1993-01

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January 1993

Technical Report CAS/CNS-93-018

Proceedings of the world congress on neural networks, Portland, IV, 491-494. Hillsdale, NJ: Erlbaum Associates.

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Abstract

The 2–channel Ellias–Grossberg neural pattern generator of Cohen, Grossberg, and Pribe [1] is shown to simulate data from human bimanual coordination tasks in which anti–phase oscillations at low frequencies spontaneously switch to in–phase oscillations at high frequencies, in–phase oscillations can be performed at both low and high frequencies, phase fluctuations occur at the anti–phase to in–phase transition, and a "seagull effect" of larger errors occurs at intermediate phases.

Human Bimanual Coordination Effects

In the Yamanishi et al [6] finger tapping task, subjects were required to bimanually tap keys in time to visual signals. The timing signal was varied across ten relative phases: $(0.0, 0.1, 0.2, \ldots 1.0)$, where $0.0 = 0°$ and $1.0 = 360°$. The authors observed two properties in the responses of their subjects, see Figure 1. 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 oscillations with 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 0° and 360°) or pure anti–phase (0.5 or 180°). 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 Tuller and Kelso [5]. The appearance of the plot of the standard deviation of the errors been called the "seagull effect" [5].

Kelso [4] describes an 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 [5] summarize 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

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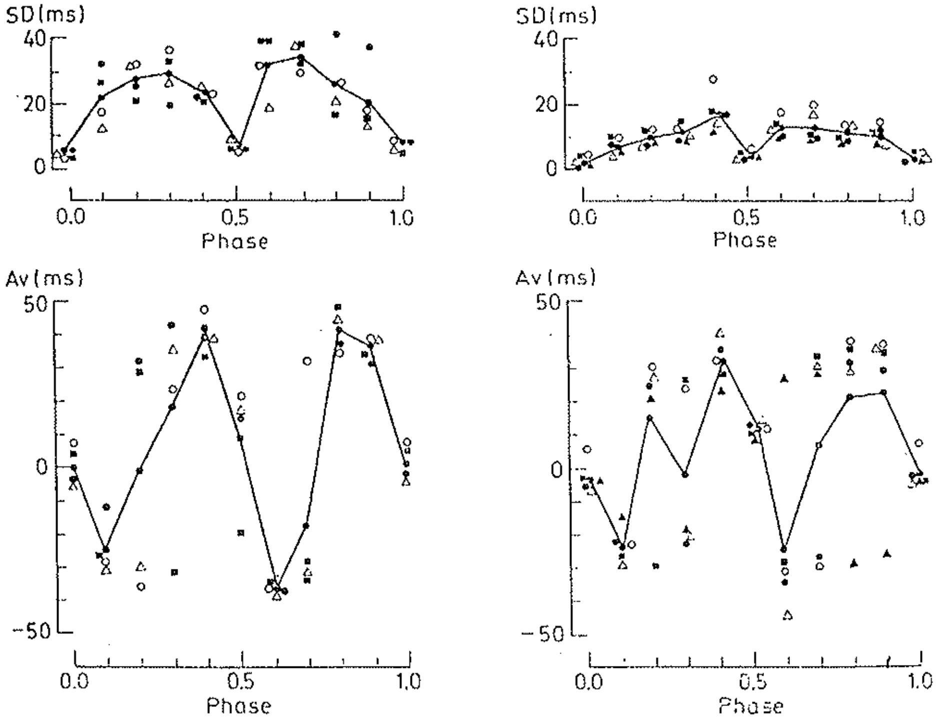
[*] Supported in part by AFOSR (AFOSR 90-0128 and AFOSR F49620-92-J-0225).

[†] Supported in part by AFOSR (AFOSR 90-0175), NSF (NSF IRI-90-24877), and ONR (ONR N00014-92-J-1309).

[‡] Supported in part by DARPA (AFOSR 90-0083) and ONR (ONR N00014-92-J-1309).



Unskilled subjects

Skilled subjects

Figure 1: An example illustrating both the tendency to slip from intermediate phase relationships toward purely in-phase and anti-phase relationships and the "seagull effect"(Yamanishi el al [6]).

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°, and 360° (the "seagull effect" described above).

Model of a Two–Channel Neural Pattern Generator

The model is a version of the cooperative–competitive nonlinear feedback network introduced by Ellias and Grossberg [2]. The 2-channel pattern generator, briefly summarized in Cohen, Grossberg, and Pribe [1], is depicted in Figure 2 and obeys the equations:

$$\frac{d}{dt}x_1 = -Ax_1 + (B - x_1)[f(x_1) + I_1] - (C + x_1)[D_{11}g(y_1) + D_{12}g(y_2)], \tag{1}$$

$$\frac{d}{dt}y_1 = E[(1 - y_1)[x_1]^+ - y_1], \tag{2}$$

$$\frac{d}{dt}x_2 = -Ax_2 + (B - x_2)[f(x_2) + I_2] - (C + x_2)[D_{21}g(y_1) + D_{22}g(y_2)], \tag{3}$$

and

$$\frac{d}{dt}y_2 = E[(1 - y_2)[x_2]^+ - y_2], \tag{4}$$

where $D_{12} = D_{21}$, $[\omega]^+ = max(\omega, 0)$, and

$$f(\omega) = \frac{F_1([\omega]^+)^2}{F_2 + ([\omega]^+)^2}, \quad g(\omega) = \frac{G_1([\omega]^+)^2}{G_2 + ([\omega]^+)^2}. \tag{5}$$

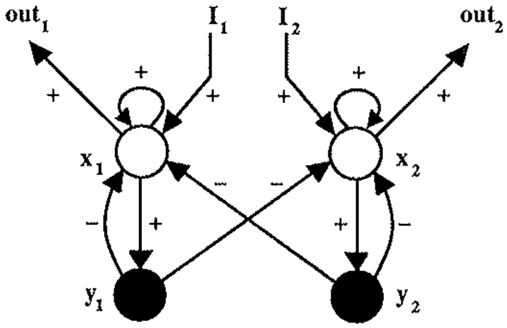
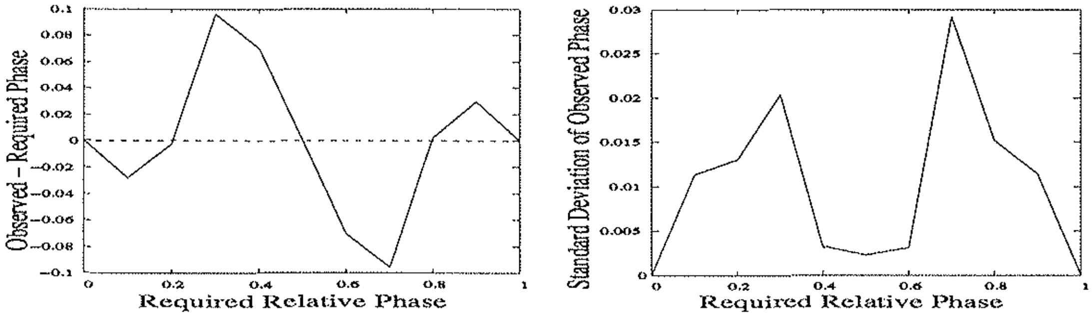


Figure 2: This two channel neural pattern generator exhibits oscillatory behavior consistent with human performance in bimanual coordination tasks.



(A) *(B)*

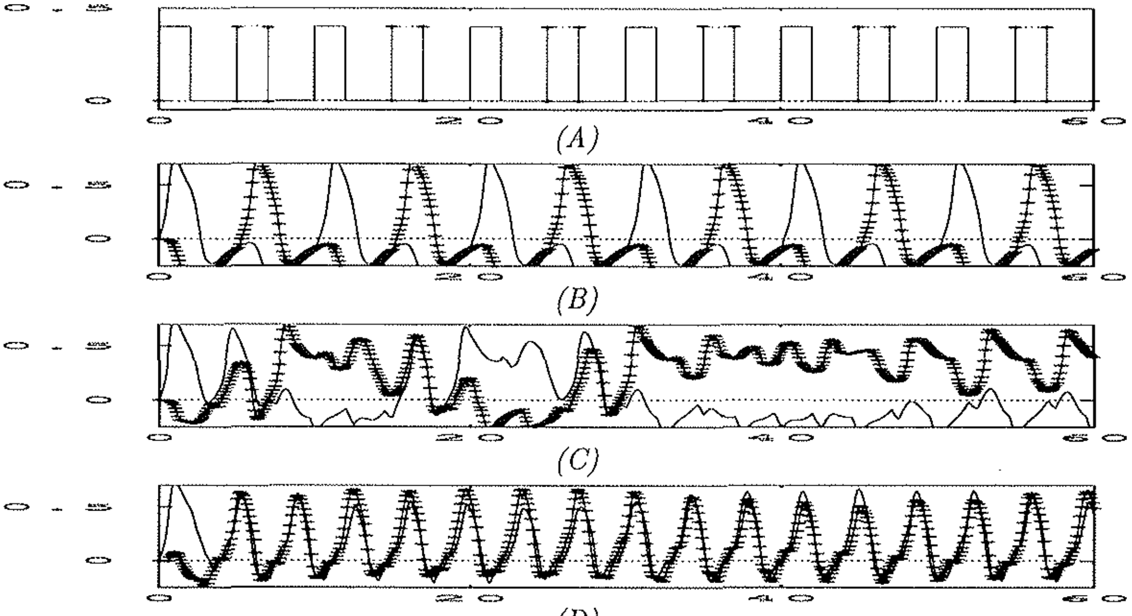
Figure 3: *(A)*: The model exhibits the tendency to slip from intermediate phase relationships toward purely in-phase and anti-phase relationships. This plot shows the mean of the (observed – required) phase (there are 145 points per mean). *(B)*: The model exhibits the 'seagull' effect: Intermediate 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.

Here x_i is the activity, or potential of a fast excitatory neuron or population, y_i is the activity of a slow inhibitory interneuron or population, and I_i is an external input. The excitatory and inhibitory activities obey a shunting equation [3], and interact with each other via nonlinear sigmoid signals.

Simulation Results

The neural pattern generator reliably reproduces all four effects in response to input pulses, I_i, that mimic experimental conditions: (1) Increasing the frequency of anti–phase square wave (Figure 3A) input caused a bifurcation from anti-phase (Figure 4B) to in-phase (Figure 4D) oscillations. (2) There was no reverse transition in response to in-phase inputs (not shown). (3) Phase fluctuations were exhibited in between the anti-phase and in-phase regimes (Figure 4C). (4) The "seagull" effect was observed (Figure 3B). The tendency to slip from intermediate phase relationships toward purely in-phase and anti-phase observed by Yamanishi was also occurs.

These results support the hypothesis that oscillations during human bimanual coordination are emergent properties of a neural network whose finger commands compete via slow inhibitory feedback interactions, excite themselves vias fast excitatory interactions, and are nonlinearly coupled to shunting membrane processes via nonlinear sigmoid signals.



(A)

(B)

(C)

(D)

Figure 4: 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) give rise to the anti-phase oscillation in (B). The input frequency in (A) is low, 0.1 pulses per unit time; (C) at intermediate input frequencies (0.4), fluctuations occur; (D) at high input frequencies (0.85), in-phase oscillations obtain. $A = 1.0$, $B = 1.1$, $C = 2.5$, $D_{ii} = 0.8$, $D_{ij} = 0.45$, $E = 1.0$, $F_1 = 9.0$, $G_1 = 3.9$, $F_2 = 0.5$, $G_2 = 0.5$. The input, I_i, when on was 0.4 and when off was 0.0, and the duration of each pulse was 2.0. $t_{max} = 60.0$, and $\Delta t = 0.01$. The initial conditions were reset to zero before each run.

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