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Strategies of Balancing: Regulation of Posture as a Complex Phenomenon

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Strategies of Balancing: Regulation of Posture as a Complex Phenomenon

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by
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Keywords: Chaos, Postural Stability, Pain

ABSTRACT

Strategies of Balancing: Regulation of Posture as a Complex Phenomenon

by

Allison Hilbun

The complexity of the interface between the muscular system and the nervous system is still elusive. We investigated how the neuromuscular system functions and how it is influenced by various perturbations. Postural stability was selected as the model system, because this system provides complex output, which could indicate underlying mechanisms and feedback loops of the neuromuscular system. We hypothesized that aging, physical pain, and mental and physical perturbations affect balancing strategy, and based on these observations, we constructed a model that simulates many aspects of the neuromuscular system. Our results show that aging changes the control strategy of balancing from more chaotic to more repetitive. The chaotic elements ensure quick reactions and strong capacity to compensate for the perturbations; this adeptly reactive state changes into a less reactive, slower, probably less mechanically costly balancing strategy. Mental tasks during balancing also decreased the chaotic elements in balancing strategy, especially if the subject experienced chronic pain. Additional motoric tasks, such as tying knots while balancing, were correlated with age but unaffected by chronic pain. Our model competently predicted the experimental findings, and we proceeded to use the model with an external data set from Physionet to predict the balancing strategy of Parkinson's patients. Our neurological model, comprised of RLC circuits, provides a mechanistic explanation for the neuromuscular system adaptations.

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CHAPTER 1

INTRODUCTION

Postural stability is indicative of a person's ability to adeptly maintain an upright stance during static and dynamic conditions. Although most individuals do not monitor their own balance capabilities as a health indicator, recent research has shown a correlation between lifespan and postural stability (Cooper et al. 2014). Although it is unclear why instability is related to mortality, balance disturbances do precede tangible symptoms. Observably, elderly people generally struggle with postural instability (Blaszczyk et al. 1993; Amoud et al. 2007). Unexpected falls in elderly people are still a common cause of death and catastrophic injury (Melzer et al. 2004). The causes of the decline in postural stability include a general decrease in the sensitivity of neural receptors, decreased processing speed of the brain's central processing systems along with cognitive impairment and the decreased potential of power production from cross bridges of motor systems (Blaszczyk et al. 2006; Horak 2006). More specifically, aging progressively affects the neuromuscular systems in older people by increasing muscle activation of the vastus lateralis and biceps femoris muscles, which affects the feedback mechanisms of balancing (Laughton et al. 2003). Research has shown that there are differences between both the visible sway and the balancing patterns between older and younger people, especially in the mediolateral direction (Blaszcyk et al. 1993; Laughton et al. 2003 Amoud et al. 2007). When participants are asked to do static stances, center of pressure data are often examined in the medial-lateral and anteroposterior directions independently, and greater deviations of trajectories are considered evidence of age, incompetence, or pathology (Wikstrom et al. 2005). Although the decline in postural stability with age is observable and documented, how the control strategy changes with age is still unclear. It is the goal of this work, through statistical mechanics, to further reveal differences between people in balancing which have not yet been observed, and thus improve the efforts to detect markers for declining health status.

Interpretation of results of postural stability studies is intricate, because results vary based upon several factors such as age and lifestyle choices. Interestingly, the data gleaned from postural stability studies are not intrinsically predictable. For example, a study by Simmons (2005) revealed that in unfamiliar, perturbing situations, highly trained ballet dancers were inferior to controls in maintaining balance. Their attempts to rectify perceived instability involve different joints than controls (Simmons 2005). It is therefore the invisible control strategy and not necessarily the magnitude of movement or apparent balancing appearance which is important for identification of risks. We specifically have explored the relationship between postural stability and aging and chronic pain. Our assumption is that the differences discovered between groups will elucidate the underlying mechanisms behind the change in balancing strategy that accompanies age. Based upon balance analysis, there has already been a difference discovered between the young and the elderly center of pressure displacement by fractal analysis (Amoud et al. 2007). Amoud et al. (2007) discovered an increase in the Hurst exponent of balancing data in elderly people. How this control strategy changed through the years, however, was not identified.

The analysis methodology in this paper depends upon chaos indicators and diffusion coefficients. The theory behind the diffusion coefficient originated from when Albert Einstein (1905) examined the random movement of a particle suspended in a liquid and determined that its movement was mutually exclusive of other particles. He quantified the particle's 'mean square displacement' (Equation 1), where D is the diffusion coefficient. Mandelbrot et al. (1968) showed that this can be written as in Equation 2. In this equation, H is the Hurst exponent, and it is a value between 0 and 1. A Hurst exponent of 0.5 is a completely random walk; other works use the Hurst exponent instead of the diffusion coefficient, but both values reflect the randomness of a particle’s movement, or in this case, the predictability of the center of pressure of the balancing foot which is a metaphor for a particle.

$\langle \Delta x \rangle = \sqrt{2D\Delta t}$ Equation 1.

$\langle \Delta x^2 \rangle = \Delta t^{2H}$ Equation 2.

The second group we compare with healthy young people are people with chronic pain. We visited the Johnson City Chiropractic Clinic, and the results of that study are detailed on page 28. The pains were greatly varied and were not categorized in this study, because chronic pain from all sources affects the brain similarly, with increase gray matter volume in the hippocampus and parahippocampal gyrus, regardless of the source of the pain (Smallwood et al., 2013). Research has indicated that chronic pain negatively affects the postural stability of sufferers (Lee et al. 2012; Mann et al. 2010). Mann et al. (2010) showed that women who suffered from chronic lower back pain had significantly impaired postural control strategies, as evidenced by increased center of pressure velocity. The removal of visual feedback (eyes closed condition) further impaired the postural stability (Mann et al. 2012). Lee et al. (2012) also showed postural instability in patients with chronic lower back pain when compared with controls in the eyes closed condition. Researchers measured results by using the time of successful stability holding and the essential range of kinematic movements of various body segments and compared these with data from the force plate. They concluded that controls had significantly better stability indices than those with lower back pain for the eyes closed case of the dominant foot (Lee et al. 2012). There is logically a connection between pain and balance disturbances according to the results discussed below: it is known that various alterations in subconscious bodily trajectories often accompany neurological and mental disorders (Brand 1998, Aybek et al. 2012). Chronic pain results in altered balancing strategies due to accompanying basal ganglia modification, similar to what is seen in people with depression (Lafer et al. 1997; Meyer et al. 2006). Aybek et al. (2012) examined the differences between spontaneous hand movements in unmedicated, depressed individuals in comparison with healthy controls. Because fractal patterns are decreased in diseased and elderly EEG signals, but prominent in healthy controls, this group endeavored to explore the fractal dynamics of hand movements in carefully matched depressed groups and controls. The depressed individuals had scored greater than 21 on the Hamilton depression rating scale. Participants were given accelerometers to wear on their wrist and encouraged to go about their daily activities as normal between 10 am and 4 pm. Participants were not aware of the details of the study. After the hours of recording, angular velocity was analyzed along with the trajectories of the rotations of the hand. A detrended fluctuation analysis (DFA) was used to compare the fractal properties of the groups. It is apparent that the healthy controls exhibited fractal patterns for hand movement measurements (alpha values close to 1) (Aybek et al. 2012). In addition, major depression has been shown to negatively affect the basal ganglia (Lafer et al. 1997). In a study by Lacerda et al., 2003, it has been shown via MRI that the volume of the basal ganglia was significantly diminished when compared with healthy controls. The authors did, however, discover differences between the global pallidus between groups. The left side of the putamen was also significantly different than controls and appeared to correlate with the length of the depression. They asserted that structure indeed of the basal ganglia was altered in the course of the development of depression (Lacerda et al. 2003). There has also been a connection drawn between autism and magnitude of balance sway. Similar to the Radonovich et al. (2013) have explored the relationship between postural stability and autism. Children between the ages of 3 and 16 years of age, comprised of a control group and children with diagnosed autism spectrum disorder, were asked to stand on a force plate with feet at comfortable width for 20 seconds while ground reaction forces were collected. They then ultimately measured the magnitude of the postural sway of the participants based on the center of pressure dispersion, and compared these results with a Repetitive Behavior Scale-Revised (RBS-R) test. They discovered a significant correlation between the increased range of the postural sway and the repetitive behaviors, however, whether the control strategy of balancing was different between groups, as opposed to just of greater amplitude in the autistic group, was unexplored (Radonovich et al. 2013).

Although a connection between postural instability and pain and brain conditions such as autism and depression has been drawn, there has not been a chaos analysis on signals from stability data that can be used to characterize such data and differentiate them from healthy data. Further, there is a lack of understanding of the alteration of control strategies used by pained individuals and whether they are similar to what is observed in older people or not.

To test the reasons behind the changes in control strategy with age and pain condition, we present two modeling papers: a model for wasp interactions, and a model for balancing based on an electrical circuit. The wasp paper gave a foundation for the construction of our neurological circuit model due to its description of biological phenomena based upon the flow of electrons through linked electrical circuits. The neurological model helps elucidate how simple alterations of parameters may recreate the results we have observed and thereby generally reveal positive treatment strategies based upon electronics. This model explores the damage caused by such illnesses as Parkinson’s Disease (PD). According to Kano et al. (2011), PD creates binding problems for dopamine, serotonin, and noradrenaline in the limbic system which are also risk factors for depression, which is linked with pain. In vivo studies have used [^{11}C] RTI-32 in positron emission tomography as a marker for binding of dopamine and noradrenaline, revealing a decrease in binding in the diseased group (Kano et al. 2011). Imaging studies on untreated depressed individuals have also shown decreased ability for ligand binding for dopamine receptors (Robinson 2007). This binding difficulty is modeled by the reduction of the capacitance of our circuit, detailed on page 74, in the central nervous system tier.

Our cumulative hypotheses are as follows:

- Older people have less chaotic balancing data and more repetitive recovery patterns.
- Chronic pain decreases the chaotic components of balancing.
- The change in control strategy with age and pain can be modeled by decreased capacitance.

CHAPTER 2

The effect of age on balancing behavior: complexity analysis of parallel force trajectories

Hilbun, A. and Karsai, I.

Abstract.

Background: The study of postural instability via stabilograms is important to understand and monitor the risk of falls. The propensity to fall is not always identifiable by observing a patient's movements macroscopically; it is more important to determine underlying control strategy to recognize pathology. In this study, we used chaos indicators to identify how the control strategy changes with age.

Methods: Thirty-five healthy people ages 18-72 performed three tasks while balancing on one foot on a force plate: standard balancing task, mental task (balancing while answering basic arithmetic questions), and knot-tying task (balancing while tying two knots in a piece of ribbon). Mediolateral force trajectories were analyzed to determine control strategy via Hurst exponents, correlation dimensions, Lyapunov exponents, and phase-space plots.

Results: We found increased pattern repetition in balancing with increased age, as evidenced by the emergence of a double attractor pattern in phase-space plots and the increase of Hurst exponents with age from approximately 0.3 to 0.8. Correlation dimensions were not different among age groups. As people age, they tend to develop strong feed forward control strategies for balancing, and lose the complexity of micro movements intrinsic to young age.

Conclusions: There is an open loop control strategy for balancing that emerges in older adulthood, and there are attractors inherent to balancing which begin to develop in middle age.

Keywords: Postural stability, elderly, fall risk, control strategy, chaos

Background

Postural stability reflects the ability to maintain an upright stance, constantly monitoring and adapting the center of mass of the body. The prevalence of reduced postural stability in the elderly is high (Amoud et al., 2007; Blaszczyk et al., 1993). Unexpected falls in elderly people remains a common cause of death and injury (Melzer et al., 2004). For people over the age of 65, 30% will suffer a fall within a year (Melzer et al., 2004, Blaszczyk et al., 2006). The decline in postural stability is caused by a decrease in the sensitivity of neural receptors, a decrease in the speed of the central processing systems of the brain, cognitive decline, and the decreased potential of power production in motor systems (Blaszczyk et al., 2006, Horak, 2006). Laughton et al. (2003) showed that old age affects the neuromuscular systems in older people by increasing muscle activation of the vastus lateralis and biceps femoris muscles. This in turn affects the feedback mechanisms of balancing. Balance studies have shown that there are differences between the balance ability and patterns of older and younger people, especially in mediolateral sway (Blaszcyk et al., 1993; Amoud et al., 2007; Laughton et al., 2003). Blaszczyk et al. (1993) showed that both the anterioposterior (AP) and mediolateral (ML) directions in the circular voluntary sway test were higher in the younger group when compared with the older group. Although there is agreement in the literature that significant differences exist in balancing proficiency between older and younger adults, the control strategy that is altered with age and the best method for quantifying the change of the stability control strategy is unclear.

In many studies, the center of pressure data of the base of the support (the foot) is plotted with an *x* and *y* axis showing the movement of the center of pressure along the two-dimensional plane of the force plate (Blaszczyk et al., 1993). The width of this two-dimensional path is a simple and common method of quantifying stability (Blaszczyk et al., 1993). However, it has been shown that highly trained, healthy ballet dancers have wider balance paths than untrained individuals (Simmons, 2005). Thus the actual degree of sway does not necessarily indicate proficiency. The method of balancing is more important than the sway radius. Other studies (Duarte et al., 2000; Collins and DeLuca, 1993) have attempted to use statistical mechanics to not only measure differences between groups, but to try to comprehend the changes in the control strategies which caused those discrepancies. The use of innovative methods for quantifying signals has become highly valuable in medical research; for example, there has been recent advancement in cardiac analysis due to nonlinear modeling of heart rhythms (Gois and Savi, 2009).

In this study, we quantify balancing data with different chaos indicators, for the purpose of detecting balance differences with age. Because there is a change in energy dispersal based upon the randomness of motion and because younger people more efficiently use energy, there may be a tendency towards decreased randomness in balancing with age (Alekseev and Strunin, 1973). Additionally, persistent balancing patterns, which include the use of repetitive patterns, will be more mechanically inefficient than more random patterns. For this reason, we hypothesize that the change of proficiency of balance strategy is continuous, with a gradual tendency towards less random movements. We also hypothesize that younger individuals have negative feedback control systems for balancing, and this is also paired with more chaotic elements in their balancing data, which altogether provides a fast adaptive balancing system.

Methods

Thirty-five subjects, both sexes (18 males and 17 females) aged between 18 and 72 with body mass index averaging 28.02 (BMI 20.5-42.8) voluntarily participated in this study. These participants had no lower body disabilities or significant health problems. Participants verbally attested that they did not have any neuropathy or previous history of falls. Each participant signed an informed consent document; the study was approved by the Institutional Review Board of East Tennessee State University. Prior to trials, participants were required to perform a ‘timed get up and go’ test in which they were seated in a chair and upon hearing ‘go’, they were asked to rise and walk 10 ft., then turn around, walk back to the chair, and sit back down in the chair. If they were unable to accomplish this within 10 seconds, then the person was excluded from the study. A Pasco two-dimensional force plate was used to measure parallel force trajectories; this device has been used in studies where force plate portability is vital (Vilar et al., 2013; Sato & Heise, 2012; Penitente et al., 2010). Parallel force data from single foot stance movements were collected with 100 data points per second. Prior to data collection, weight and height were measured.

Three different actions were studied: standard test, the mental test, and the knot tying test. For the standard test, participants initially stood with the dominant foot on the force platform, and the other foot on a support platform with the same height as the device. Upon the start of each trial, the participant would shift his or her weight onto the foot which was on the force plate and maintain balance on that foot for a total of 12 seconds. Dominant legs were determined by the participant’s verbal affirmation of their dominant leg. Hands were placed at the hips for these trials

For the mental test, participants were asked to balance on one foot for 12 seconds while verbally responding to short addition and subtraction questions.

For the knot tying test, participants were asked to balance on one foot for 12 seconds while tying two knots in a 20 cm long piece of ribbon.

Mathematical Methods

To establish a characterization of the balancing data obtained from the test subject, we needed to separate the trends, chaotic and random elements of the complex data. Hurst exponents were used to analyze the force plate data in order to determine the control strategy of the participant (Collins and DeLuca, 1993). A Hurst exponent between 0.5 and 1 is called persistent, meaning that there with each new datum point, it is likely that the data will continue in the pattern that it had been following before the new data. A Hurst exponent between 0 and 0.5 is called anti persistent, meaning that with each new data point, it is likely that the data will begin an opposite pattern as it had been following. Aste (2013) proposed to obtain the generalized Hurst exponent by a different method. First he describes how the random variables change in time (Equation 1), where X(t) is the time series, τ is a time delay, and q refers to the analysis of q order moments. Then he describes how this random walk leads to the Hurst exponent, H (Equation 2), where v is a time resolution (Aste, 2013; Matteo et al., 2003).

$$\boldsymbol{K_q(\tau) = \frac{\langle |X(t+\tau) - X(t)|^q \rangle}{\langle |X(t)|^q \rangle}} \qquad \text{Equation 1}$$

$$\boldsymbol{K_q(\tau) \sim \frac{t}{v}^{q(H(q))}} \qquad \text{Equation 2}$$

Phase-space plots visually show both the data and its motion all on the same plot. They can reveal attractors in data. We have taken the balancing data and represented them as phase-space plots for each individual person to observe the patterns in balancing strategy. These phase-space plots are dependent upon each datum point and the derivative of the data.

Assuming that data displays fractal properties, in other words having self-similarity when observing the data in smaller and smaller increments, the correlation dimension can be used to further examine the patterns in complex data. Traditionally, the correlation dimension is calculated by taking each new data point and constructing a circle of radius ‘r’ around the data point (its phase-space volume) then observing what fraction of points are covered by this circle. The radius ‘r’ is then expanded and another fraction of points covered is found. Log log plots of the fraction of covered points vs. the radius chosen are found and then the slope is assumed to be the correlation dimension (Osorio et al., 2001). Our correlation dimension is estimated as the degree of the polynomial of best fit of this produced function. Our code for this function depends upon the fast fourier transform of the data, as shown in Equations 3 and 4, where T is the time series.

$$radius = \frac{frequency^2}{T_i} \qquad \text{Equation 3}$$

$$covered = \int \frac{1}{1000 * N} * |fft(T)|^2 \qquad \text{Equation 4}$$

Lyapunov exponents measure the dependency of the system on its initial conditions. The Lyapunov exponents show how much the balancing strategy changes in time and how much the initial balancing behavior impacts the later balancing strategy. This exponent is determined by how the trajectories of a time series diverge in time. The trajectories are written as 'x(t)' and 'x(t) + $\delta x(t)'$. The largest Lyapunov exponent was calculated (Equation 5), where γ is the dominant Lyapunov exponent and is essentially the average of the rate of separation of the trajectories in the time series (Cvitanovic et al., 2004). If this dominant Lyapunov exponent is less than zero, then the system is assumed to be without a chaotic nature, and it dissipates into a fixed point attractor, similar to the time path of a damped harmonic oscillator. If this Lyapunov exponent is approximately equal to 0, then it is assumed that the system is stable and may have two uncoupled oscillators. For example, a phase-space plot of two undamped simple harmonic oscillators which have different heights of swing would show two concentric circles of different diameter but centered around the same point (Elert, 1995). A Lyapunov exponent greater than 1 has great trajectory divergence and may show either chaos or random movement.

$$\|\delta x(t)\| \approx e^{\gamma t} \|\delta x_0\| \qquad \text{Equation 5.}$$

Statistics

Residual plots for the standard balancing trial showed normal distribution and skew, indicating the model is capable of accounting for the various chaos indicators and has fulfilled the conditions of normality. A generalized linear model approach was accomplished to test for the relationship between the chaos parameters (Hurst exponents, Lyapunov exponents, and correlation dimensions) and the age of the participant. Residual analysis provided evaluation of the statistical model and the model was altered until the residuals did not show a discernible pattern, hence suggesting only random error has not been explained. The alpha value was set at 0.05 (NumXL 2015, MATLAB 2015, XL version 2010). Data for the cognition and concentration tasks were fit with a polynomial assuming minimal number of coefficients to describe the nature of the data.

Results

Control Strategy

Hurst exponent is not dependent upon the sex or BMI of the test subjects and no significant interaction terms were found amongst the studied variables (GLM, $p > 0.05$, $df = 33$). Significant relationships were found between the age and the Hurst exponents (GLM, $p < 0.05$, $df = 33$). There is a positive relationship between age and open loop control strategy for balancing based on the Generalized Hurst exponent, for the trials of standard balancing on the dominant leg (Figure 2.1).

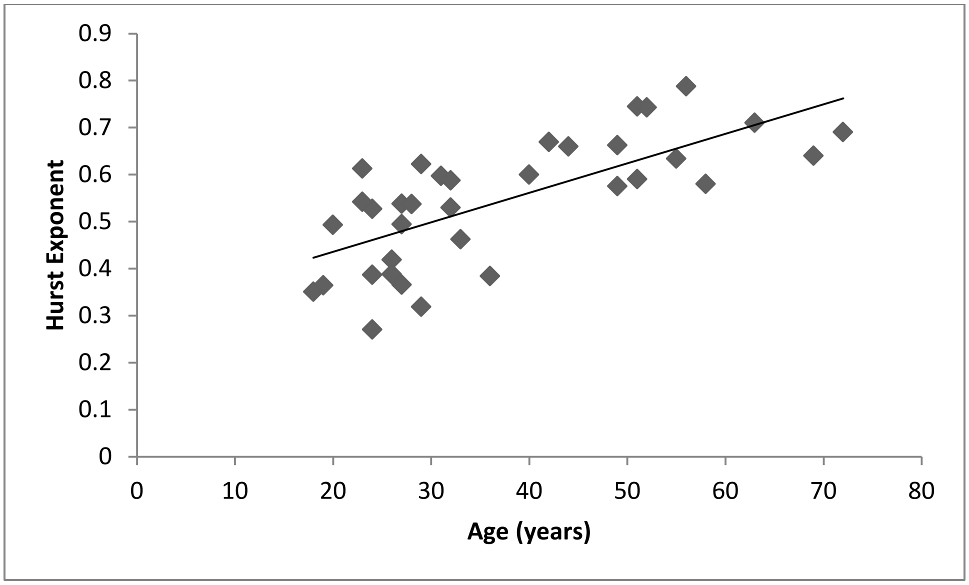

Fig 2.1. Control strategy as a function of age for dominant stance. Generalized Hurst exponents vs. age were plotted for the mediolateral force trajectories while balancing on one foot, unperturbed. Control strategy increases with age; GLM: $y = 0.0063x + 0.3103$, $r = 0.71$, $p < 0.001$, $df = 33$

There was also a curvilinear relationship between age in years and the generalized Hurst exponent for the knot tying tasks and the concentration tasks based on our regression analysis (Figures 2.2 and 2.3). We used a parabola to fit the data with the assumption that there is a maximum around the age of 60 for the perturbing tasks. This assumption is based on Clapp et al., (2011) who showed that the ability to focus on both the concentration task and the balancing simultaneously deteriorates after 60 years of age.

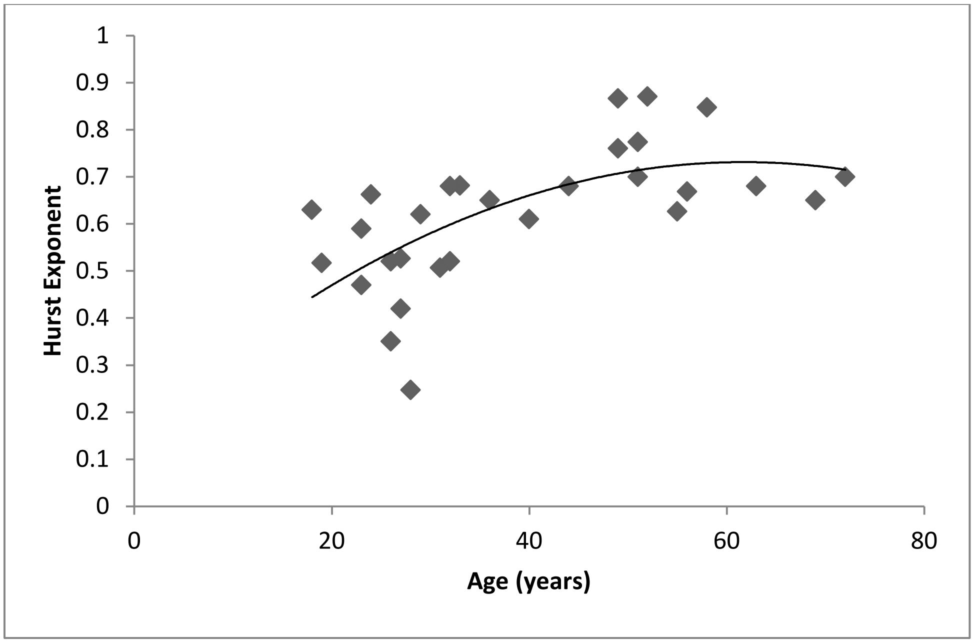

Fig 2.2. Control strategy vs. age for knot tying task. Generalized Hurst exponents vs. age were plotted for the mediolateral force trajectories while balancing on one foot while tying knots in a ribbon. Control strategy increases curvilinearly with age; polynomial:#y = $-0.0002x^2 + 0.0193x + 0.1405$, $r = 0.64$, $p < 0.001$, *df* = 27

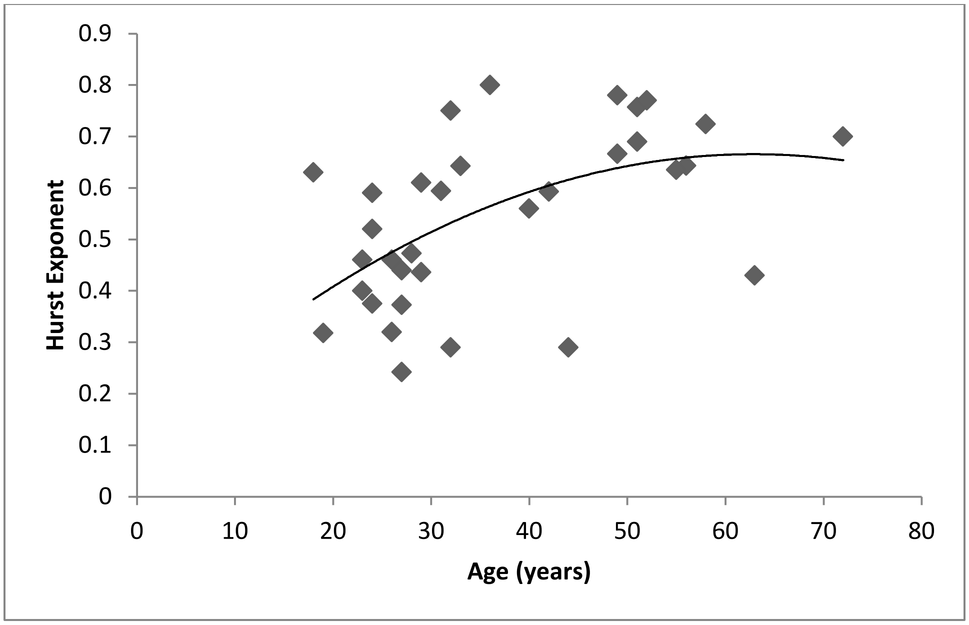

Fig 2.3. Control strategy vs. age, mental task Generalized Hurst exponents vs. age were plotted for the mediolateral force trajectories while balancing on one foot and answering basic arithmetic questions. The control strategy increases curvilinearly with age; polynomial:#y = -0.0001x^2 + 0.0176x + 0.1114, r = 0.54, p < 0.01, *df* = 32

Repetition of Balancing Patterns

We used phase-space plots to analyze how repetitive the balancing movements of particpants were. In general, the phase-space plots of data from younger and older individuals revealed a double attractor pattern for the older people, and a lack of such a pattern for the younger people for the standard trials on the dominant foot (Figure 2.4). This means that the older people tended to repeat their balancing movements for the whole balancing test. In Figure 2.4, an example of a phase-space plot of an older individual is shown beside the phase-space plot of a younger individual. There is a striking difference in the balancing patterns: 78% of people over the age of 45 had phase-space plots that revealed a double attractor pattern, while only 14% of people below age 45 show a double attractor pattern.

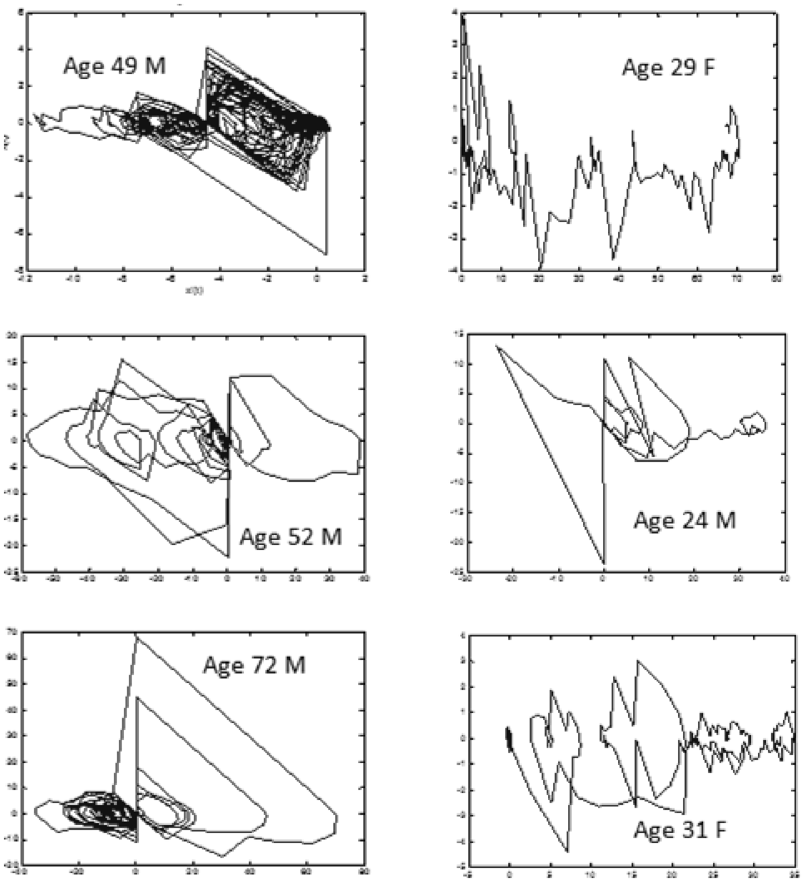

Figure 2.4. Characteristic phase-space plots. These figures are examples of the apparent attractors evident in the phase-space plots of older people (left column). Younger subjects rarely (14%) exhibited similar space plot with attractors (right column).

Dimensionality and time-dependency of balancing

Correlation dimensions are not dependent upon the sex, BMI, or age of the test participants (GLM, $p > 0.05$, *df* = 33). The participants of this study were all free of significant health issues, thus revealing that age does not affect the general geometric span of the data. Repeated patterns have been shown in older people (Figures 2.1-2.4), however since the dimensionality is unchanged, it is the timing and repetition of elements that marks the difference between the force data of younger and older individuals and not the magnitude of all changes. The descriptive statistics for the correlation dimensions are presented in Table 1. There are thus possible strange attractors with fractal dimension between 2 and 3 for healthy individuals balancing.

Task	Mean	Standard Deviation	Range	Kurtosis
Standard	2.63	0.70	3.03	0.20
Knot tying	2.58	0.78	3.98	1.66
Mental	2.54	0.90	4.15	0.61

Table 1. Descriptive statistics of dimensionality. There is no significant difference between older and younger people in the correlation dimensions of their mediolateral force trajectories; healthy people, regardless of age, have force data in the dimension of approximately 2.5. The mental tasks and knot-tying task is not different than the standard task (t-test, t stat mental = 1.67, t stat knot-tying =1.67; $p > 0.05$, $p <0.05$.

There is a negative linear relationship between the largest Lyapunov exponent and age (Figure 5). The largest Lyapunov Exponents for young people are predominately positive, indicating strong chaotic components.

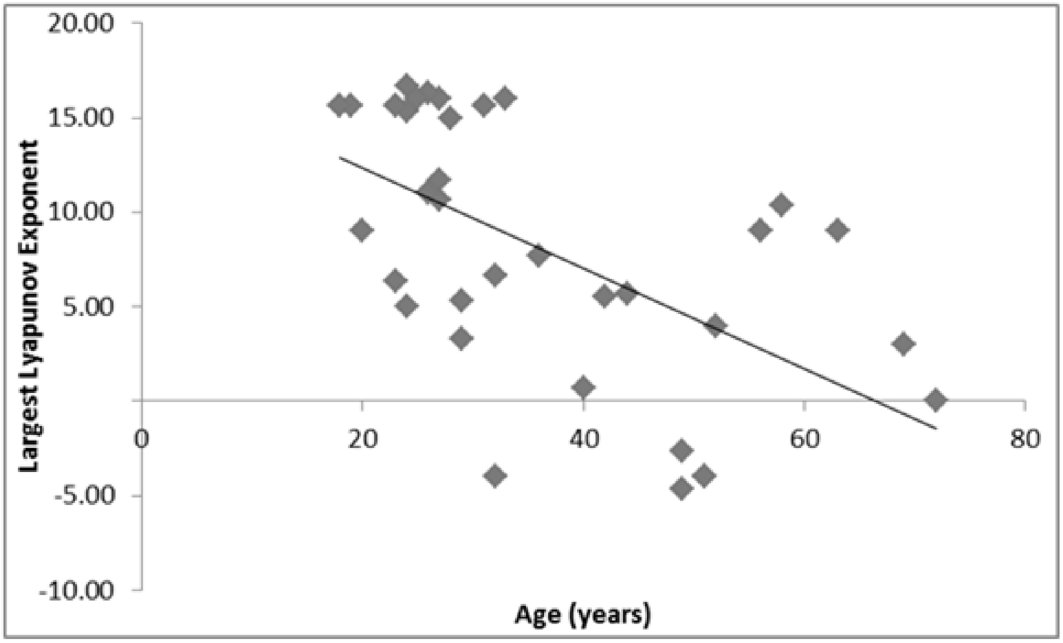

Fig 2.5. Time-dependency of balancing: largest Lyapunov exponents vs. age. Lyapunov exponents from mediolateral force data for each trial (general, knot tying, and mental tasks) were averaged and the results plotted against age. There is a negative linear relationship between the time-dependency of the data and age; linear model:# $y = -0.2648x + 17.632$, $r = 0.57$, $p < 0.01$, $df = 32$

Discussion

There is a clear open-loop control strategy which emerges with age. Hurst exponents increase with age for the standard balancing task, indicating a continual decline in the brain's ability to quickly process information and provide feedback to the central and peripheral nervous systems and the limbs. For the mental and knot-tying tasks, the polynomial fit reveals that people reach the higher Hurst exponent levels at a younger age for the mental and knot-tying tasks. The results of the mental task rely upon a participant's ability to quickly understand the researcher ask the questions and to quickly process the information. There is damage of mitochondrial DNA and subsequent apoptosis of cochlear cells with age (Iwasaki et al. 2014). This may negatively affect balancing even at late middle-age. Rankin et al. (2000) showed that there was reduced muscle activity when balancing if given math problems to accomplish, both for young and older adults. The math tasks in their study affected the older and younger people equally. Since the muscle activity was similarly altered between age groups, it may be that the feedback mechanisms of the central brain processing centers are struggling to quickly provide feedback during cognition tasks, while in younger people, the decreased muscular activation quickly was processed by the brain and balance strategy quickly adapted. Further, the results of the knot-tying task rely upon the ability to concentrate on performing a fine motor control task while still remaining balanced on one foot. The balancing strategy becomes thus more random with age because of delays in muscle activation and diminished strength; the older people have a problem remaining upright while balancing and concentrating on something else. Conceivably, problems with sensory input cause physiological delays, thereby causing older participants to have more of a struggle with knot tying efficiently and therefore having a delay in activation of their feedback mechanisms for balancing (Blaszczyk et al., 2006). Regarding the specific balancing pattern of choice, it is possible that the double attractor pattern shown in the older individuals results from the subjects' view of the trials as biphasic. In other words, they think about the task as 1. Get on the force plate and 2. Hold the balancing position. The younger people may think about the task as one distinct balancing challenge. The dimensionality is not altered by age in healthy people. The data thus has similar geometric complexity, but since there are significant differences in Hurst exponents and Lyapunov exponents, there is a change in the speed at which the body tries new patterns.

There have been disagreements regarding the most appropriate method of analyzing balancing data. Collins and DeLuca (1993) were one of the first to propose to model their center of pressure data as a random walk. Their method was to split up their data into time intervals of equal length and then find the square of the displacement of each time interval, (Collins and DeLuca, 1993). They then made log log plots of the mean of this displacement squared vs. the time interval and determined the slope of this line to be the Hurst exponent. They found two different lines of different slopes and surmised that the first line was a Hurst exponent for the short term and the second line was the Hurst exponent upon longer balancing periods. This method has been questioned; Delignières et al. (2003) wrote that the Hurst exponent being two different values based upon time was only measured due to the inappropriate use of bounds in the system. The Hurst exponent has been appropriately used to describe motion of subatomic particles, yet biological systems such as a foot on a force plate has bounds that a subatomic particle does not experience. Delignières et al. (2003) showed that this problem may be solved by simply integrating the data. Calculation of the Hurst exponent, which relates to the randomness of data in relation to a suspended particle in a liquid's random movements, is used for procedural modeling due to its nature to show the strength of feedback mechanisms. Amoud et al. (2007) used statistical mechanical methods to quantify balancing data. They calculated the Hurst exponents via the detrended fluctuation analysis method as well as the stabilogram diffusion analysis method and found an increase in Hurst exponent with old age, indicating a tendency toward positive feedback in older people. Our study used the generalized Hurst exponent, which should avoid the bounding issues of the original estimation tool of Collins and DeLuca (1993).

Conclusions

Our general findings were in agreement with Amoud et al. (2007), in that the Hurst exponents showed increased pattern generation with age, and we were able to further conclude that there are intrinsic attractors associated with balancing disorders. Additionally, we were able to show differences in chaotic components in balancing in only 12 seconds and from mediolateral force trajectories on an inexpensive force plate, which will be useful as a quick and easy test for the health and complexity of an individual’s processing systems.

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CHAPTER 3

The effect of pain on balancing behavior: complexity analysis of parallel force trajectories

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Abstract

We analyzed the balancing data of people with chronic pain to determine how their control strategy differs from that of healthy people. Unlike the healthy people, the balancing strategy of people with chronic pain is not dependent upon age, except for in the standard balancing task. People with chronic pain fall into one of two categories: random patterns of balancing or highly persistent balancing strategies for standard balancing. For perturbation tasks, people with chronic pain exhibited persistent balancing strategies at a young age.

Background

It is estimated that more than 100 million Americans suffer from chronic pain, caused by a combination of physiological and psychological issues (Ehde et al., 2014). Among the lifestyle challenges caused by chronic pain such as loss of function and loss of life fulfillment due to agony, one dangerous problem associated with chronic pain is postural instability, which can lead to further life attrition and even catastrophic injury (Lee et al., 2012; Mann et al., 2010).

Mann et al. (2010) showed that women who suffered from chronic lower back pain had significantly impaired postural control strategies, as evidenced by increased center of pressure velocity. The removal of visual feedback (eyes closed condition) further impaired the postural stability (Mann et al., 2012). Lee et al., 2012 also showed postural instability in patients with chronic lower back pain when compared with controls in the eyes closed condition. Although this connection between postural instability and chronic pain sufferers has been drawn, it is unclear how the control strategy of balancing changes due to pain. Identification of a control strategy for people with chronic pain will help elucidate the brain mechanisms marred with long-term pain.

In this study, we quantify balancing data from pain patients with different chaos indicators, for the purpose of detecting balance differences between them and healthy controls, as recently observed (Hilbun and Karsai, 2016). We hypothesize that the chronic pain patients are not able to balance as mechanically efficiently as healthy people, due to pain signals from sensory neurons disrupting the most efficient energy dissipation capability (Alkseev and Strunin, 1973). We predict that this mechanical inefficiency will decrease chaotic components in their balancing data.

Methods

Twenty subjects, both sexes (10 males and 10 females) aged between 18 and 59 with body mass index averaging 30.31 (BMI 23.8-45) voluntarily participated in this study. These participants had a verbally affirmed chronic pain. The pains were greatly varied and were not categorized in this study, because chronic pain from all sources affects the brain similarly, with increase gray matter volume in the hippocampus and parahippocampal gyrus, regardless of the source of the pain (Smallwood et al., 2013). Chronic pains included headaches, general soreness, whiplash, lower back pain, upper back pain, hip pain, shoulder pain, elbow pain, knee pain, muscular pain such as hamstring injuries, and combinations of these pains. Participants were all being treated for their pain and thus had no noticeable balance problems. Every participant signed an informed consent document; the study was approved by the Institutional Review Board of East Tennessee State University. Before commencing trials, participants performed a ‘timed get up and go’ test in which they were seated in a chair and upon hearing ‘go’, they were asked to stand up and walk 10 ft., then pivot, walk back to the chair, and return to a seated position. If they were unable to accomplish this task within 10 seconds, they were not permitted to participate further. As in the work by Hilbun and Karsai (2016), a Pasco two-dimensional force plate was used to measure parallel force trajectories. Parallel force trajectories from single foot stance were collected at 100 Hz.

The methodological protocol, including the mathematical analysis, was the same as in Hilbun and Karsai, 2016: Three different actions were studied: standard test, the mental test, and the knot tying test. For the standard test, participants initially stood with the dominant foot on the force platform, and the other foot on a support platform with the same height as the device. Upon the start of each trial, the participant would shift his or her weight onto the foot which was on the force plate and maintain balance on that foot for a total of 12 seconds. Dominant legs were determined by the participant’s verbal affirmation of his or her dominant leg. Hands were placed at the hips for these trials

For the mental test, participants were asked to balance on one foot for 12 seconds while verbally responding to short addition and subtraction questions.

For the knot tying test, participants were asked to balance on one foot for 12 seconds while tying two knots in a 20 cm long piece of ribbon.

Mathematical Methods

Hurst exponents were used to analyze the force plate data in order to determine the control strategy of the participant (Collins and DeLuca, 1993). A Hurst exponent between 0.5 and 1 is assumed to be persistent; A Hurst exponent between 0 and 0.5 is anti-persistent. We analyzed the data for Hurst exponents as in Hilbun and Karsai (2016), based upon the generalized Hurst exponent approach of Aste (2013). He described the change in random variables in time (Equation 1), where X(t) is the time series, $\boldsymbol{\tau}$ is a time delay, and q is the q order moments. The random walk is then related to the Hurst exponent, H (Equation 2), where v is a time resolution (Aste, 2013; Matteo et al., 2003).

$$\boldsymbol{K_q(\tau) = \frac{\langle |X(t+\tau)-X(t)|^q \rangle}{\langle |X(t)|^q \rangle}} \qquad \text{Equation 1}$$

$$\boldsymbol{K_q(\tau) \sim \frac{t}{v}^{q(H(q))}} \qquad \text{Equation 2}$$

We use phase-space plots to reveal attractors; we have also calculated correlation dimensions based upon the degree of polynomial of best fit of the functions, assuming self-similarity in the fluctuations of the force data (Hilbun and Karsai, 2016). Our code for this function depends upon the fast fourier transform of the data, as shown in Equation 3, where T is the time series.

$$Correlation\ Dimension = \int \frac{1}{1000*N} * |fft(T)|^2 \qquad \text{Equation 3}$$

We calculated the largest Lyapunov exponents to measure how the system changes in time and thus its relationship with initial conditions (Hilbun and Karsai, 2016). The largest Lyapunov exponent was calculated (Equation 5), where γ is the dominant Lyapunov exponent and is an average of the rate of dispersion of the trajectories (Cvitanovic et al., 2004). We assume that dominant Lyapunov exponents greater than 1 indicate either chaos or random movements, equivalent to 0 represent a stable system, and less than 0 indicate a fixed attractor.

$$\|\delta x(t)\| \approx e^{\gamma t}\|\delta x_0\| \qquad \text{Equation 5.}$$

<u>Statistics</u>

We used a generalized linear model approach to test the relationship between the chaos parameters (Hurst exponents, Lyapunov exponents, and correlation dimensions) and the age, sex, pain profile, and BMI of the participant. The alpha value was set to 0.05 (MATLAB 2015, XL version 2010).

Results

Control Strategy

Hurst exponents are not dependent upon the sex or BMI of the test subjects and no significant interaction terms were found amongst the studied variables (GLM, $p > 0.05$, *df* = 19, Figure 3.1). Significant relationships were found (Hilbun and Karsai, 2016) between the age and the Hurst exponents for healthy people for the standard balancing task and the concentration task (GLM, $p < 0.05$, *df* = 33, Figure 3.1). Pain does not affect this relationship for those tasks (GLM, $p > 0.05$). Significant relationships were also found (Hilbun and Karsai, 2016) between the age and the Hurst exponents for healthy people for the mental task (GLM, $p < 0.05$, *df* = 33, Figure 3.1). Pain affects this relationship (GLM, $p < 0.05$). Additionally, when a Hurst exponent is between 0.46 and 0.54, the behavior of the signal closely resembles a random walk (Mitra, 2012). For the standard balancing task, most people with chronic pain (80%) fell either into a random walk group (N = 7) or a strongly persistent group with $H > 0.7$ (N = 8).

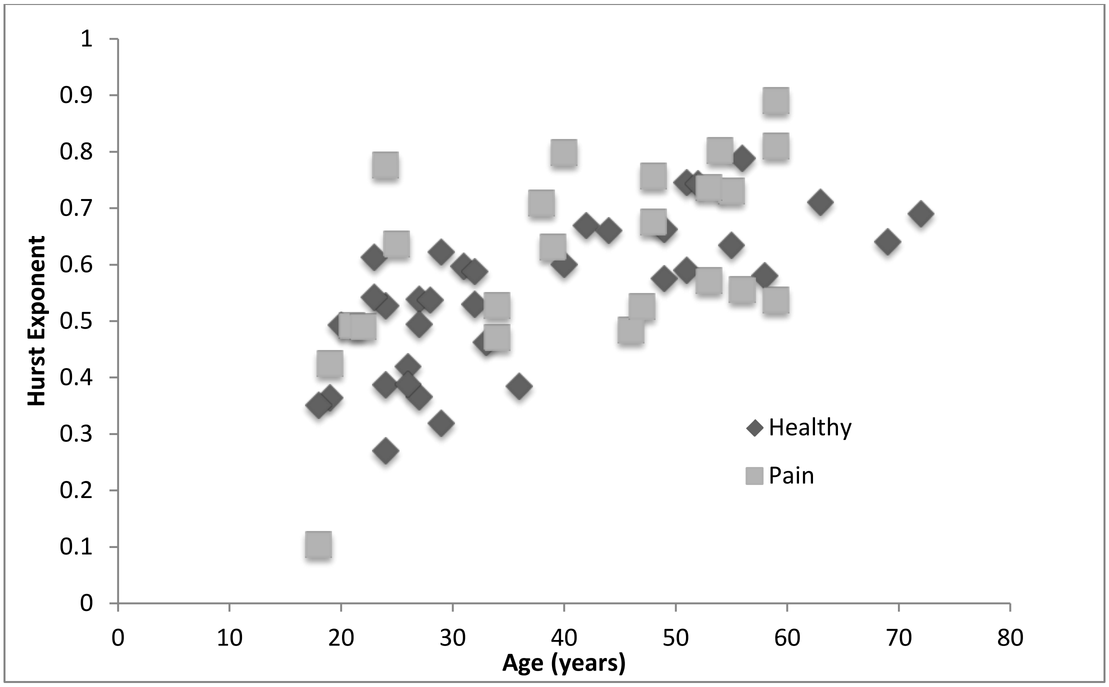

Fig 3.1. Control strategy as a function of age for dominant stance. Generalized Hurst exponents vs. age were plotted for the mediolateral force trajectories while balancing on one foot, unperturbed, and compared to those of healthy people (Hilbun and Karsai, 2016). Control strategy increases with age for both conditions; GLM: $y = 0.0063x + 0.3103$, $r = 0.71$, $p < 0.05$; $y = 0.0068x + 0.3329$, $r = 0.56$, $p < 0.05$, *df* = 19.

There was no relationship between the age and Hurst exponent for the knot tying task for people with chronic pain (Figure 3.2., GLM, $p > 0.05$) Pain does, however, significantly affect this relationship for the mental task (Figure 3.3, GLM, $Persistency = 0.004 * age + \begin{array}{ll} healthy & -0.099 \\ pain & 0 \end{array} + 0.514$, $p < 0.05$).

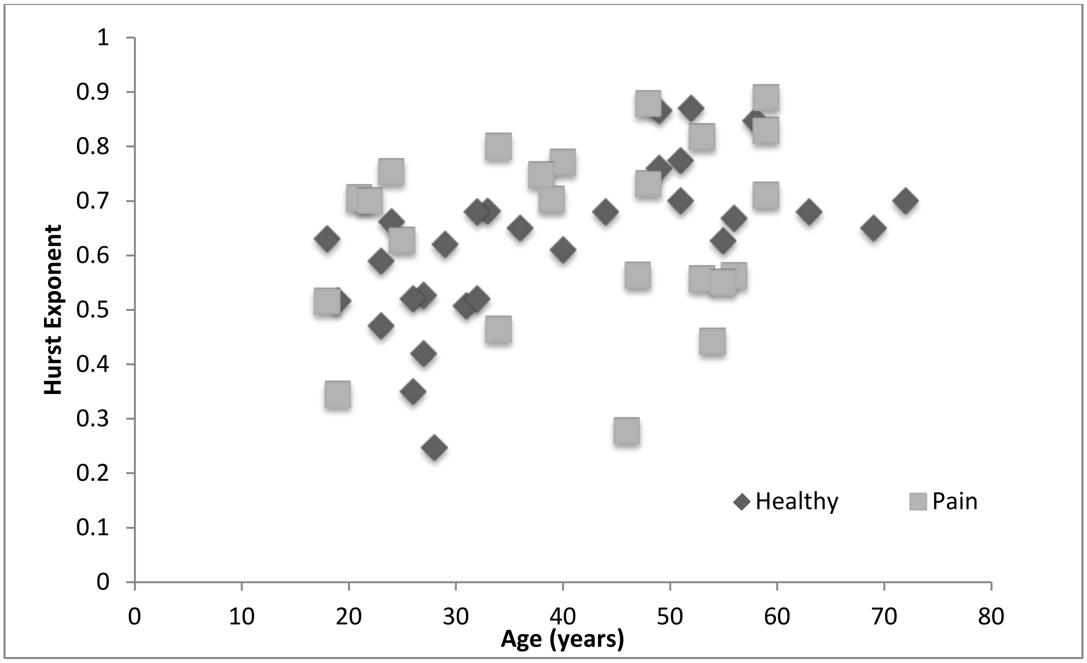

Figure 3.2. Control strategy vs. age for knot tying task. Generalized Hurst exponents vs. age were plotted for the mediolateral force trajectories while balancing on one foot while tying knots in a ribbon. Control strategy increases curvilinearly with age; polynomial:#y = $-0.0002x^2 + 0.0193x + 0.1405$, r = 0.64, p < 0.001, *df* = 27. Generalized Hurst exponents vs. age were plotted for the mediolateral force trajectories while balancing on one foot while tying knots in a ribbon for people with chronic pain; GLM: r = 0.1072, p > 0.05, *df* = 19.

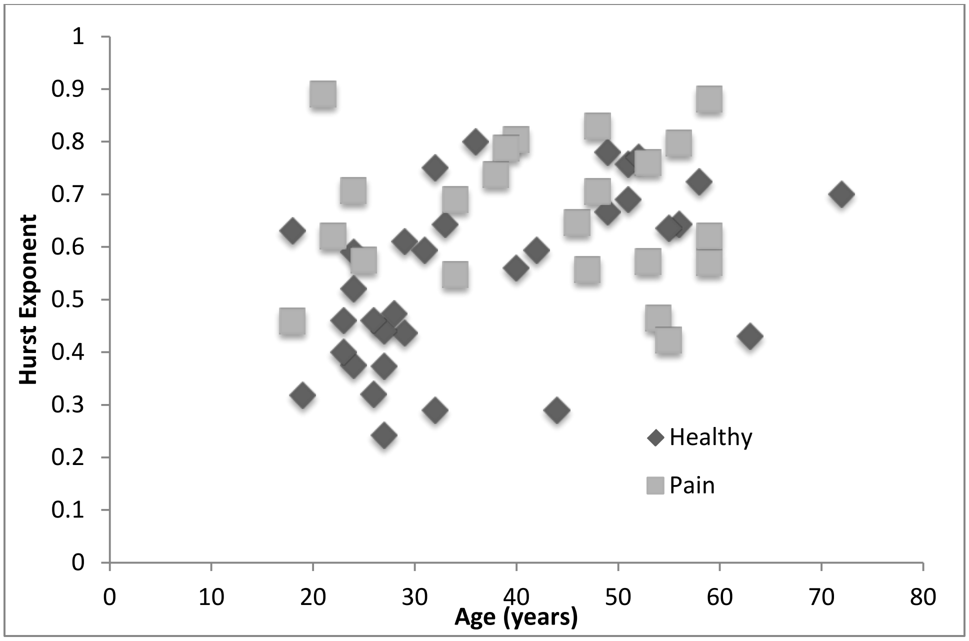

Fig 3.3a,b. Control strategy vs. age, mental task. Generalized Hurst exponents vs. age were plotted for the mediolateral force trajectories while balancing on one foot and answering basic arithmetic questions. The control strategy increases curvilinearly with age; polynomial:#y = -0.0001x^2 + 0.0176x + 0.1114, r = 0.54, p < 0.01, *df* = 33. Generalized Hurst exponents vs. age were plotted for the mediolateral force trajectories while balancing on one foot and answering basic arithmetic questions for people with chronic pain;

GLM: $Persistency = 0.004 * age + \begin{array}{cc} healthy & -0.099 \\ pain & 0 \end{array} + 0.$

Repetition of Balancing Patterns

We used phase-space plots to analyze the pattern repetition in balancing. There is a double attractor pattern which emerges with older age; we have previously shown that 78% of participants over the age of 45 had an emergent double attractor pattern (Hilbun and Karsai, 2016). This pattern was only observed in 36% of people with pain ages 40 and older (30% 45 and older, Figure 3.4). Older people with pain may not be using the same balancing patterns as their painless counterparts due to preoccupation with their pain, and that pain signal's disruption of the central pattern generators which would typically be present.

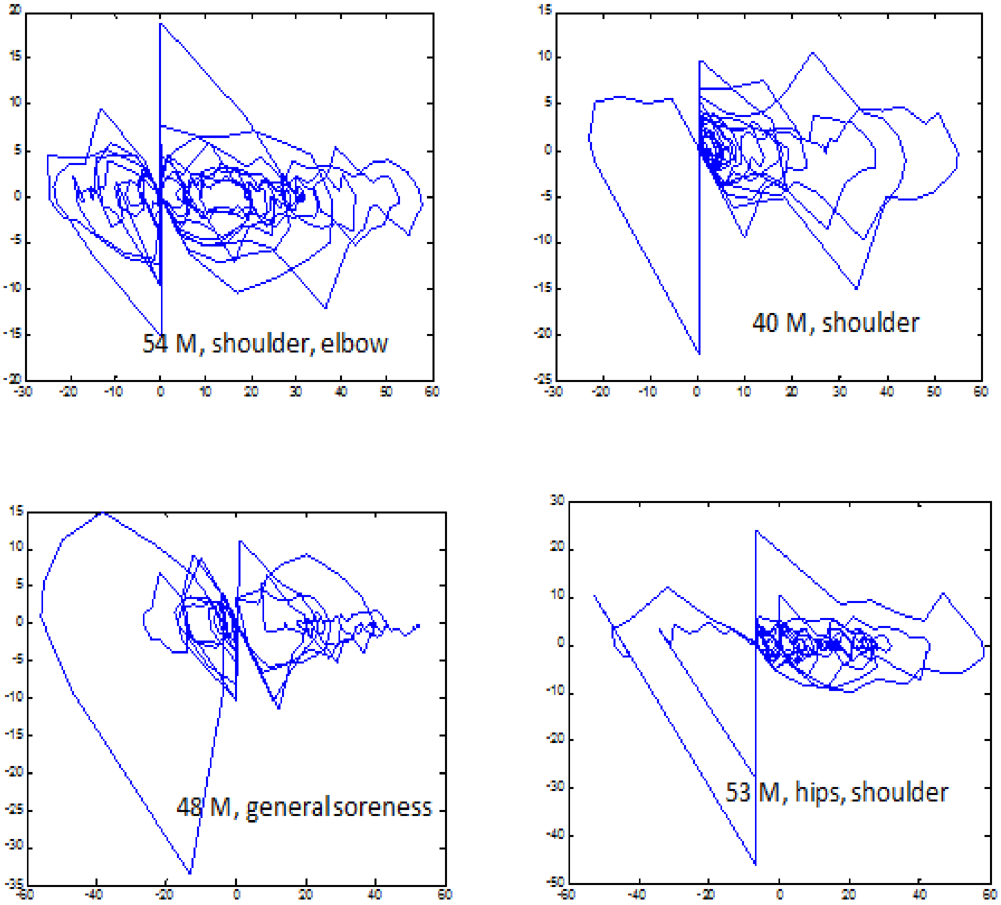

Figure 3.4. Characteristic phase-space plots. The double attractor patterns that were present in people with pain are shown.

Dimensionality and Time-Dependency of Balancing

Correlation dimensions are not dependent upon the sex, BMI, or age of the test participants for people with chronic pain. (GLM, $p > 0.05$, *df* = 19). We compared the descriptive statistics of the correlation dimensions of the healthy people (Hilbun and Karsai, 2016) with those of the people with chronic pain. There are thus possible strange attractors with fractal dimension between 2 and 3 for healthy and pained individuals balancing. The arithmetic means between groups were statistically equivalent, but the standard deviations in the standard balancing task were significantly different ($F = 2.56$, $p < 0.05$).

Task	Mean	Mean pain	Std. dev.	Std.dev. Pain
Standard	2.63	2.67	0.7	0.44
Knot tying	2.58	2.58	0.78	0.62
Mental	2.54	2.96	0.9	0.68

Table 1. Descriptive statistics of dimensionality. All participants, regardless of age, have force data in the dimension of approximately 2.5. The standard deviation for the standard task for people with chronic pain is different than that of the healthy people, but not for the other tasks ($F = 2.6$, $p < 0.05$).

There is a negative linear relationship between the largest Lyapunov exponent and age for healthy people, but not for people with chronic pain (Figure 3.5, Hilbun and Karsai, 2016). The largest Lyapunov Exponents for young people are predominately positive, indicating strong chaotic components.

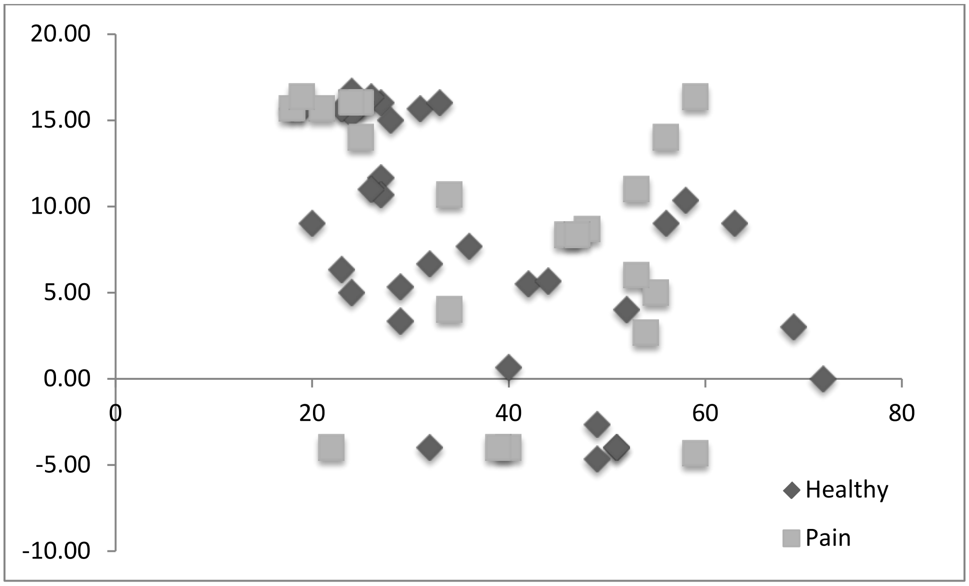

Fig 3.5. Time-dependency of balancing: largest Lyapunov exponents vs. age. Lyapunov exponents from mediolateral force data for each trial (general, knot tying, and mental tasks) were averaged and the results plotted against age for the people with chronic pain, and then compared with those of the healthy people (Hilbun and Karsai, 2016). There is a negative linear relationship between the time-dependency of the data and age for healthy people, but not people with pain; linear model:#$y = -0.2648x + 17.632$, $r = 0.57$, $p < 0.01$, $df = 32$.

Discussion

There is a clear open-loop control strategy which emerges with age in healthy people (Hilbun and Karsai, 2016). Interestingly, existence of pain affects the control strategy during the mental task, but not the knot-tying task. It is likely that the knot-tying task, which is a sensory task, literally interrupts the afferent pathway of pain traffic. There is a positive correlation between math scores and calculation activation in the bilateral anterior cingulate cortex (Price et al., 2013). It is thus possible that the processing of pain and mathematical reasoning are largely processed in the anterior cingulate cortex and that a math task is not capable of taking precedence over pain processing. For healthy people, the control strategy passes through a range that is approximately Brownian at around age 30. For the people with pain, the values are approximately either random or strongly persistent, which shows that the pain either distracts the brain from choosing a solid pattern to follow, or it causes the individual to be even more resistant to feedback mechanisms than their healthy counterparts. It has been shown that while performing basic arithmetic, both the agonist muscle (gastrocnemius) and the antagonist muscle (tibialis anterior), which both are integral in maintaining ankle positioning for solid stability, have reduced activity (Rankin et al., 2000). Additionally, there is decreased in amplitude of muscle activity in the gastrocnemius muscle when comparing older people with younger people at time 350-500 milliseconds after beginning balancing (Rankin et al., 2000). Of significant importance is that balancing requires significant attention, and that with old age, the changes observed in muscle activity occur too quickly for the changed reaction to be a result of the monosynaptic system and thus must originate in higher brain centers (Rankin et al., 2000). It is cognitive functioning that is changed with age, thus the increased attentional demands with the perturbing balancing tasks create signal overloads which disrupt the typical balancing capabilities. People with pain react in various ways to the demands, which may be a result of differing magnitude of pain or differences in prioritizing focus.

Conclusions

In general, our findings show that the existence of any category of chronic pain alters the control strategy of balancing such that the patterns are either random or strongly persistent. Additionally, many young otherwise healthy people with pain exhibit persistent balancing strategies. Importantly, the existence of chronic pain alters the control strategy of balancing while performing mental arithmetic.

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CHAPTER 4

Task allocation of wasps governed by common stomach: a model based on electric circuits

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Abstract

Simple regulatory mechanisms based on the idea of the saturable 'common stomach' can control the regulation of construction behavior and colony-level responses to environmental perturbations in *Metapolybia* wasp societies. We mapped the different task groups to mutual inductance electrical circuits and used Kirchoff's basic voltage laws to build a model that uses master equations from physics, yet is able to provide strong predictions for this complex biological phenomenon. Similar to real colonies, independently of the initial conditions, the system shortly sets into an equilibrium, which provides optimal task allocation for a steady construction, depending on the influx of accessible water. The system is very flexible and in the case of perturbations, it reallocates its workforce and adapts to the new situation with different equilibrium levels. Similar to the finding of field studies, decreasing any task groups caused decrease of construction; increasing or decreasing water inflow stimulated or reduced the work of other task groups while triggering compensatory behavior in water foragers. We also showed that only well connected circuits are able to produce adequate construction and this agrees with

the finding that this type of task partitioning only exists in larger colonies. Studying the buffer properties of the common stomach and its effect on the foragers revealed that it provides stronger negative feedback to the water foragers, while the connection between the pulp foragers and the common stomach has a strong fixed-point attractor, as evidenced by the dissipative trajectory.

Introduction

Insect societies function as superorganisms (Holldobler and Wilson, 2008) in which parallel processing is ubiquitous. The parallel processing not only makes the system more reliable (Barlow and Proschan, 1975), but it also makes possible the emergence of a complex system of the network of specialized units (Karsai and Wenzel, 1998, Seurant and Stanley, 2012). Division of labor is one of the most studied and intriguing phenomena in insect societies. One of the most complex types of labor organization mechanisms is called task partitioning, which describes a situation when a given task, such as nest construction, is partitioned into subtasks. These subtasks are commonly connected sequentially and carried out by different more or less specialized individuals, such that it can be observed on the working process of the bucket brigade (Anderson et al., 2002). The assignment of a given worker to a given subtask is commonly dynamic, because it depends on the progress of the work, the number of participants, and other factors, and it poses a decision problem at the individual level for task switching (Sinha et al., 2006). In the insect society, each agent has only a local perception and only local information about the overall situation, and these societies have no foreman or other central task allocation unit, therefore the whole system is self-organizing itself to establish close to optimal performance via allocating different numbers of workers to different task groups.

Swarm founding *Metapolybia* wasps exhibit flexible and adaptive task specialization, in which distinct subsets of the complex nest construction task are partitioned between cooperative teams of nest mates (Karsai and Wenzel, 1998; 2000; Karsai and Balazsi, 2002; Agrawal and Karsai, 2016). The building task is partitioned into four subtasks, and all subtasks are carried out by generally different individuals. Some workers specialize in water collecting and bringing the water to the nest, where it is stored in the crop of other wasps. These water storer wasps form a “common stomach” where the water can be downloaded or taken out, if needed. Other specialized wasps called pulp foragers collect water from the common stomach and fly out to collect wooden pulp. The water they bring from the nest is needed to macerate the plant materials (cellulose) into building material. This building material then is transported to the nest, where it will be distributed to builder wasps, which built the pulp into the nest. Field experiments and modeling of this system revealed that the saturation of the common stomach is used by the wasp as an information center (Karsai and Schmickl, 2011). For example, if the common stomach is saturated with water, the water foragers have difficulty downloading their water load, while the pulp foragers can take water from the common stomach very easily. This indicates that in the colony, there would be more water providers than necessary. Consequently, some of the water foragers would give up water foraging and switch into water users such as pulp foragers or builders. However, these switches also have costs (Hamann et al., 2013); therefore a large common stomach also can play a role as a buffer (Karsai and Runciman, 2011), so small fluctuations would not trigger task switching, and the wasps would operate with high task fidelity (Karsai and Phillips, 2012). This would in turn ensure additional benefits to the colony, such as the ability to learn the position of water and pulp resources.

Task partitioning itself is an old and general challenge not only in insect societies (Deneubourg and Goss, 1989; Seeley et al., 1991; Schmickl et al., 2012) but also in computational distributed systems (Bannister and Trivedi, 1983; Klügl et al., 2003), or in robot groups (Gerkey and Matari´c, 2004; Lemaire et al., 2004). Due to the hiatus of master equations in biology, task partitioning is commonly described and modeled with agent-based approaches or by the use of empirical functions. For example the ‘‘response threshold models’’ assume that workers vary intrinsically in task preference (Robinson and Page, 1989) and these threshold functions are commonly described by some form of sigmoid curve (Boneabou, 1999). Karsai and Balazsi (2002) used a Weibull function, commonly used to describe stress and aging processes, for modeling task partitions and Karsai and Schmickl (2011) built a complex system dynamic model that used combinations of linear functions to describe material flow and task switching in *Metapolybia* societies. These models are based on empirical data, fitted functions, and simple reasonable assumptions which well predicted the operation of natural colonies.

Our goal in this paper is different. We will show that the essence of this complex biological phenomenon can be described by master equations using the physical systems of inductance circuits. We have built a model from electric circuits that will provide similar predictions to that which we observed in real colonies and empirical models. Models based upon electrical circuits have been adeptly used to model such systems as the nervous system; Hodgdon and Huxley (1952) provided a circuit model, based upon resistors and a capacitor, to model nerve impulses. Their research has been confirmed and expounded upon for further elucidation of cellular processes such as anesthesia (Heimburg and Jackson, 2007). Furthermore, it has been asserted that the properties of neural circuits and animal behavior are linked (Newcomb et al., 2012). Coupled circuits involving capacitors, resistors, and inductors were chosen for this model due to the circuits' inherent abilities to essentially explain storage through inductors and capacitors, loss due to environmental factors through resistors, and a general structure that would allow for a circular flow of a supply of particles: water in the biological system and electrons in the physical circuit. We will carry out a series of perturbation experiments in our model and we will compare the predictions or our model to field experiments and the predictions of other models constructed for the same system.

Theory/Calculations

Our model is based upon a simple physical system: an electrical circuit. It consists of four circuits, each of which acts as a different functional part of the wasp colony. The four parts of the wasp system which are modeled are the water foragers, the common stomach, the pulp foragers, and the builders. The electrons flowing through the circuits are used to model water flow through the system. In other words, each circuit corresponds to a group of wasps that are engaged in the same task, and the flow of electrons represents the flow of water through the system. Each task group (water foragers, pulp foragers, common stomach wasps, and builders) are represented by an RLC circuit. These circuits are related to simple harmonic oscillators. The inductance (L) acts as the mass of a harmonic oscillator system; the resistance (R) causes damping, and the capacitance (C) behaves like the spring constant of a mass oscillating on a spring. Each of the individual RLC circuits is connected by mutual inductance, representing the connectedness of these tasks (Figure 4.1). Mutual inductance was chosen as a connection between the circuits because the change of mutual inductance in one coil induces a current in the second coil. The water foragers acquire water, and then the water foragers directly affect the common stomach, the common stomach directly affects the pulp foragers, and the pulp foragers directly affect the builders. Because the water foragers collect water and increase the supply of the common stomach, we use mutual inductance to model this work-based exchange of materials and information. Because in order to forage pulp, the pulp foragers need water from the common stomach, there is once again a work-based exchange of materials and information. The builders need supplies from the pulp foragers to build, so these circuits are also connected by mutual inductance. Sinks of water for construction and drinking/cooling are modeled via resistors.

The current model is different from previously published models of task allocation of wasp societies (Karsai and Balazsi, 2002, Karsai and Schmickl, 2011, Karsai and Runciman, 2011; Karsai and Phillips, 2012; Hamann et al., 2013), because these models used either an agent-based approach or a combination of empirical and linear equations. Our present electrical circuit approach models the flow of water through the wasp system using master equations, which are based upon a well-studied physical system (Giancoli, 2000). This new model also allows us to derive new testable predictions on the connectedness of the system as a whole and the connectedness of the common stomach with the pulp foragers.

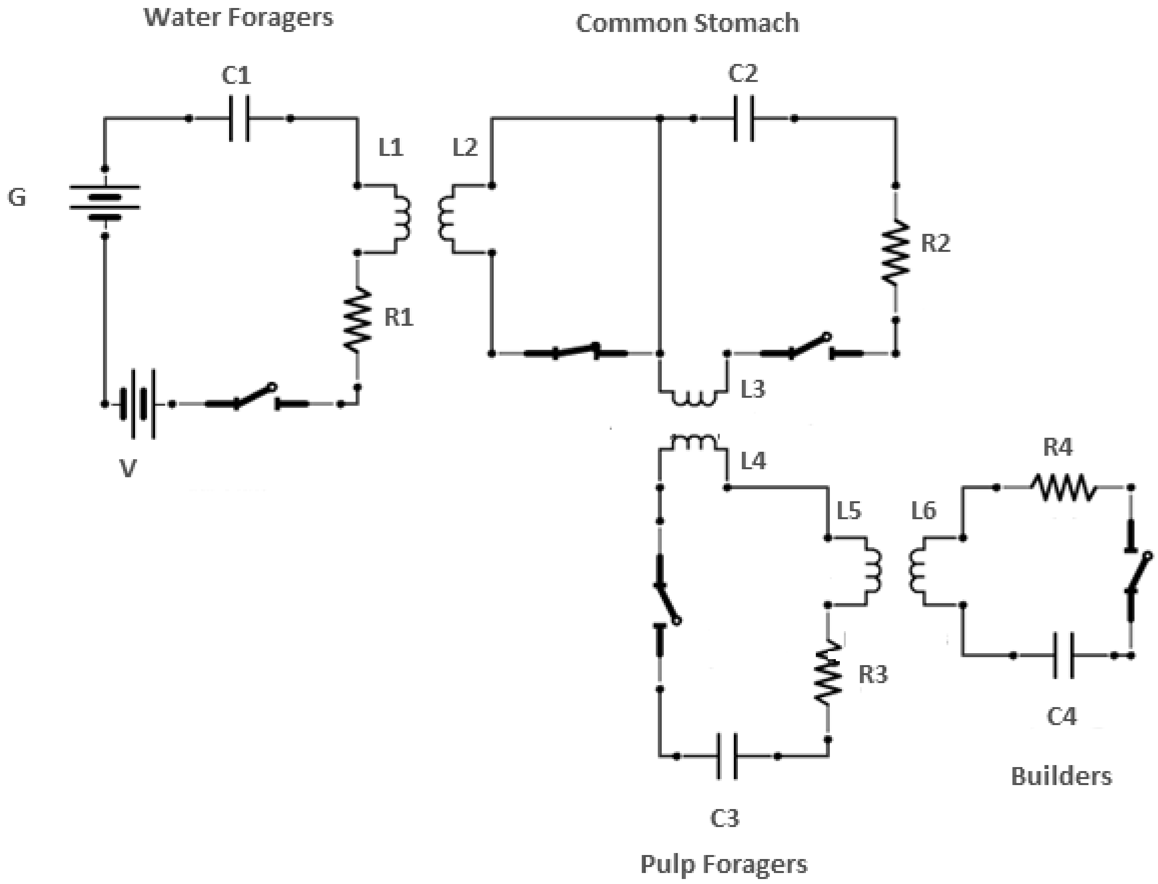

Figure 4.1. Circuit diagram model of task partitioning of *Metapolybia* wasps. The four circuits represent the group of wasps belonging to the four task groups. Elements of circuits are described in Table 1.

The Model:

The Water Foragers

The task of the water foragers is to collect water and transfer the water to the common stomach. The circuit which models the water foragers comprises a capacitor (C1), a resistor (R1), and an inductor (L1). This circuit also has two voltage sources, (V and G), allowing current to flow in two different directions and for directionality to be adjusted. The water forager circuit's inductor (L1) is placed in close proximity to the inductor (L2) of the common stomach to allow for flow between the circuits. The work of the water foragers are regulated by how full the common stomach is and how much water is generated by the main water source (G).

The Common Stomach

The common stomach RLC circuit is comprised of a resistor (R2), a capacitor (C2) and two inductors (L2 and L3). The function of the common stomach is such that water foragers can download water into it and the pulp foragers can upload water from it. This flow of materials is modeled by L1 and L2 as well as L3 and L4 inductors being placed in close proximity (Fig 1). The L1 from the water foragers allows electrons to flow through the common stomach, and the L3 from the common stomach allows electrons to flow to the pulp foragers. There is a wire which divides the circuit so that this circuit will have two switches, each affecting a different inductor, allowing for feedback. One switch opens when the other switch closes, and vice versa. This causes changes in the magnetic field so that voltage can be induced in adjacent circuits (Faraday's Law). Additionally, because the common stomach is a temporal storage place, it has a high capacitance capability (Table 1). The resistor (R2) of the common stomach reflects the common stomach's potential use of the water for other reasons than construction, such as consumption and cooling. It has been shown that as the common stomach saturates, it decreases the flow into the common stomach, which means that the percentage of water foraging has decreased (Karsai and Schmickl, 2011). We modeled this property by simply placing the common stomach near both the inductor coils of the water foragers and the pulp foragers. Its central location here allows it to act as a buffer and also provide feedback to the system.

The Pulp Foragers

The pulp forager RLC circuit is a combination of a capacitor (C3), resistor (R3), and two inductors (L4 and L5) in series, and it is connected to the common stomach via the inductor L4 and it is connected to the builders via L5 (Figure 4.1). To simplify the system, we assumed that the pulp foragers simply convert water to watery pulp, therefore the water is lost only in small quantities through R3 (some water evaporates during pulp making).

The Builders

The builders' RLC circuit is a combination of a capacitor (C4), resistor (R4), and an inductor (L6) in series, and it is connected to the pulp foragers via the inductor L5 (Figure 4.1). The resistor (R4) in this circuit drains the circuit of electrons and this loss of energy from the system represents the wasp building process, where the water is in the form of pliable building material, which will dry out after the construction finished.

General Assumptions

In our model, electron flux is representative of water flow. Wasps belonging to the same task are grouped into a single circuit. The main source of electrons to the system is originated from the batteries of the water forager circuit (G and V). The wires in the system do not allow for dissipation of energy; the wires are completely efficient, as decrease of current is only supposed to occur at the resistors. There are no time delays in the circuit wires. Additionally, it is assumed that the changes in current causing voltage to be induced are equal to the charge on the adjacent circuit. The second derivative term, representing the voltage which is induced from one coil to the next, is thus equivalent to the charge of the adjacent circuit in this system. When perturbation experiments were carried out, if something was removed from the system, we assumed that this quantity was not replaced; therefore the system reached a new equilibrium based on the changes. The switches in the system can be opened and closed at appropriate times in order to cause a change in magnetic field and subsequently create a voltage in the proximal coil. Additionally, all switches in the system are assumed to open and close in such a way as to allow continuous electron flow between circuits and thus the circuit is assumed to allow for both the transfer of electrons through the inductors and also return to a state of equilibrium.

In the circuit models, the electrons are generated by batteries, while in the wasp colonies, the water is collected by water foragers. This difference between the two systems is especially important for studying the effect of perturbations on the water foragers. In wasp colonies, the effect of a perturbation is commonly propagated through the whole system, but the continuous generation of electrons in a water forager circuit could flood the water forager circuit with electrons, therefore the backpropagation of the perturbation could not be detected easily. To keep the model simple, but make the effect of perturbation detectable, the mutual inductance between the common stomach and water foragers (M1) has 2 different values (either $M1_a$ or $M1_b$, depending upon the origin of the current change). $M1 = M1_a$ when current change originates within the water foragers and $M1 = M1_b$ when current change originates within the common stomach (or the pulp foragers or builders which in turn change the current in the common stomach). We assumed that the effect of common stomach to the water foragers is larger than the opposite effect, hence $M1_a < M1_b$ (Table 1). This could be conceptualized as a step up transformer and this setup improves the detection of the effect of perturbations to the water forager circuit.

The parameters of this model were not possible to obtain directly from the biological system, but we parameterize this model to adhere the biological system as closely as possible. We also follow the simplicity principle and therefore, if there is no indication in the biological system that similar parameters should be markedly different (for example water use for drinking of different types of wasps (R1-R3)) then we use the same values for the resistors except for R4, which also represents the water loss via the evaporation of water from the freshly constructed structure (Table 1). Generation of water is assumed to have a steady (V) and a fluctuating (G) component, which was described by a simple sinus function. The values of capacitors are different, because it represents the size of the task group of the wasps in the colony. The colonies generally operate only with few water foragers, more pulp foragers and larger number of builders and common stomach wasps (Karsai and Wenzel, 2000). We used inductance values to fine tune the basic model to predict realistic ratios between the task groups (Table 1).

Behavior of the 4 Circuits

Our model consists of four RLC circuits coupled by mutual inductance, simulating the wasp colony’s water and pulp foraging, the operation of the common stomach, and the building.

The different behavior of the 4 tasks (change of charge on the 4 loops), is solved by Kirchoff's basic voltage laws. The four loops are described separately by simple second order differential equations (Equations 1-4) to study the responses of the tasks independently; P, W, C, and B refer to the charge on each RLC circuit for the pulp forager, water foragers, the common stomach, and the builders, respectively.

The change of charge in time in the water forager circuit is described by

$$W''[t] = \frac{\left(C''[t]*M1 - R1*W'[t] - \left(\frac{W[t]}{C1}\right) + V_{Battery}\right)}{L1} \qquad \text{(Equation 1)}$$

Where the $C''[t] * M1$ term represents the mutual inductance term of the water foragers connected with the common stomach, and M1 = $M1_a$ with current change originating in the water foragers and M1 = $M1_b$ for current change originating from the common stomach; R1*W[t] is the voltage drop due to the resistor representing the water use of the water foragers. W[t]/C1 is subtracted as the voltage drop across the capacitor, showing the water foragers' ability to retain small quantities of water. The water inflow is modeled via the battery voltages, V and G (Figure 4.1). These are summed and are referred to as $V_{Battery}$. The right hand side of the equation is divided by L1, which was derived as $W''[t]$ multiplied by L1 as the change of current times the inductance of this circuit, also caused by mutual inductance. The equation is set equal to zero, and then solved for $W''[t]$, causing all terms to be divided by the L1 inductor.

The change of charge in time in the common stomach circuit is described by

$$C''[t] = \frac{\left(W''[t]*M1-P''[t]*M2-R2*C'[t]-\left(\frac{C[t]}{C2}\right)\right)}{L2+L3} \qquad \text{(Equation 2)}$$

$W''[t] * M1$ represents the first mutual inductance term of the water foragers acting with the common stomach, and M1 = $M1_a$ with current change originating in the water foragers and M1 = $M1_b$ for current change originating from the common stomach; $P''[t] * M2$ represents the second mutual inductance term of the common stomach creating mutual inductance with the pulp foragers. These two terms allow the transfer of water to the common stomach by water foragers and from the common stomach by the pulp foragers. The $R2 * C'[t]$ term is subtracted as the voltage drop across this resistor, showing the small loss of water from the common stomach. The $\frac{C[t]}{C2}$ term is subtracted for the capacitor; this is a large capacitor, because the common stomach plays the role of water storage, buffer and eventually regulating the wasp activity. The nominator on the right hand side of the equation is divided by L2 + L3, because the derivation was that $C''[t] * (L2 + L3)$ represents the second aspect of the mutual inductance, which is dependent upon the inductance of the individual coils that are in the common stomach coil. The equation is solved for $C''[t]$, so the right hand side of the equation is divided by L2 + L3.

The change of charge in time in the pulp forager circuit is described by:

$$P''[t] = \frac{\left(C''[t]*M2 - B''[t]*M2 - R3*P'[t] - \left(\frac{P[t]}{C3}\right)\right)}{L4+L5}$$ (Equation 3)

where $C''[t] * M2$ represents the mutual inductance term of the pulp foragers connected with the common stomach and $B''[t] * M2$ represents the mutual inductance term of the pulp foragers with the builders. These two terms allow the transfer of water from the common stomach to the pulp foragers and from the pulp foragers to the builders. $R3 * \mathrm{P}'[t]$ is simply the voltage drop across the resistor from Ohm’s Law, showing water use (other than pulp collecting behavior) of the pulp foragers. P[t]/C3 is subtracted as the voltage drop across the capacitor, showing the pulp foragers’ ability to store small quantities of water. The nominator of the right hand side of the equation is divided by L4 + L5, which was derived as the change of current times the inductance of this circuit, also caused by mutual inductance. The final equation shown above is set equal to $P''[t]$, so the right hand side is all divided by L4 + L5, the inductance of the pulp forager coil and thus its ability to accept water from the common stomach.

The change of charge in time in the builder circuit is described by

$$B''[t] = \frac{\left(P''[t]*M2 - R4*B'[t] - \left(\frac{B[t]}{C4}\right)\right)}{L6}$$ (Equation 4)

$P''[t] * M2$ represents the first mutual inductance term of the pulp foragers acting with the builders. This models the water arriving to the builders as a wet pulp. The $R4 * \mathrm{B}'[t]$ term is subtracted as the voltage drop across this resistor, modeling the evaporating water leaving the freshly constructed nest material. The $\frac{B[t]}{C4}$ term is subtracted for the capacitor showing the builders' ability to store small quantities of water. The numerator on the right hand side of the equation is divided by L6, because the derivation was that $B''[t] * L6$ represents the second aspect of the mutual inductance, which is dependent upon the inductance of the individual coils that are in the common stomach coil. The equation is solved for $B''[t]$, so the right hand side of the equation is divided by L6.

Table 1.

Parameters of the Model

Parameter/variable	Description	Value/unit
C1	Capacitor WF	0.5 F
C2	**Capacitor CS**	**10 F**
C3	**Capacitor PF**	**3 F**
C4	**Capacitor B**	**10 F**
R1	**Resistor WF**	**5** ©
R2	**Resistor CS**	**5** ©
R3	**Resistor PF**	**5** ©
R4	**Resistor B**	**10** ©

G	**WF Battery part 1**	**Sin[1.5t]*e^{-t} V**
V	**WF Battery part 2**	**1 V**
L1	**Inductance WF**	**5 H**
L2	**Inductance CS + WF**	**10 H**
L3	**Inductance CS + PF**	**5 H**
L4	**Inductance PF+CS**	**5 H**
L5	**Inductance PF+B**	**5 H**
L6	**Inductance B**	**5 H**
$M1_a$	**Mutual Inductance WF’ CS**	**0.1 H**
$M1_b$	**Mutual Inductance CS’ WF**	**0.2 H**
M2	**Mutual Inductance CS” PF, PF” B**	**0.1 H**

* WF = water foragers, CS = common stomach, PF = pulp foragers, B = builders

Results

The circuit model produced plausible predictions for the colony level behavior of wasp societies (Karsai and Wenzel, 2000) and comparable results to the earlier empirical models (Karsai and Balazsi, 2002; Karsai and Schmickl, 2011).

Assuming zero initial charge on all circuits, there was a sharp increase of charge in the water forager circuit at the very beginning of the simulation, which quickly reached equilibrium. This was followed by an increase of charge in the common stomach circuit. Finally, the pulp foragers and the builder circuits increased in a delayed manner and reached equilibrium at approximately 1200 seconds (Figure 4.2), when the electrons generated by the battery propagate through the system, damped by the resistors. Overall, the model predicted a continuous construction where the charge of PF was larger than of WF, similar to wasp colonies, where there are more pulp foragers than water foragers. The charge on the builders is higher than that of the foragers, which was also found in actual colonies, where more builders exist than foragers. The common stomach has a higher charge than the foragers and this in fact is important to ensure the buffering ability of the common stomach. The values at which these circuits stabilize are independent of the initial charge on the circuits.

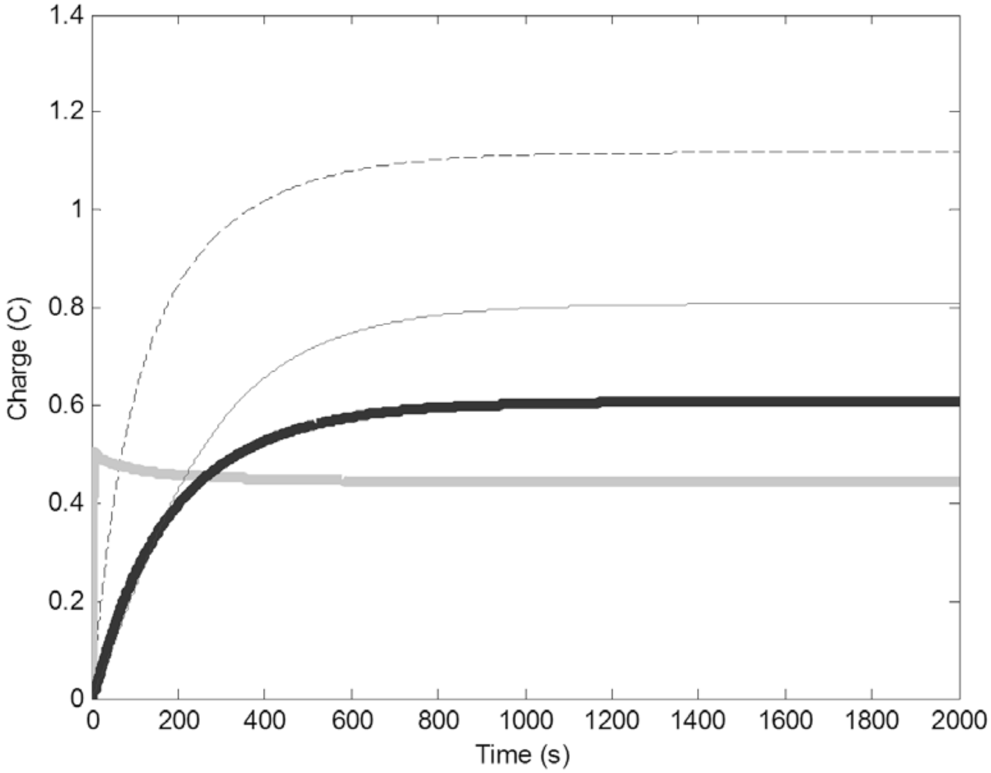

Figure 4.2. Change of charge on the four circuits after the batteries V and G are turned on (t=0). Common stomach: dashed line, builders: thin black line, water foragers: thick gray line, pulp foragers: thick black line. The model used the basic parameters (Table 1).

Perturbation Experiments

In order to further test the robustness of the model, perturbation experiments were carried out and the model predictions were compared to field data and the predictions of previous models, qualitatively. Removing or adding components of the system or materials will force the system to adapt. For example, spraying water on wasp nests increases construction, because the water foragers can get water quickly on site, which in turn increases the water level of the common stomach. This will promote more pulp foraging; with more pulp arrives to the nest with a higher rate, more construction will result (Karsai and Wenzel, 2000).

All simulations started as the normal run, but after the system stabilized at time t = 2000 seconds we made a sudden change in a single parameter and followed the change of the charge of the four circuits (the water foragers, the pulp foragers, the common stomach, and the builders). The direction of the change of different circuits is compared to the observed change in the number of pulp and water foragers (Karsai and Wenzel, 2000).

To simulate capturing water foragers (removing members of this task group), we suddenly decreased their number by reducing C1 from 0.5 F to 0.25 F and reducing R1 from 2 to 1 © (Figure 5.3). The reduced number of water forager was unable to refill the common stomach, this in turn resulted in reduction of charge on all circuits. There is a concurrent drop of reserve water in the common stomach, which decreases the number of pulp foragers that can use the water to forage. New equilibriums were established, accommodating the lower electron flow.

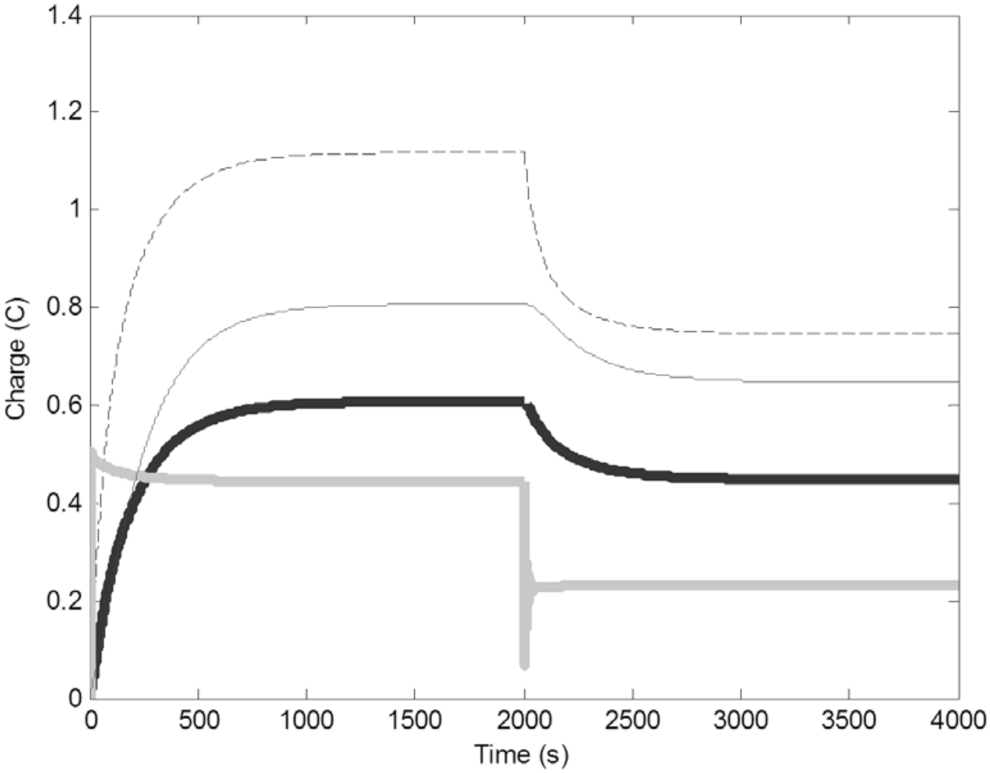

Figure 4.3. Removal of water foragers (decrease of C1 from 0.5 to 0.25 F and R1 from 5 to 2 ©); Common stomach: dashed line, builders: thin black line, water foragers: thick gray line, pulp foragers: thick black line.

To simulate addition of extra water to the environment, we increased the water output by adding 0.5 V to the fluctuating battery component (G). Because of the direction of the wires, increasing G would result in a decrease in the charge on the water foragers, but the change in current should induce voltage in the other circuits (Figure 4.4). The charge on the water foragers decreased and the charge on the common stomach increased. This in turn increased the charge of the pulp forager and builder circuits. This behavior is very similar what we can observe in wasp colonies after the rain. Increased water availability will make the refilling of the common stomach easy, therefore part of the water foragers are converted to pulp foragers and builders.

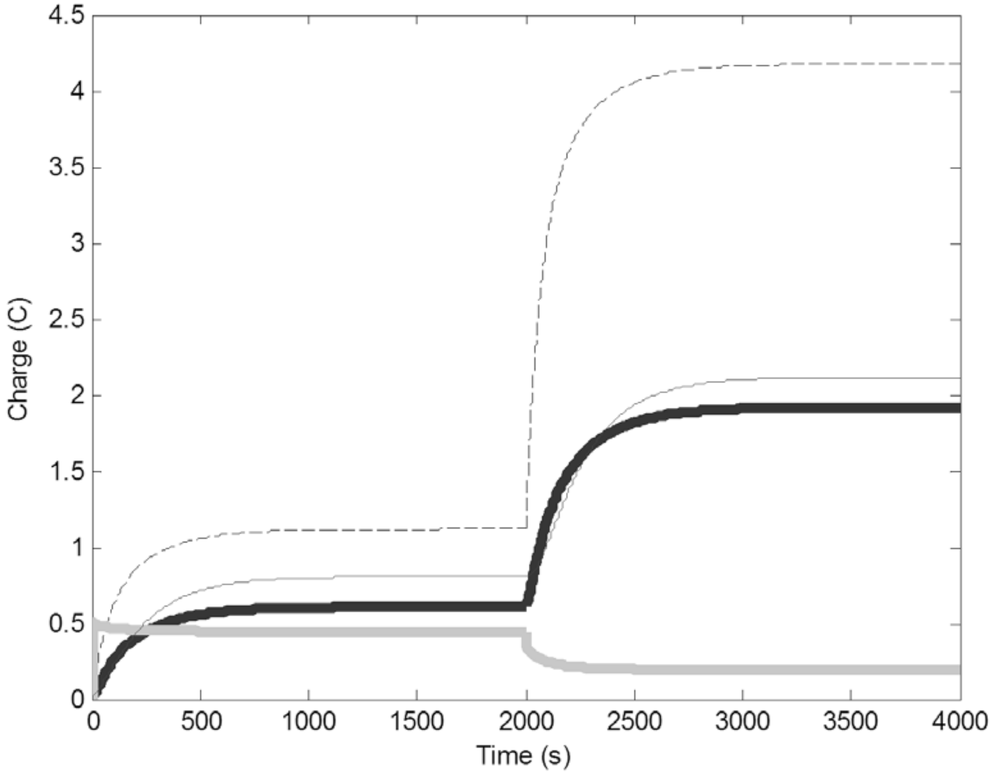

Figure 4.4. Addition of water to the environment (0.5 V added to G, increase of water output from the environment): Common stomach: dashed line, builders: thin black line, water foragers: thick gray line, pulp foragers: thick black line.

Modeling the removal of pulp foragers was carried out by assuming the physical circuit decreased proportionally in size, causing a decrease in C3 from 3 to 1 F and a decrease of R3 from 5 to 2 ©. Fewer pulp foragers collected less pulp, therefore the colony had needed less water, so both the number of builders and water foragers decreased. The amount of water in the common stomach decreased as well (Figure 4.5).

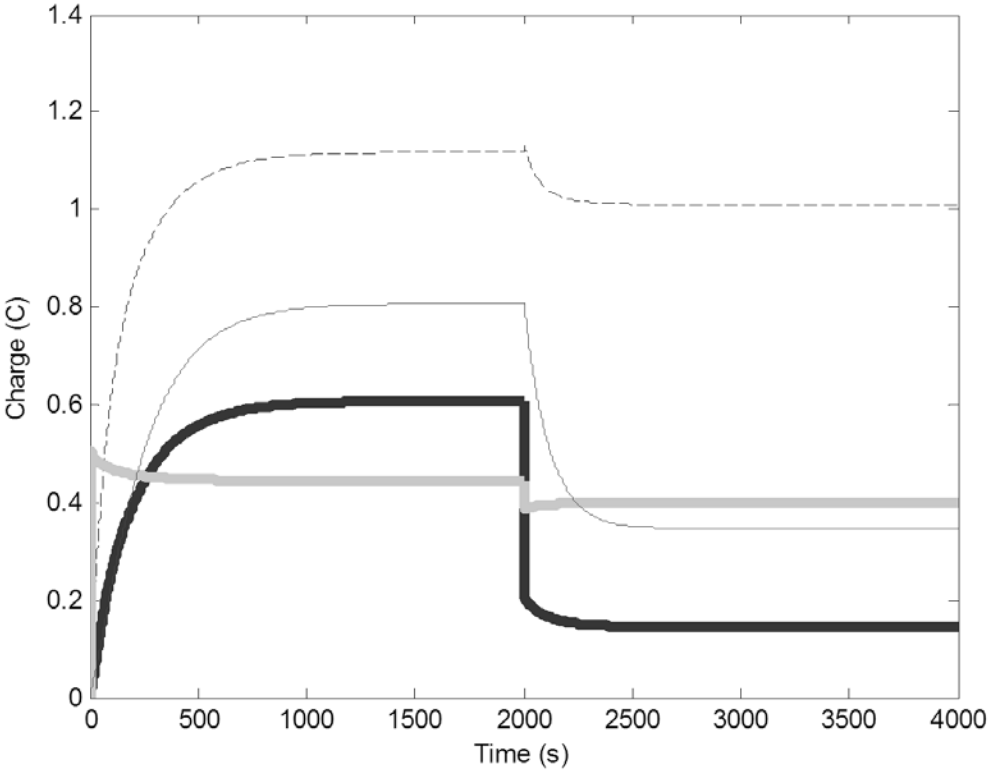

Figure 4.5. Change in time of charge when pulp foragers are removed (C3 reduced from 3 to 1 F and R3 reduced from 5 to 2 ©). Common stomach: dashed line, builders: thin black line, water foragers: thick gray line, pulp foragers: thick black line.

Decreasing the number of builders was modeled by assuming the physical circuit decreased proportionally in size, causing a decrease of C4 from 10 to 5 F, and a decrease of R4 from 10 to 5 ©. (Figure 4.6). Decreasing building capacity decreased the demand of pulp and in turn the water, which would be why the number of foragers dropped. Due to less water use, the water in the common stomach increased, but the influx and outflux of water into the common stomach became much slower.

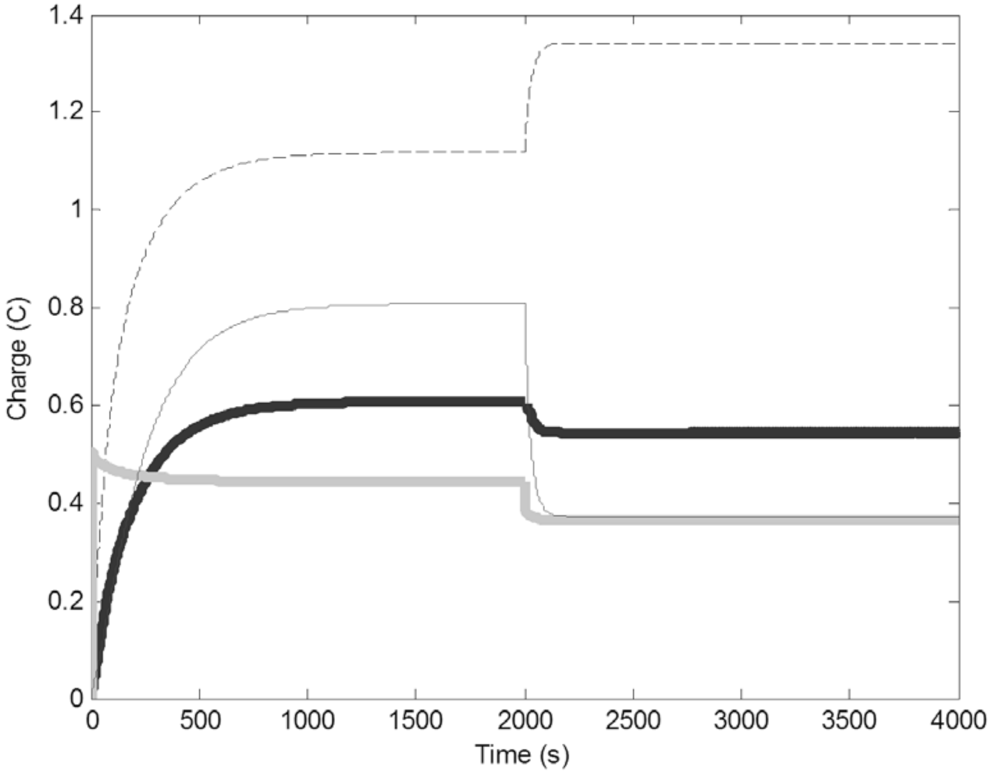

Figure 4.6. Change of charge in time when builders are removed (C4 is reduced from 10 to 5 F, and R4 is reduced from 10 to 5 ©). Common stomach: dashed line, builders: thin black line, water foragers: thick gray line, pulp foragers: thick black line.

Leakage of the common stomach was modeled by the drain of 0.05 V from the location of the resistor R3 in the common stomach (Figure 4.7). This caused a significant decline in the charge on the Common Stomach, and this in turn decreased pulp foraging and building. The number of water foragers increased as a compensatory effect for increasing water influx into the system.

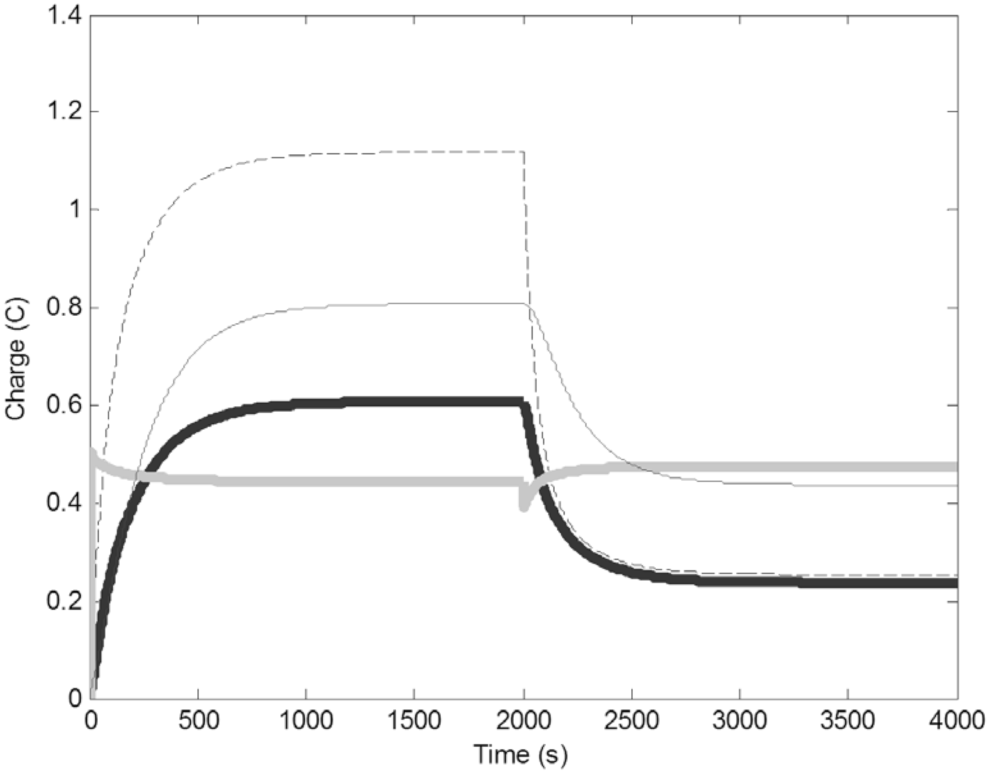

Figure 4.7. Change of charge in time implementing a leaky common stomach (0.05 V drained from R3): Common stomach: dashed line, builders: thin black line, water foragers: thick gray line, pulp foragers: thick black line.

To simulate change in the capacity of the common stomach we reduced C2 from 10 to 3 F. This would mean that the common stomach wasps did not have their full ability to store water or the number of water storer wasps decreased. Since they were not capable of storing adequate amounts of water, the water foragers were forced to increase to attempt to sustain the demand for water for the builders and pulp foragers (Figure 4.8). However even with larger water foraging the pulp foraging and building decreased into a lower equilibrium.

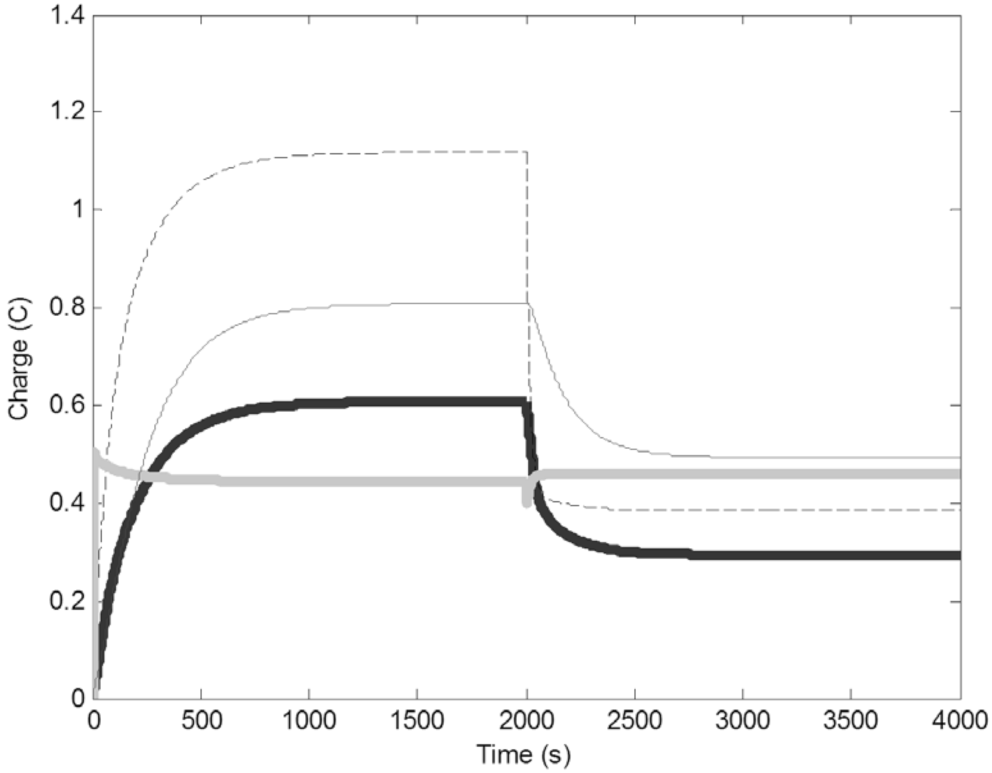

Figure 4.8. Change in charge of circuits when the storage capacity of the common stomach is reduced (C2 reduced from 10 F to 3 F.): Common stomach: dashed line, builders: thin black line, water foragers: thick gray line, pulp foragers: thick black line.

Mutual inductance (M1 and M2) of the system, which serve as the linkage between the task groups, were manipulated to test the reliance of the common stomach and the pulp foragers on the water foragers. M1 and M2 were reduced from 0.1 H to 0.075 H, 0.05 H, and 0.01 H, to represent a 25%, 50%, and 90% reduction, respectively. This resulted in the plummeting of the charge on the pulp foragers and builders (Figure 4.9). Our standard simulations had high mutual inductance between the circuits, because the wasp society we studied is highly connected. Decreasing the mutual inductance means that the task groups became less coupled. This resulted in large drop in the charge of all circuits indicating that this system is not effective with low linkage. Decreasing the inductance simulates the situations where the task groups are loosely connected and the society operates with less specialized individuals (Karsai and Wenzel, 1998).

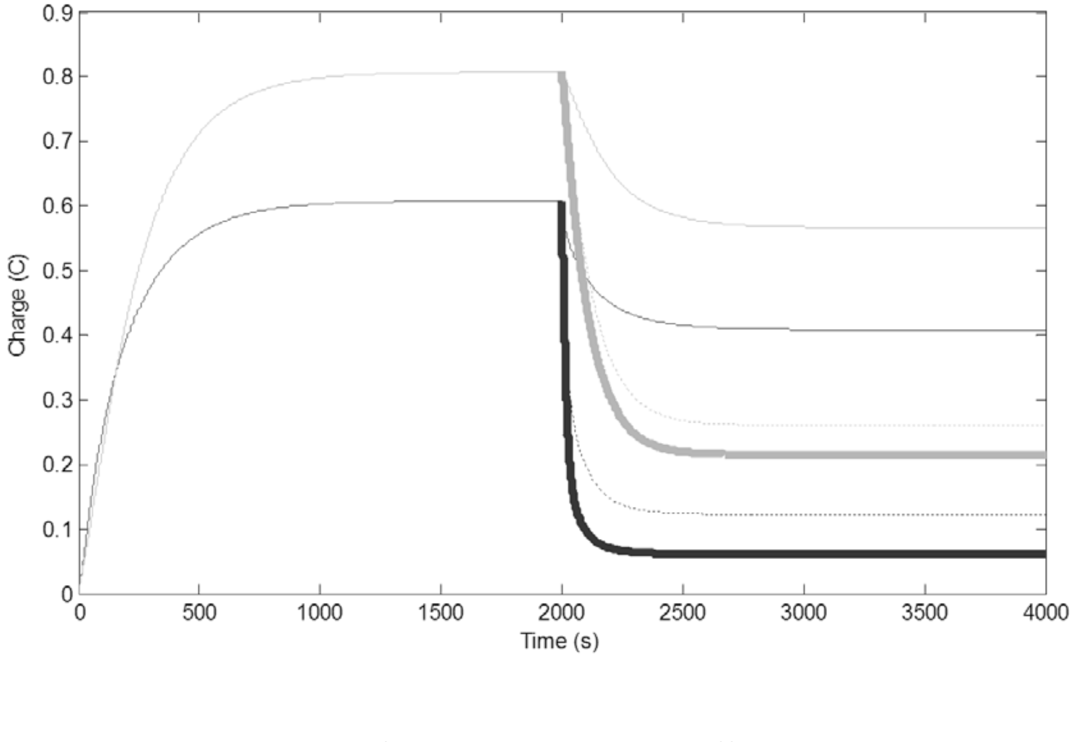

Figure 4.9. Change of charge in time with different coupling intensity between the circuits (M1 and M2 were reduced from 0.1 H to 0.01 H

(thickest line), from 0.1 H to 0.05 H (dot/dashed line), and from 0.1 H to 0.75 H (medium thick line); pulp foragers (black), builders (gray). With decreased coupling, the charge on the circuits drops due to decreased current passed through each circuit by the inductors.

Simulating difficulty to obtain water from the common stomach by the pulp foragers indicates a situation when conserving water is important to the colony. This was achieved by decreasing the coupling between the two circuits by decreasing the mutual inductance between the common stomach and the pulp foragers (M2) from 0.1 to 0.05 H. This resulted in the significant decline in charge of the common stomach, foragers, and the builders (Figure 4.10). This reflects the difficulty in sustaining pulp foraging and thus building if the transfer of water is hindered between the common stomach and the pulp foragers.

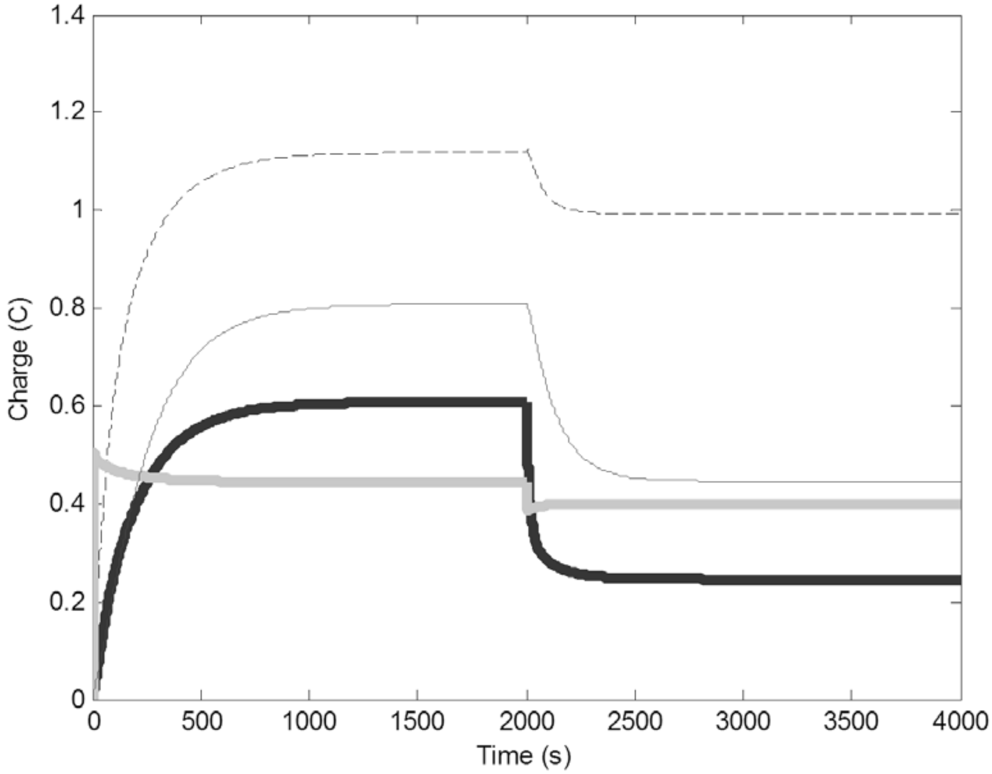

Figure 4.10. Change in charge of circuits when the connectivity between the common stomach and the pulp foragers is reduced (mutual inductance M2 between common stomach and pulp foragers reduced from 0.1 to 0.05 H). Common stomach: dashed line, builders: thin black line, water foragers: thick gray line, pulp foragers: thick black line.

To demonstrate that the common stomach has different types of relationships with the foragers, the charge of the common stomach was plotted vs. the charge of the foragers. In these experiments, we assumed low water consumption (R2 reduced from 5 © to 0.000001 © (Figure 4.11). The phase-space plots show that the number of water foragers quickly stabilize, while the common stomach oscillated in a damped fashion. The pulp foragers relationship is different, their charge oscillates longer following the oscillations of the common stomach and they together slowly decay toward a stable point. This suggests that the common stomach's relationship with the water foragers involves more feedback than the relationship between the common stomach and the pulp foragers.

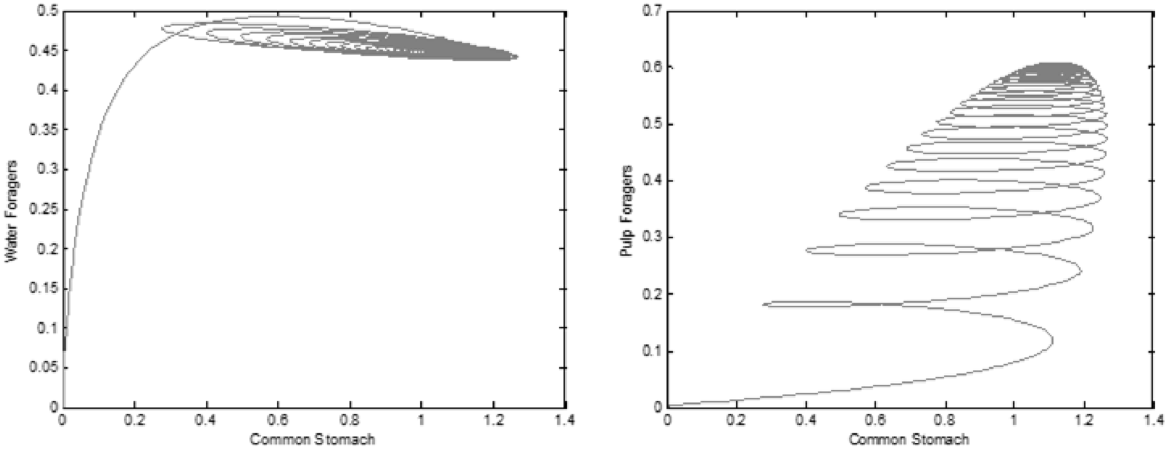

Figure 4.11a. Charge in time: Common Stomach plotted against water foragers with low common stomach resistance (R2 reduced from 5 to 0.000001 ©). b: Charge in time: Common Stomach plotted against pulp foragers with low common stomach resistance (R2 reduced from 5 to 0.000001 ©), The start point is at the origin.

Discussion

The common stomach as a regulatory mechanism for task partitioning and work allocation has been shown in wasps (Karsai and Wenzel, 1998; 2000; Karsai and Balazsi, 2002, Hamann et al, 2013; Karsai and Runciman, 2011; Karsai and Phillips, 2012), ants (Schmickl and Karsai, 2014) and bees (Schmickl and Karsai, 2016). These agent-based or system dynamic models are based on empirical functions and observations and provide numerically calculated predictions for comparison with empirical data and other models. Our goal in this paper was to apply master equations of circuit dynamics to describe our biological system and to show that the circuit model we present here is not only able to provide similar predictions to empirical models, but it is also able to explore new relationships between variables, and hence can promote new experimentation.

Our circuit system is very minimalistic, but it is capable of modeling the task allocation of the social wasps and the predictions of the model are very similar to what we can observe in the field or using empirical models (Karsai and Wenzel, 2000; Karsai and Balazsi, 2002; Karsai and Phillips, 2012). The system is strongly controlled by the common stomach, which is akin in several ways to the information center introduced by Seeley (1985). The water providers and users are interacting indirectly through the common stomach, which not only provides information on the status of water flow, but also buffers the system. The system works independently of the initial conditions shortly set into an equilibrium, which provides optimal work/task allocation for a steady construction, depending on the influx of accessible water. The system is very flexible and in the case of perturbations, it reallocates its workforce and adapts to the new situation with a different equilibrium level.

This flexibility of task reallocation correlates with other life-history parameters, such as colony size, body size, and nesting habits (Karsai and Wenzel, 1998). The wasp colonies we modeled here are of medium size, and individual workers are not strongly fixed in a task. The individuals can change their behavioral profile quickly (Karsai and Wenzel, 2000), therefore we assumed that every worker wasp is identical to the others and they differ only in which task group to which they belong. This allowed us to simplify this system into group levels and describe the groups as circuits. Our model has intrinsic differences between the parameters of the circuits, but each circuit is intrinsically the same type of circuit (RLC).

Perturbation of the circuit model predicted changes that similar to the field observation on *Metapolybia* (Karsai and Wenzel 2000) and *Polybia* (Jeanne 1996) wasps. Addition of water to our system increased pulp foraging and construction, but decreased water foraging. The removal of water foragers also decreased the charge on all involved circuits, meaning that the system was set to a lower equilibrium until new wasps could be recruited for water foraging. Decreasing pulp foragers showed a decrease in charge to all circuits except for a slight increase in charge for the common stomach, due to its central position and enhanced storage capacity. The circuit model was able to predict all major perturbations qualitatively the same manner as it was observed in the field and in other models (Karsai and Wenzel, 1998; 2000; Karsai and Balazsi, 2002; Karsai and Phillips, 2012)

Karsai and Wenzel, 1998 analyzed several life history parameters of many wasp species and their main finding was that simple individual level behaviors and interactions will lead to variances in life history, such as how flexible the behavioral repertoire of the individual is and how connected the subsystems are via interactions. The two extremes of this scale are the small societies with independently acting jack-of-all-trade individuals and the strongly connected more rigid behavioral or age based caste systems of large colonies. Our model, via manipulating the mutual inductance terms and the storage capacity of the common stomach, allowed us to predict what would happen if these interactions (or the connectedness of the circuits) are weakened. The model predicted a large decrease of construction related activities including drop of water content in the common stomach. In fact, the nest construction based on common stomach is not viable in societies with small number of wasps. *Metapolybia* and *Polybia* wasps are breeding via colony fission, therefore their colony size normally does not go too low (Forsyth, 1978). Wasps with small societies are using jack-of-all-trade workers and they do not have common stomachs. (Karsai and Wenzel, 1998).

Our model also was able to explain the differences regarding how water foragers and pulp foragers connect to the common stomach. Pulp foragers generally spend more time and a higher number of interactions with common stomach wasps than water foragers do (Karsai and Wenzel, 2000). Our model predicted different dynamics between the two forager types with the common stomach. In the phase-space plots, the relationship between the foragers and the common stomach both have point attractors, however, the water foragers observably orbit around the common point attractor and quickly reach a close spot to that attractor, but then spirals away from it (Figure 4.11a). The phase-space plot of pulp foragers vs. the common stomach reveals a consistent dissipation towards the point attractor (Figure 4.11b). This suggests that the common stomach's relationship with the water foragers involves more negative feedback than the relationship between the common stomach and the pulp foragers. We propose that the task allocation via the common stomach is a very efficient regulatory mechanism, because through a network of worker interactions, a set of positive and negative feedbacks are connected and balanced by a robust buffer system.

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CHAPTER 5

Modeling neuromuscular control strategies via electrical circuits

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Abstract

The control systems for maintaining postural stability have been modeled by an electrical circuit. This model is capable of predicting control strategy as well as attractors of the system, based upon the manipulation of the capacitors, resistors, and inductors. Healthy people have increased capacitance and inductors out of phase, when compared with the elderly, people with chronic pain, and Parkinson's patients.

Introduction

We have developed a simple model which represents the complexity of the central and peripheral nervous system and their connection with the muscular system. This model is based upon basic circuit theory, and it is capable of simulating the neuromuscular connection. Recent research has emerged which models such aspects of the neuromuscular connections as the nerve-muscle interface, muscular contraction, and muscular contraction in connection with the spinal cord (Peasgood et al., 2003, Valero-Cuevas et al., 2011). These models are effective, but are at the cellular level. Additionally, current models have not been capable of representing the variability of force with muscular contraction increase, and there is a gap in knowledge regarding the connection between spinal circuitry and muscles (Valero-Cuevas et al., 2011). The goal of this study was to produce a large-scale model of the connection between the central nervous system, the peripheral nervous system, and the muscles, which could quantify the effectiveness of the bodily system as a whole, based upon overall current. This model could thus be capable of revealing how the body operates as a whole unit, and can be used to simulate the differences in neurological tasks between people of different ages and health statuses.

We have previously shown that postural stability is negatively affected by age and chronic pain. There is an increase of feedforward control mechanisms intrinsic to balancing with increased age, and with pain, there is a tendency to behave either randomly or with very persistent strategies (Hilbun and Karsai, 2016, Duarte et al., 2000). Because decline in postural stability is caused by a decrease in the sensitivity of neural receptors, a decrease in the speed of the central processing systems of the brain, and a decreased potential of power production in motor systems, we use our postural stability analysis to study the complex neurological system and thus our model (Blaszczyk et al., 2006).

We also test the model on force data from people with Parkinson’s Disease. Parkinson’s Disease (PD) is a neurodegenerative illness affecting nearly 1 million Americans (Parkinson’s Disease, 2015). Major symptoms include dramatically slowed movements, cognitive impairment, and tremors. At the time when motor symptoms in people are significant enough that diagnosis is given, there has already been a roughly 70% loss of dopamine producing cells in the substantia nigra. Recent research has sought biomarkers for PD, because early detection and treatment may be pivotal for prevention of death and loss of autonomy (Parkinson’s Disease, 2015, Yulmetyev et al., 2003). There is a reduced occurrence of chaos in movement with PD, and Levadopa, the most common drug of treatment, brings back chaos intrinsic to healthy motor movement (Yulmetyev, 2003).

Theory/Calculations

Moreover, we have developed a neurological circuit model to explain the results of balancing and gait data. The predictions of the model were compared to balancing data of healthy people and people with chronic pain (Hilbun and Karsai, 2016). Our model has three tiers which represent the central nervous system (with a battery source V1), the peripheral nervous system (with a battery source V2), and the muscular system (Figure 5.2). The bottom tier represents the central nervous system. The middle tier represents the peripheral system, because it is the mechanical connection between the central nervous system and the muscular system, and the top tier represents the muscular system, which is connected in parallel with the central nervous system and the peripheral nervous system. We assume that the charge on the circuit model (Figure 5.1) is equivalent to the efficiency of the neurological system, and thus predictive of the control strategy. Our model is based upon RLC circuits with two variable battery sources (V1 and V2). The central nervous system has been modeled by RLC circuits, which allows for neuronal cell membranes to be passive through resistors and capacitors (Dwyer et al., 2010). The inductor allows for resonance within the system and thus the ability to act as a band-pass filter (Dwyer et al., 2010). All resistors are for the purpose of damping the signals to prevent over heating, while regulating the ease of flow of current. The bottom current loop, labeled ‘A’ consists of a resistor (R1), inductor (L1), capacitor (C1) and the battery (V1) in series, and in parallel with the other battery (V2) and R3 (Equation 1). Likewise, the top current loop, labeled ‘B’, consists of a resistor (R2), inductor (L2), and capacitor (C2) in parallel with the second battery (V2) and R3 (Equation 2). There is a conservation of current at point C (Equation 3).

The output charge from loops A and B represents the Hurst exponents during standard balancing. The charge of P[t] plotted vs. B[t] represents the phase-space plots of the force plate data and reveals the attractors in the system. The parameters were chosen such that there would be realistic charge values such that Hurst exponents could be directly paralleled.

Central Nervous System

The central nervous system (CNS) tier consists of a battery (V1), a capacitor (C1), a resistor (R1), and an inductor (L1). The battery (V1) paralleles the input of the central nervous system (CNS) in maintaining postural stability. The capacitor in the CNS (C1) also allows for the storage of information as it is sent to the brain, after which it is further processed. The resistor (R1) allows for control and dissipation and the inductor (L1) allows for the filtering of elevated current flow, which represents the brain’s resistence to such diseases as epilepsy, Parkinson’s Disease, and Huntington’s Disease.

Peripheral Nervous System

The peripheral nervous system (PNS) tier consists of a battery (V2) and a resistor (R2). The PNS has been studied in the treatment of neurological illnesses via neural stimulation, and such stimulation has been done by the application of a battery to the PNS (Slavin, 2016). Therefore, a properly functioning PNS has an inherent battery capable of adequate levels of bodily stimulation. The PNS also has a resistor, which represents the axoplasm and any existing cell membranes with a myelin sheath (Thompson et. al, 2004).

Muscular System

The top tier of the circuit (R2, L2 and C2) represents the muscular structure of the body. The inductor (L2) along with the capacitor (C2) allows for the storage of energy in both the magnetically and electrically; this represents the muscle contractions' dependency on chemical energy (through ATP production) as well as electrical energy (through nerve synapses). Additionally, the muscle system's memory storage capability has been observed; muscle fiber area is maintained for long periods of time even during lack of use (Staron et al., 1985).

Circuit Sensitivity

The sensitivity of our circuit and the robustness of our model is strong. Because this model consists of RLC circuits, we used the standard transfer function for a low-pass filter, and by using resultant resistance, capacitance, and inductance values, observed the frequency response change based on the doubling and halving of the resistance values. (Fig 5.1., Table 1).

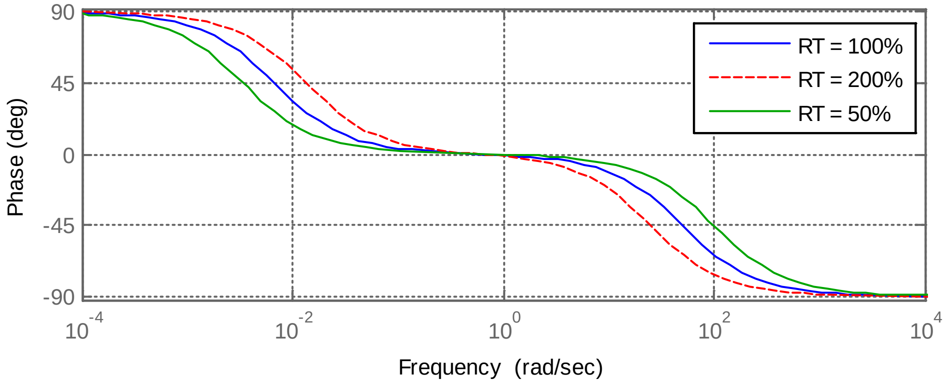

Fig 5.1. Frequency response (based upon transfer function from input to output voltage, based upon initial resistance values): (100%), double the resistance values (200%) and half of the resistance values (50%).

General Assumptions

The wires in the system do not allow for dissipation of energy; the wires are completely efficient, as decrease of current is only supposed to occur at the resistors. There are no time delays in the circuit wires. Unless otherwise stated, circuit parameters are as listed in Table 1.

$$A''[t] = \frac{\mathrm{V1} - (P\prime[t] * \mathrm{R2}) - \frac{A[t]}{\mathrm{C1}} - (A\prime[t] * \mathrm{R1})}{L}$$

Equation 1. Loop A

Where V1 is the time variant voltage source, $(P'[t] * \mathrm{R2})$ is subtracted due to the voltage drop across R2, $\frac{A[t]}{\mathrm{C1}}$ is subtracted due to the charge stored in the capacitor, and $-(A'[t] * \mathrm{R1})$ is subtracted due to the voltage drop across R1, controlling the ease of flow of current. The A’’[t]*L is the inductance term, and is also subtracted, but the equation is solved for A’’[t] for simplicity.

$$B''[t] = \frac{\mathrm{V2} - (P'[t] * \mathrm{R2}) - \frac{B[t]}{\mathrm{C2}} - (B'[t] * \mathrm{R3})}{\mathrm{L2}}$$ Equation 2. Loop B

Where V2 is the time variant voltage source, $(P'[t] * \mathrm{R2})$ is subtracted due to the voltage drop across R2, $\frac{B[t]}{\mathrm{C2}}$ is subtracted due to the charge stored in the capacitor, and $-(B'[t] * \mathrm{R3})$ is subtracted due to the voltage drop across R3, controlling the ease of flow of current.. The $B''[t]$*L is the inductance term, and is also subtracted, but the equation is solved for $B''[t]$ for simplicity.

$$P'[t] = A'[t] + B'[t]$$ Equation 3.

Where $A'[t]$ is the current flowing toward point C from the central nervous system tier, and $B'[t]$ is the current flowing toward point C from the muscular tier, which sum to give the current through the peripheral nervous system tier via the junction law.

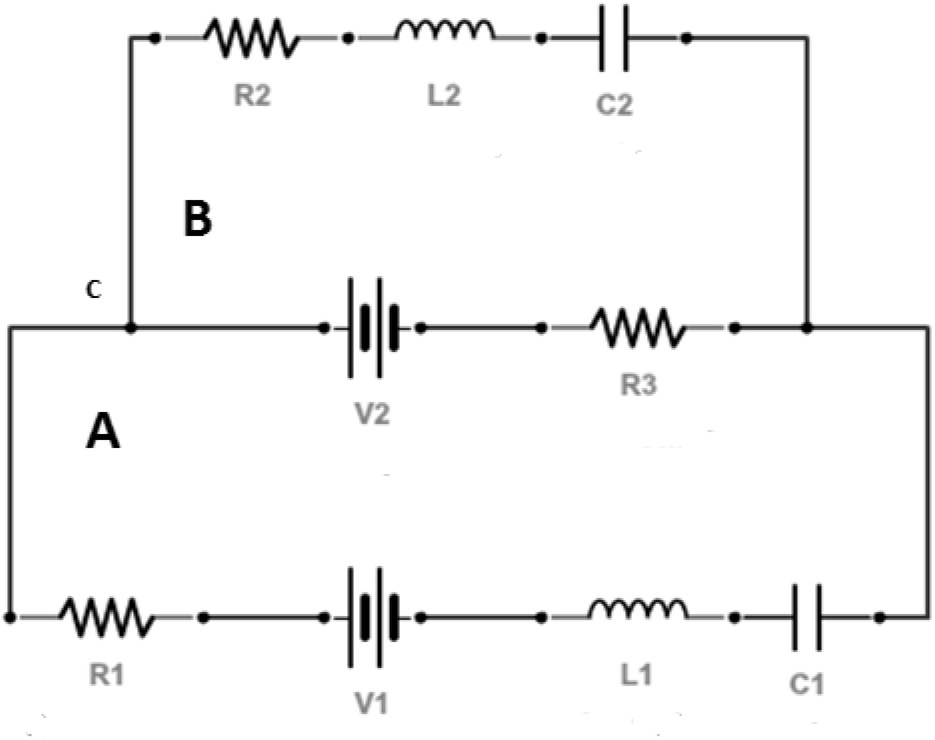

Fig. 5.2. Circuit model: This circuit presents the model for the control system in postural stability. The bottom tier represents the central nervous system. The middle tier represents the peripheral nervous system. The top tier represents the muscular reactivity (A[t] = Current loop 1, Central Nervous System, B[t] = current loop 2, Muscular System, C[t] = current junction, Peripheral Nervous System).

Table 1.

Parameters of the Model

Parameter/variable	Description	Value/unit
C1	**Capacitor CNS**	**30 F**
C2	**Capacitor PNS**	**10 F**

R1	**Resistor CNS**	**0.001** ©
R2	**Resistor PNS**	**0.001** ©
R3	**Resistor Muscles**	**0.001** ©
V1	**Battery CNS**	$\mathbf{0.1 * Sin(t)}$ **V**
V2	**Battery PNS**	$\mathbf{0.1 * Sin(t)}$ **V**
L1	**Inductance CNS**	**40 H**
L2	**Inductance Muscles**	**20 H**

* CNS = central nervous system, PNS = peripheral nervous system

Results

We measured the current flowing through each tier of the system. The control strategy is based on the Hurst exponent for standard balancing and is estimated by summing the current flowing through each tier of the circuit. The linear equation modeling the increased Hurst exponent with age (Hilbun and Karsai, 2016) was y = 0.0063x + 0.3103; therefore, people between 14 and 22 are likely to have an anti-persistent control strategy, with a Hurst exponent between 0.4 and 0.45 for balancing. The parameters from Table 1 produce a Hurst exponent of approximately 0.4 (Table 1, Figure 5.3).

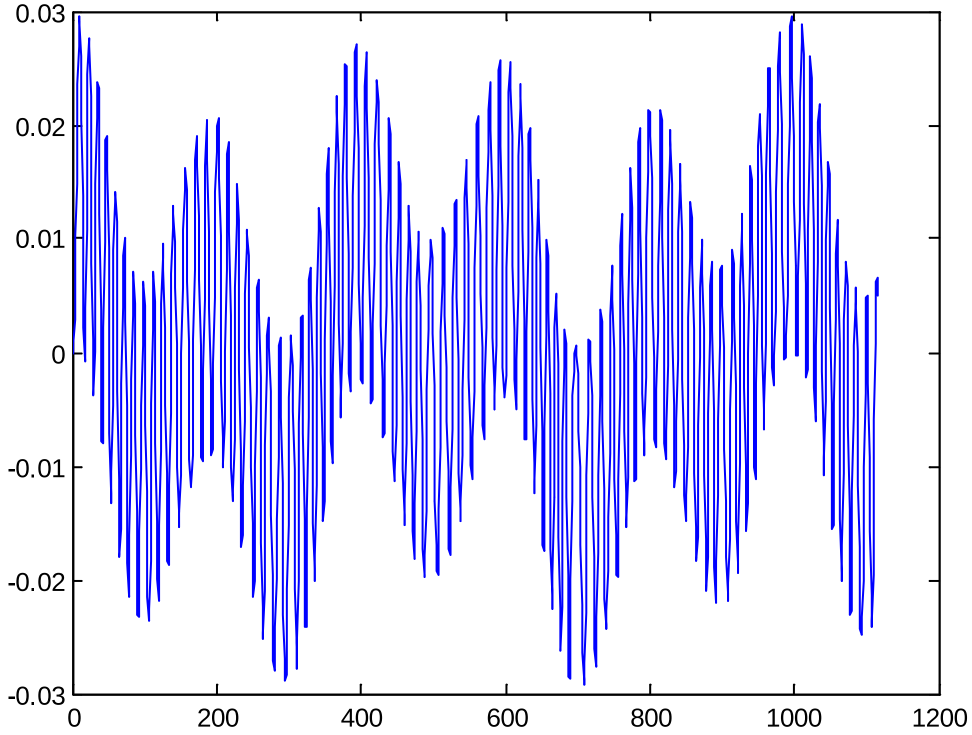

Figure 5.3. Charge on each tier of circuit in time for a young person (age approximation: 14-22, Hurst exponent = 0.42)

Testing the model for older people

We were able to model the control strategy of older individuals (age greater than 45 years) by paralleling the calculated Hurst exponents with the charge on each tier of the circuit (Hilbun and Karsai, 2016). The linear equation modeling the increased Hurst exponent with age (Hilbun and Karsai, 2016) was $y = 0.0063x + 0.3103$; the age of onset of strongly persistent control strategy ($H > 0.60$) would thus be only 46 years of age. To model the change in the system for an approximately 46 year old person, we assume that the central nervous system has decreased storage capability, so we reduced C1 from 30 to 3 F. Muscles also decline in strength with age, so we reduced C2 from 10 to 1 F. We also increased the resistance on all resistors from 0.001 © to 0.1 © because current does not flow as freely in older people. This resulted in the current having a persistent pattern (Hurst exponent = 0.68, Figure 5.4). In our recent study (Hilbun and Karsai, 2015), we showed that in most older people, their phase-space plots of mediolateral force trajectories while balancing revealed a double attractor pattern (Figure 5.4). For the parameters, which gave the figure 8 pattern (Figure 5.6), the charge on the system oscillates in such a way that the inductors were in phase for the emergence of this pattern (Hilbun and Karsai, 2015, Figure 5.5). There may be thus a linking of these two distant inductors, which causes the feedforward information exchange.

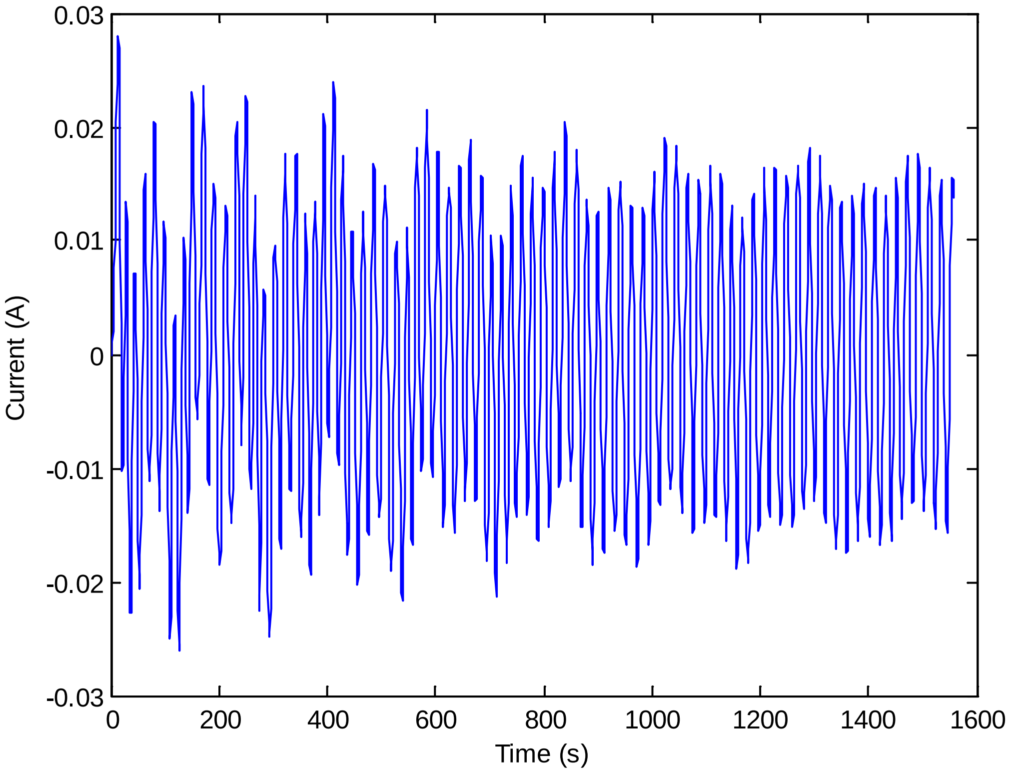

Figure 5.4. Summed current from circuit system, age > 45: C1 from 30 F to 3 F, and C2 from 10 F to 1 F, Resistance increase from 0.001 to 0.1 © on all resistors, Hurst exponent = 0.63.

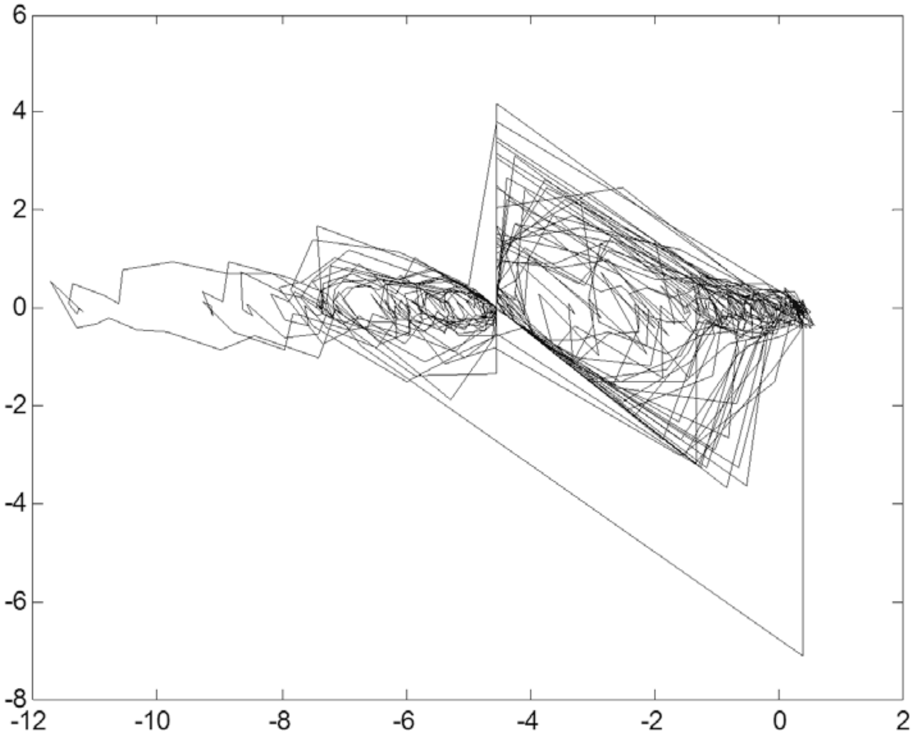

Figure 5.5. From Hilbun and Karsai, 2015: Characteristic phase-space plot of mediolateral force data in older people

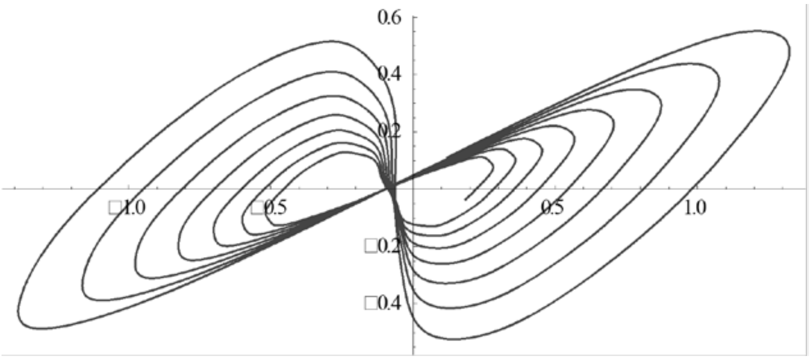

Figure 5.6. Phase-space plot of P[t] vs. B[t], where P[t] is the peripheral nervous system and B[t] is the muscular system, with C1 = 3 F, C2 = 1 F, L1 = 40 H, and L2 = 30 H, R1 = R2 = R3 =0.1;

Chronic Pain

We also analyzed how the model relates to people with chronic pain. In collecting mediolateral force data in people with pain, we found that there was no relationship between age, sex, or BMI and control strategy for the perturbation tasks (Hilbun and Karsai, 2016, GLM, $p<0.05$). Therefore, there is an increased occurrence of closed loop control strategy at young age if pain exists. According to our model, with significant pain, C1 and C2 are decreased as in old age, but the resistance remains the same. This is very similar to that which was seen in the older people (Figure 5.4), however, the inductors are not in the same phase, so the figure 8 pattern is not generally observed. The Hurst exponent is 0.63 for this perturbation (Figure 5.7).

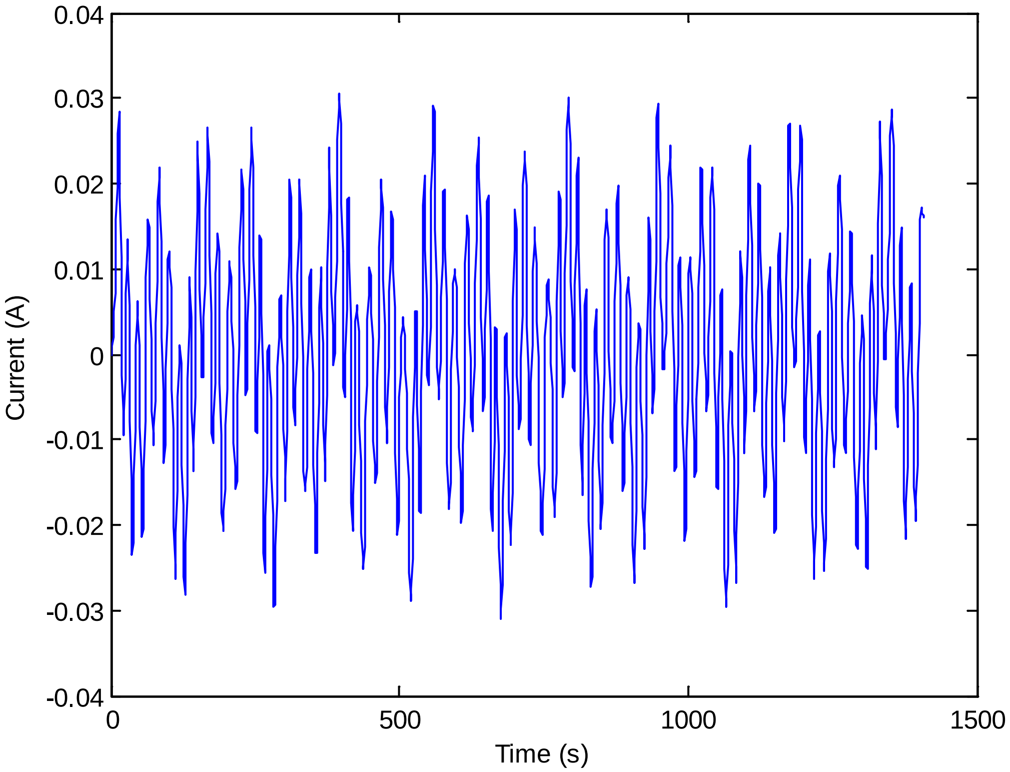

Figure 5.7. Summed current for people with chronic pain: C1 from 30 F to 3 F, and C2 from 10 F to 1 F, Hurst exponent = 0.63

Further Analysis

We extrapolated the use of this model further to include analysis of data from a different source than stationary balancing. We used raw data from Physionet people with Parkinson’s patients (Physionet, Yogev et al., 2005). Participants walked on a force treadmill while resultant forces were calculated during 30 seconds of walking. We analyzed the Hurst exponents using the generalized Hurst exponent. (Aste, 2013; Hilbun, 2016). Walking is more common than balancing on one foot, so the body was more effective at performing this task, so the persistence of force data where less pronounced than for one-foot balancing, but were significantly different than age-matched controls (t-stat = 1.68, $p < 0.01$). According to our model, C1 is decreased in Parkinson's patients, a more significant decrease than with age-matched controls. C1 was reduced to 1 F and C2 was reduced to 0.5 F. In addition, the brain inductance is decreased with Parkinson's Disease, so we decreased the inductor of the central nervous system, L1, from 40 H to 4 H. Because the majority of people with Parkinson's Disease is over 60 years of age, the resistance on all resistors are again increased to 0.1 © (Yulmetyeve et al., 2003). This results in a more pronounced persistent pattern (H = 0.81), (Yulmetyev et al., 2003, Figure 5.8).

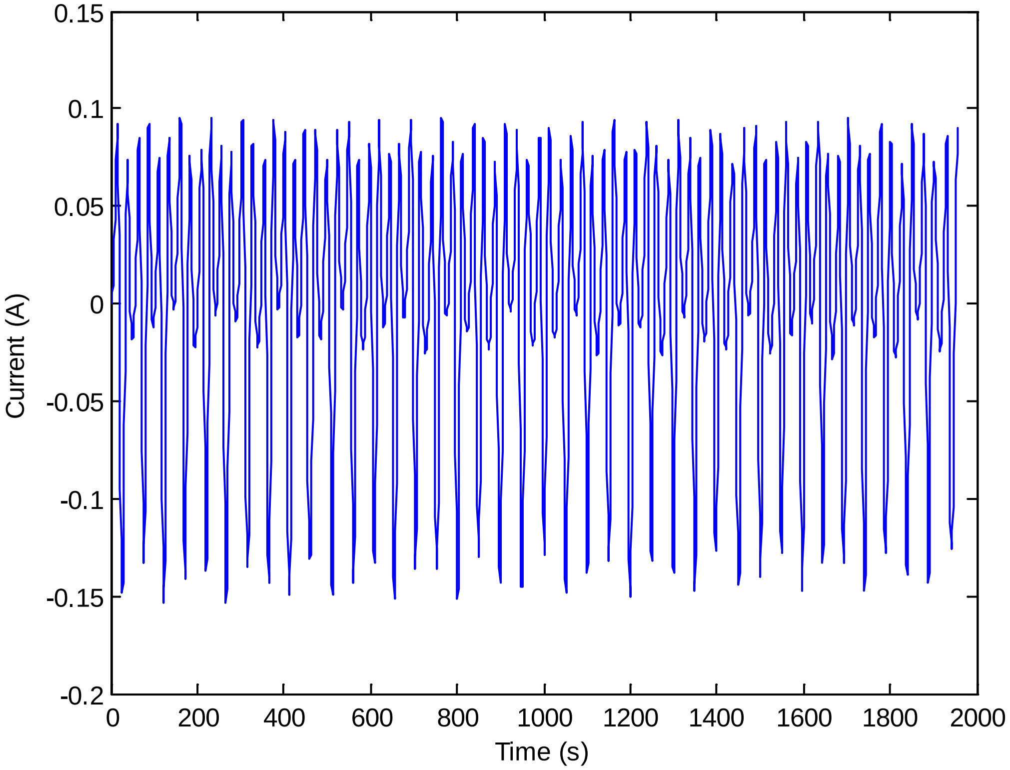

Figure 5.8. Summed current for people with Parkinson's Disease: C1 from 30 F to 1 F, and C2 from 10 F to 0.5 F, L1 from 40 H to 4 H, Hurst exponent = 0.81

Discussion

In essence, there is a decrease in C1 and C2 with age, which causes the increase in persistent control strategy in old age and with pain profiles. With increased age, there is also a tendency to have increased inductance and specifically to have a resonant ratio of L1 to L2 with respect to the other parameters, which produces the double attractor pattern which is common to the force phase-space plots of older people. The major difference between the pain patients and the older people is that the pain patients do not have the L1 and L2 values in phase due to differing resistance values. This indicates that with age, there is a feedforward relationship that is kept between L1 and L2. Although there is discomfort with pain, the existence of pain may interrupt this relationship, because the brain is focused on the pain signals, which disturbs the signal from the muscles to the brain; therefore the phase relationship between L1 and L2 is more chaotic, as in younger people.

For Parkinson’s patients, there is also a decrease in C1, but it is of a greater magnitude than with healthy older people. Because the main importance of this capacitor is to store charge in the central nervous system part of the circuit, it is probably that the decreased efficiency of this capacitor relates to a storage issue within the brain. It has been shown that if there are mutations in genes that encode beta-glucocerebrosidase (GBA), lysosomal storage is marred and people have a higher proclivity to develop Parkinson’s Disease (Parkinson’s Disease, 2015). Additionally, there is a significant in inductance for Parkinson’s patients when compared with that of healthy older individuals. Regarding the decreased inductance, there has been a patent for an implantable inductor in the brain to help induce signals which are diminished in Parkinson’s disease (US8412332). Physical circuitry involving such efficient inductors, along with capacitors with storage potential equivalent to that of this model may be useful as treatment inside the brain.

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CHAPTER 6

DISCUSSION/CONCLUSIONS

We have shown the emergence of a clear open-loop control strategy with age. Hurst exponents increase linearly with age for standard one-foot balancing, which shows predictable and progressive decline of the brain's ability to efficiently process information and provide feedback to the central and peripheral nervous systems and the limbs. This same relationship is observed in people with chronic pain. For the mental and knot-tying tasks, the polynomial fit of data in healthy people shows that people reach persistent levels at a younger age, most likely because of divided cognitive function demands. Additionally, the performance on the arithmetic task requires the participant to quickly understand the researcher's prompts and to quickly process the information, do arithmetic, and respond. As there is known damage of mitochondrial DNA and subsequent apoptosis of cochlear cells with age, this may be at play even at middle-age (Iwasaki et al. 2014). Similarly, Rankin et al. (2000) showed that there was reduced muscle activity when balancing if given math problems to accomplish, both for young and older adults. In their study, the math tasks affected the older and younger people equally in terms of electromyography. Considering that the muscle activity was similarly altered between age groups in this study by Rankin et al. (2000), but we have shown that the addition task decreases the strength of feedback mechanisms, it may be that the increased focus on balancing actually is what actually detracts from the antipersistent behavior of healthy people; in younger people, the decreased muscular activation quickly was processed by the brain and balance strategy quickly adapted. For people with pain, the age-dependency of balancing while answering the arithmetic questions disappeared. People thus behaved similarly to older people at a much younger age. Further, the results of the knot-tying task rely upon the ability to concentrate on performing a fine motor control task while still remaining balanced in one foot. The balancing strategy becomes thus more random with age because of delays in muscle activation and diminished strength, the older people have a problem remaining upright while balancing and concentrating on something else. Conceivably, problems with sensory input cause physiological delays, thereby causing older participants to have more of a struggle with knot tying efficiently and therefore having a delay in activation of their feedback mechanisms for balancing (Blaszczyk et al. 2006). Regarding the specific balancing pattern of choice, it is possible that the double attractor pattern shown in the older individuals results from the subjects' view of the trials as biphasic. They segment the balancing task into two parts: getting comfortably balanced and remaining comfortably balanced. The younger people just swiftly move on the plate and adjust when necessary. The dimensionality is not altered by age in healthy or pained people. The data thus has similar geometric complexity, but since there are significant differences in Hurst exponents and Lyapunov exponents, there is a change in the speed at which the body tries new patterns. Lyapunov exponents in people with pain are without age dependency as well, which indicates that relationship to initial conditions in people with pain is weaker than in healthy people, indicating traffic from diverted focus. Finally, the manipulation of capacitance and inductance models the observed balancing changes. For this reason, further research endeavors should explore treatment methods which specifically target the storage capabilities of the nervous systems, such as more precise neurostimulation.

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Professional Experience:	Math Teacher and Physical Education Instructor for grades 7-10, Stonebridge School, Chesapeake, Virginia, 2009 – 2010 Head Cheerleading Coach, The University of Northern Colorado, Greeley, Colorado, 2011 – 2012 Instructor of Record, Biochemistry Lab, East Tennessee State University, Johnson City, Tennessee, 2013-2014
Publications:	Hilbun, A., Karsai, I., The effect of age on balancing behavior, 2015 (Under Review), Journal of NeuroEngineering and Rehabilitation Hilbun, A., Karsai, I., Task allocation of wasps governed by common stomach: a model based on electrical circuits, 2016, (Submitted Manuscript), Journal of Physical Biology Hilbun, A., Karsai, I., The effect of pain on balancing behavior, 2016 (prepared Manuscript) Hilbun, A., Karsai, I., A simple neurological circuit model for balancing, 2016 (prepared Manuscript)

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Sigma-Xi Grant-In-Aid of Research, 2015: ‘Balance Data as a Diagnostic Tool’

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