illustrated in Figure 4A.

PC analysis of the magnitudes of the individual finger peak forces has shown significant differences between the data sets for the first and last PCs (Fig. 4B). PC1 accounted, on average, for 55.65 ± 12.26% of the total variance for the actual data sets and for 37.19 ± 5.14% of the variance for the surrogate data set. However, the biggest relative difference between the data sets was seen in the amount of variance accounted for by the last PC (PC4). For the surrogate data set, this amount was about four times higher than for the actual data set (3.96 ± 1.57% vs. 15.64 ± 1.16% for the actual and surrogate data sets respectively). There was also a difference between the actual and surrogate data sets in the amount of variance accounted for by PC3, namely 20.73 ± 2.25% vs. 14.55 ± 4.93% for the surrogate and actual data sets respectively. All the mentioned differences were significant at $p < 0.05$ according to the Wilcoxon's singed-rank test. There were no significant differences between the two sets in the amount of variance accounted for by PC2.

We also ran a combined PCA that included all eight variables. The percentages of variance accounted for by individual PCs for the actual and surrogate data sets are presented in Figure 5. Note that the first two PCs accounted for about 80% of the total variance for the actual data set, but only for about 41% of the total variance for the surrogate data set. To analyze whether the timing and magnitude variables contributed significantly to common PCs (we will address these as "mixed PCs"), we accepted an arbitrary but customary cutoff of 0.4 as a minimal significant loading value. The first two PCs for all ten subjects showed significant loading either only on subgroups of timing variables or only on subgroups of magnitude variables. Over all 80 individual PCs (8 PCs x 10 subjects), there were only six cases of mixed PCs, and these PCs were always among the PC3-PC8 groups accounting for small amounts of variance (see filled bars in Fig. 5). In contrast, the surrogate data set (open bars in Fig. 5) showed eleven cases of mixed PCs out of the total of twenty PC1-PC2 and a proportional number of mixed PCs for PC3-PC8.

Discussion

As in several earlier studies (Kudo et al. 2000; Muller and Sternad 2003), we have assumed that task-specific covariation of characteristics of individual finger force profiles, $F_i(t)$, that could be present in an actual data set, was eliminated by selecting $F_i(t)$ from different trials and creating a surrogate data set. Comparison of characteristics of dispersion has revealed higher variability for the peak value of total force and lower variability for the deviation of the time of the total force from its desired time for the surrogate set as compared to the actual data set. We interpret the former finding as pointing at the presence of negative covariation among individual finger force magnitudes within the actual set, i.e. a synergy that stabilized the peak value of total force about the required value of 15 N. The latter finding suggests that the timings of the individual force profiles in the actual data set with respect to t_0 covaried positively, for example, if one finger speeded up, other fingers were also likely to speed up. This covariation led to higher indices of dispersion in the timing of the total force, i.e. there was no timing synergy among individual finger force pulses that would help stabilize the time of F_{PEAK} at the required time t_0.

Synergies that stabilize magnitude of the total force

A series of earlier studies used the framework of the uncontrolled manifold (UCM) hypothesis to analyze finger coordination in relatively slow force production tasks (Latash et al. 2001, 2002a,b; Scholz et al. 2002, 2003). The UCM hypothesis assumes that the controller selects a UCM corresponding to a desired value of a performance variable (such as total force) and then structure the finger force variance such that most of it is confined to the UCM. Those studies failed to show finger synergies that would stabilize total force when the force changed relatively rapidly and its magnitude was relatively low. Findings within the current study suggest a very different picture: Individual finger forces showed predominantly negative covariation such that the total force was stabilized despite the very fast rate of force change (much higher than in the cited studies). This was seen at early phases of the force pulse when the total force was low.

Principal component analysis of the peak magnitudes of individual finger forces showed a redistribution of the amount of variance between PC1 and PC3/PC4 in the surrogate data set as compared to the actual data set. According to the UCM hypothesis, stabilization of total force is associated with creation of a manifold (UCM) in the finger force space and the finger force variance is mostly restricted to that UCM. For a particular value of the total force, the UCM in three-dimensional. The fourth dimension is orthogonal to the UCM; variance along that dimension is expected to be low. For a perfect data set representing an ellipsoid oriented parallel to the UCM, with its shortest axis orthogonal to the UCM, PC4 is expected to be parallel to the shortest axis. Hence, comparison of the amount of variance accounted for by PC4 provides a crucial test of the hypothesis on total force stabilization. Our analysis has shown significantly lower amount of variance accounted for by PC4 for the actual data set as compared to the surrogate data set providing an additional confirmation of the hypothesis on stabilization of the total peak force by covariation of individual finger forces. Changes in the amount of variance accounted for by PC3 were is the same direction as for PC4. They may reflect the fact that actual ellipsoids of data point distributions were not oriented perfectly parallel to the UCM such that projections onto the two shortest axes reflected the smaller amount of variance orthogonal to the UCM.

There are a number of differences between the earlier studies and the current one. The earlier studies used a different set of variables, modes (cf. Danion et al. 2002), rather than finger forces. The modes take into account the phenomenon of enslaving, i.e. unintended force production by fingers when another finger of the hand produces force (Li et al. 1998; Zatsiorsky et al. 1998, 2000). However, enslaving in our experiments could only create positive covariation among finger forces, while the findings in the current study suggest predominance of negative covariation. That is, taking enslaving into account would only strengthen the effects. Another major difference is that force pulses in the current study were so fast (average rise time of about 160 ms) that visual feedback based corrections were unlikely to play any role. In earlier studies, even the fastest force patterns were much slower and supposed to follow a certain visually presented template; hence, they were supposed to be performed under continuous feedback control. The current findings may be interpreted as showing that naturally occurring variations in the sharing pattern of the total force among the fingers can occur even during the fastest force pulses and these variations keep the magnitude of the total force relatively unchanged.

There is an early effect in Figure 3A suggesting a transient period of positive covariation of finger forces early in a ramp trial that destabilizes the total force but may play a role in stabilization of the total pronation/supination moment (cf. Latash et al. 2001). Although the effect is small, it corroborates earlier observations in young control subjects (Scholz et al. 2002; Latash et al. 2002a), healthy elderly (Shinohara et al. 2003), and persons with Down syndrome (Latash et al. 2002b). This "opposite of a force stabilizing synergy" effect was studied in depth for cyclic and ramp force production at different rates (Latash et al. 2002b). In a recent study (Shim et al. 2003), it has been shown that there likely is a critical time at which the positive covariation (that destabilizes the total force) switches to a negative covariation, which we interpret as a force-stabilizing synergy. Since a switch from positive to negative covariation was seen during the first several tens of ms (Fig. 3), it was likely to be of a purely central origin, not relying on proprioceptive feedback control processes (cf. Todorov and Jordan 2002). However, currently we have no proofs for such a central back-coupling mechanism.

Synergies that stabilize timing of the total force

A number of earlier studies have shown that relative timing of action by individual effectors during a multi-effector action is rather stable over repetitions of the task and even under changes in its characteristics. For example, in a study of professional typists, Terzuolo and Viviani (1980) showed that natural variations in the speed of typing of a standard phrase preserved the relative timing of individual key strokes by the fingers of the typist. Later studies have suggested that relative timing was not an invariant property of a motor act but an emergent property that could change under certain changes in task parameters (reviewed in Turvey 1990b).

In an earlier paper (Latash et al. 2002b), we reported observations suggesting that the controller had problems in compensating timing errors in the outputs of individual fingers. The current study shows the lack of such compensation explicitly. It suggests that individual finger force pulses are strongly synchronized and they keep this synchrony over trials such that all fingers speed up or slow down together. Principal component analysis of the times of the peak forces of individual fingers provided additional support for this conclusion: For the actual data set, PC1 accounted for over 90% of the total variance, while for the surrogate data set, PC1 accounted for less than 40% of the variance.

In the current study we address a possibility of timing adjustments among outputs of individual elements within a single realization of the task. The question we ask is: “If one finger in a particular trial develops its peak force too quickly, will other fingers slow down to reach the peak closer to the prescribed time?” To answer this question, we analyzed a set of realizations of the discrete task. Our subjects relaxed completely between any two attempts at force production to minimize possible effects of one task realization on another. This approach is very different from analysis of consecutive cycles in an ongoing cyclic task, as was done in a variety of studies of rhythmic actions (Keele et al. 1985; Wing and Kristofferson 1973; Semjen et al. 1984; Turvey et al. 1989). In those studies, the question was: “If one cycle is performed too quickly, will the next cycle be performed slower, quicker, or without a change in the pace?”. This question can be and has been applied to a single effector performing the task (Roberts et al. 2000; Sternad et al. 2000), while our question can be applied only to a set of effectors (fingers in our study).

The apparent failure of the controller to create timing synergies may be tentatively interpreted within the theoretical framework suggested by Schöner (1995). This framework assumes a hierarchical system of control, which involves, in particular, a timing level, and a synergy level. At the timing level, relative timing of effector involvement is defined. At the synergy level, the task is shared among the effectors. Within this general scheme, results of the current study suggest that the controller was able to stabilize the magnitude of the total force by negative covariation in individual finger forces, i.e. a synergy was created at the synergy level. However, if a timing error occurred, it was likely to be equal in all effectors. In other words, there was no synergy at the timing level.

Acknowledgments

This study was supported in part by NIH grants AG-018751, NS-35032, and AR-048563.

References

Bernstein NA (1967) The co-ordination and regulation of movements. Pergamon Press, Oxford

Danion F, Schöner G, Latash ML, Li S, Scholz JP, Zatsiorsky VM (2003) A force mode hypothesis for finger interaction during multi-finger force production tasks. Biol Cybern 88: 91-98.

Keele S, Pokorny R, Corcos D, Ivry R (1985) Do perception and motor production share a common timing mechanism: A correlational analysis. Acta Psychol 60: 173-191

Kudo K, Tsutsui S, Ishikura T, Tomoki I, Yamamoto Y (2000) Compensatory coordination of release parameters in a throwing task. J Mot Behav 32: 337-345.

Latash ML, Scholz JF, Danion F, Schöner G (2001) Structure of motor variability in marginally redundant multi-finger force production tasks. Exp Brain Res 141: 153-165.

Latash ML, Kang N, Patterson D (2002a) Finger coordination in persons with Down syndrome: Atypical patterns of coordination and the effects of practice. Exp Brain Res 146: 345-355.

Latash ML, Scholz JF, Danion F, Schöner G (2002b) Finger coordination during discrete and oscillatory force production tasks. Exp Brain Res 146: 412-432.

Latash ML, Scholz JP, Schöner G (2002c) Motor control strategies revealed in the structure of motor variability. Exer Sport Sci Rev 30: 26-31.

Li Z-M, Latash ML, Zatsiorsky VM (1998) Force sharing among fingers as a model of the redundancy problem. Exp Brain Res 119: 276-286.

Muller H, Sternad DS (2003) A randomized method for the calculation of covariation in multiple nonlinear relations illustrated with the example of goal-directed movement. Biol Cybern 89: 22-33.

Roberts S, Eykholt R, Thaut MH (2000) Analysis of correlations and search for evidence of deterministic chaos in rhythmic motor control by the human brain. Phys Rev E 62: 2597-2607.

Scholz JP, Danion F, Latash ML, Schöner G (2002) Understanding finger coordination through analysis of the structure of force variability. Biol Cybern 86: 29-39.

Scholz JP, Kang N, Patterson D, Latash ML (2003) Uncontrolled manifold analysis of single trials during multi-finger force production by persons with and without Down syndrome. Exp Brain Res 153: 45-58

Schöner G (1995) Recent developments and problems in human movement science and their conceptual implications. Ecol Psychol 8:291–314

Semjen A, Garcia-Colera A, Requin J. (1984) On controlling force and time in rhythmic movement sequences: the effect of stress location. Ann N Y Acad Sci 423: 168-182

Shim JK, Latash ML, Zatsiorsky VM (2003) The central nervous system needs time to organize task-specific covariation of finger forces. Neurosci Lett 353: 72-74.

Sternad D, Dean WJ, Newell KM (2000) Force and timing variability in rhythmic unimanual tapping. J Mot Behav 32: 249-267

Terzuolo CA, Viviani P (1979) The central representation of learned motor patterns. In: RE Talbott, DR Humphrey (eds.) Posture and Movement, pp. 113-121, New York: Raven Press

Todorov E, Jordan MI (2002) Optimal feedback control as a theory of motor coordination. Nat Neurosci 5(11): 1226-35

Turvey MT (1990a) Coordination. Amer Psychol 45: 938-953

Turvey MT (1990b) The challenge of a physical account of action: A personal view. In: Whiting HTA, Meijer OG, van Wieringen PCW (eds.) The Natural-Physical Approach to Movement Control, pp. 57-92, Amsterdam: VU Univ Press

Turvey MT, Schmidt RC, Rosenblum LD (1989) "Clock" and "motor" components in absolute coordination of rhythmic movements. Neurosci 33: 1-10

Wing AM, Kristofferson AB (1973) Response delays and the timing of discrete motor responses. Percept Psychophys 14: 5-12

Zatsiorsky VM, Li Z-M, Latash ML (1998) Coordinated force production in multi-finger tasks. Finger interaction, enslaving effects, and neural network modeling. Biol Cybern 79: 139- 150.

Zatsiorsky VM, Li Z-M, Latash ML (2000) Enslaving effects in multi-finger force production. Exp Brain Res 131: 187-195.

TABLE 1

Means and standard deviations of characteristics of the actual (A) and surrogate (S) data sets

VARIABLE	MEAN	St. Dev.	Significance (MEANS)	Significance (St. Dev.)
F_{PEAK} (N) – A	15.03	1.44	A > S *	A < S *
Φ_{PEAK} (N) – S	13.15	2.12		
t_{PEAK} (ms) – A	62.80	47.94	|A| > |S| *	A > S *
τ_{PEAK} (ms) – S	47.99	38.52		
t_{START-} (ms) – A	192.12	81.72	|A| < |S|*	A > S
τ_{START} (ms) – S	244.75	71.34		
Δt (ms) – A	165.89	44.55	A < S *	A < S *
$\Delta\tau$ (ms) – S	224.91	70.79		

Means and standard deviations across subjects are shown (n = 8). * - statisically significant difference at $p < 0.001$.

Figure Captions

Figure 1. A: A scheme of the experimental setup. B: A typical total force profile (solid curve) and its first derivative (dashed curve) that was used to define the time of pulse initiation (t_{START}). Time zero corresponds to the required time of the peak of the force pulse.

Figure 2. Typical sets of force profiles for an actual data set (A) and for a surrogate data set (B). Total, I, M, R, and L stand for total, index, middle, ring, and little finger forces, respectively. Time zero corresponds to the required time of the peak of the force pulse.

Figure 3. The difference between total force variances of the surrogate and actual data set ($\Delta Var = Var\Phi - VarF$). In panel A, ΔVar was computed using variances in absolute units (N^2). In panel B, ΔVar was computed using variances divided by the average force squared. Averaged across subjects data are shown with standard error bars.

Figure 4. Percentage of the total variance accounted for by each principal component for the PCA ran on finger force times (panel A) and finger force magnitudes (panel B) for the actual (filled bars) and surrogate (open bars) data sets. Averaged across subjects data are shown with standard error bars.

Figure 5. Percentage of the total variance accounted for by each principal component (PC) within PCA ran on finger force magnitude and timing variables together for the actual (filled bars) and surrogate (open bars) data sets. Averaged across subjects data are shown with standard error bars.

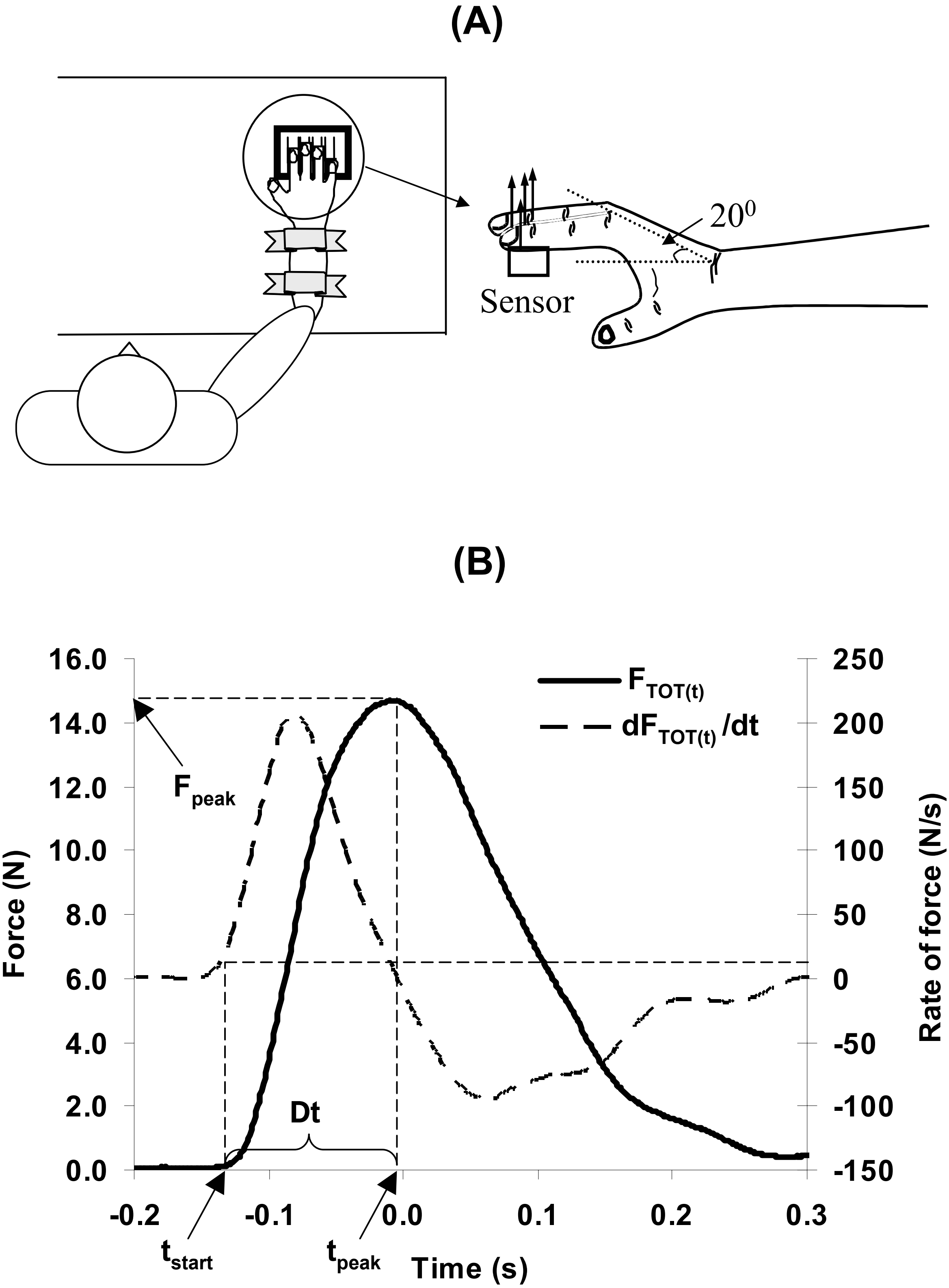
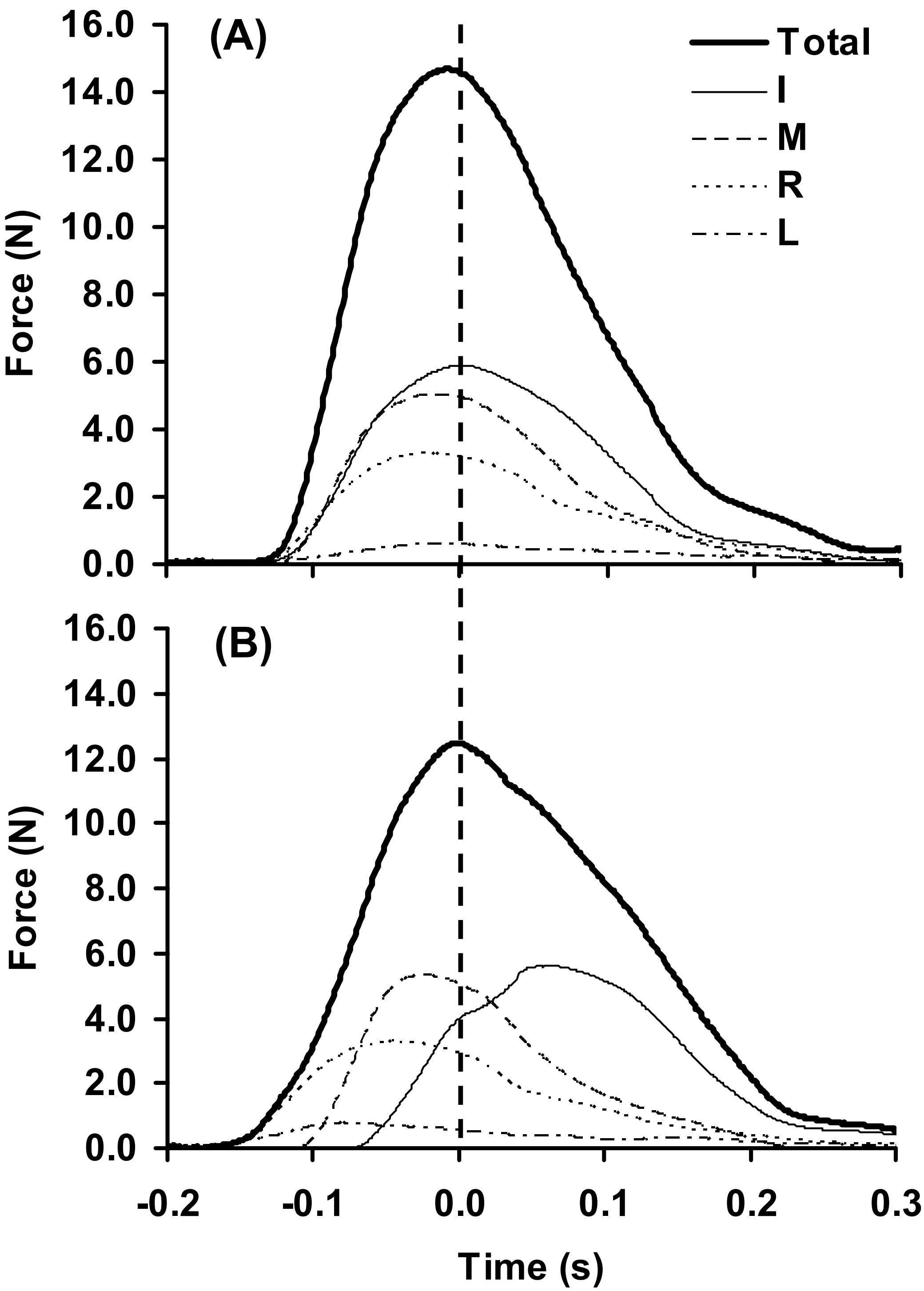

(A)
20⁰
Sensor
(B)
Force (N)
Rate of force (N/s)
Time (s)
16.0
14.0
12.0
10.0
8.0
6.0
4.0
2.0
0.0
250
200
150
100
50
0
-50
-100
-150
-0.2
-0.1
0.0
0.1
0.2
0.3
F_TOT(t)
dF_TOT(t) /dt
F_peak
Dt
t_start
t_peak

Figure 1



(A)
(B)
Total
I
M
R
L
Force (N)
0.0
2.0
4.0
6.0
8.0
10.0
12.0
14.0
16.0
Time (s)
-0.2
-0.1
0.0
0.1
0.2
0.3

Figure 2

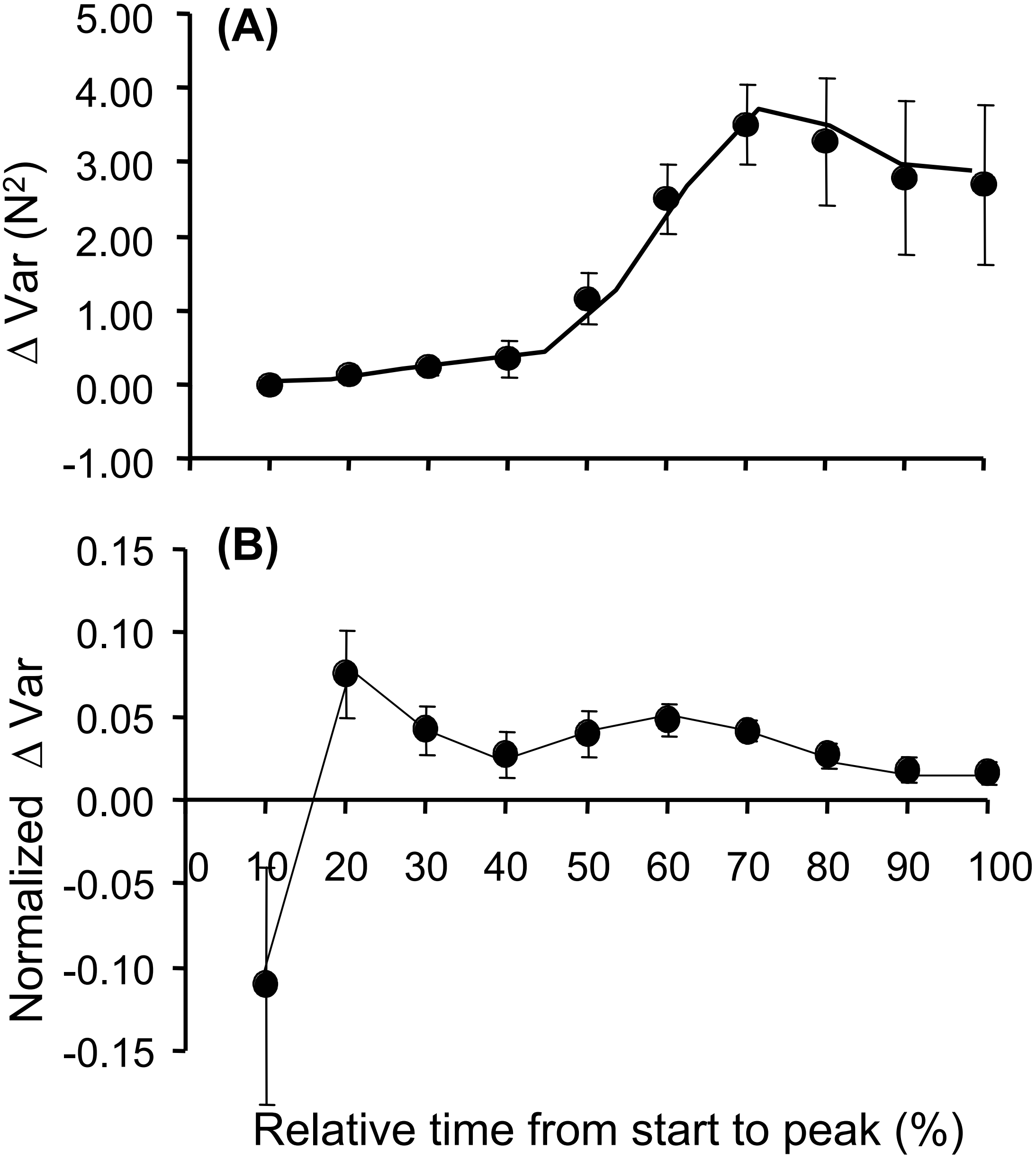

(A)
5.00
4.00
3.00
2.00
1.00
0.00
-1.00
Δ Var (N²)
(B)
0.15
0.10
0.05
0.00
-0.05
-0.10
-0.15
Normalized Δ Var
0
10
20
30
40
50
60
70
80
90
100
Relative time from start to peak (%)

Figure 3

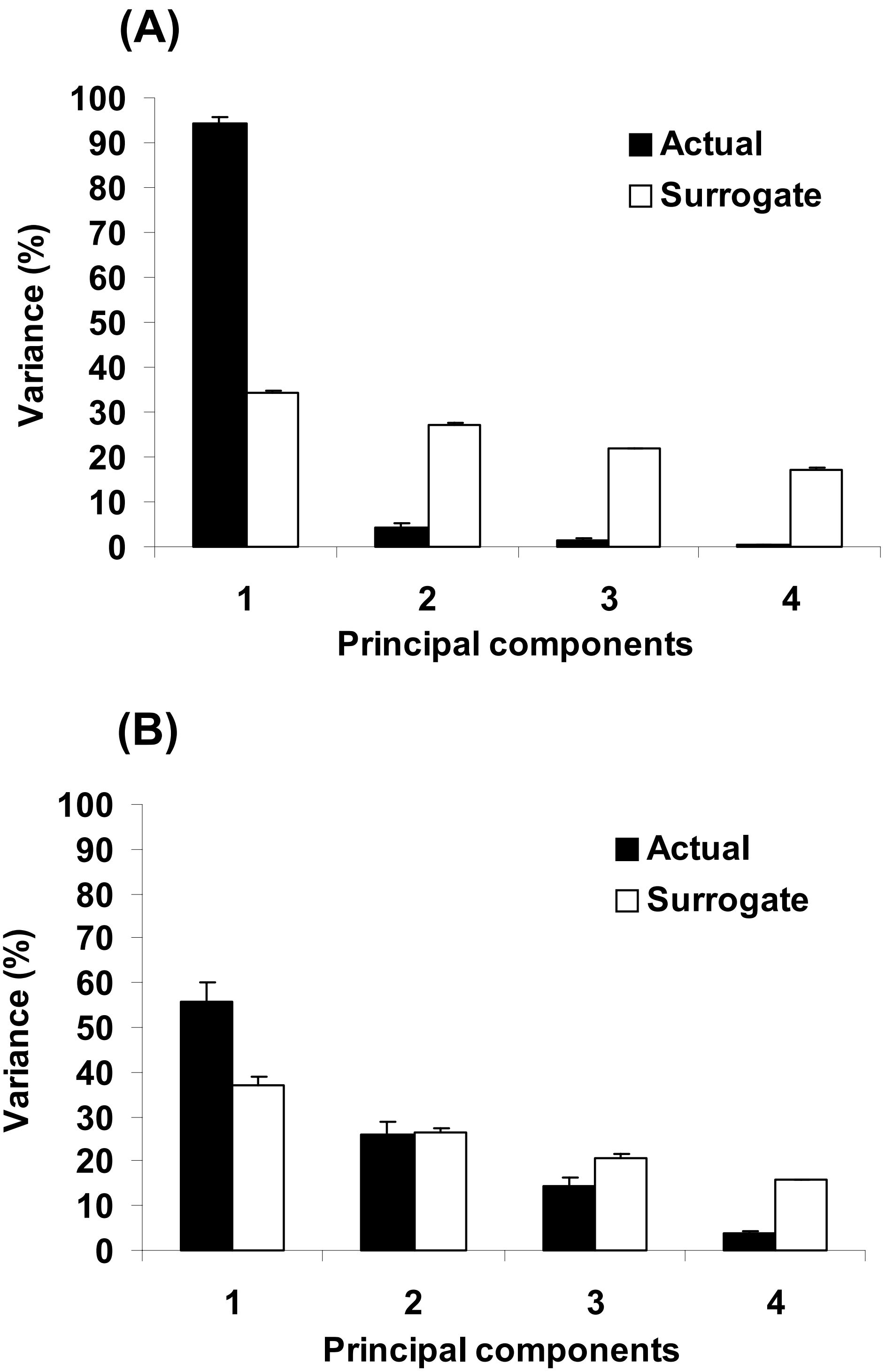

(A)
100
90
80
70
60
50
40
30
20
10
0
Variance (%)
Actual
Surrogate
1
2
3
4
Principal components
(B)
100
90
80
70
60
50
40
30
20
10
0
Variance (%)
Actual
Surrogate
1
2
3
4
Principal components

Figure 4

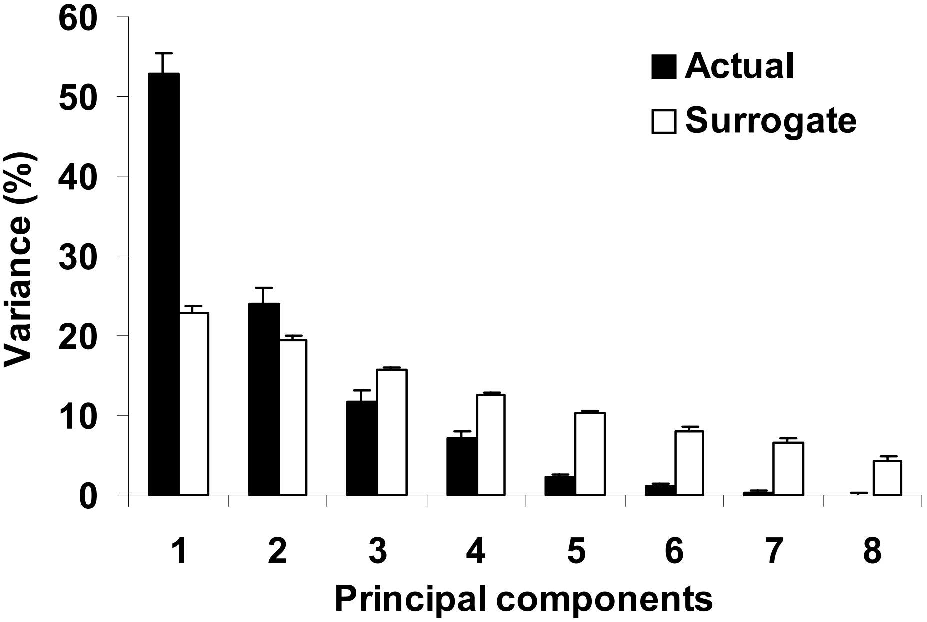

60
50
40
30
20
10
0
Variance (%)
■ Actual
☐ Surrogate
1
2
3
4
5
6
7
8
Principal components

Figure 5