Shared and specific muscle synergies in natural motor behaviors

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*PNAS, vol 102, no. 8, 2005*

Computational Intelligence Seminar A - SS06

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Division of talk

- Fast recap
  - Motion as an ‘ill-posed’ problem
  - The problem of inverse dynamics and its probable solutions
  - Motor Primitives
    - Force fields as possible motor primitives
    - Muscle synergies as possible motor primitives
- Introduction to the current paper
- Methods
- Results
- Conclusions
Fast recap of background material
Motion as an ‘ill-posed’ problem

Consider: Arm movement from point A to point B in space
- Infinite number of possible hand trajectories
- Multiple combinations of joint motions at shoulder, elbow and wrist for each trajectory
- Multiple muscle combinations can result in same joint torques

In essence: selecting an appropriate movement for a goal, is an extremely complex task
- High dimensionality of search space
- Nonlinear and dynamical nature of transformation between muscle activity and movement
The problem of inverse dynamics

**Direct dynamics**: Calculating trajectory $X(t)$ from force $F(t)$

**Inverse Dynamics**: Calculating force $F(t)$ from trajectory $X(t)$

- Transformation from planned limb movement to a set of motor commands involves the solution of the inverse dynamics problem
- This involves the transformation from desired motion to forces that are needed to drive the limb

\[
D(q, \dot{q}, \ddot{q}) = \tau(t)
\]

- Does the brain carry out such inverse dynamics calculations?
Probable solutions

- Solutions based on feedback
- Solutions based on feed-forward
- Memory based computations
- Internal models composed of Motor Primitives
What are Motor Primitives?

Motor Primitives can be thought of as the basic building blocks or discrete modules that can be combined in linear or non-linear fashion to generate a vast repertoire of movements.

Possible candidates:
- Force Fields
- Muscle Synergies

NOTE: The idea of Motor Primitives is based on the hypothesis that the motor output has a modular organization.
Force fields as motor primitives

- Electrical stimulation of lumbar spinal cord of frog imposes a specific balance of muscle activation.
- Mechanical responses of activated muscles measured by attaching the limb to a force transducer.
- Direction and amplitude of contracting force measured at different points in the limbs workspace.
- Evoked contractions direct the limb to an equilibrium point in space.
- Collection of measured forces correspond to a well structured spatial pattern – a vector field.
Vector summation and emergence of motor primitives

- Force-fields follow the principle of vectorial addition
- Movement and posture can be explained based on a combination of few basic elements (motor-primitives)
- These active force-fields stored in spinal cord can be combined through superposition to generate a vast range of movements.
Muscle synergies as motor primitives

**Muscle Synergies** – can be defined as the *coherent activations, in space or time, of a group of muscles*

Muscle synergies have been proposed as the building blocks or primitives that can be used to generate motor behavior

- Term came into use due to studies on the organization of spinal cord
- According to this hypothesis, supraspinal and afferent signals flexibly combine a few muscle synergies to generate a variety of movements
Introduction to the current paper
Key-points

- Paper investigates whether CNS uses a modular architecture
- EMG recordings made from 13 muscles in the hind limb of frogs during jumping, walking and swimming
- Use of a multidimensional factorization technique to extract
  - Invariant amplitude and timing relationships among muscle activations
The two models of muscle synergies

- Instantaneous muscle activation
  - Synchronous muscle synergies (combinations of non-negative Vectors)
  - Spatial organization in muscle patterns
  - DECOMPOSITION
  - Time-varying muscle synergies (combinations of temporal sequences of non-negative Vectors)
  - Specific characteristics in muscle activation waveforms
Model 1 – Synchronous muscle synergy
Model 1 – Synchronous muscle synergy

- Is a vector of real numbers, each component of which represents the activation of a particular muscle.
- A *muscle activation waveform* is generated by scaling each component of synchronous muscle synergy vector by the same time varying coefficient.
- A *muscle pattern* is then constructed by summing the muscle activation waveforms generated by different synergies.

Thus a synchronous muscle synergy captures a set of fixed amplitude relationships among the muscle activations; i.e. an invariant spatial organization of the muscle patterns.
Model 1 – Synchronous muscle synergy

- Muscle pattern is generated by recruitment of $N$ synchronous synergies as the linear combination of $N$ non-negative vectors

\[ m(t) = \sum_{i=1}^{N} c_i(t) w_i \]

- Or, when MP is sampled at discrete time intervals,

\[ M = WC \]

$m(t)$ = $P$ dimensional vector, representing the activation of $P$ muscles at time $t$

$c_i(t)$ = a nonnegative coefficient scaling the amplitude of $i^{th}$ synergy at time $t$

$M = P \times K$ matrix

$W = P \times N$ matrix

$C = N \times K$ matrix
Model 2 – Time-varying muscle synergy

Fig. 1. Time-varying synergies model. In this simulated example, two time-varying synergies (a) are scaled in amplitude and shifted in time (b), and then combined to construct two different patterns (c). (a) The rows in each synergy (W₁ and W₂) represent the activation time courses of the three muscles (m₁ to m₃), with the amplitude, shown in color code, normalized within each synergy to the value of the maximum sample. The profile in the box below each synergy represents the time course of the synergy averaged across muscles. (b) To generate a specific muscle pattern, every muscle in each synergy is first scaled in amplitude by a non-negative coefficient (c₁ in the illustration representing the time course of the three muscles of W₁) and shifted in time by an onset delay (t₁). The three curves in a box represent W₁ before (dashed traces) and after (solid traces) scaling and shifting. (c) The elements of the first synergy (magenta shaded area) are then summed together with corresponding elements of the second synergy (green shaded area) to generate the complete pattern (solid line). In this illustration, the amplitude coefficients (c₁ and c₂) are represented as the height of the rectangles below the muscle patterns, and the onset delays (t₁ and t₂) are represented by the horizontal position of the left edge of the rectangle.
Model 2 – Time-varying muscle synergy

- Is a time sequence of vectors representing a collection of muscle activation waveforms
- A muscle pattern is constructed by scaling different synergies, each sequence multiplied by a single amplitude coefficient, shifting the synergy onset in time, each sequence shifted by a single timing coefficient, and finally summing them muscle by muscle
Model 2 – Synchronous muscle synergy

- Muscle pattern is generated by recruitment of \( n \) instances of \( N \) time-varying synergies as the linear combination of \( N \) non-negative vectors \( \mathbf{w}_i(\tau) \)

\[
\mathbf{m}(t) = \sum_{j=1}^{n} c_j \mathbf{w}_I(j)(t-t_j)
\]

- where \( \{\mathbf{w}_i(\tau)\}_{i=1}^{N} \) is the \( i^{th} \) synergy, i.e. a sequence of \( P \) dimensional vectors, representing the activation of \( P \) muscles over time

\( c_j \) = a nonnegative coefficient scaling the amplitude of \( j^{th} \) synergy

Differently from model 1, a given muscle pattern \( \mathbf{m}(t) \) can be reconstructed by multiple instances of same \( N \) synergies
Model 2 – Synchronous muscle synergy

\[ m(t) = \sum_{j=1}^{n} c_j W_{I(j)}(t - t_j) \]

- Differently from model 1, a given muscle pattern \( m(t) \) can be reconstructed by multiple instances of same \( N \) synergies.
- The \( j^{\text{th}} \) instance is simply a shifted version of \( i^{\text{th}} \) synergy (use of an index function \( i = I(j) \in [1, \ldots, N] \) to map instances to synergy).
- All synergies are compactly represented as the matrix \( W = [W^1 \ W^2 \ldots W^N] \), with \( P \) rows and \( Q \times N \) columns.
- A time shifting matrix \( \Theta_i[k, K] \) is introduced to align, by matrix multiplication of \( W \) with \( \Theta_i \), the first sample of the \( i^{\text{th}} \) synergy with the \( k^{\text{th}} \) sample of a muscle pattern (\( K \) samples long). So the above equation can be written in matrix notation as:

\[ M = W \left( \sum_{j=1}^{n} c_j \Theta_{I(j)}[k_j, K] \right) = WH \]
Model 2 – Time-varying muscle synergy

- If the vectors in the sequence that define the time varying synergy are all in the same direction, then it reduces to Model 1.

- In general, the sequence of vectors may represent a collection of asynchronous muscle activation waveforms, and hence a time varying synergy captures spatiotemporal invariants in the muscle patterns.
Methods

Three adult bullfrogs (*Rana catesbeiana*) were used in the experiments.
Electrode Implantation

Muscles were implanted with bipolar intramuscular electrodes

13 muscles that were implanted

1. Rectus internus major (RI)
2. Adductor magnus (AD)
3. Semi-membranosus (SM)
4. Vasta internus (VI)
5. Vasta externus (VE)
6. Peroneus (PE)
7. Gastrocnemius (GA)
8. Rectus anterior (RA)
9. Ventral head of semitendinosus (ST)
10. Sartorius (SA)
11. Biceps, or iliofibularis (BI)
12. Iliopsoas (IP)
13. Tibialis anterior (TA)
Data collection and preprocessing

- A lightweight miniature flat cable attached to the connector on the back of frogs to record EMG data
- EMG signals were differentially amplified (gain 5000), band-pass filtered (10-1000 Hz), digitized (1 Khz), and stored on a computer hard-drive
- All behavioral sessions were videotaped (29.97 frames per second), synchronized with EMG recordings
- Data analysis performed using software written in MATLAB
- With the help of the video, the EMG records were segmented into behavioral episodes (e.g. 1 jump)
- Raw EMG data for each segment was then digitally rectified and low pass filtered (20Hz cutoff), and integrated over 25 ms intervals
- Resulting samples were normalized for each animal and each muscle to the amplitude of the maximum sample of integrated EMG activity in that muscle over all episodes of all behaviors
Synergy extraction algorithm – Model 1

- Used a nonnegative matrix factorization algorithm
- Algorithm starts with random nonnegative synergies and coefficients and proceeds to minimize the total reconstruction error by iterating a coefficient update step, and a synergy update step
- Convergence criterion of 5 consecutive iterations for which the increase of the reconstruction $R^2$ was $< 10^{-4}$
- To minimize the probability of finding a local minima, optimization process was repeated 5 times, and solution with highest value of $R^2$ was selected
Synergy extraction algorithm – Model 1

- The equation $M = WC$ is initialized with random nonnegative synergies ($W$) and coefficients ($C$).

- Coefficient update rule:
  \[
  C_{ij} = C_{ij} \frac{(WTM)_{ij}}{(WTWC)_{ij}}
  \]

- Synergy update rule:
  \[
  W_{ij} = W_{ij} \frac{(MCT^T)_{ij}}{(WCC^T)_{ij}}
  \]
Synergy extraction algorithm – Model 2

- Used an optimization algorithm that allows the reconstruction of each EMG segment by combinations of an arbitrary number of synergy instances.

- The algorithm starts by initializing N synergies with random nonnegative values.

- It proceeds to minimize the total reconstruction error, by iterating over 3 steps:
  1. Selection of synergy instances by matching pursuits algorithm
  2. Determination of scaling coefficients
  3. Updating of the synergies
Synergy extraction algorithm – Model 2: Selection of synergy instances by matching pursuits

- For each EMG segment of length K, and N synergies Q samples long →
  - A dictionary is created with all of possible synergy instances obtained by shifting each normalized synergy from the beginning to the end of the segment, one sample at a time
  - For an EMG segment of K samples, results in a dictionary of N x (K+Q -1) elements

- The matching pursuits then selects those elements in dictionary whose combinations best match the pattern by following steps
  1. The scalar product of muscle pattern with all of the elements of the dictionary are computed
  2. The dictionary element with the largest scalar product is selected
  3. The selected element is multiplied by its scalar product and subtracted from the muscle pattern
  4. The scalar product of the residual muscle pattern with all of the remaining dictionary is computed…
Synergy extraction algorithm – Model 2: Determination of scaling coefficients and updating the synergies

- For each EMG segment and given the set of N synergies, once n instances have been selected, the scaling coefficients ($\{c_i\}_{i=1,...,n}$) that best reconstruct that episode are determined by *back-projection*

- Update rules similar to Model 1 are used, with the matrix $H$ used instead of $C$
Shared and specific synergies

- Shared Synergies – Synergies common to all behaviors
- Specific Synergies – Synergies specific to a subset of behaviors
- Both kind of synergies were extracted by modification to the synergy extraction algorithm
Significance of extracted synergies

- To verify that the particular synergies extracted by algorithms, were not selected as a result of a bias in the method
  - $R^2$ values were compared for
    - reconstruction of real data from extracted synergies
    - reconstruction of structure-less data from synergies extracted from those simulated data
- Constructing structure-less data for synchronous synergies
  - Randomly reshuffle the samples for each muscle independently – same amplitude distribution as the real data, but correlation is destroyed
- Constructing structure-less data for time-varying synergies
  - Reshuffle the samples for each muscle over the entire dataset, and assign them to episodes of the same duration as the real data
  - Low-pass filter the shuffled waveforms (10Hz), to maintain the frequency composition of simulated data same as real data
Synergy similarity

- The *cosine* of the angle between two synergies was used as a measure of their similarity.

- **Synchronous Synergies** – Simply the scalar product of the two normalized synergies

- **Time-varying synergies** – The maximum of the normalized scalar products between two time-varying synergies shifted by $k_1$ and $k_2$ samples over all possible relative delays ($k_1 - k_2$)
Synergy set comparison

- Two sets of synergies were compared by
  - Computing the similarities between their best matching pairs
  - And by counting the number of pairs with similarity above chance
  - Pairs of synergies were matched by starting with the pair with highest similarity, and then removing the pair, and matching the remaining elements
Results
Summary of data collected

<table>
<thead>
<tr>
<th>Behavior</th>
<th>No. of episodes</th>
<th>No. of samples</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>F10</td>
<td>F11</td>
</tr>
<tr>
<td>Jumping</td>
<td>218</td>
<td>117</td>
</tr>
<tr>
<td>Swimming</td>
<td>135</td>
<td>40</td>
</tr>
<tr>
<td>Walking</td>
<td>166</td>
<td>36</td>
</tr>
</tbody>
</table>

Behavioral episodes either produced spontaneously, or as a result of gentle cutaneous stimulation

Great variability observed in each behavior
Spatial structure captured by synchronous synergies

- Synchronous synergies for individual behaviors for each frog were extracted, with number of synergies in each set varying from 2 to 8.

- The fraction of total variation in data explained by the combination of the synergies in each set increased with the number of synergies.

<table>
<thead>
<tr>
<th>Frog</th>
<th>Behavior</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
<th>7</th>
<th>8</th>
</tr>
</thead>
<tbody>
<tr>
<td>F10</td>
<td>Jumping</td>
<td>0.75</td>
<td>0.82</td>
<td>0.86</td>
<td>0.90</td>
<td>0.92</td>
<td>0.94</td>
<td>0.95</td>
</tr>
<tr>
<td>F11</td>
<td>Jumping</td>
<td>0.71</td>
<td>0.85</td>
<td>0.89</td>
<td>0.91</td>
<td>0.93</td>
<td>0.95</td>
<td>0.96</td>
</tr>
<tr>
<td>F17</td>
<td>Jumping</td>
<td>0.71</td>
<td>0.80</td>
<td>0.86</td>
<td>0.90</td>
<td>0.92</td>
<td>0.94</td>
<td>0.96</td>
</tr>
<tr>
<td>F10</td>
<td>Swimming</td>
<td>0.78</td>
<td>0.84</td>
<td>0.89</td>
<td>0.91</td>
<td>0.93</td>
<td>0.95</td>
<td>0.96</td>
</tr>
<tr>
<td>F11</td>
<td>Swimming</td>
<td>0.68</td>
<td>0.77</td>
<td>0.82</td>
<td>0.88</td>
<td>0.91</td>
<td>0.94</td>
<td>0.95</td>
</tr>
<tr>
<td>F17</td>
<td>Swimming</td>
<td>0.59</td>
<td>0.69</td>
<td>0.76</td>
<td>0.81</td>
<td>0.86</td>
<td>0.90</td>
<td>0.94</td>
</tr>
<tr>
<td>F10</td>
<td>Walking</td>
<td>0.56</td>
<td>0.72</td>
<td>0.85</td>
<td>0.89</td>
<td>0.92</td>
<td>0.94</td>
<td>0.96</td>
</tr>
<tr>
<td>F11</td>
<td>Walking</td>
<td>0.68</td>
<td>0.79</td>
<td>0.89</td>
<td>0.91</td>
<td>0.94</td>
<td>0.95</td>
<td>0.97</td>
</tr>
<tr>
<td>F17</td>
<td>Walking</td>
<td>0.55</td>
<td>0.73</td>
<td>0.80</td>
<td>0.87</td>
<td>0.91</td>
<td>0.93</td>
<td>0.95</td>
</tr>
</tbody>
</table>

Table 3. Number of pairs of synchronous synergies with similarity above chance between the sets with five elements extracted from the same behavior in different frogs.

<table>
<thead>
<tr>
<th>Behavior</th>
<th>F10–F11</th>
<th>F10–F17</th>
<th>F11–F17</th>
</tr>
</thead>
<tbody>
<tr>
<td>Jumping</td>
<td>5</td>
<td>5</td>
<td>5</td>
</tr>
<tr>
<td>Swimming</td>
<td>5</td>
<td>2</td>
<td>3</td>
</tr>
<tr>
<td>Walking</td>
<td>5</td>
<td>3</td>
<td>3</td>
</tr>
</tbody>
</table>

$R^2$ values from pooled data ➔ jumping – 0.87, swimming – 0.87, walking – 0.84
Shared and specific synchronous synergies

- Can some synergies might be shared across behaviors?

- To investigate this, the set of 5 synergies extracted from each behavior were compared. Similarities were found between
  - 3 pairs of synergies for jumping and swimming
  - 4 pairs of synergies for jumping and walking
  - 3 pairs of synergies for swimming and walking
Shared and specific synchronous synergies

- R² value for reconstruction of entire dataset with this set of shared and specific synergy – 0.87
- R² values for jumping – 0.86, swimming – 0.86, walking – 0.81
- Thus a single set consisting of a mixture of shared and specific synergies can reconstruct the patterns for individual behaviors with essentially the same accuracy
Spatiotemporal structure revealed by time-varying synergies

- Time-varying synergies for individual behaviors for each frog were extracted, with number of synergies in each set varying from 2 to 8.

- The fraction of total variation in data explained by the combination of the synergies in each set increased with the number of synergies.

<table>
<thead>
<tr>
<th>Frog</th>
<th>Behavior</th>
<th>Fraction for each no. of synergies</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>2</td>
<td>3</td>
</tr>
<tr>
<td>F10</td>
<td>Jumping</td>
<td>0.78</td>
</tr>
<tr>
<td>F11</td>
<td>Jumping</td>
<td>0.79</td>
</tr>
<tr>
<td>F17</td>
<td>Jumping</td>
<td>0.75</td>
</tr>
<tr>
<td>F10</td>
<td>Swimming</td>
<td>0.74</td>
</tr>
<tr>
<td>F11</td>
<td>Swimming</td>
<td>0.64</td>
</tr>
<tr>
<td>F17</td>
<td>Swimming</td>
<td>0.53</td>
</tr>
<tr>
<td>F10</td>
<td>Walking</td>
<td>0.52</td>
</tr>
<tr>
<td>F11</td>
<td>Walking</td>
<td>0.59</td>
</tr>
<tr>
<td>F17</td>
<td>Walking</td>
<td>0.53</td>
</tr>
</tbody>
</table>

Table 5. Number of pairs of time-varying synergies with similarity above chance between the sets with five elements extracted from the same behavior in different frogs.

<table>
<thead>
<tr>
<th>Behavior</th>
<th>F10–F11</th>
<th>F10–F17</th>
<th>F11–F17</th>
</tr>
</thead>
<tbody>
<tr>
<td>Jumping</td>
<td>5</td>
<td>4</td>
<td>4</td>
</tr>
<tr>
<td>Swimming</td>
<td>4</td>
<td>3</td>
<td>3</td>
</tr>
<tr>
<td>Walking</td>
<td>5</td>
<td>3</td>
<td>4</td>
</tr>
</tbody>
</table>

R² values from pooled data → jumping – 0.81, swimming – 0.80, walking – 0.70
Shared and specific time-varying synergies

- The set of 5 synergies extracted from each behavior were compared. Similarities were found between
  - 4 pairs of synergies for jumping and swimming
  - 3 pairs of synergies for jumping and walking
  - 3 pairs of synergies for swimming and walking
Shared and specific time-varying synergies

- $R^2$ value for reconstruction of entire dataset with this set of shared and specific synergy – 0.79
- $R^2$ values for jumping – 0.81, swimming – 0.75, walking – 0.66
- Thus a single set consisting of a mixture of shared and specific synergies can reconstruct the patterns for individual behaviors with essentially the same accuracy
Conclusions

- A small number of synergies can explain a large fraction of variation in the muscle patterns.
- The synergies extracted from the same behavior in different frogs were in most cases similar.
- Some synergies are shared across behavior while others are behavior specific.
- Results support the hypothesis that the motor output has modular organization.
- Also an indication that some, but not all modules are shared across behaviors.
Thank You.
References

1. d`Avella et. al. *PNAS*, vol 102, no.8, 2005