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ABSTRACT

How do humans and other animals accomplish coordinated movements? How are novel combinations of limb joints rapidly assembled into new behavioral units that move together in in-phase or anti-phase movement patterns during complex movement tasks? A neural model simulates data from human bimanual coordination tasks. As in the data, anti-phase oscillations at low frequencies switch to in-phase oscillations at high frequencies, in-phase oscillations occur both at low and high frequencies, phase fluctuations occur at the anti-phase in-phase transition, a "seagull effect" of larger errors occurs at intermediate phases, and oscillations slip toward in-phase and anti-phase when driven at intermediate phases.
Humans and other animals effortlessly control their limbs to accomplish coordinated movements. In particular, novel combinations of joints can be rapidly assembled into new behavioral units, or synergies, that are capable of moving together in in-phase or anti-phase movement patterns to carry out complex movement tasks like tool use, dancing, piano playing, and the like. In order to study this competence, an experimental paradigm has previously been developed in which humans are asked to move fingers from both hands at variable frequencies and to do so in in-phase or anti-phase rhythms. Data from these experiments exhibit characteristic properties which provide clues to how new combinations of joints can be rapidly bound together to generate coordinated movement patterns.

This article describes a neural network model that suggests how novel joint combinations can be rapidly bound together in rhythmic patterns. These patterns are emergent properties due to network interactions. They are not explicitly represented or programmed in the network. The model simulates parametric properties of human movement data as emergent, or interactive, properties of nonlinear network interactions. This network takes the form of a central pattern generator (CPG) that coordinates the movement across limb joints when volitional input signals perturb the network.

For example, in a bimanual finger tapping task, Yamanishi et al.\textsuperscript{1} required subjects to tap keys in time to visual cues. The timing of the cues was varied across ten relative phases: \((0.0, 0.1, 0.2, \ldots, 1.0)\), where \(0.0 = 0^\circ\) and \(1.0 = 360^\circ\). The authors observed two properties in the responses of their subjects. First, the subjects' fingers tended to slip from intermediate relative phase relationships toward purely in-phase (0.0 and 1.0) or anti-phase (0.5) relationships. Second, the observed in-phase and anti-phase oscillations exhibited less variability than intermediate phase relationships. That is, when the subjects were asked to synchronize to signals whose phase relationships varied from 0.0 to 1.0, the standard deviation of the errors was lowest when the phase relationship was near in-phase (0.0 and 1.0) or pure anti-phase (0.5). The standard deviation of the errors increased as the subjects were required to move away from the in-phase or pure anti-phase oscillations. These two properties
were also observed by Schoner and Kelso\textsuperscript{2} and by Tuller and Kelso\textsuperscript{3}. The appearance of the plot of the standard deviation of the errors has been called the “seagull effect”\textsuperscript{3}; see Figure 1A. The CPG model exhibits the seagull effect, as well as the slip toward pure in-phase and pure anti-phase oscillations (Figure 1B).

Figure 1

Kelso\textsuperscript{4} described a related experimental task in bimanual coordination which involved moving fingers or limbs in in-phase or anti-phase oscillations. For example, adduction of the right index finger simultaneously with abduction of the left index finger is an anti-phase movement. Concurrent abduction (or adduction) of both fingers is an in-phase movement. The rate of movement of the fingers was signaled by a metronome. Tuller and Kelso\textsuperscript{3} summarized the following four qualitative behaviors found in the bimanual tasks:

1. If a subject was asked to produce a 180° anti-phase oscillation, the subject could do so at low frequencies, but as frequency increased, the subject eventually switched to an in-phase oscillation.

2. When instructed to perform an in-phase oscillation, the subject could do so at both low and high frequencies.

3. Fluctuations in which no clear phase relationship dominates occur before the transition from anti-phase to in-phase oscillations. There does not appear to be a clear transition point between ranges of frequencies where only in-phase output occurs and the lower frequencies where both anti-phase and in-phase frequencies occur.

4. Subjects phase errors were minimal at required phases of 0°, 180°, as in the “seagull effect” described above.

Figure 2

The CPG model reliably reproduces all four effects in our simulations; see Figures 2 and 3. In order to simulate these four properties, the model was presented with a pulsed wave
anti-phase oscillatory input to each channel, as shown in Figure 3A. These pulsed inputs represent the descending volitional commands to move the fingers as required. The square waves were either equal to a constant input level when on, or set to zero when off. The input level and the duration of the “on” portion of the signal were held constant for each of the simulations. For each simulation, only the frequency of these pulses was varied. The duration of the “on” portion of the signals was 2.0 in all simulations. Shorter duration signals did not reliably produce oscillations in both channels. In order to generate Figure 2, we computed, for 145 points, the relative phases of the output signals using the times at which they exceeded a threshold. As the frequency was varied, the model showed a switch from anti-phase (Figure 2B) to in-phase (Figure 2D) oscillations. It did not show the reverse transition in response to in-phase inputs, as in the data. The system also exhibited fluctuations in between the anti-phase and in-phase regimes (Figure 2C).

**Figure 3**

The CPG consists of nerve cells, or cell populations, that obey membrane equations\textsuperscript{5}, also called shunting equations\textsuperscript{6}. The cells excite themselves via feedback signals while they inhibit themselves and other populations (Figure 4). These anatomical connections form an on-center off-surround network, a design that is ubiquitous in the nervous system\textsuperscript{6–9} and that has been used to explain other types of motor behavior\textsuperscript{10}. For purposes of motor control, it is also relevant that cells in the motor cortex are linked together via widespread inhibitory connections.\textsuperscript{11} When a subset of model cells is driven by in-phase inputs or by anti-phase inputs of increasing frequency, as in Figures 2 and 3, then the network interactions generate observed properties of variable frequency finger movements as emergent properties of the entire network.

**Figure 4**

The Kelso data and our simulations suggest the prediction that this type of opponent CPG acts as a kind of nonlinear low pass filter; that is, at high frequencies of stimulation,
the output of the system converges to the response obtained from the network when pulsed inputs are replaced by a tonically active nonspecific signal of the same amplitude that is input equally to all the cells. The model's ability to resolve the input arousal signal is inversely related to its frequency. If the model exhibits a prescribed phase response to a sustained arousal level, then the output of the system converges to this response irrespective of the phase relationships which occur in high frequency inputs of the same amplitude.

Including an afferent feedback signal from the limbs, say from tactile sensations, proprioception, or joint receptors, would not necessarily improve the ability of such a CPG to stay phase-locked to the input signal. The afferent signal will either overlap in time with the input signal or it will not. If it does overlap, then it will have the effect of increasing the amplitude of the input. Increased amplitude has not, in our simulations, improved the ability of the model to accurately follow the phase of the input. On the other hand, if the efferent signal lags the input, then this signal tends to further smooth, or increase the frequency of, the total input to the oscillator, and thus helps to favor the rhythm that would be generated by a tonically active nonspecific signal.

The opponent CPG model thus shows how a ubiquitously occurring neural design—namely, a recurrent on-center off-surround network whose cells obey membrane equations—can give rise to activation patterns that are characteristic of coordinated rhythmic movements. The patterning of inputs to such a network organizes it to behave as if it possesses special linkages between particular joints, whereas in reality, the inhibitory connections can be quite widespread and nonspecific. The model hereby illustrates how neural interactions can coordinate novel combinations of movements that are not specified in the wiring diagram of the brain.
The CPG is defined by the shunting on-center off-surround recurrent network

\[
\frac{dx_1}{dt} = -Ax_1 + (B - x_1)[f(x_1) + I_1] - (C + x_1)[D_{11}g(y_1) + D_{12}g(y_2)],
\]

(1)

\[
\frac{dy_1}{dt} = E[(1 - y_1)[x_1]^+ - y_1],
\]

(2)

\[
\frac{dx_2}{dt} = -Ax_2 + (B - x_2)[f(x_2) + I_2] - (C + x_2)[D_{21}g(y_1) + D_{22}g(y_2)],
\]

(3)

\[
\frac{dy_2}{dt} = E[(1 - y_2)[x_2]^+ - y_2],
\]

(4)

where \(x_i\) is the rapidly changing potential of the \(i\)th excitatory cell population, and \(y_i\) is the slowly changing potential of the \(i\)th inhibitory cell population. Parameter \(A\) is the passive decay rate, \(B\) and \(C\) are the excitatory and inhibitory saturation potentials of the membrane, or shunting, terms \(B - x_i\) and \(C + x_i\), \(I_i\) is the input to the \(i\)th population to itself, \(D_{ij}g(y_j)\) is the inhibitory feedback signal from the population \(j\) to population \(i\), with inhibitory path strength \(D_{ij}\), and \([x]^+ = \max(x, 0)\). The feedback signals in the on-center off-surround network are sigmoid functions of activity\(^{6,12}\), namely,

\[
f(x) = \frac{F_1([x]^+)^2}{F_2 + ([x]^+)^2} \quad \text{and} \quad g(x) = \frac{G_1([x]^+)^2}{G_2 + ([x]^+)^2}.
\]

(5)
REFERENCES


FIGURE CAPTIONS

Figure 1: (A) An example illustrating both the "seagull" effect and the tendency to slip from intermediate phase relationships toward purely in-phase and anti-phase relationships. [Reprinted with permission from Yamanishi, Kawato, and Suzuki.] (B) The model exhibits the "seagull" effect: Intermediate phase relationships are more variable than purely in-phase or purely anti-phase relationships. The standard deviation of the observed relative phases is plotted against the required relative phase. The model exhibits the tendency to slip from intermediate phase relationships toward purely in-phase and anti-phase relationships. This plot shows the mean of the (observed—required) phase. There are 145 points per mean.

Figure 2: Bifurcation from anti-phase to in-phase oscillation in response to anti-phase inputs of increasing frequency. The anti-phase inputs \( I_i \) in (A) replace the GO signal in Figure 2. They give rise to the anti-phase oscillation in (B). The input frequency in (A) is low, .1 pulses per unit time; (C) at intermediate input frequencies (0.4), fluctuations occur; (D) at high input frequencies (0.85), in-phase oscillations obtain. \( A = 1.0, B = 1.1, C = 2.5, D_{ii} = 0.8, D_{ij} = 0.45, i \neq j, E = 1.0, F_1 = 9.0, G_1 = 3.9, F_2 = 0.5, G_2 = 0.5. \) The duration of each pulse was 2.0. The integration step size was 0.01. The duration of each pulse was 0.05. The initial conditions were reset to zero before each run.

Figure 3: As the frequency of the in-phase inputs is parametrically increased, the oscillator output also stays in-phase: No bifurcations occur. The in-phase input shown in (A) produces the output shown in (B). The in-phase output for inputs with higher frequency in-phase oscillations are shown in (C) and (D). The parameters and input frequencies are as in Figure 2, except the input is always in-phase.

Figure 4: The CPG is defined by a recurrent on-center off-surround network whose cells obey membrane, or shunting, equations. See text for details.
Figure 1

(A) SD (ms) and Av (ms) for unskilled subjects.

(B) Standard deviation of observed phase and observed - required phase.
Figure 2