VARIABILITY IN THE ACQUISITION AND CONTROL OF A THROWING TASK

A Thesis in
Kinesiology
by
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ABSTRACT

Our motor system has the ability to reliably achieve the task goal while revealing substantial variability. The inherent system variability and perturbations from external environment continuously challenge the central nervous system (CNS) during the control of movement. The general purpose of this study is to investigate the role of variability (both internal and external to the system) in the control of movement and motor learning. A virtual throwing task was adopted as a model task where different movement executions lead to the same task performance. Subjects manipulated a lever arm with a single-joint elbow movement and released a virtual ball that traversed a concentric force field to hit a target. From basic mechanics, release angle and velocity at ball release fully determined the ball trajectory and hitting success. Based on this task a nonlinear solution manifold representing the set of all solutions to the task was calculated. Experiment 1 tested whether subjects were sensitive to motor variability and find solutions in the solution manifold with least error-sensitivity and whether subjects preferred solutions with minimum velocity. Results showed that with practice solutions became aligned with the solution manifold and concentrated at the most error-tolerant locations. The individually chosen velocities at release covered a wide range suggesting that subjects did not gravitate to minimum velocity. Even with prolonged practice, subjects still had substantial variability in error-sensitive dimension. Experiment 2 investigated whether the control of movement accuracy and variability could benefit from the enhancement of potentially perturbing information. Based on stochastic resonance (SR), detection of sensory signals can be enhanced in the presence of externally added noise. Error-dependent noise was added to the angle of ball release; this essentially enhanced the result variability of throws via visual feedback to the subjects. In addition, the threshold signaling successful hits was lowered. Results showed that subjects significantly improved accuracy and reduced motor variability with enhanced error information compared with controls. This improved performance was retained for a prolonged period even after removal of the enhanced error information. These results showed that the CNS can alter its motor strategy to compensate for perturbations from the internal system and external environment. The control of movement can be enhanced by external noise via SR. Experiment 3 examined different magnitudes of noise to examine whether SR was present. Four different levels of error-dependent noise were added to the angle of ball release. The results showed that an optimal level of noise best enhanced the control of movement accuracy and variability comparing with three other noise levels. This work indicated that with externally added optimal level of noise, the CNS could adapt and further decrease its internal noise. Taken together, the three studies provided insight on how the CNS selects control strategies in the present of sensorimotor variability and perturbations from the environment. It extended our understanding on the role of intrinsic and extrinsic variability during the control of movement. It suggested possible intervention protocols for motor learning and rehabilitation.
<table>
<thead>
<tr>
<th>Chapter</th>
<th>Title</th>
<th>Section</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>3</td>
<td>Introduction</td>
<td>3.1 Introduction</td>
<td>60</td>
</tr>
<tr>
<td></td>
<td></td>
<td>3.2 Method</td>
<td>65</td>
</tr>
<tr>
<td></td>
<td></td>
<td>3.3 Results</td>
<td>71</td>
</tr>
<tr>
<td></td>
<td></td>
<td>3.4 Discussion</td>
<td>78</td>
</tr>
<tr>
<td></td>
<td>References</td>
<td>82</td>
<td></td>
</tr>
<tr>
<td>4</td>
<td>Stochastic Resonance in Visual Perception Benefits Motor Control</td>
<td>3.1 Introduction</td>
<td>86</td>
</tr>
<tr>
<td></td>
<td></td>
<td>3.2 Method</td>
<td>89</td>
</tr>
<tr>
<td></td>
<td></td>
<td>3.3 Results</td>
<td>93</td>
</tr>
<tr>
<td></td>
<td></td>
<td>3.4 Discussion</td>
<td>99</td>
</tr>
<tr>
<td></td>
<td>References</td>
<td>102</td>
<td></td>
</tr>
<tr>
<td>5</td>
<td>General Discussion</td>
<td>3.1 Introduction</td>
<td>104</td>
</tr>
<tr>
<td></td>
<td>REFERENCES</td>
<td>112</td>
<td></td>
</tr>
</tbody>
</table>
CHAPTER 2

Figure 1: Workspace, execution space and solution manifold. Panel A shows the workspace with the position of the center post and target of Experiment 1. Three ball trajectories exemplify how different release variables can lead to the same result with zero error, \( d = 0 \) (1, 2). Trajectory 3 shows a trajectory with non-zero error, \( d = 30 \). Panel B shows the execution space and solution manifold. White areas denote zero-error solutions, increasing error is shown by increasingly darker grey shades, black denotes a post hit. The release variables of the first and second trajectory which hit the target correspond to points 1 and 2 (denoted by stars) on the solution manifold, the variables of the third trajectory correspond to the triangle in a grey-shaded area. ..........................14

Figure 2: Experimental setup. Participants stand in front of the setup with their forearm resting on the horizontal lever arm. The rotation of the arm is recorded by the potentiometer, when the finger opens the contact switch the ball in the virtual simulation is released. Online recordings of the arm movements are displayed on the projection screen. .................................................................18

Figure 3: A: Simulation of Hypothesis 1: the probability of success is equal to 1 for all zero-error solution. B: Simulation of Hypothesis 2: White areas represent the highest probability of success. The most error-tolerant solution is close to \(-\pi/4\) rad and 5 rad/s.23

Figure 4: Histogram of all subjects’ trials plotted in execution space. The maximum of the distribution is close to the predicted location with the highest probability of success............................................................26
Figure 5: Projection of the histograms’ distributions to the angular dimension. Top panel shows the projected distribution of Hypothesis 1 (Figure 3A); the middle panel shows the projected distribution of Hypothesis 2 (Figure 3B); the bottom panel shows the distribution of the human data.

Figure 6: Individual distribution of trials of sessions 2 and 3 in execution space. The 360 trials of each of the 9 participants are represented by the 95% confidence ellipses. The center of ellipse is the mean value of release angle and velocity, the orientation of ellipse is the orientation of eigenvector of the covariation matrix of angle and velocity, the length of the major and minor axes are twice the square root of the eigenvalues.

Figure 7: Results of the TNC decomposition. Contribution of the three components, T-Cost (black), N-Cost (gray), and C-Cost (white), to performance improvement. The bars represent the standard error across subjects. The embedded figure shows the exponential fits of each component.

Figure 8: Workspace, execution space and solution manifold of Experiment 2. Panel A shows the workspace with the position of the center post and the target used in the experiment. Panel B shows the associated execution space and solution manifold. White areas denote perfect solutions, increasing error is shown by increasingly darker grey shades, black denotes a post hit. Three different ball trajectories in the work space are produced by different release angles and velocities. The first and second trajectories which hit the target corresponding to the first two points in the solution manifold, denoted by stars, the third trajectory which missed the target corresponds to the triangle.
Figure 9: **A**: Simulation of Hypothesis 2 (identical to Experiment 1). The highest probability of success can be found across velocity dimension with an angle around of approximately 1.4 rad. **B**: Simulation of Hypothesis 3. The probability of success is lower for high velocity due to the simulated signal-dependent noise. The highest probability of success can be found for an angle of $\pi/2$ rad with a velocity around 5 rad/s.

Figure 10: Histogram of all subjects’ trials of four sessions plotted in execution space (720 trials per subject). The distribution is spread along a long range of velocities from 2.5 to 20 rad/s at an angle of 1.6 rad.

Figure 11: Projection of the distributions to the velocity dimension. The top panel shows the distribution predicted by Hypothesis 2 (Figure 9A); the middle panel shows the distribution predicted by Hypothesis 3 (Figure 9B); the bottom panel shows the distribution of the human data.

Figure 12: Individual distribution of trials of sessions 2 to 5 in execution space. The 720 trials of each of the 9 participants are represented by the 95% confidence ellipses. The center of ellipse is the mean value of release angle and velocity, the orientation of ellipse is the orientation of eigenvector of the covariation matrix of angle and velocity, the length of the major and minor axes are twice the square root of the eigenvalues.

Figure 13: Results of the TNC decomposition. Contribution of the three components, tolerance (black), noise reduction (gray), and covariation (white), to performance improvement. Each bar represents the standard error across subjects. The embedded figure shows the exponential fits of each component.

CHAPTER 3
Figure 1: Stochastic resonance paradigm. The system only had response when signal input crosses the system threshold (All variables are in arbitrary units). (a) The noisy signal input is below threshold; therefore the system had no output. All variables are with arbitrary units. The noisy signal plus an extra noise makes threshold crossing happen. Each threshold crossing is denoted by a pulse in the output as shown at the upper part of panel a. The pulse output carries information about the signal input. (b) The noisy signal input is below the original threshold 1. However, when the system threshold is lowered to threshold 2, the pulse output is generated where threshold crossing occurs…………….62

Figure 2: Workspace, execution space and solution manifold. (a) The workspace with the position of the center post and target. Three ball trajectories exemplify how different release variables can lead to the same result with zero error, d = 0 (trajectory 1, 2). Trajectory 3 shows a trajectory with non-zero error, d = 30 cm. (b) The execution space and solution manifold. White areas denote zero-error solutions, increasing error is shown by increasingly darker grey shades, black denotes a post hit. The release variables of the first and second trajectory which hit the target correspond to points 1 and 2 (denoted by stars) on the solution manifold, the variables of the third trajectory correspond to the point 3 in a grey-shaded area……………………………………………………………………………………………64

Figure 3: Experimental setup. Participants stand in front of the setup with their forearm resting on the horizontal lever arm. The rotation of the arm is recorded by the potentiometer, when the finger opens the contact switch the ball in the virtual simulation is released. Online recordings of the arm movements are displayed on the projection screen………………………………………………………………………………………………..65
Figure 4: Solution manifold with simulated noise added to the release angle. Noise was added to the angle when the actual release angle $\alpha$ deviated from the center angle $\alpha_c$ with $\alpha \in (1.0, 1.88)$. When the release angle was out of this range, no noise was added. The noise intensity increase linearly with the deviation of $\alpha$ from $\alpha_c$. …………………68

Figure 5: Execution distribution of typical subjects in each group. Execution of the last two sessions of each block (Session 4 and 5 of block 3) was plotted on the execution space. (a) One typical subject from the noise group. (b) One subject from the threshold group. (c) One from the control group. The 95% confidence ellipses were used to visualize the distribution. ………………………………………………………………………………………………………72

Figure 6: (a) Average success rate of each session of 6 subjects in each group. Error bars denote the standard deviation of the success rate in each group. The stars in the bars of sessions 4 to 6 shows the mean perceived success rate when noise was added or the error threshold was lowered; the error bars on the stars denote the standard deviation of the success rate across subjects. The 3-way (Group x Block x Session) ANOVA showed a significant main effect of Block ($F(2, 30)=58.30$, $p<0.0001$), and Session ($F(2, 30)=9.73$, $p=0.001$), an interaction between Block and Session ($F(4, 60)=4.30$, $p=0.004$) and an interaction between Block and Group ($F(4, 60)=5.75$, $p=0.001$). An additional 2-way (Group x Session) ANOVA focusing on Block 3 showed a significant main effect for Group ($F(2,15)=5.02$, $p=0.021$) but no significant effect for Session ($F(4, 60)=1.33$, $p=0.27$), nor for the interaction between Session and Group ($F(8, 120)=1.03$, $p=0.427$). The relevant pairwise Posthoc comparisons are reported in the text. (b) Average continuous error over time (averaged trials) in the noise group. Circles denote the average actual error over time in the noise group (average is formed over 20 trials for each of the
6 subjects). An exponential function $y = a \cdot e^{x/\tau} + c$ (with $x$ being the average trial number and $y$ being the error) was fitted to Block 1; the same function was fitted throughout Block 2 and 3. The filled dots in Block 2 represent the averaged perceived error when noise was added.

Figure 7: Distance error and standard deviation (SD) of release angle over time. For better illustration, averages trials were calculated over 20 successive trials for each subject’s sequence. An exponential function $y = a \cdot e^{x/\tau} + c$ (with $x$ being the average trial number and $y$ being the calculated variables) was fitted to the block 1 of the data with 95% prediction interval; the same function was fitted through block 2 and 3 also with 95% prediction interval in the noise and threshold group. A linear function was fitted through block 2 and 3 in the control group, because no trend of decline was found in the success rate. (a) The comparison of distance error between the noise group and the control group. The gray solid lines denote the fitted exponential function of the noise group, and the light gray bands represent the 95% prediction interval. The black solid lines denote the fitted exponential and linear function of the control group, and the region within the dash lines represents the 95% prediction interval. (b) The comparison of SD of release angle between the noise group and the control group, and the notations were the same as shown in panel a. (c) The comparison of distance error between the threshold group and the control group. The gray solid lines denote the fitted exponential function of the threshold group, and the dark gray bands represent the 95% prediction interval. The black solid lines denote the fitted exponential and linear function of the control group, and the region within the dash lines represents the 95% prediction interval. (d) The
comparison of SD of release angle between the threshold group and the control group; the
notations were the same as shown in panel e……………………………………………77

CHAPTER 4

Figure 1: Workspace, execution space and solution manifold. (a) The workspace with the
position of the center post and target. Three ball trajectories exemplify how different
release variables can lead to the same result with zero error, \( d = 0 \) (trajectory 1, 2).
Trajectory 3 shows a trajectory with non-zero error, \( d = 30 \) cm. (b) The execution space
and solution manifold. White areas denote zero-error solutions, increasing error is shown
by increasingly darker grey shades, black denotes a post hit. The release variables of the
first and second trajectory which hit the target correspond to points 1 and 2 (denoted by
stars) on the solution manifold, the variables of the third trajectory correspond to the
point 3 in a grey-shaded area………………………………………………………………….88

Figure 2: Experimental setup. Participants stand in front of the setup with their forearm
resting on the horizontal lever arm. The rotation of the arm is recorded by the
potentiometer, when the finger opens the contact switch the ball in the virtual simulation
is released. Online recordings of the arm movements are displayed on the projection
screen………………………………………………………………………………………89

Figure 3: Solution manifold with simulated noise added to the release angle. Noise was
added to the angle when the actual release angle \( \alpha \) deviated from the center angle \( \alpha_c \nabla \)
with \( \alpha \in (1.0, 1.88) \). When the release angle was out of this range, no noise was added.
The noise intensity increase linearly with the deviation of \( \alpha \) from \( \alpha_c \) ………………90
Figure 4: Average success rate over sessions. (a) Average percentage of target-hits per session (240 trials) over 6 subjects of each group; error bars represent the standard deviation of success rates over 6 subjects. Noise was manipulated in Session 4 to 6, and the mean and standard deviation of success rate are their actual performance. (b) Subjects perceived success rate represented by the mean and standard deviation over 6 subjects in each group during Session 4 to 6. The perceived success rates in group 1 to 3 were lower than their actual success rate.

Figure 5: Performance error over average trials for each group. Each panel represents the average error for each group. Average trials were calculated over 10 successive trials for each subject’s sequence and then were averaged across 6 subjects. This calculation yielded 144 values which were denoted as circles. An exponential function \( y = a \exp(-x/\tau) + c \) was fitted to the average errors in block 1 (72 values). A linear function \( y = a \cdot x + b \) was fitted to the data in block 2 (72 values). The same averaging procedure was performed on the perceived error in block 2 where noise was added to. The perceived errors were denoted as stars. In Group 0, the noise magnitude is 0; therefore the actual error is the same as the perceived error. For better illustration, the stars were not shown in Group 0. In Group 1 to 3, with larger magnitude of noise added in block 2, the difference between the actual error and the perceived error became larger.

Figure 6: Standard deviation (SD) of angle over average trials for each group. Each panel represents the SD angle for each group. SD angle were calculated over 10 successive trials for each subject’s sequence and then were averaged across 6 subjects. This calculation yielded 144 values which were denoted as filled circles. An exponential
function \( y = a \cdot \exp(-x / \tau) + c \) was fitted to the SD angle in block 1 (72 values). A linear function \( y = a \cdot x + b \) was fitted to the data in block 2 (72 values).

**Figure 7:** The final performance error and SD angle after the noise manipulation. The average performance error and SD angle of the session 6 (the last 24 average trials from Figure 4 and 5) in each group were chose, and the mean and standard deviation was calculated for the 24 values. The average error was shown as a dash with error bars denoting the standard deviation. The average SD angle was shown as solid squares with error bars denoting the standard deviation.

**Figure 8:** The improvement of performance error and SD angle after the noise manipulation. The difference between session 3 and 6 (i.e. the last session/the last 24 average trials of each block) in performance error and SD angle were calculated. The mean and standard deviation was presented. The error improvement was shown as a dash with error bars denoting the standard deviation. The SD angle improvement was shown as solid squares with error bars denoting the standard deviation.
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CHAPTER 1

Introduction

1.1 Flexibility and variability

Human behavior is amazingly rich and varied. Rarely do humans perform the same action twice in exactly the same manner. For example, people reach an object with different limb joint configurations; they locomote and avoid obstacles while maintaining different body postures. In sports activities, athletes throw darts using different arm configurations; basketball players shoot the ball into the basket with always different body postures. All these examples demonstrate the flexibility of the central nervous system (CNS) in the control of movement. This flexibility is a result of the redundancy of the sensorimotor system. Originally highlighted by Bernstein (1967), redundancy means that the same task goal can be obtained by many infinitely different executions. For example, when pointing to a target with the finger multiple combinations of joint angles of the arm can achieve the same spatial position of the finger. However, it is not clear how the CNS choose one specific solution out of others to meet the task demand.

The CNS coordinates the large number of degrees of freedom (DoF) in slightly different ways over repeated actions, which gives rise to the variability in movement. Studies on motor learning have repeatedly demonstrated that variability both in movement execution and task performance is relatively high at an early stage of practice. At later stages of practice, couplings are formed between the DoF, which leads to low variability and high accuracy in the task performance.

The analysis of variability over repeated actions has been recognized as a window into the determinants of acquisition and control of actions (Davids, Bennett, & Newell,
Variability is not necessarily random but has structure that expresses strategies or constraints of the central nervous system. Various approaches have been developed to characterize the structure and dimensionality of variability (e.g. 1/f noise, entropy) (Gilden, Thornton, & Mallon, 1995; Newell, Vaillancourt, 2001; Riley, Balasubramaniam, & Turvey, 1999). Several studies have documented that variability in movement execution is compensatory resulting in less variance in a task-relevant variable than without such covariation (Cusumano & Cesari, 2006; Martin, Norris, Gregor, & Thach, 2002; Müller & Sterad, 2004, 2008; Scholz & Schöner, 1999). Distributional properties of variability over repeated performances can be decomposed revealing different routes for the CNS to reduce variability and increase accuracy (Cohen & Sterad, accepted; Müller & Sterad, 2003, 2004). All these approaches have provided important tools to help understand the underlying process of performance and learning.

1.2 Success with variability

Our motor system has the ability to achieve task goals reliably and at the same time allows considerable variability at different stages of action. This poses a difficult problem for researchers to understand how the CNS organizes the redundant system in controlling movement under uncertainty. The uncontrolled manifold (UCM) (Latash, Scholz, & Schöner, 2002; Scholz & Schöner, 1999) proposed that the variability is constrained into a subspace where the task goal is obtained in equivalent fashion, and variability is channeled into the task relevant dimensions. Based on the similar notion, Todorov and Jordan (2002) have addressed the issue of redundancy using the minimum intervention principle (Gelfand & Tsetlin, 1962). One assumption of this approach is that the motor command is corrupted by signal-dependent noise proposed by Harris and Wolpert (1998)
where the noise increases with the signal amplitude. The idea of Todorov and Jordan’s approach is that the motor system can be modeled based on the framework of optimal feedback control, which postulates that deviations from an average hand trajectory are corrected only if they interfere with the task performance, because the corrective signal introduces variability elsewhere in the system due to signal-dependent noise.

The above approaches focused on the covariance structure of the execution variability (i.e. no control will be exerted along the solution manifold). Sternad and colleagues (Cohen & Sternad, accepted; Müller & Sternad, 2003, 2004) have developed the so-called TNC-method for decomposing variability into three conceptually different contributions: tolerance, noise, and covariation. The three components capture the cost to the task performance of the location of a data set (T), the dispersion of the execution variables (N), and the exploration of the redundancy in the execution space (C). This method captures the features of the structure of the variability during learning and control of movement.

1.4 Sensorimotor noise

One source of variability, generally referred to as intrinsic neuromotor noise, originates from all levels of the biological system, both sensory and motor. For example, when we estimate the size of an object via visual perception or the weight of the object via the haptic information our estimates are not exact but there is uncertainty. When executing a movement, the neuronal activity in the brain is mixed with noise, and the complex biomechanical elements also have substantial noise. Therefore there is always discrepancy between the desired and the actual motor output. Although it was proposed
that the CNS can integrate multiple sensory modalities to increase the estimate accuracy (Ernst & Banks, 2002), the effect of random noise can never be eliminated.

**Motivation of Experiment 1:** Given the redundancy of the system and the ubiquitous sensorimotor noise, little is understood how the CNS selects from the infinite number of possible motor strategies under the circumstance of intrinsic noise. With prolonged practice, subjects always have residual variability in their performance. One central question is whether actors prefer strategies that allow maximum variability in movement execution while incurring minimum error in the task performance. Given a certain level of variability in motor outcome, the knowledge of a large neighborhood solution is important especially when the system is nonlinear and has discontinuities. This experiment proposed a novel statistical analysis to quantify the sensitivity to error for performance strategies with a given level of sensorimotor noise.

1.4 Stochastic resonance induced motor control and learning

It is widely acknowledged that the ubiquitous noise originating from the neuromotor system and also from the external environment influences both the sensory input and the motor output. Even in the performance of expert athletes who have undergone extensive practice, there is always a certain level of noise. This is particularly evident when movements are performed under invariant conditions. However, in the last few decades there has been increasing recognition that noise also has positive effects. One example for such positive role is stochastic resonance (SR), where by adding specific level of noise to the input the system response to the input signal is enhanced (Benzi, Sutera, & Vulpiani, 1981; McNamara & Wiesenfeld, 1989). More specifically, for a dynamical system the addition of a optimal level of noise to the system input can maximize the detection of
weak signal input (Wiesenfeld & Moss, 1995). It has been used to improve signal detection in a variety of biological systems (Moss, Ward, & Sannita, 2004) ranging from single neuron activity recording (Longtin, Bulsara, & Moss, 1991) to tactile sensation (Collins, Imhoff, & Grigg, 1996) and visual perception (Collins, Imhoff, & Grigg, 1996; Simonotto et al., 1997). An fMRI study on visual perception indicated that the subjects who perceived a grayscale graph had the highest neural activation in the visual cortex only when an optimal amount of noise was applied to the graph (Simonotto et al., 1999).

When performing movements, sensory information is continuously integrated into the motor system. The sensory system provides the information about the state of the body and the state of the environment, which allows the CNS to correct movement errors online or in a trial-by-trial manner. The manipulation of sensory information and sensory feedback has significant effect on motor control and learning. For example, when proprioception is prohibited, subjects experience considerable difficulties during locomotion (Lajoie et al., 1996). Without vision, subjects revealed significant higher postural sway than with vision (Dornan, Fernie, & Holliday, 1978). These evidences demonstrated that sensory information is critical to accurate motor control. Based on SR, researchers have shown that the motor system benefited from enhanced sensory information. In specific, subliminal mechanical noise applied to the soles of the feet could increase somatosensory information, which ultimately enhanced human balance stability both in healthy people and in patients with diabetic neuropathy and patients with stroke (Priplata et al., 2002; Priplata et al., 2006).

**Motivation of Experiment 2:** While several studies have already shown that the presence of external noise can improve sensory information and improve human balance
control, what has not yet been examined is to what degree biological systems adapt to the added noise. This study investigated whether the control of movement accuracy and variability benefits from the enhanced sensory information. From an applied perspective, intervention strategies in clinical protocols can facilitate improvement of motor functions. Whether the functional effect can be maintained after the removal of intervention is of great importance for patients. However, no further investigations have been conducted on subjects’ response when the enhanced sensory information was removed. In particular, this study asks how subjects respond when the enhanced error information is removed again. Further, tuning system parameters (e.g. system time constant, amplitude of potential) has been proposed as an alternative way of inducing SR (Xu, Duan, & Chapeau-Blondeau, 2004). This experiment also tested whether lowering the error signaling threshold can get similar results as by adding noise.

**Motivation of Experiment 3:** The CNS has different sensitivity and responds differently to error information during motor learning and adaptation (Diedrichsen, Hashambhoy, Rane, & Shadmehr, 2005; Smith, Ghazizadeh, & Shadmehr, 2006). The noise magnitude in Experiment 2 was chosen using experimenter’s intuition (i.e. a chosen noise level that effectively enlarged performance error while still unnoticeable by the subjects). However, it is not clear whether there is an optimal level of noise added to the sensory information can best enhance the control of movement. Extending the concept of SR to motor adaptation, if external noise is added to the system in an optimal level, the system may maximize the accuracy and minimize movement variability. Based on this prediction, the purpose of this experiment is to investigate whether an optimal level of
noise added to the system, via optimally enhancing sensory error information, can ultimately best enhance the control of movement both in accuracy and variability.
CHAPTER 2

Neuromotor Noise and Sensitivity to Error in the Control of a Throwing Task

Chapter 2 contains an original manuscript prepared for submission to a journal

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Abstract

In redundant motor tasks where the same result can be obtained in different ways, the putative neuromotor noise in the sensorimotor system leads to “repetitions without repetition”. The present study showed that with practice i) subjects find those solutions that are most tolerant to error, and ii) subjects channeled their variability into task-irrelevant dimensions. Using a throwing task in a virtual set-up where angle and velocity at ball release fully determined the result, our statistical approach permitted quantitative predictions about solution strategies and their sensitivity to error. Based on a mathematical model of the task the nonlinear manifold containing the set of all solutions was calculated and provided a priori predictions about successful and error-tolerant strategies. Two experiments contrasted three hypotheses: 1) subjects are sensitive to their motor variability and find solutions on the manifold with maximum error-tolerance; 2) subjects choose any solution on the manifold with equal probability; 3) subjects choose solutions with minimum velocity to avoid higher variability at higher signal strengths. Results were consistent with Hypothesis 1 showing that with sufficient practice solutions concentrated at the most error-tolerant locations and aligned with the direction of the solution manifold. The individually chosen velocities at release covered a wide range, ruling out Hypothesis 3. A novel analysis of covariation, noise, and tolerance supported these findings showing that covariation or alignment with the solution manifold is achieved with practice. These findings highlight that subjects can channel their motor variability into error-tolerant dimensions.
Neuromotor Noise and Sensitivity to Error in the Control of a Throwing Task

Variability has been a pervasive theme in the long history of motor control research and has been recognized as a window into the determinants of acquisition and control of actions (Davids, Bennett, & Newell, 2006; Newell & Corcos, 1993). Decrease of error but also motor variability as a consequence of practice is a widely documented indicator of skilled performance and improvement (Adams, 1987; Schmidt & Lee, 1999; Woodworth, 1899). Emphasis has been predominantly on variability in the performance outcome, such as spatial or temporal errors from the target, as also highlighted in the Fitts task (Fitts, 1954; Plamondon & Alimi, 1997). Some more recent studies have focused on the variability at different stages in movement generation, for example during the planning stage (Churchland, Afshar, & Shenoy, 2006a; Gordon, Ghilardi, & Ghez, 1994), during the execution of movements (van Beers, Haggard, & Wolpert, 2004b), and in the processing of sensory estimates (Osborne, Lisberger, & Bialek, 2005). Still other approaches have focused on the structure in the temporal evolution of variability in a landmark variable using linear and nonlinear times series analysis techniques (Gilden, Thornton, & Mallon, 1995; Hausdorff, 1995; Riley, Balasubramaniam, & Turvey, 1999).

Control strategies have been proposed that minimize variability at given stages of movement generation (Flash & Hogan, 1985; Harris & Wolpert, 1998; Todorov, 2004; Uno, Kawato, & Suzuki, 1989; Viviani & Flash, 1995).

One key problem where variability is central and can leverage insight into motor control is redundancy in movements or tasks, i.e., where more than one solution can achieve the same task goal. For example in a multi-joint pointing movement more than one joint-angle combination leads to a given accuracy in the endpoint. Over repetitions of
the “same” movement, there will be variations as a result of the ever-present neuromotor noise. This variability is not necessarily random but rather expresses strategies or constraints of the central nervous system. For example, several studies documented that in multi-joint pointing and throwing movements variations in joint angles show significant negative correlations, providing support that variability in joint space is compensatory resulting in less variance in a task-relevant variable than without such covariation (Arutyunyan, Gurfinkel, & Mirskii, 1968; Bernstein, 1967; Cusumano & Cesari, 2006; Martin, Norris, Gregor, & Thach, 2002; Müller & Sternad, 2004a, 2008; Scholz & Schöner, 1999; Stimpel, 1933). However, these approaches did not directly relate variability in execution to variability or consistency in result. Such direct comparison is of course hampered by the fact that different variables have different units and are therefore not directly comparable. To make such comparison possible we have developed a two-level approach that evaluates variability in execution and its effect on the result (Müller & Sternad, 2003, 2004a, 2004b, 2008). In previous work we showed that distributional properties of variability over repeated performances can be decomposed revealing different routes for the central nervous system to reduce variability and increase accuracy (Boonstra, Wei, & Sternad, submitted; Cohen & Sternad, submitted; Müller & Sternad, 2004b).

Based on this two-level task analysis, the focal question addressed in the present study is whether actors prefer strategies that allow maximum variability but with minimum penalty. Given the ubiquitous neuromotor noise, are actors sensitive to those task solutions that allow maximum noise while resulting in minimum deviations on endpoint accuracy? To answer this question sensitivity analyses are necessary that assess
the penalty incurred by deviations from a given solution. In mathematics, sensitivity or stability analyses are typically confined to assess the consequences of small deviations from a single solution, i.e., typically the fixed-point solution of a model. Specifically, local linear stability analysis evaluates whether (infinitesimally) small perturbations destabilize a solution and relaxation time provides a quantitative measure for how fast a system returns to a stable solution. However, such an approach is ignorant to the effects of slightly larger errors. Knowledge of a larger neighborhood, however, is particularly important when the system is nonlinear and has discontinuities. Local stability analysis is also unrealistic when considering that in human performance perturbations or errors are not infinitesimally small but rather have a sizable variance. Hence, it is important to assess error sensitivity not only at a point but in a neighborhood around a chosen solution. The present study presents a novel statistical analysis to assess the sensitivity to error for performance strategies with a given variance.

To this end we examine a throwing task called skittles that can be represented by two levels based on basic mechanical analysis\(^1\). In the experimentally controlled task two variables, angular position and velocity at release of a ball, fully determine the balls’ trajectory and its error from hitting a target. We distinguish between the execution level and the result level. Execution variables are those that bring about the movement, i.e., the arm movements and the two variables at release. Result variables refer to the movement outcome as defined by the task, i.e., the error to the target. The functional relation between execution and result is known from basic mechanics. The key characteristic is that the number of execution variables is larger than the result variables, i.e., the execution system is redundant with respect to the result. Hence, the execution and result
variables span a multi-dimensional space that will be referred to as execution space. Different combinations of execution variables that lead to the same result with zero error form a set that will be called the solution manifold.

Based on this task representation, we present a new statistical method to predict and assess strategies of the sensorimotor system with respect to their equivalence and sensitivity. In addition, we will apply a method for decomposing variability into three conceptually different contributions: tolerance, noise, and covariation (TNC) (Cohen & Sternad, submitted; Müller, Frank, & Sternad, 2007; Müller & Sternad, 2003, 2004a, 2004b, 2008; Smeets & Louw, 2007). The present study will apply this method to further characterize assess the solutions chosen by the subjects.

The Experimental Task and Hypotheses

The model task for the present study is skittles where the person throws a ball attached to a pendulum around a pole to hit a skittle at the opposite side. The trajectory of the ball is fully determined by the angular position and velocity at release of the ball. In the experiment subjects used a lever arm manipulandum and performed a throwing movement in a virtual environment to hit a target. The virtual environment simulated the pendular throw similar to skittles or tetherball. In top-down view, the ball trajectory describes an elliptic trajectory around a center post from which it is suspended (concentric force field, Figure 1A, view as subjects see it during the experiment). The target is located at the opposite side of the post. Performance results are quantified by the minimum distance ($d$) between the ball and the target. The mathematical relation between the two execution variables and the result variable is fully deterministic and known
(Müller & Sternad, 2004b). Hence, this task is a representative example for goal-oriented skills where a redundant number of execution variables fully determine the result.

The two successful trajectories in Figure 1A illustrate how different combinations of the two execution variables can lead to the same result ($d = 0$). The relation between execution and result variables is captured in the execution space (Figure 1B). Every throw defined by the variables angle and velocity corresponds to one point in this space. Different levels of success, as quantified in $d$, are displayed by different grey shades: perfect solutions, $d = 0$, are displayed in white; solutions with increasing error are shown by increasingly darker grey shades; black denotes a post hit. Note that different positions of the target and the center post create very different execution spaces and solution manifolds.

**Figure 1**: Workspace, execution space and solution manifold. Panel A shows the workspace with the position of the center post and target of Experiment 1. Two ball trajectories exemplify how different release variables can lead to the same result with zero error, $d = 0$ (trajectory 1, 2). Trajectory 3 shows a trajectory with non-zero error, $d =$
30cm. Panel B shows the execution space and solution manifold. White areas denote zero-error solutions, increasing error is shown by increasingly darker grey shades, black denotes a post hit. The release variables of the first and second trajectory which hit the target correspond to points 1 and 2 on the solution manifold, the variables of the third trajectory correspond to the point 3 in a grey-shaded area.

Given that neuromotor noise leads to variability over repeated throws that never goes to zero, two experiments address the hypothesis that with practice subjects find solutions that are tolerant or insensitive to variability. In overview, the first experiment contrasts two hypotheses: Hypothesis 1 predicts that subjects are sensitive to their motor variability and find solutions that maximize expected performance, i.e., they show sensitivity to error-tolerant dimensions in execution space. In addition, the distribution of solutions will align with the solution manifold, maintaining variability in execution but minimizing error and variability in the result. The alternative Hypothesis 2 states that subjects find successful solutions but without any sensitivity to error tolerance. The second experiment presents a control for Hypothesis 1 and examines whether signal-dependent noise may account for the results. Using a variation of the task where solutions have the same error tolerance for a large range of velocities, Hypothesis 3 states that solutions with low velocity are preferred. These hypotheses are further detailed and quantified in the methods for each experiment.

Experiment 1

Method
Participants. Nine graduate students (7 male, 2 female, 22 to 30 years of age) from the Pennsylvania State University volunteered to participate in this experiment. All reported themselves to be right-handed. They were informed about the purpose of the experiment, but were naive about the nature of the manipulations in the experiment. Prior to data collection, subjects were instructed about the experimental procedure upon which they signed an informed consent form in agreement with the Institutional Review Board of the Pennsylvania State University.

Task and Apparatus. Participants performed the virtual throwing task in a 2D virtual environment. On the screen they saw a lever arm that corresponded to their arm movements that threw a ball towards a target skittle on the other side of the center post. The virtual ball’s trajectory was triggered by the subject when he/she released a switch on the manipulandum; the ball should hit a target skittle located on the other side of the center post (Figure 1A). Participants operated a real lever arm in the horizontal plane with their forearm resting on a splint that was cushioned with foam to provide comfortable support (Figure 2). The height of the lever was adjusted so that each participant could comfortably stand upright and his/her forearm could be placed horizontally on the lever arm. The elbow joint was aligned with the axis of rotation of the lever arm. The length of the lever arm was adjustable to the subject’s elbow length. The end of the lever was poised on a needle bearing to allow free rotation in one angular dimension, which was measured by a potentiometer (Vishay Spectrol, CA) with a sampling rate of 700 Hz. The lever arm could move over the entire 360 deg range and the potentiometer could measure the entire range. Depending on the instruction the participant could stand to the right or left of the vertical fixation, depending on whether
he or she aimed to throw the ball in a clockwise or counterclockwise direction around the center post.

In this forearm position, the participant grasped a ball that was affixed to be comfortably within grasp (Figure 2B). By flexing the index finger the participant closed a contact switch that was attached on the ball. Extending the index finger, corresponding to opening the grasp to throw the ball, opened the switch and triggered the release of the ball on the visual display. The ball trajectory was computed from the online measurements of angular position and numerically differentiated velocity at release according to the model described in (Müller & Sternad, 2004b). For each throw (trial) the angle of the ball at the moment of release and the minimum distance to the target was recorded. If the ball hit the center post, the ball trajectory was terminated and the distance to the target was penalized with the relatively large error of 60cm. The visual display (75 Hz update rate) was presented on a back projection screen that had an effective width of 1.80m and height of 1.40m and was positioned 0.6 m in front of the participants. The ball’s trajectory was displayed for 1s, which was sufficient for the ball to go past the target skittle. The visual display and the data acquisition were programmed in Visual C++ (Microsoft, version 6.0); the virtual display was implemented by Open GL Graphics (Silicon Graphics, version 1.2). Given that the projection screen was vertical and the lever arm moved horizontally, there was a 90 deg angle transformation between the behavior and the virtual presentation. None of the participants reported any trouble with this transformation.
Figure 2: Experimental setup. Participants stand in front of the setup with their forearm resting on the horizontal lever arm. The rotation of the arm is recorded by the potentiometer, when the finger opens the contact switch the ball in the virtual simulation is released. Online recordings of the arm movements are displayed on the projection screen.

**Task and Procedure.** Participants were instructed to hit the target with the virtual ball as accurately as possible. Perfect hits were signaled with a color change of the target from yellow to red. The experimenter also emphasized that they should avoid hitting the center post as a post hit was penalized with a large error. A perfect hit meant that the center of the ball went exactly through the center of the target; simply touching the target was not sufficient. After the throw, a zoomed window of the target and the ball trajectory
appeared on the screen to give subjects visual feedback about the closeness of their trajectory to the target. After a self-timed short break subjects initiated the next trial. The zoomed window remained on the screen until they started the next trial. Typically, one trial lasted 1 - 2 s with approximately 4 s between trials.

Each subject performed 3 sessions each consisting of 3 blocks with 60 trials in one block, yielding a total of 540 trials. Between each block, participants rested for a few minutes. The total duration of each session was approximately 15 min. The sessions were collected on three consecutive days. In session 1 participants were instructed to try different release angles and release velocities to find strategies that achieved successful solutions. In the subsequent sessions subjects were instructed to maintain the strategy, or strategies, that proved most successful in the first session. Subjects were instructed to avoid hitting the center post as they would receive a penalty in terms a large error.

*Execution Space and Hypotheses.* Figure 1A shows the workspace as subjects saw it on the projection screen during the experiment. Defining the origin (0, 0) at the center of the workspace as shown in Figure 1A, the position of the center post was at (0.105, -0.60m) with a radius of 0.33m. The target skittle was located at the coordinates (0.35, 1.25m) with a radius of 0.05m. Figure 1B represents the associated execution space with the nonlinear solution manifold shown in white. The grey shades denote executions with increasing distance error. Note, the solution manifold is defined by zero error solutions. The black areas denote those strategies that hit the center post and are assigned an error of 0.60m. Hence, there are discontinuities in the space. The locations of the target and the center post were so designed for this experiment that successful solutions were to a large part relatively insensitive to release angle, i.e., approximately parallel to the x-axis.
Given this representation of the task, it is expected that actors will choose a strategy that will be on or close to the solution manifold. As a result of the redundancy of the task, each solution on the manifold is equivalent. However, the different locations on the solution manifold have very different sensitivity to errors, as Figure 1B illustrates by the changing width of the light grey shades surrounding the white solution manifold. The least sensitive or most error-tolerant area in this execution space is at angle values around -0.7 rad and velocity values around 3 rad/s. If actors were “aware” (not necessarily consciously) that they have only limited control over their actions, a useful strategy would be to execute the task with variables that permit variability without incurring too much error. Following this logic, Hypothesis 1 predicts that subjects are sensitive to their motor variability and with practice gravitate towards solutions close to the manifold with the least sensitivity to error.

To quantify such prediction the expected performance for each location in execution space, $E(D)$, was evaluated by assessing a neighborhood around a focal location $(\alpha, v)$; the neighborhood simulated a given dispersion around a location. To this end, the execution space was divided into 360*360 bins and $E(D)$ was evaluated for each bin $(\alpha_i, v_j)$, with $i = 1, 2 \ldots 360, j = 1, 2 \ldots 360$. (The total grid was defined over all possible angles from $-\pi$ to $+\pi$ rad and velocities between 0 and 20 rad/s. The maximum velocity was experimentally determined as the upper limit that subjects could perform.) Before calculating $E(D)$ the individual result values were transformed in order to display positive values with post hits set to zero and larger $D$ represents better performance:

$$D(\alpha_i, v_j) = |d(\alpha_i, v_j) - 60 cm|$$
where \( d(\alpha, v) \) is the closest distance between the target and the ball trajectory for an execution determined by \( \alpha \) and \( v \). 60cm is the maximal distance to target, i.e., the penalty for a post hit.

For each location \((\alpha, v)\) a matrix with probability weights was defined including all cells that were within two standard deviations of angle and two standard deviations of velocity. (Note that \((\alpha, v)\) is the center cell of the matrix). These standard deviations were \( s_\alpha = 0.12 \) rad and \( s_v = 0.60 \) rad/s, as determined posthoc from the grand average over sessions 2 and 3 from all 9 participants\(^2\). This yielded a matrix of 15 (angle, \( k = -7 \) to 7) \times 23 (velocity, \( n = -11 \) to 11) cells with the probability distribution \( p(\alpha + k, v + n)\):

\[
p(\alpha + k, v + n) = pdf\left(\frac{\alpha - \alpha_{\text{center}}}{s_\alpha}\right) \cdot pdf\left(\frac{v - v_{\text{center}}}{s_v}\right),
\]

\[
p(\alpha_{\text{center}}, v_{\text{center}}) = pdf(\alpha_{\text{center}}, v_{\text{center}})
\]

where \( pdf \) is the probability density function of the bivariate normal distribution with mean \((\alpha, v)\) and standard deviation \((s_\alpha, s_v)\).

\[
E(D_{ij}) = E(D(\alpha, v)) = \frac{1}{15 \times 23} \sum_{k = -7}^{7} \sum_{n = -11}^{11} p(\alpha + k, v + n) \cdot D(\alpha + k, v + n)
\]

Finally, all \( E(D_{ij}) \) values were normalized to 1 by dividing by the largest value because the Gaussian weighting produced values were no longer comparable to the original distance errors.

When the weight matrix was outside the boundary of the execution space, the outside cells of the weight matrix were eliminated and only the remaining cells were used.
in the calculation. By moving the matrix across the execution space these calculations were performed for all 360x360 grid points. This prediction is illustrated in Figure 3A: expected performance $E(D)$ was highest at $\alpha = -0.7$ rad and $v = 3$ rad/s, the most error-tolerant solution. These calculations for expected performance $E(D)$ are equivalent to the algorithm calculating expected utility in decision theory with $D(\alpha, v)$ the utility or cost function (Berger, 1985; Trommersh"{a}user, Maloney, & Landy, 2003).

Alternatively, a successful strategy could consist of solutions that vary but all lie on the solution manifold – without preference for any specific location. This limit case is expressed in the null Hypothesis 2 that states that over repeated trials all executions on the solution manifold are equally likely. To visualize this hypothesis the execution space is divided into a grid of 36*36 bins. If a bin intersects the solution manifold, i.e., it contained at least one solution with zero error, the value of 1 is assigned. For all other solutions, the value zero was assigned (Figure 3B). Note that the predictions in Hypotheses 1 and 2 are expressed in continuous and discrete form, respectively: expected performance in Hypothesis 1 is a continuous prediction, while $E(D)$ in Hypothesis 2 is a discrete variable.
Figure 3: A: Simulation of Hypothesis 1: White areas represent the highest expected performance. The most error-tolerant solution is close to -0.7 rad and 3 rad/s. B: Simulation of Hypothesis 2: the expected performance is equal to 1 for all zero-error solution.

Confidence Ellipses. To quantify the distribution of data in execution space for each subject the covariance matrix of the execution variables was calculated and visualized by its 95% confidence ellipse. Three parameters described the confidence ellipse: 1) the mean of release angle and velocity determined the center of the ellipse, 2) the eigenvectors were calculated to determine the orientation of the ellipse, and 3) the square
roots of the eigenvalues determined the size of the semi-major and semi-minor axes of the ellipse. Given that the confidence ellipse depended on the number of samples we pooled the data of sessions 2 and 3.

Variability Decomposition. In order to further understand the contributions to variability in a redundant task, Müller and Sternad (2003, 2004) and (Cohen & Sternad, submitted) developed an approach for decomposing variability in the result variable based on the redundancy of execution variables. This method decomposes the error in performance into the three components Tolerance, Noise, and Covariation (TNC). The analysis is statistical in nature and analyzes the properties of a set of data, e.g., a block of 60 trials. The distributional properties of a block of trials in execution space are evaluated and the contribution of the three components to accuracy in performance is differentiated. The present study applied the calculations as developed by Cohen and Sternad (submitted) where the three components were estimated in terms of the cost in the result variable that each data set incurred.

More specifically, the cost of Tolerance, or T-Cost, quantified how much better the given data set could be if it were at a better location in execution space with respect to the solution manifold. The second component Noise, or N-Cost, quantifies the contribution of stochastic dispersion to the result. Assuming a given block of data scattered in execution space, its average result is compared with the result from that set or point that has minimum result error. The difference in results between the actual and best set determines the cost due to noise, N-Cost. The third component Covariation evaluates the alignment of a set of data with the solution manifold. To estimate C-Cost for a data set, an optimized data set was generated in which the means and distributions of the angles
and velocities were maintained, while the individual pairings were recombined to achieve the best possible performance of the entire set. The difference between the best result of the permuted virtual data sets and the actual data determines the cost due to \textit{Covariation}, \textit{C-Cost} (for details see Appendix and Cohen & Sternad, submitted).

For these calculations the series of 540 trials of each participant was parsed into 9 blocks of 60 trials each. For each block the calculations of the three costs were conducted separately. For each data block a virtual set was calculated that optimized a given component.

\textit{Statistical Analyses.} Multivariate analyses of variance were conducted on the TNC components using a MANOVA with session as repeated measure and the three components as three dependent variables. For the multivariate tests the Hotelling’s Trace was adopted and Greenhouse-Geyser adjustments were applied when sphericity was violated in the dependent measures. Several $t$-tests and the non-parametric test Wilcoxon signed rank test were applied. A significance level of $p < 0.05$ was used for all analyses. All statistical analyses were performed with SPSS (version 16.0). Exponential fits were calculated using the Levenberg-Marquardt nonlinear regression technique in Matlab (version 7.1, Mathworks).

\textit{Results}

\textit{Performance Improvement.} Figure 4A shows the distance error over trials across all three sessions. The data points represent the medians with the corresponding interquartile ranges shown by the error bars. For each estimate the data of 9 participants were pooled over 15 trials. Medians were taken because the discontinuously high penalties for the post
hits would have unduly skewed the means. It can be seen that after large errors in the first half of session 1 participants reached a relatively constant level of performance throughout the rest of the experiment. The initially large errors in session 1 are partly due to the fact that participants were instructed to explore different strategies until they found one that achieved good hitting success. In sessions 2 and 3 they were instructed to continue with that strategy that proved to be the best one and to fine-tune it. Hence, the average change in error in session 1 was large (12.02 cm) compared to the smaller changes in session 2 (0.56 cm) and session 3 (0.34 cm). Given this qualitative difference in the amount of improvement, the data from session 1 were excluded from subsequent analyses and the data of sessions 2 and 3, in which subjects had achieved a relatively skilled level, were pooled.

Figure 4: **A**: Time series of errors (median and interquartile range) averaged across 9 participants. The trials were also averaged such that for every non-overlapping series of 15 trials the median is plotted with the corresponding interquartile ranges shown by the error bars. **B**: Histogram of all subjects’ trials plotted in execution space. The maximum
of the distribution is close to the predicted location with the highest expected performance.

**Pooled Distributions.** A first focus was on the skilled performance that participants had reached in sessions 2 and 3. Figure 4B shows a histogram with all 360 trials of sessions 2 and 3 of all 9 participants plotted in execution space. The histogram is shown on the same 36x36 grid as used for Hypothesis 2. The distribution is clearly non-uniform and clustered around its mode at a release angle of -0.73 rad and velocity 2.65 rad/s. This mode is close to the maximum \( E(D) \) as predicted by Hypothesis 1 (-0.7 rad, 3.0 rad/s). Note that the highest frequency of trials is also close to the locations with the highest risk, i.e., executions that lead to a post hit (black color).

To quantitatively compare the data distributions with the predictions of the hypotheses, the two-dimensional distributions were projected onto the angular dimension. For Hypothesis 1 the cells with 95% and higher than the maximum \( E(D) \) were projected onto the angular dimension. Figure 5 shows the projected distributions of release angle of the two hypotheses (top and middle panel) and the data (bottom panel). Two \( t \)-tests for matched pairs contrasted data with each of the two hypotheses. There was no significant difference between Hypothesis 1 and the data, \( t(35) = -1.38, p = 0.18 \); in contrast, the difference between Hypothesis 2 and the data was significant, \( t(35) = 4.83, p < 0.0001 \). Based on these results Hypothesis 2 could be rejected.
Figure 5: Projection of the histograms’ distributions to the angular dimension. Top panel shows the projected distribution of Hypothesis 1 (Figure 3A); the middle panel shows the projected distribution of Hypothesis 2 (Figure 3B); the bottom panel shows the distribution of the human data.

Individual Distributions. Figure 6 illustrates the distributions of the 360 trials separately for the 9 individuals in terms of their mean and confidence ellipses. The 95% confidence ellipses visualize the orientation and extent of the correlation of angle and velocity for each participant. The figure suggests that individuals showed overall smaller distributions that covered the area with highest tolerance. Some, but not all, of the ellipses had a tendency to align with the direction of the solution manifold, indicating that some individuals showed sensitivity to the error-tolerant dimension in the execution space. However, note that despite the visual impression, the orientation of the ellipses and their alignment with the manifold cannot be quantified, for example by principal components, because the execution space is not a metric space. One way to overcome this
problem and quantitatively assess the covariation of the data is to calculate the TNC-
Costs. This analysis assesses cost in result space and is therefore not affected by the
different dimensions of execution space.

Figure 6: Individual distribution of trials of sessions 2 and 3 in execution space. The 360
trials of each of the 9 participants are represented by the 95% confidence ellipses. The
center of ellipse is the mean value of release angle and velocity, the orientation of ellipse
is the orientation of eigenvector of the covariation matrix of angle and velocity, the
length of the major and minor axes are twice the square root of the eigenvalues.

For this analysis the data were grouped into blocks of 60 trials. This block size was
sufficiently large to permit statistical evaluation but small enough to also allow an
assessment of how such properties change across practice sessions. Figure 7 illustrates
the contribution of the three components, T-Cost, N-Cost, and C-Cost, over the 9 blocks
of all three sessions. It shows that all three components contributed to the improvement
and decreased over practice as expected. A MANOVA with session as the repeated factor
and the three components as three dependent variables was applied to these results. The multivariate effect for session was significant, \( F(6, 26) = 4.52, p < 0.005 \) (Hotellings Trace). Univariate tests of the MANOVA identified the changes in \( N\text{-Cost} \) and \( C\text{-Cost} \) across sessions as significant, with \( F(1.56, 12.48) = 6.69 \) and \( F(1.20, 9.61) = 6.82, p < 0.05 \), respectively. \( T\text{-Cost} \) did not show significant changes. Pairwise comparisons identified significant changes in \( N\text{-Cost} \) and \( C\text{-Cost} \) between sessions 1 and 3.

The time development of the three components was also fitted with exponential functions and is shown in the insert. The fits highlight the sharp decrease in all costs in session 1 and the plateauing in sessions 2 and 3. Visual comparison shows that \( C\text{-Cost} \) dropped from a high initial level to approach \( N\text{-Cost} \) in session 3. Both \( N\text{-Cost} \) and \( T\text{-Cost} \) showed little change after the first session and \( T\text{-Cost} \) had the overall lowest value, indicating that this component was exploited more than the other two components. Most pertinently, the time course of \( C\text{-Cost} \) supports the expectation that individuals use covariation between execution variables to align their distributions with the solution manifold.
Figure 7: Results of the TNC analysis. Contribution of the three components, \( T\)-Cost (black), \( N\)-Cost (gray), and \( C\)-Cost (white), to performance improvement. The bars represent the standard error across subjects. The embedded figure shows the exponential fits of each component.

Discussion

The task of skittles is a model example for a redundant task where subjects reorganize their performance in the course of practice. With experimental control the redundancy was reduced to a 2-to-1 mapping that is sufficient for an infinite number of solutions to occur. Additionally, the task is interesting as the solution manifold forms a nonlinear set in execution space. The actual movement lasts approximately 350ms such that online corrections based on sensory feedback are unlikely and performance improvement happens across many trials. The approach of this study is a statistical one where we examine distributional properties over many repetitions. Our rationale is that variability across repetitions is unavoidable but that actors choose strategies that are
tolerant to error and that channel variability in task-irrelevant dimensions. As expected actors show significant improvement within the experimental time course such that it permits the assessment of changes with practice as well as of skilled performance. The time course of improvement shows that within one experimental session subjects attain a relatively skilled level of performance that is nevertheless fine-tuned over the two subsequent sessions.

With a focus on skilled performance in the latter part of practice the results in this experiment gave support for Hypothesis 1. This hypothesis quantified the idea that actors chose strategies that were tolerant to error and that they channeled their variability to solutions with highest probability of success. The null Hypothesis 2 that predicted a uniform distribution on the solution manifold was clearly rejected on the basis of 9 participants’ performance. Hence, the neighborhood of the solutions and the expected performance mattered in what types of movement they executed.

The rationale and the results of our study are in overall accordance with a series of experiments by Trommershäuser and colleagues (Trommershäuser, Gepshtein, Maloney, Landy, & Banks, 2005; Trommershäuser et al., 2003). Using a speed-accuracy task where the target area is bounded by a penalty area (in different distances and with different penalties) the distribution of hits is examined with respect to the expected gain (reward and penalty). Importantly, hitting success was binary (positive for the target area and negative for the penalty area) and the cumulative score over series of trials was presented to the subjects with the instruction to maximize this score. Formalized in a decision theoretical framework where a gain function is optimized based on the weighted sum of the gain and the subject’s inherent variability, the results showed systematic
effects of the penalty on the distributions. The results therefore supported the conclusion that selection of a movement strategy is determined by the subject’s inherent variability. Note though that their work places emphasis on selection of strategies whereas the present study emphasizes the sensitivity to error and the principle of minimum intervention (see also (Todorov & Jordan, 2002) and discussion).

While the pooled data of all participants in the present study matched the predictions of Hypothesis 1 very well, inter-individual analysis also revealed that - not unexpectedly – each actor had a clear preference for a strategy. One other interesting aspect in the present task is that the most error-tolerant strategy was also adjacent to “risky” executions where throws lead to post hits. Yet, this risk of penalty did not seem to prevent some actors from choosing this strategy. Note though, the post hits had no immediate consequences to our subjects, unlike in Trommershäuser’s work where a running score is diminished by penalties. Rather, the focus was on the continuous distance to the target, which was prerequisite to the sensitivity analysis central to our study.

Closer inspection of the individuals’ distributions in execution space revealed that actors showed different degrees of covariation within sets of trials. However, it was already emphasized that inspection of the distributions in execution space alone does not permit such a conclusion as the units of the two execution variables are not the same. Hence, to further evaluate covariation the relation of the two execution variables had to be examined with respect to the result. For this analysis the result data were decomposed into the three components, \textit{T-Cost}, \textit{C-Cost}, and \textit{N-Cost} that also permitted an assessment of the changes over time. All three components contributed with a sharp decline in
session 1 followed by a leveling off in sessions 2 and 3. The contributions from \textit{T-Cost} showed that a good location was found early in practice and maintained. \textit{N-Cost} was also relatively invariant after a drop at the very beginning. Interestingly, \textit{C-Cost} indeed showed continued decrease suggesting a fine-tuning by shaping the distributions into alignment with the solution manifold.

One caveat may be brought forward in the interpretation of the results of experiments. The predicted error-tolerant strategy was coincident with solutions of lowest release velocities. In previous work is has been shown that variability scaled with movement speed such that performance at higher velocities is more variable (Schmidt, Zelaznik, Hawkins, Frank, & Quinn, 1979; Worringham, 1991, 1993). Assuming movement velocity reflects a magnitude of the motor control signal, this observation is consistent with variability increasing with signal strength. Physiologically, this behavioral observation has been related to the organizational properties of the motor unit pool such as recruitment order and twitch amplitudes (Jones, Hamilton, & Wolpert, 2002). Even though these muscle-physiological studies are confined to isometric contractions, it can be generalized that solutions with high velocity should be avoided if variability is to be reduced or optimized (Hamilton & Wolpert, 2002; Harris & Wolpert, 1998; van Beers, Haggard, & Wolpert, 2004a). The results may therefore also suggest that actors simply chose solutions at the lowest possible velocities to avoid “signal-dependent” noise. To test this alternative explanation a second experiment was designed that could distinguish between the two alternative explanations. The skittles task was modified to create an execution space with a solution manifold that permitted a large range of velocities with equal probability of success.
Experiment 2

Methods

Participants. Nine graduate students (4 male, 5 female) from the Pennsylvania State University volunteered to participate in this experiment. They all reported themselves to be right-handed, and their age ranged between 21 and 30 years. None of them had participated in Experiment 1. They were informed about the purpose of the experiment, but were naive about the manipulations in the experiment. Prior to data collection, subjects were instructed about the experimental procedure upon which they signed an informed consent form in agreement with the Institutional Review Board of the Pennsylvania State University.

Apparatus and Procedure. Using the same apparatus as in Experiment 1, each subject performed 5 sessions each consisting of 3 blocks of 60 trials each, yielding a total of 900 trials. Between each block, subjects could rest for a few minutes. Similar to Experiment 1, subjects were instructed to first explore the entire execution space in session 1; in sessions 2 to 5 they were instructed to maintain and fine-tune the solutions that they regarded best.

Execution Space and Hypotheses. Figure 8A shows the virtual environment that subjects saw during the experiment. The target (radius 0.05 m) was located at the coordinates (0.05, 1.058m); the slightly smaller center post (radius 0.25 m) was now centered at (0, 0). Figure 8B represents the associated execution space with the new solution manifold. The set of successful solutions was approximately parallel to the
velocity dimension; hence, solutions were sensitive to release angle but insensitive to release velocity.

**Figure 8:** Workspace, execution space and solution manifold of Experiment 2. Panel A shows the workspace with the position of the center post and the target used in the experiment. Panel B shows the associated execution space and solution manifold. White areas denote perfect solutions, increasing error is shown by increasingly darker grey shades, black denotes a post hit. Three different ball trajectories in the workspace are produced by different release angles and velocities. The first and second trajectories that hit the target corresponding to the first two points in the solution manifold, the third trajectory which missed the target corresponds to the point 3.

Hypothesis 1 with its prediction that a weighted neighborhood determines the expected performance was quantified and visualized in the same manner as in Experiment 1. Figure 9A presents the results of these matrix-based calculations and shows how the expected performance values (normalized to 1 and shown in white) were
approximately parallel to the velocity dimension.

The alternative Hypothesis 3 that subjects optimize their performance by minimizing their “signal strength”, i.e., velocity, was quantified in the following manner. Identical to the calculations of Hypothesis 1, the expected performance $E(D)$ was evaluated for each of the 360*360 bins in execution space. Different from Experiment 1 the size of the probability matrix was scaled proportional to velocity. To this end, it was first verified that the standard deviations of both angle and velocity indeed increased with increasing release velocity. Plotting standard deviations of subjects’ blocks of data against the respective means and performing a linear regression yielded the following regression equations: $SD\alpha = 0.05 + 0.04v$, $SDv = 0.23 + 0.04v$. Hence the matrix size and weights were adjusted and changed from 7x21 at low velocities to 43x51 for higher velocities.  

Specifically, define $SD\alpha_j$ and $SDv_j$ as the variability of release velocity $v_j$. Then the matrix size at $v_j$ is:

$$K_j = 2 \cdot SD\alpha_j \cdot \frac{360}{2\pi} = SD\alpha_j \cdot \frac{360}{\pi}$$

$$N_j = 2 \cdot SDv_j \cdot \frac{360}{20} = SDv_j \cdot 36$$

Note that $2\pi$ and 20 are the range of execution space; 360 is the bin number of each dimension.

$$E(D_j) = \frac{1}{K_j \cdot N_j} \sum_{k=-K_j}^{K_j} \sum_{n=-N_j}^{N_j} p(\alpha_{ik}, v_{jn}) \cdot D(\alpha_{ik}, v_{jn})$$

$$E(D_j) = \frac{1}{21 \cdot 25} \sum_{k=-21}^{21} \sum_{n=-25}^{25} p(\alpha_{ik}, v_{jn}) \cdot D(\alpha_{ik}, v_{jn}) \text{ for the highest velocities}(j = 360), \text{ where}$$
Hypothesis 3 is visualized in Figure 9B. Due to the higher variability at higher velocity, the expected performance was lower at higher than at smaller velocities. Specifically, the highest value of expected performance was at an angle of 1.4 rad and a velocity of 2.7 rad/s.

\[
p(\alpha_{i+k}, v_{j+n}) = pdf\left(\frac{\alpha_i - \alpha_{i+k}}{0.05 + 0.04 * v_j}\right) * pdf\left(\frac{v_j - v_{j+n}}{0.23 + 0.04 * v_j}\right)
\]

Figure 9: A: Simulation of Hypothesis 1 (identical to Experiment 1). The highest expected performance can be found across velocity dimension with an angle around of
approximately 1.4 rad. B: Simulation of Hypothesis 3. The expected performance is lower for high velocity due to the simulated signal-dependent noise. The highest expected performance can be found for an angle of 1.4 rad with a velocity around 2.7 rad/s.

Data Analyses. Most analyses were identical to Experiment 1. The distributions of the individuals’ data in execution space were illustrated with the same confidence ellipses. The TNC-cost analysis was applied in identical manner to blocks of 60 trials but now for a total of 15 blocks over the 5 sessions.

Results

Performance. Figure 10A shows the median and interquartile ranges of the error pooled over 9 participants and 15 trials over the course of five sessions. As in Experiment 1, the performance improved relatively fast in the first session and the error decreased to reach a relatively steady level after session 2. The changes in the median error were 1.68 cm (session 1), 0.51 cm (session 2), 0.35 cm (session 3), 0.07 cm (session 4), and 0.14 cm (session 5). Given this qualitative difference in the amount of improvement and given that in session 1 subjects were instructed to explore the entire execution space and their performance was expected to be variable with large errors, the following analyses pooled the data of sessions 2 to 5 where performance had converged towards what subjects regarded as their best solutions.

Pooled Distributions. Figure 10B shows the histogram in the execution space pooling all trials of all participants in sessions 2 to 5. The data were distributed across a large range of velocity values, between 2.5 and 15.3 rad/s. To quantitatively compare the
distributions of the data with the ones predicted by the hypotheses, the data and the hypothesized distributions were projected onto the velocity dimensions (Figure 11). Hypothesis 1 is shown in the top panel, the middle panel shows the distribution predicted by Hypothesis 3, and the bottom panel shows the distribution of the human data. Statistical comparisons were performed with the Wilcoxon signed rank test because the distribution of the paired differences between hypotheses and data were not normal. The test results did not detect a difference between Hypothesis 1 and the data ($p = 0.84$). Instead, the difference between Hypothesis 3 and the data was significant ($p < 0.0001$), rejecting Hypothesis 3.

*Figure 10:* A: Time series of errors over trials (median and interquartile range). The errors are averaged over 9 participants. The trials were also averaged such that for every non-overlapping series of 15 trials the median is plotted with the corresponding interquartile ranges shown by the error bars. B: Histogram of all subjects’ trials of four sessions plotted in execution space (720 trials per subject). The distribution is spread along a long range of velocities from 2.5 and 15.3 rad/s at an angle of 1.4 rad.
**Figure 11:** Projection of the distributions to the velocity dimension. The top panel shows the distribution predicted by Hypothesis 1 (Figure 9A); the middle panel shows the distribution predicted by Hypothesis 3 (Figure 9B); the bottom panel shows the distribution of the human data (Figure 10B).

*Individual Distributions.* Figure 12 shows the confidence ellipses for each participant calculated from the pooled data from the four sessions (using 720 trials for each ellipse). The individuals’ means were distributed across different velocities and reflected the different preferences between individuals. Importantly, the velocities of these means ranged between 4.18 to 13.5 rad/s and did not cluster at the lowest velocities as predicted by Hypothesis 3. Many ellipses also showed a vertical orientation parallel to the solution manifold.
Figure 12: Individual distribution of trials of sessions 2 to 5 in execution space. The 720 trials of each of the 9 participants are represented by the 95% confidence ellipses. The center of the ellipse is the mean value of release angle and velocity, the orientation of the ellipse is the orientation of the eigenvector of the covariation matrix of angle and velocity, the length of the major and minor axes are twice the square root of the eigenvalues.

The TNC-cost analysis was performed to further scrutinize changes in the structure of variability across the five sessions. Figure 13 shows that all three components were significant contributors to performance improvement over practice, although C-Cost only showed a large drop in the initial blocks. These qualitative impressions were verified by the MANOVA with showed a significant multivariate effect for session, $F(12, 86) = 46.17, p < 0.0001$ (Hotellings Trace). Univariate tests identified changes in T-Cost, N-Cost, and C-Cost across sessions that were significant with $F(1.40, 11.20) = 18.97, p < 0.001$, $F(1.38, 11.02) = 22.11, p < 0.001$, and $F(1.06, 8.05) = 6.12, p < 0.05$, respectively. Pairwise comparisons across sessions were significant for T-Cost and N-Cost documenting the large change from session 1 to sessions 2, 3, 4, and 5. This pattern of
change was identical for the two costs. In contrast, $C\text{-}Cost$ did not show pairwise differences. This different pattern is understandable as covariation cannot be computed for a solution manifold that is parallel with one of the axes. The fact that $C\text{-}Cost$ is not zero at the beginning is due to the fact that this cost was evaluated across the entire execution space where the solution manifold is different. The exponential fits in the insert of Figure 13 reiterate these results in continuous representation.

**Figure 13:** Results of the TNC cost analysis. Contribution of the three components, $T\text{-}Cost$ (black), $N\text{-}Cost$ (gray), and $C\text{-}Cost$ (white), to performance improvement. Each bar represents the standard error across subjects. The embedded figure shows the exponential fits of each component.

Discussion
The major objective of the second study was to replicate Experiment 1 in a variation that removes the potential confound that the results could have been due to subjects minimizing release velocity. Experiment 2 created a new execution space with a solution manifold that was parallel to velocity with an error tolerance that was approximately equal along a range of release velocities. Hence, in this variation subjects were free to choose any release velocity, including minimizing velocity, and achieve the same consistency in the results with a similar dispersion in release angle. Results showed that actors did not have a preference for minimum velocity but rather chose a relatively large range of velocities, in contradiction to Hypothesis 3. The results were again consistent with Hypothesis 1, showing that the data clustered in alignment with the solution manifold where the error tolerance is identical along a range of velocities. The elliptic orientation of the individual data clusters showed that actors are aware of their variability and channel it into directions that were insensitive to error in the result.

The TNC-results further supported these interpretations and also highlighted how the structure in the data changed through the sessions. The results for T-Cost and N-Cost showed that both were increasingly reduced to improve performance. The changes in T-Cost gave evidence that with practice subjects increasingly moved to a location in execution space, or to a strategy, that was less prone to error. Simultaneously, the dispersion was reduced, expressed in N-Cost. Note that covariation could not be assessed in C-Cost as the orientation of the manifold was parallel to velocity.

General Discussion
The sensorimotor system is a highly complex dynamical system with many hierarchically nested processes of an immense range of spatial and temporal scales, from the level of action potentials and motor units to that of intersegmental dynamics. It is therefore not surprising that at the level of observed actions there is always variability. Many sources for this variability have been identified in neurophysiological studies: For example Churchland and colleagues have demonstrated that fluctuations in single neuron activity in the dorsal premotor cortex and M1 of monkeys during the preparatory stage of highly practiced reaching movements accounts for half of the observed variability in the velocity profiles of reaching trajectories (Churchland, Afshar, & Shenoy, 2006b). Complementary to this finding, a study by (van Beers et al., 2004a) attributed a part of the observed noise originating during the execution. This conclusion was based on behavioral results where variations in the planning and localization stages were experimentally controlled and the modeling demonstrated that this noise was a mixture of signal-dependent and independent noise. Muscle physiological studies demonstrated that the signal-dependent magnitude of noise, specifically the scaling of force variability with force magnitude in isometric force production, was induced by properties of the motor neuronal pool, specifically twitch amplitude and recruitment order (Jones, Hamilton, & Wolpert, 2001). Lastly, a study on song learning in juvenile songbirds revealed that variability was significantly reduced when pharmacologically inactivating a basal ganglia related circuit. This circuit projects its output to the motor pathways and thereby significantly contributes to variability in the produced sequences (Ölveczky, Andalman, & Fee, 2005). Interestingly, any further modification of the vocal sequence and learning is inhibited thereafter. A review of other physiological underpinnings of variability in
perceptual-motor level can be found in (Bays & Wolpert, 2007). Taken together, these complex processes in the underlying neurophysiological substrate give rise to fluctuations that are never completely suppressed and, as it may be speculated, should not be suppressed.

While all these studies identified sources of variability, they also implied a generally random structure. The present study aimed to tease apart different aspects of variability, both random and non-random, from behavioral data at the background of a statistic analysis of the task. One way to cope with undesired variability is to channel it into directions that have little effect on the end result within a given task. For example, in pistol shooting the linkage of joints in the arm may vary within a single aiming movement and across different trials without necessarily affecting the outcome of the aiming. In fact, it has been shown that covariation across joints of the extended arm occurs such that variations in joint angles have little effect on the endeffector or the orientation of the barrel (Arutyunyan et al., 1968; Cusumano & Cesari, 2006; Scholz, Schöner, & Latash, 2000). Similarly, studies on dart throwing (Müller & Loosch, 1999), boule throwing (Dupuy, Mottet, & Ripoll, 2000) and basket ball (Kudo, Tsutsui, Ishikura, Ito, & Yamamoto, 2000) showed that the release parameters co-varied. These demonstrations highlight the omnipresent problem how the central nervous system solves redundant tasks, the problem of allowing for variability but preempting the penalty of errors in the outcome.

The particular issue that variability is channeled into dimensions that do not matter to the performance outcome is not entirely new and has been investigated and supported in several previous studies. For example, channeling of variability into “do-not-care”
directions has been the result in the stochastic optimal control model developed by (Todorov & Jordan, 2002). Similarly, the approach using the so-called UnControlled Manifold analysis (UCM), is based on the idea that variance deforms into an ellipsoid with its major direction along the uncontrolled manifold, the null space for a given control variable (Latash, Scholz, & Schöner, 2002; Scholz & Schöner, 1999). However, the present study adds several new important aspects to this otherwise similar notion.

First, the TNC-representation is not confined to a metric space, e.g., a space spanned by joint angles and it assesses variability with respect to a task-defined goal function. Although the UCM-method derives the null space with respect to a hypothesized controlled variable, the dispersion in performance variables is assessed around the mean performance without relating the variance to a task-defined success in performance. For example in a pistol shooting task, the multi-joint arm movements have been analyzed with respect to the orientation of the pistol barrel in a shooting task (Scholz et al., 2000). The important difference to the presented approach is that there is no analysis of a desired orientation of the barrel that would lead to a perfect shot. The present approach affords the calculation of execution space that presents the complete representation of executions with their associated performance results. Therefore, it can also make a priori predictions where and how variability should be distributed. This is expressed in Hypothesis 1.

Importantly, this analysis reveals not only the set of solutions but also to what degree deviations are penalized by errors, i.e., the sensitivity or tolerance to error, that leads another set of predictions about the most error-tolerant strategies. Hypothesis 1 is that in skilled performance actors are aware of the limited resolution in their control and take this into account when planning and executing a movement. To quantify this hypothesis
we simulated that subjects do not plan in terms of a single solution but they take a small “area” of solutions into account. This approach differs from the conventional sensitivity analysis that is anchored around a single point in the space of execution variables (Cusumano & Cesari, 2006; Todorov & Jordan, 2002). The quantification of Hypothesis 1 and even more so Hypothesis 3 pays tribute to the actual variability of actors and evaluates the expected performance for such variability.

Hypothesis 1 – actors are sensitive to their internal variability – was supported in two experiments that tested two different task variations. In Experiment 1 the solution manifold was L-shaped but the highest probability of success was at relatively low velocities. Subjects avoided solutions in which error tolerance was quite small and selected solutions with higher expected performance. Interestingly, the error-tolerant strategies were also close to solutions that received a penalty for hitting the center post. Despite this “risk” actors still preferred those strategies with a large neighborhood of similarly good solutions. This portion of the solution manifold was parallel but also slightly slanted with respect to the angle dimension. Hence, covariation between the execution variables improved performance. This expectation was directly quantified by the TNC-analysis that showed the decrease in C-Cost, i.e., increase in covariation from session 1 to 3.

Experiment 2 was designed to replicate the result with an entirely new solution manifold and at the same time rule out a potential confound. Target skittle and center post were so positioned that the solution manifold was parallel to the velocity dimension; therefore, successful solutions could be found across a range of velocity dimension and they all had a comparable sensitivity to error. The results were again in support of
Hypothesis 1 that error-tolerant solutions were preferred. No support was obtained for Hypothesis 3 that subjects were sensitive to their velocity dependent variance and found solutions with minimum velocity in solution manifold. This is noteworthy as the analysis of standard deviations and velocity and its associated standard deviations did show that higher release velocities were associated with higher standard deviations. Yet, these higher standard deviations in the velocity dimension did not matter in this task. Hence, avoidance of higher velocities was not necessary to achieve the task.

This dispersion is visible in the pronounced alignment of the confidence ellipses in Experiment 2, which appeared higher than in Experiment 1. Another explanation for this difference is that subjects received two more practice sessions in Experiment 2. The ellipses were drawn for 720 trials each, which enhanced the shape and orientation of the data distribution.

In summary, two experiments examined a virtual throwing task and presented an analysis that provided a priori hypotheses about which strategies actors should employ if they optimized error-tolerance. Analysis of the relation between the variability in execution to the success in the task revealed that actors only decreased their motor variability in execution variables that mattered for the success of the task. The findings gave strong support that subjects were sensitive to their motor variability and preferred error-tolerant strategies.
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Appendix

Analysis of T-, N-, and C-Costs

To extract the three components for a set of data, 60 consecutive trials each described by two execution variables (release angle and release velocity) and one result variable (distance to target or error) were analyzed as a set. For each set of data the mean result was calculated. For the calculation of each component, the data were transformed in a specific way to create another set with optimal results in terms of one component while other features of the data set remained unchanged. The mean result for this optimized data set was calculated. The algebraic difference between the mean result from the actual data set and the mean result from the optimized data set expressed the cost of the specific component.

T-Cost expresses the cost to performance of a given data set not being centered in the best region of execution space. To estimate T-Cost for a data set, an optimized data set was generated in which the mean of the release angles and the mean of the release velocities were set at the values that yielded the best overall result, while the dispersion along each axis was preserved. To this end, a grid of 600 x 600 possible center points for the data set was created over a range of values in execution space determined by the limits of the task. The optimization procedure moved the whole data set through the grid and evaluated its mean result at each location. For data points that extended beyond the grid, the values were calculated on the extended execution space. The location that yielded the best overall performance result was compared with the result of the actual data set. The algebraic difference between the actual result and the result at the optimized center defined T-Cost.
C-Cost expresses the cost to performance of a given data set not fully exploiting redundancy in the execution space. To estimate C-Cost for a data set, an optimized data set was generated in which the means and distributions of the angles and velocities were maintained, while the individual pairs were recombined to achieve the best possible performance. This idealized data set was found with a greedy hill climbing algorithm using a pairwise matching procedure. To implement this, first the pairs of angles, $a_i$, and velocities, $v_i$, were rank ordered from best to worst according to the error result, $r_i$, with $i = 1, 2, 3, \ldots, 60$. Next, the angle from the worst performing pair $a_{60}$ was paired with $v_{59}$, and $a_{59}$ was paired with $v_{60}$, i.e., $v_{59}$ and $v_{59}$ were swapped; the mean result of $r_{59}$ and $r_{60}$ was determined. If the mean result improved over the original $r_{59}$ and $r_{60}$, the swap was accepted. As a next step $v_{60}$ was swapped with $v_{58}$ and the resulting mean error of $r_{58}$ and $r_{60}$ was evaluated. If the mean result improved, the swap was accepted. This procedure continued until $a_{60}$ was paired with $v_{1}$, i.e., $v_{60}$ was swapped with $v_{1}$. After this sequence of 59 comparisons, the same procedure was repeated with $a_{59}$. Hence, the batch consisted of $59 \times 59 = 3481$ comparisons. The number of profitable swaps was recorded for each batch. Then, this entire batch of procedures was repeated on the improved set until the number of swaps converged to zero (no further swaps could profitably be made). The algebraic difference between the mean result of the actual data set and the mean result of the optimally recombined set defined C-Cost. Note that this method can find optimal covariation between execution variables even in situations in which the solution manifold is nonlinear, as in this task.

N-Cost. To estimate the cost to performance of a given data set not reflecting optimal compression of dispersion in execution variables, a virtual data set was created in which
the mean and pairings of the angles and velocities were maintained, while variability was reduced to achieve the best possible mean result. To find the optimal reduction of dispersion, first the mean of the angle and velocity was determined. Then, the data set was “shrunk” in 100 steps to collapse onto the mean. For the shrinking procedure, first the radial distance of each point to the mean was determined. Second, this radial distance was divided into 100 steps, each bringing every data point 1% closer to the mean angle and mean velocity until all 60 points collapsed at the mean. At each step the overall mean result was evaluated. The step that led to the best overall performance was selected as the set with optimal dispersion. The algebraic difference between the mean result of the optimal data set and the mean result of the actual data set defined $N$-Cost. Note that this method allows for the possibility that the mean may not be located on the best possible point in execution space with the best result.
References


Footnotes

1: Skittles is a British pub game, similar to the American tetherball. A ball is attached to a string on a central vertical pole. The ball is thrown around the pole in a pendular fashion with the goal to hit a set of skittles that is placed at the other side of the pole. As in bowling, the goal is to hit as many skittles as possible. The present experiment simplified this game to only one target “skittle” and represented the pendular ball and pole in a top-down view.

2: The hypotheses were first calculated using variability estimates from pilot data. After having finished the analyses of the present experiments, the parameters of the hypothesis simulations were adjusted to obtain the best possible hypotheses to test the data of the two experiments.
CHAPTER 3

Stochastic Resonance in Skill Performance and Retention
Adaptation and After-Effects with Added Noise and Threshold Manipulations

Chapter 3 contains an original manuscript prepared for submission to a journal

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Abstract

Based on stochastic resonance, detection of sensory signals can be enhanced in the presence of noise. We showed that control of movement accuracy and variability benefits from enhancement of seemingly perturbing information. Using a goal-directed throwing task in a virtual environment, error-dependent noise was added to the arm position at ball release; in a complementary condition, the threshold signaling successful hits was lowered. Results showed that subjects significantly improved accuracy and reduced motor variability with enhanced error information compared to controls. This enhanced performance was retained for a prolonged five-session period after noise was removed and the threshold was raised. These results demonstrated the relevance of stochastic resonance for the control of movements. The findings have implications for training and rehabilitation as signal detection and control processes in the sensorimotor system can be improved with enhanced error information.
It is generally assumed that noise both from external and internal sources presents a challenge for the sensorimotor system to perform movements with high accuracy and low variability (Bays & Wolpert, 2007; van Beers, Baraduc, & Wolpert, 2002). However, it is also recognized that noise or rather variability in performance aids the exploration of behavioral possibilities and thereby increases flexibility and adaptation to new task demands (Newell & McDonald, 1992; Ölveczky, Andalman, & Fee, 2005). Here we show that task performance can benefit from adding noise, leading to immediate and longer-term performance improvements. The theoretical framework of stochastic resonance (SR) guided the experimental manipulations that led to more accurate performance.

It is beyond doubt that the sensorimotor system is a highly complex dynamical system with many hierarchically nested processes of an immense range of spatial and temporal scales, from the level of action potentials and motor units to that of intersegmental dynamics. Importantly, many of these nonlinearities in sensory processes are thresholds. Such nonlinear threshold systems exhibit stochastic resonance, a phenomenon where the response of the system to the input signal is enhanced by adding noise (Benzi, Sutera, & Vulpiani, 1981; McNamara & Wiesenfeld, 1989). More specifically, the addition of a random interference can enhance the detection of a weak input (Wiesenfeld & Moss, 1995). This phenomenon has been used to improve signal detection in a variety of different dynamical systems, both biological and physical, ranging from neural networks, tactile and visual sensation (Collins, Chow, & Imhoff, 1995; Collins, Imhoff, & Grigg, 1996; Longtin, Bulsara, & Moss, 1991; Moss, Ward, & Sannita, 2004; Simonotto et al., 1997; Collins, 1999; Russell, Wilkens, & Moss, 1999).
Most pertinent to the present study, Collins and colleagues reported that applying subliminal mechanical noise to the feet enhances human balance control both in healthy young people, elderly and in diabetic patients (Priplata et al., 2002; Priplata et al., 2006).

The classical paradigm demonstrating SR in nonlinear systems requires the concurrence of a sub-threshold signal input, added noise, and a threshold (Fig. 1a). In such a system, information about the signal is encoded by its crossing of a given threshold. The original signal input is always below threshold and the system therefore does not respond to the stimuli. If external noise is added, the signal may cross the threshold leading to a sequence of pulses representing the output. This output contains probabilistic information about the original sub-threshold input signal, and thus allows it to be detected and further processed. Tuning system parameters has been proposed as another way of inducing SR. For example adjusting system parameters such as time constants or amplitudes of potential, an ‘optimal’ system emerged and that enhanced signal transmission (Xu, Duan, & Chapeau-Blondeau, 2004). Therefore, besides adding noise, an alternative way of increasing the occurrences of threshold crossings is to lower the threshold. Fig. 1b illustrates that with threshold 1, the input signal is always below threshold and shows no response to the input signal. When threshold 1 is lowered to threshold 2, a similar output as in Fig. 1a is achieved. Note that the input signal itself is noisy and this noise component is called internal noise to distinguish it from the externally added noise.
Figure 1: Stochastic resonance paradigm. The system only had response when signal input crosses the system threshold. (a) The noisy signal input is below threshold; therefore the system had no output. All variables are with arbitrary units. The noisy signal plus an extra noise makes threshold crossing happen. Each threshold crossing is denoted by a pulse in the output as shown at the upper part of panel a. The pulse output carries information about the signal input. (b) The noisy signal input is below the original threshold 1. However, when the system threshold is lowered to threshold 2, the pulse output is generated where threshold crossing occurs.

To make the analogy with the sensorimotor system explicit: The input signal is the to-be-detected stimulus or sensory information. It is conceivable that if noise is added to the input stimulus, then the system may adapt to suppress spurious output and lower its internal noise as compensation for the added noise. Alternatively, lowering the threshold
may similarly lead to an increased spurious output. Again, one way for the biological system to maintain performance with tolerable noise is to decrease its internal noise. While the benefit of adding external noise has been demonstrated in biological systems, the complementary manipulation of lowering the threshold to enhance response to information has not been tested specifically in biological systems. This may be due to the fact that the system’s threshold is typically fixed internally or it changes randomly inaccessible to the experimenter. However, when the task has an external threshold that can be artificially set, its manipulation becomes possible. The present study manipulates both noise and threshold with the hypothesis that equivalent adaptations will be achieved (Hypothesis 1).

While several studies have already shown that noise produces adaptations that can be understood as stochastic resonance, it has not yet been examined whether these adaptations persist after removal of the added noise. As has been argued before, learning is only achieved when the system’s improvement persist for a prolonged time (Schmidt & Lee, 2005). Therefore, the present study also tests such retention of performance improvement due to noise and threshold manipulations. To this end, noise is removed and the threshold is reset to its initial value and performance is tested for another five days. Evidently, when using noise as an intervention method, it is highly desirable that such adaptations persist. On the other hand, it can similarly be expected that subjects return to their initial more variable strategy when noise is removed or threshold was increased to the initial value. Hence, we formulate this expectation as Hypothesis 2.

A throwing task called skittles served as the model task (Figure 2). The task is representative for goal-oriented skills where the execution of a discrete movement
involves a redundant number of variables that fully determine the result. Inspired by the British game skittles, a ball suspended on a central vertical pole is swung around this pole in a pendular fashion. The goal is to hit a target skittle placed at the other side of the pole. In the top down view presented to the subject on a projection screen (Figure 2a), the ball trajectory traverses around the pole in a concentric force field describing an elliptic trajectory. Feedback information about performance success is given by showing how close the thrown ball hits the target.

**Figure 2:** Workspace, execution space and solution manifold. (a) The workspace with the position of the center post and target. Three ball trajectories exemplify how different release variables can lead to the same result with zero error, \( d = 0 \) (trajectory 1, 2). Trajectory 3 shows a trajectory with non-zero error, \( d = 30 \) cm. (b) The execution space and solution manifold. White areas denote zero-error solutions, increasing error is shown by increasingly darker grey shades, black denotes a post hit. The release variables of the first and second trajectory which hit the target correspond to points 1 and 2.
(denoted by stars) on the solution manifold, the variables of the third trajectory correspond to the point 3 in a grey-shaded area.

The virtual set-up afforded both the manipulation of external noise and error signaling threshold. Three groups of subjects trained for one session until they achieved a plateau in their skill level; in session 2, noise was added to the release angle in Group 1; the error signaling threshold was lowered in Group 2; Group 3 served as a control group without any manipulations; in session 3, the experimental conditions were the same as in session 1 for all three groups.

Methods

Participants. Eighteen subjects (11 male, 7 female, 24 to 46 years of age) from the Pennsylvania State University volunteered to participate in this experiment. All reported themselves to be right-handed. They were informed about the purpose of the experiment, but were naive about the nature of the manipulations in the experiment. Prior to data collection, subjects were instructed about the experimental procedure upon which they signed an informed consent form in agreement with the Institutional Review Board of the Pennsylvania State University. Six subjects (4 male, 2 female) were randomly assigned to the noise group, six subjects (3 male, 3 female) to the threshold group, and six (4 male, 2 female) to the control group.

Apparatus. The apparatus is the same as shown in Chapter 2.

Task and Procedure. Each subject performed the task for a total of 11 sessions performed on 11 days with a maximum of 2 days between these testing sessions. The
sessions were parsed into 3 blocks. Block 1 consisted of 3 sessions and was regarded as general practice of the virtual task. Block 2 (3 sessions) presented the respective experimental conditions. Block 3 (5 sessions) tested the retention of skill under the original conditions. In each session subjects performed 240 trials to render a total of 2640 trials. After each set of 60 trials, subjects were encouraged to take a short rest.

The target skittle (radius 5 cm) was located at the x-y coordinates (0.05, 1.055 m) in the workspace; the center post (radius 25 cm) was centered at the coordinates (0, 0) (Figure 2a). The distance-error signaling threshold was 1.1 cm for all 3 groups with exception of Block 2 of the threshold group, where it was decreased to 0.65 cm. Subjects were instructed to try their best to hit the target with the virtual ball. Importantly, they received no information about the manipulations, neither in Block 2 nor Block 3, where the original conditions were reestablished. The experimenter emphasized that they should avoid hitting the center post as a post hit was penalized with a large error. At the end of each trial, a zoomed window showed the segment of the trajectory closest to the target to inform subjects about their performance. This zoom window was presented for 2 s. If the ball hit the target and the distance error, defined as the minimum distance between the center of the ball and the center of the target skittle, was smaller than the error threshold, the color of the target changed from the regular yellow to red, signaling the success of the trial. Figure 2b represents the solution manifold as determined by the locations of the target skittle and the center post. The locations were so chosen that the solution manifold was oriented vertically and successful solutions were only sensitive to release angle but not to release velocity. This choice facilitated the noise manipulations explained below.
Typically, one throw lasted 1 s with approximately 4 s between throws. The duration of each session was approximately 15 min.

**Noise Manipulation.** In Block 2 of the noise condition, noise was added to the release angle so that the accuracy of the ball trajectories was partly outside the control of the subjects. To this end, the angle at the center of the solution manifold, $\alpha_c$, was determined to be at 1.44 rad. Noise was added to the angle when the actual release angle, $\alpha$, deviated from $\alpha_c$. Specifically, when the release angle $\alpha$ was collected by the computer, a random number was added and the ball trajectory was calculated based on the noisy release angle. A previous study using the same target constellation with the same solution manifold showed that after practice 95% of all trials were within $\alpha \in (1.0, 1.88 \text{ rad})$, corresponding to a maximum error $d = 3.6 \text{ cm}$. Noise intensity increased linearly with the deviation from $\alpha_c$:

$$\alpha_{\text{noise}} = \alpha + (\alpha - \alpha_c) \cdot \xi_U$$

(1)

where $\alpha_{\text{noise}}$ is the noisy release angle, $\xi_U$ is uniformly distributed noise on the interval from 0 to 2 rad. This range was chosen to present a sufficiently large perturbation that was also sufficiently undetectable by the subject. This design also ensured that a larger intensity of noise was added when subjects displayed larger variability in the release angle. Note that the added noise $(\alpha - \alpha_c)$ was signed and error-dependent: for $\alpha$ smaller (larger) than $\alpha_c$, the noise was negative (positive) amplifying the deviation from the solution manifold and creating larger visible errors. This design ensured that the added noise always enhanced the error information but in a random manner. Figure 4 represents the effect of the noise on the solution manifold. Note that the added noise only affected
the visually displayed trajectory, i.e., only the consequence and not the actual performance of the task. There was no mechanical perturbation and subjects did not notice that noise was added.

**Figure 4:** Solution manifold with simulated noise added to the release angle. Noise was added to the angle when the actual release angle $\alpha$ deviated from the center angle $\alpha_c$ with $\alpha \in (1.0, 1.88)$. When the release angle was out of this range, no noise was added. The noise intensity increase linearly with the deviation of $\alpha$ from $\alpha_c$.

**Data Processing.** Despite the instruction subjects occasionally hit the center post incurring a large penalty ($d = 60$ cm). To avoid undesired skewing in the further processing of the sequence of errors these high penalties were “smoothed” by applying a bootstrap method. First, the data were parsed into a series of non-overlapping windows with a size of 30 data points. The window size was chosen to be large enough to obtain sufficiently reliable estimates and small enough to not be confounded with changes due to learning. Second, within each window the post hit/outliers were removed and the maximum of the remaining data points was determined. Third, the post hits that were
removed from the original data were replaced by this maximum multiplied with a gain of 1.5. To avoid that all replaced values within a window were assigned the same maximum value, the data were resampled every time (using bootstrapping) (Zhu & Zhang, 2004).

All numerical analyses were performed with Matlab (The Mathworks, version 7.2.0).

Confidence Ellipses. To quantify the distribution of data in execution space for each subject the covariance matrix of the execution variables was calculated and visualized by its 95% confidence ellipse. Three parameters described the confidence ellipse: 1) the mean of release angle and velocity determined the center of the ellipse, 2) the eigenvectors were calculated to determine the orientation of the ellipse, 3) the square roots of the eigenvalues determined the magnitude of the semi-major and semi-minor of the ellipse.

Statistical Analyses. A mixed-design ANOVA was applied to the binary success rate data, with Group as the between-subjects factor, and Block as the within-subjects factor, which was nested in the factor Session (in Block 3 only the first 3 sessions were entered to ensure a balanced design). An additional 3 (Group) x 5 (Session) ANOVA was performed on the success rates in Block 3 with Session as a repeated factor. Posthoc tests with Bonferroni adjustments were performed following the ANOVA. The percentage data was transformed by the arcsin square root algorithm before performing the statistical analysis to satisfy the assumption of normality (Zar, 1999).

To quantify and statistically test the differences between the three groups, the exponential function $y = a \times \exp(-x/\tau) + c$, and the linear function $y = a \times x + c$ were fitted to the performance error and the SD angle data of the individual subjects in each group using the Matlab function ‘nlinfit’ from the Statistics Toolbox. We fitted the
trimmed mean error of 20 trials based on least squares. The trimming consisted of
discarding the data with the largest error, leaving 19 values from which we calculated the
mean. We also fitted the trimmed SD angle of 20 trials. Similarly, the largest deviation
from the mean of 20 trials was discarded, leaving 19 values from which the SD angle was
calculated. The rationale behind this approach is that the mean or SD (over all 20 values)
was too sensitive to occasional outliers and the median or the interquartile range was too
insensitive to large performance errors. This procedure produced 132 performance errors
or SD angle values per actor.

For the control group a single exponential curve was fitted to the data from all 3
blocks combined. For the threshold and noise group, one exponential curve was fitted to
the data in block 1 and one exponential curve was fitted to data in block 2 and 3. If the
exponential fit did not converge, a linear function was fitted to the data. In the
performance error fitting, two subjects (block 1 for both of them) in the noise group and 3
subjects (block 1 for one actor, block 2 and 3 for 2 subjects) in the threshold group were
fitted by linear function. In the SD angle fitting, two subjects (block 2 and 3 for both of
them) in the noise group, 3 subjects (block 1 for one subject, block 2 and 3 for one
subject, block 1 and block 2 and 3 for one subject) in the threshold group and 2 subjects
in the control group were fitted by linear function.

The fitted parameters between groups were compared using \( t \)-tests. In block 1 two-
sample \( t \)-tests were performed on the asymptotic level (parameter \( c \)); in block 2 one-
sample \( t \)-tests were applied on the amplitude (parameter \( a \)) of the exponential function in
the experimental groups; in block 3 two-sample one-tailed \( t \)-tests were conducted on the
asymptotic level (parameter \( c \)). The confidence level was set to 0.05 in all statistical tests.
Statistical analyses were performed with SPSS (SPSS Inc., v15.0). Exponential fits were calculated using the Levenberg-Marquardt nonlinear regression technique in Matlab (Mathworks, v. 7.2.0).

Results

*Distribution in Execution Space.* The data distributions of one typical subject from each group are illustrated in Figure 5. The subjects’ distributions are highlighted by the confidence ellipses. Qualitative comparison between performance in Block 1 and 2 shows lower dispersions in the angle dimension in the noise and threshold group in Block 2 as noise was added to the release angle and the threshold was lowered. Note that in Block 2 and 3 the variability in velocity did not change as task success was not sensitive to release velocity. After reestablishing initial conditions in Block 3 this low dispersion was maintained in both experimental groups. In contrast, the control group showed no change throughout the 3 blocks. As there was no change in the velocity dimension, no further analysis was performed on the velocity variable.
Figure 5: Execution distribution of typical subjects in each group. Execution of the last two sessions of each block (Session 4 and 5 of block 3) was plotted on the execution space. (a) One typical subject from the noise group. (b) One subject from the threshold group. (c) One from the control group. The 95% confidence ellipses were used to visualize the distribution.
Success Rates. The percentages of successful target hits per session (240 trials) were averaged across all 6 subjects per group and are shown in Figure 6a. After short initial practice performance improved in all three groups in Block 1 and all subjects reached a comparable performance level (no significant differences between groups in Session 3 ($p_s > 0.05$, posthoc). In Block 2, when noise was added or the threshold was lowered, subjects in the two experimental conditions continued to improve their performance, which was significantly higher than in Block 1 ($p_s < 0.0001$, posthoc); in contrast, no significant improvement was found in the control group ($p = 0.061$, posthoc). These results supported Hypothesis 1. The perceived success rates in Block 2, denoted by the stars, were significantly lower as to be expected and were even slightly lower than during the initial practice in Block 1. However, they also showed an increase across sessions 4, 5, and 6. During the five retention sessions of Block 3, where noise was removed and the threshold was reset to the initial value, subjects maintained their improved performance, which was significantly higher than the control group ($p_s < 0.05$, posthoc). The success rates of the two experimental groups did not change ($p = 0.24$ and 0.19) and remained significantly higher than the control group ($p = 0.021$).
Figure 6: Average success rate of each day over 6 subjects in each group and average distance error over time in the noise group. (a) Error bars denote the standard deviation of the success rate in each group. The stars on session 4 to 6 shows subjects perceived success rate when noise was added or error threshold was lowered in the noise and threshold group, and the error bars on the stars denote the standard deviation of the success rate across subjects. Add ANOVA results (b) Circles denote the average actual error over time (average 20 trials for each subjects, and average them over 6 subjects). An exponential function $y = a \cdot \exp(-x/\tau) + b$ (with x being the average trial number and
y being the calculated variables) was fitted to block 1 of the data; the same function was fitted through block 2 and 3, because no trend of decline was found in the success rate. The stars in block 2 shows the perceived error when noise was added.

*Continuous Performance Changes.* A depiction of the time course of the continuous measures of performance is shown in Figures 6b and 7. To compress and filter the data for better illustration, averages were calculated over 20 successive trials for each subject’s sequence and then averaged across subjects. Figure 6b shows the data of the noise group, both in terms of their perceived error as a result of the added noise and the actual error that their release parameters would have achieved. The results illustrate that when approaching the end of Block 1, subjects’ improvements in performance had leveled off. However, when noise was added in Block 2, subjects continued to improve their noisy and actual performance errors. Note that the perceived errors in Block 2 were higher than those at the beginning of practice. Importantly, the performance continued at the same level across 5 sessions of Block 3, consistent with the results of the binary success rates.

Figure 7 illustrates the time course of the error and release angle and their respective standard deviations (SD) by means of their exponential fits with the 95% confidence intervals (shaded area). As there was no significant change between Block 2 and 3, the exponential fits were performed over the two blocks. Figure 7a and 7b illustrate the performance changes for the noise group in contrast to the control group; Figure 7c and 7d illustrates the results of the threshold group. In both the error and angle measures, the
fitted exponentials of the control group remained higher than those of the experimental
groups, although their confidence intervals overlapped.

To quantify group differences, the exponential function \( y = a \exp(-x/\tau) + c \), and
the linear function \( y = a \cdot x + c \), was fitted to the performance error for individual subject
in each group. \( t \)-tests were applied on the fitted parameters to compare the group
differences. In Block 1, no difference was found in the asymptotic levels (parameter \( c \))
between the experimental groups and the control group (Threshold vs. Control group:
\( t(10)=0.01, p=1.0 \); Noise vs. Control group: \( t(9)=1.78, p=0.108 \), two-sample \( t \)-test). In
Block 2, where error information was enhanced, the experimental groups showed
significant improvement in performance error (parameter \( a \)) (Threshold group: \( t(3)=2.25, 
p=0.055 \); Noise group: \( t(4)=2.69, p=0.027 \), one sample \( t \)-test). When the enhanced error
information was removed in Block 3, the improved performance error in the two
experimental groups was retained and was significantly lower than in the Control group
(parameter \( c \)) (Threshold vs. Control group: \( t(10)=-3.93, p=0.0014 \); Noise vs. Control
group: \( t(9)=-2.14, p=0.0306 \), two-sample one-tailed \( t \)-test).

The same procedure was performed on the SD angle data for all individual subjects in
each group. At the end of Block 1, there were no differences of SD angle in the
asymptotic levels (parameter \( c \)) between the experimental groups and the control group
(Threshold vs. Control group: \( t(10)=0.55, p=0.593 \); Noise vs. Control group: \( t(9)=1.57, 
p=0.152 \), two-sample \( t \)-test). In Block 2, when the error information was enhanced, the
experimental groups showed significant improvement in SD angle (parameter \( a \))
(Threshold group: \( t(5)=2.83, p=0.018 \); Noise group: \( t(4)=1.67, p=0.0853 \), one sample \( t \)-test). When the enhanced error information was removed in Block 3, the improved SD
angle in the experimental groups was retained and was significantly lower than the
Control group (parameter c) (Threshold vs. Control group: \( t(10) = -5.65, p=0.001 \); Noise
vs. Control group: \( t(9) = -2.16, p=0.0297 \), two-sample one-tailed \( t \)-test).

Figure 7: Distance error and standard deviation (SD) of release angle over time. For
better illustration, averages trials were calculated over 20 successive trials for each
subject’s sequence. An exponential function \( y = a \exp(-x/\tau) + b \) (with x being the
average trial number and y being the calculated variables) was fitted to the block 1 of the
data with 95% prediction interval; the same function was fitted through block 2 and 3
also with 95% prediction interval. (a) The comparison of distance error between the
noise group and the control group. The gray solid lines denote the fitted exponential
function of the noise group, and the light gray bands represent the 95% prediction

77
interval. The black solid lines denote the fitted exponential function of the control group, and the region within the dash lines represents the 95% prediction interval. **(b)** The comparison of SD of release angle between the noise group and the control group, and the notations were the same as shown in panel **a.** **(c)** The comparison of distance error between the threshold group and the control group. The gray solid lines denote the fitted exponential function of the threshold group, and the dark gray bands represent the 95% prediction interval. The black solid lines denote the fitted exponential function of the control group, and the region within the dash lines represents the 95% prediction interval. **(d)** The comparison of SD of release angle between the threshold group and the control group; the notations were the same as shown in panel **c.**

**Discussion**

Based on stochastic resonance identified in nonlinear physical systems, several studies demonstrated that also biological systems can enhance performance in the presence of added noise (Richardson, Imhoff, Grigg, & Collins, 1998). This is probably due to the enhanced detection of sensory signals. The control of balance benefits from such enhanced perceptual information which makes changes in the center of pressure more detectable (Priplata, Niemi, Harry, Lipsitz, & Collins, 2003). The present study extended these findings in two ways: *i*) the study showed that added noise and lowering an error signaling threshold have equivalent effects on improving performance accuracy, consistent with stochastic resonance; *ii*) improvement of accuracy and reduction of variability is retained after removal of experimental interventions and hence have a
prolonged effect on improving performance. This effect has implication for intervention strategies in rehabilitation.

Enhanced error and learning. The concept of stochastic resonance has been applied to various biological systems to enhance signal detection (See Moss, Ward, & Sannita, 2004 for a review). Collins and colleagues have implemented this method into the enhancement of postural stability (Priplata et al., 2002). However, to our best knowledge, no study has been found that applied stochastic resonance to motor learning. Our results suggested that the enhanced error information via stochastic resonance could further improve performance of subjects who already in skilled level. Indeed there were studies that used error augmentation method (i.e. kinematic error was amplified with a certain gain) to enhance learning. For example, Patton and colleagues (Patton, Stoykov, Kovic, & Mussa-Ivaldi, 2006) found that with augmented error feedback subjects had a higher adaptation rate to the force field perturbation than the control. However, the choice of error amplification gain is somewhat arbitrary. Whereas using the mechanism of stochastic resonance, the present study provided theoretical basis for the intervention manipulations for motor learning and rehabilitation.

Retention. Although studies on motor adaptation reported that subjects need a slow process to adapt to a novel motor task (e.g. perturbations were added to the task) while initial behavior was rapidly restored after perturbation was removed (Davidson & Wolpert, 2004; Shadmehr, Brandt, & Corkin, 1998), other researchers also proposed that absence of kinematic error information may delay the adaptation back process (Scheidt, Reinkensmeyer, Conditt, Rymer, & Mussa-Ivaldi, 2000). Their results suggested that the retention of this improved performance was still found even with prolonged practice. In
our experiment, after noise was removed or the threshold was reset to normal, subjects received less error feedback compared to the first 2 blocks. Therefore, maintaining their adapted performance did not result in an increased error that would necessitate a change or even reversal in the adaptations.

Another possible explanation is that the enhanced error information increased subjects’ sensorimotor gain due to the increase of the motoneuron recruitment stimulated by the error information. After multiple days practice and learning, the cortical network connection was strengthened and even involved growth of new connections, which arise long term functional effect (Kandel, 2000). Furthermore, the changed conditions due to removal of noise or raised threshold do not introduce increased error. Therefore, there is no need to change back to the initial performance.

*Noise Magnitude*. An optimal intensity of added noise was not investigated in this study; the noise intensity was chosen using experimenter’s intuition. The intuitive criterion was that the noise sufficiently enhanced error information but the manipulation was undetectable by the subjects. Different noise intensities may affect the results. Stochastic resonance expects that there is an optimal level where the system shows resonance – best response to noise. Although previous research has found that the best perception for different subjects benefited from the same optimal intensity of added noise in visual system (Simonotto et al., 1999), it is not necessarily the case that the same optimal noise intensity can best enhance motor control for different populations (e.g. healthy people versus patients). Thus, further research is needed to investigate whether optimal noise intensity exists that can best enhance learning for different individuals and different populations. Further research is needed to explore the effect generalization to
other movements, such as more complex upper limb movements and movements in lower limbs.

The results corroborated the relevance of stochastic resonance for the generation of movements and suggested that subjects were sensitive to their internal noise and could reduce it in the presence of external noise. The results have implications to intervention strategies rehabilitation training for patients because signal detection and control processes in the sensorimotor system may be enhanced with added noise. Importantly, these effects can persist even after removal of external noise.
References


CHAPTER 4

Stochastic Resonance in Visual Perception Benefits Motor Control

Chapter 3 contains an original manuscript prepared for submission to a journal

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Abstract

In nonlinear threshold systems noise can enhance the detection of sensory signals via the mechanism of stochastic resonance. This study showed that the control of movement benefited from optimally enhanced visual error feedback. Using a throwing task with accuracy requirements in a virtual environment where the result of the throw is sensitive to the ball release angle, four different magnitudes of error-dependent noise were added to the angular position of the manipulandum at ball release that determined the trajectory of the ball. This added noise essentially enhanced the error and variability of the throws that subjects observed after their throw. Consistent with the previous study, performance variability increased due to the added noise. In addition, the results showed that there is an optimal level of noise that maximally enhanced the control of movement accuracy and variability. This work indicated that when noise is added that has an optimal magnitude, the central nervous system can adapt and further decrease its internal noise.
Stochastic resonance in visual perception benefits motor control

Noise has typically been viewed detrimental to signal detection and information processing. In biological systems, noise from internal and external sources continues to challenge the control process of the central nervous system. However, some studies also pointed out positive roles of noise. For example, the phenomenon of stochastic resonance (SR) was originally found by Benzi and colleagues (Benzi, Sutera, & Vulpiani, 1981) in the study of global climate modeling, in which the response of a nonlinear system to a weak periodic input signal is amplified by adding an optimal level of noise (McNamara & Wiesenfeld, 1989).

In contrast to the traditional view of noise, the constructive role of noise via the mechanism of stochastic resonance has been documented in a variety of biological systems (Moss, Ward, & Sannita, 2004). For instance, it was demonstrated that the sensitivity of auditory system is enhanced by the Brownian motion of the inner hair bundle (Jaramillo & Wiesenfeld, 1998). Collins and colleagues demonstrated that human tactile sensation could be enhanced by a non-zero level of noise, whereas excessive noise could decrease this sensation (Collins, Imhoff, & Grigg, 1996). By applying a particular level of random mechanical noise to the muscle tendon, the sensitivity of the muscle spindle receptors to weak movement signals was maximized (Cordo et al., 1996). Aside from the sensory systems, stochastic resonance was also found in the motoneuron synapse of the cat spinal cord (Martinez, Perez, Mirasso, & Manjarrez, 2007). Based on this mechanism Collins and colleagues have recently reported that noise can enhance human balance control both in healthy people and in patients by applying subliminal mechanical noise to the feet (Priplata et al., 2002; Priplata et al., 2006).
The motor output relies significantly on continuous sensory input; due to these intricate interactions it is possible to extend the SR effect from the sensory to the motor system. More specifically, the motor system can benefit from the enhanced sensory information to achieve more accurate and less variable control. However, it is not clear whether there is an optimal level of noise that best enhances the control of movement. The purpose of this study is to investigate whether there is optimally amplified visual error information via SR can improve the control of movement. Feedback about performance error is the driving force for improving accuracy in the control of movement. Mapping the sensorimotor interactions onto the mechanism of stochastic resonance, the input signal is the motor output of the CNS. If the internal motor noise on the signal is low, and the sensory error information is undetectable by the CNS, therefore the internal motor noise can be tolerated. However, the internal noise, even when below threshold, may still alter the output in a spurious fashion. If more noise at optimal level is added to the motor output, then the system may adapt to suppress spurious output and lower its internal noise to compensate for the added noise.

A throwing task called skittles served as the model task. The task is representative for goal-oriented skills where the execution of a discrete movement involves a redundant number of variables that fully determine the result. Using a lever arm manipulandum subjects performed a horizontal forearm movement to throw a virtual ball with the goal to hit a target in the virtual environment. Performance results were quantified by the deviation of the ball trajectory from the target, that is, the minimum distance \( d \) between the ball and the target. The result \( d \) was fully defined by two execution variables, angle \( \alpha \) and velocity \( v \) at the moment of release of the ball. Success of a throw was signaled
to the subject after the trial by changing the color of the target. What counts as success was determined by a threshold value for \( d \). The relation between the execution and result variables is many-to-one and is fully deterministic and known. The two successful trajectories in Fig. 1a illustrate how different combinations of the execution variables can lead to the same result \((d = 0)\). The relation between execution and result variables was captured in the execution space (Fig. 1b). Every throw with the variables \((\alpha, v)\) corresponds to one point in this space. Perfect solutions, \( d = 0 \), are displayed in white and form the solution manifold. Increasing error is shown by increasingly darker grey shades; black denotes a post hit. Assuming that a throwing movement is the signal, noise can be added in the virtual environment to artificially enhance the resulting variability of the throw.

**Figure 1:** Workspace, execution space and solution manifold. (a) The workspace with the position of the center post and target. Three ball trajectories exemplify how different release variables can lead to the same result with zero error, \( d = 0 \) (trajectory 1, 2). Trajectory 3 shows a trajectory with non-zero error, \( d = 30 \) cm. (b) The execution space
and solution manifold. White areas denote zero-error solutions, increasing error is shown by increasingly darker grey shades, black denotes a post hit. The release variables of the first and second trajectory which hit the target correspond to points 1 and 2 (denoted by stars) on the solution manifold, the variables of the third trajectory correspond to the point 3 in a grey-shaded area.

Method

Participants. Twenty four subjects (14 male, 10 female, 24 to 46 years of age) from the Pennsylvania State University volunteered to participate in this experiment. All reported themselves to be right-handed. They were informed about the purpose of the experiment, but were naive about the nature of the manipulations in the experiment. Prior to data collection, subjects were instructed about the experimental procedure upon which they signed an informed consent form in agreement with the Institutional Review Board of the Pennsylvania State University. They were divided into 4 groups, and six of the subjects were randomly assigned to each group.

Apparatus. The apparatus is the same as shown in Chapter 2.

Procedure. Each subject performed the task for a total of 6 sessions distributed over 6 days. The first 3 sessions (block 1) were regarded as baseline training of the virtual task. Noise magnitude was manipulated in the second three sessions (block 2) for each group. In each session subjects performed 240 trials; after each set of 60 trials, subjects could rest for a few minutes. The target skittle (with a radius of 0.05m) was located at the x-y coordinates (0.05, 1.055 m) in the workspace; the center post was centered at the coordinates (0, 0) and had a radius of 0.25m (Fig. 1a). Fig. 1b represents the associated solution manifold. The locations of the target and the center post were so chosen that the
solution manifold was oriented vertically and successful solutions were only sensitive to release angle but not to release velocity. This choice facilitated the noise manipulations explained below.

At the end of each trial, a feedback window with a zoomed display of the target and a segment of the trajectory was shown to inform subjects about their performance. If the ball hit the target and the distance error, defined as the minimum distance between the center of the ball and the center of the target skittle, was smaller than a threshold, the color of the target was changed from the regular yellow to red, signaling a close-to-perfect hit. Subjects were instructed to try their best to hit the target with the virtual ball. The experimenter emphasized that they should avoid hitting the center post because a post hit was penalized with a large error. Typically, one throw lasted 1-2 sec with approximately 4 sec between throws. The experiment duration in each session was approximately 15 min. Subjects were not informed about the change in experimental conditions.
Figure 3: Solution manifold with simulated noise added to the release angle. Noise was added to the angle when the actual release angle $\alpha$ deviated from the center angle $\alpha_c$ with $\alpha \in (1.0, 1.88)$. When the release angle was out of this range, no noise was added. The noise intensity increase linearly with the deviation of $\alpha$ from $\alpha_c$.

Noise Manipulation. Four different magnitudes of noise were added to the release angle to add variance to the ball trajectories that was outside the control of the subjects. The vertical solution manifold was chosen as it is insensitive to the release velocity. This simplified the manipulation, as it was sufficient to add noise to only one dimension, i.e., the release angle. To this end, the angle of the solution manifold $\alpha_c$ was determined to be at 1.44 rad across a wide range of velocities. Noise was added to the angle when the actual release angle $\alpha$ deviated from $\alpha_c$. A previous study using the same solution manifold showed that after practice 95% of all trials were within $\alpha \in (1.0, 1.88)$, corresponding to an error of maximally $d = 3.6$ cm. Noise intensity increased linearly with the deviation from $\alpha_c$. Figure 3 represents the effect of the noise on the solution manifold for Group 2. Note that the added noise only affected the visually displayed trajectory and did not influence the actual performance of the task. There was no mechanical perturbation. Specifically, when the value of the release angle $\alpha$ was collected by the computer, a random number was added, and then the ball trajectory was calculated based on this noisy release angle:

$$\alpha_{noise} = \alpha + (\alpha - \alpha_c) \times n \times \Xi_U$$  \hspace{1cm} (1)
Where $\alpha_{\text{noise}}$ is the noisy release angle, $n$ is the noise magnitude ($n = 0$ for Group 0, $n = 1$ for Group 1, $n = 2$ for Group 2 and $n = 3$ for Group 3), $\xi_n$ is uniformly distributed noise on the interval from 0 to 1. Note that the noise intensity term $(\alpha - \alpha_c)$ is signed. When $\alpha$ deviated to the left of $\alpha_c$ (i.e. smaller than $\alpha_c$), noise intensity was negative. Thus, the noise term pushed the actual release angle away from the solution manifold, which led to a larger error. When $\alpha$ deviated to the right of $\alpha_c$ (i.e. larger than $\alpha_c$), noise intensity was positive, increasing the release angle away from $\alpha_c$ and leading to a larger error. This design ensured that the added noise always enhanced the error information but in a random manner. Error-dependent noise was chosen over Gaussian noise because the release angle (distance error) was always noisy and Gaussian noise could eliminate an error or cause an even larger error. Therefore Gaussian noise could potentially confuse the subjects.

**Data Processing.** Even though participants were instructed to avoid the center post, they occasionally hit the post incurring very large penalties, $d = 60$ cm. To avoid undesired skewing in the processing of the sequence of errors these large errors were “smoothed” by applying a bootstrap method. First, the data were parsed into a series of non-overlapping windows with a size of 30 data points. The window size was chosen to be large enough to obtain sufficiently reliable estimates and small enough to not be confounded with changes due to learning. Second, within each window the outliers due to post hits were removed and the maximum of the remaining data points was determined using bootstrap resampling. Third, the post hits that were removed from the original data were replaced by the maximum multiplied with a gain of 1.5. The bootstrap method avoided that all replaced values within a window got the same maximum value (Zhu &
Statistical Analysis. A mixed-design ANOVA was conducted on success rate data: Group was the between-subjects factor, Block was the within-subjects factor and Session was the nested factor. Posthoc tests with Bonferroni adjustments were performed on significant ANOVA results. The percentage data was transformed by the arcsin square root algorithm before performing the statistical analysis (Zar, 1999) to satisfy the assumptions of the statistical tests. A one-way ANOVA was performed on the performance error and the SD angle among the four groups. The confidence level was set to 0.05 in all statistical tests. Statistical analyses were performed with SPSS (SPSS, version 16.0).

Results

Success Rates. The average percentage of target-hits per session (240 trials) over 6 subjects of each group is shown in Fig. 4a, error bars represent the standard deviations of success rates over 6 subjects per group. After practice in block 1, subjects in the 4 groups reached the same performance level (i.e. the same success rate) ($p_s > 0.05$, posthoc). In block 2 where different magnitudes of noise were added to the release angle, the success rates in group 2 showed a significant increase compared to block 1 ($p < 0.0001$). However, the performance was not significantly better than that of Group 0 and Group 1 ($p_s > 0.05$) due to the high variability of the success rate. Figure 4b represents the average perceived success rate of block 2 in each group with error bars denoting the standard deviations. The perceived success rates in Group 1 to 3 are lower than their actual success rate due to
the noise manipulation. The ANOVA results showed an interaction between Group and Session, $F(6, 40)=5.10, p=0.001$. The perceived success rate showed a significant increase in Group 2 ($p=0.016$, posthoc); however, no change was found in other groups ($ps>0.05$).

![Graph](image)

**Figure 4:** Average success rate over sessions. (a) Average percentage of target-hits per session (240 trials) over 6 subjects of each group; error bars represent the standard deviation of success rates over 6 subjects. Noise was manipulated in Session 4 to 6, and the mean and standard deviation of success rate are their actual performance. (b) Subjects perceived success rate represented by the mean and standard deviation over 6 subjects in each group during Session 4 to 6. The perceived success rates in group 1 to 3 were lower than their actual success rate.

Continuous evaluation of performance. A finer-grained depiction of the time course of errors and standard deviation (SD) of release angle was compared between the 4
groups (Fig. 5). To compress and filter the data for better illustration, averages were calculated over 10 successive trials for each subject’s sequence; subsequently, they were averaged across 6 subjects yielding 144 values. An exponential function was fitted to block 1, and a linear function was fitted to block 2. These results illustrate that when approaching the end of block 1, the subjects in the 4 groups had reached a plateau in terms of performance error and variability in release angle. When different magnitudes of noise were added to each group, the different groups had different perception on their performance errors, which was denoted by the stars. With larger amplitude of noise added, subjects perceived larger error than their actual performance. No noise was added to group 1, not surprisingly, no further improvement was found (linear function fitted slope = 0.00). Also no improvement was found in Group 1 and 3 where relatively small and large amplitude of noise was applied. However, when the noise magnitude was optimal, i.e. at a magnitude of 2, subjects showed further improvement in performance. Similar results were found in the SD angle.
Figure 5: Performance error over average trials for each group. Each panel represents the average error for each group. Average trials were calculated over 10 successive trials for each subject’s sequence and then were averaged across 6 subjects. This calculation yielded 144 values which were denoted as circles. An exponential function $y = a \cdot \exp(-x / \tau) + c$ was fitted to the average errors in block 1 (72 values). A linear function $y = a \cdot x + b$ was fitted to the data in block 2 (72 values). The same averaging procedure was performed on the perceived error in block 2 where noise was added to. The perceived errors were denoted as stars. In Group 0, the noise magnitude is 0; therefore the actual error is the same as the perceived error. For better illustration, the stars were not shown in Group 0. In Group 1 to 3, with larger magnitude of noise added in block 2, the difference between the actual error and the perceived error became larger.
Figure 6: Standard deviation (SD) of angle over average trials for each group. Each panel represents the SD angle for each group. SD angle were calculated over 10 successive trials for each subject’s sequence and then were averaged across 6 subjects. This calculation yielded 144 values which were denoted as filled circles. An exponential function \( y = a \cdot \exp(-x / \tau) + c \) was fitted to the SD angle in block 1 (72 values). A linear function \( y = a \cdot x + b \) was fitted to the data in block 2 (72 values).

To quantify these results and compare the effectiveness of the noise manipulation between groups, the average performance error and SD angle of session 6 (last 24 average trials) in each group were chosen, and the mean and standard deviations were calculated (Figure 7). The performance error results differed significantly between groups,
\(F(3, 95)=39.07, p<0.0001;\) Posthoc tests identified that the error in Group 2 was significantly lower than in other groups. Similarly, the SD angle during the last session was significantly different between the four groups, \(F(3, 95)=53.82, p=0.007;\) again, Group 2 showed a significantly lower level than the other groups. To quantify the relative change in performance due to the added noise in visual feedback, the difference between sessions 3 and 6 (i.e. the last session of each block) in performance error and SD angle were calculated. The means and standard deviations are presented in Figure 8. The improvement in the error was different between groups, \(F(3, 95)=31.47, p<0.0001,\) with Group 2 significantly higher than the other groups \((ps<0.05,\) posthoc\). However, when the noise magnitude was 3, improvement was even lower than for noise magnitude 0, i.e., no noise was added \((p=0.012).\) The relative improvements in SD angle showed the largest change in Group 2, but they were not statistically different between groups due the high variability of each group, \(F(3, 95)=1.37, p=0.258.\)

![Figure 7: The final performance error and SD angle after the noise manipulation. The average performance error and SD angle of the session 6 (the last 24 average trials from](image_url)

98
Figure 4 and 5) in each group were chose, and the mean and standard deviation was calculated for the 24 values. The average error was shown as a dash with error bars denoting the standard deviation. The average SD angle was shown as solid squares with error bars denoting the standard deviation.

![Graph showing error and SD angle improvement](image)

**Figure 8:** The improvement of performance error and SD angle after the noise manipulation. The difference between session 3 and 6 (i.e. the last session/the last 24 average trials of each block) in performance error and SD angle were calculated. The mean and standard deviation was presented. The error improvement was shown as a dash with error bars denoting the standard deviation. The SD angle improvement was shown as solid squares with error bars denoting the standard deviation.

**Discussion**

The present study investigated whether the enhanced sensory information can improve the control of movement based on the concept of stochastic resonance. Four different levels of error-dependent noise were added to the release angle in four groups of subjects during a throwing task. The added noise artificially enhanced the accuracy and variability of the task performance via the visual feedback at the end of each trial. The
effectiveness of the noise manipulation varied with the noise amplitude for different groups of subjects. The success rate, performance error, and the SD angle results all suggested that an optimal level of noise added to the motor output (i.e. release angle) benefited the further improvement of the control of skilled movements.

It was demonstrated that human has better visual perception on stationary images obscured with certain level of noise than without noise (Simonotto et al., 1997). An fMRI study on visual perception indicated that by applying different noise to a gray scale graph, the subjects who perceived the graph had the highest neural activation in the visual cortex in the case of optimal noise intensity (Simonotto et al., 1999). It was proposed that visual information provided one of the most important sensory cues for motor planning and motor execution (Triesch, Ballard, & Jacobs, 2002). The present study suggested that the CNS could integrate the optimally enhanced visual error information into the control of movement. It could further increase the control accuracy and decrease control variability.

One alternative explanation for the current results is that the subjects paid more attention to the task during block 2 where noise was added, because the noise manipulation essentially increased the difficulty of the task. Therefore subjects could better control their movement due to attention (Tloczynski, 1993; Wulf, 2007). However, the task is most difficult at the highest level of noise. Hence, if subjects paid more attention to their performance due to increased task difficulty, their performance improvement should have been the highest for the highest noise magnitudes. This was not supported by the results, as performance of Group 3 was inferior to other groups. The improvement in Group 3 was even worse than Group 0 where no noise was added, i.e.,
the error became worse after the noise manipulation. Therefore, this interpretation of the results cannot be upheld.

One point that requires clarification is that the optimal noise level found in this study may not be generalized to other ones; the result is specific to the task and specific to the task parameters chosen in the experiment. It is likely that the optimal noise level is different for other tasks and other experiment parameters. It is also possible that a noise level between 1 and 3 is even more effective. Therefore, the current study concludes that not all noise levels produce the same effect; rather there is sign of resonance to one magnitude.

In neuropathy patients, sensory deficits are associated with increased sensory threshold of receptors (Mizobuchi et al., 2002; Simoneau, Derr, Ulbrecht, Becker, & Cavanagh, 1996). Different studies have shown that the sensory threshold can be lowered via added noise (Dhruv, Niemi, Harry, Lipsitz, & Collins, 2002; Richardson, Imhoff, Grigg, & Collins, 1998; Simonotto et al., 1997). By applying mechanical vibrations to the feet of diabetes and stroke patients, Priplata and colleagues have shown that the thus enhanced somatosensation increased the postural stability (Priplata et al., 2006). The present study provided another possible demonstration of potential applications of the stochastic resonance mechanism to rehabilitation of motor function.
Reference


CHAPTER 5

General Discussion

During everyday activities we move with considerable variability. It has long been recognized that to achieve a given task goal more than one solution exists (Bernstein 1967). Hence, when such actions are repeated, every “repetition” is slightly different. Aside from variability due to equivalent solutions in redundant tasks, there are other sources of variability that originate in the random fluctuations of the sensorimotor system and are commonly referred to as noise. Noise is an inherent element of the biological system at all levels of analysis ranging from fluctuations in the in neural activation in the cortex to variations in the muscles’ contractile properties in the periphery. Analysis of this seemingly random variability has given some insights into the strategies or constraints of the CNS during the control of movement. Many studies have demonstrated that variability in performance variables declines with practice. However, this overt decrease in variability is only a superficial sign of changes in the nervous system. To further uncover underlying sources of such changes in variability Sternad and colleagues (Cohen & Sternad, accepted; Müller & Sternad, 2003, 2004; Müller, Frank &Sternad, 2007) developed a decomposition method that parsed changes in variability into three components. Several studies that applied this so-called TNC-analysis revealed that learners first choose an approximate solution to a given task, then further fine-tune the execution of the movement and finally minimize error in task performance while allowing variability in execution.
In contrast to the typically negative perspective on variability and noise for the control of movements, there are also potentially positive aspects of noise. One example is the phenomenon of stochastic resonance (SR). The concept of SR is that the response of a nonlinear system to a weak periodic input signal is amplified by the presence of a non-zero level of noise (McNamara & Wiesenfeld, 1989). An optimal level of noise added to the system results in the maximum detection of the signal input, whereas a larger amount of noise will degrade signal detection and system performance. The constructive role of noise via the mechanism of SR has been demonstrated in a variety of neurophysiological systems (Moss, Ward, & Sannita, 2004). Given that the motor output relies significantly on continuous sensory input, it is possible to extend the SR effect from the sensory to the motor system. More specifically, the motor system can benefit from the enhanced sensory information to achieve more accurate and less variable control.

To examine the role of variability in motor control and learning, a throwing task called skittles served as a model task. The key characteristic is that the number of execution variables is larger than the result variables, i.e., the execution system is redundant with respect to the result and many different combinations of execution variables can lead to the same result. The nonlinear relation between the execution and the result and the topology of the solution manifold can be changed by placing the target at different locations. In addition, the visual feedback of the performance result can also be manipulated by changing the threshold that provides a signal of success. These features of the task allow investigation of the question how subjects choose a movement strategy out of many others and how perceptual information affects the control of movement.
In Experiment 1, the role of variability on the selection of motor strategies was investigated. Analysis of the variability in execution with respect to the success in the task revealed that actors only decreased their motor variability in the execution variables that mattered for the success of the task. This has been shown before that the CNS selects motor strategies that only suppress the variability that interfere with the task performance (Todorov & Jordan, 2002; Scholz & Schöner, 1999). Going beyond the previous findings, our results suggested that the CNS had the capability of finding the most error-tolerant strategies given a certain degree of sensorimotor noise. Using matrix-based evaluations of the expected performance, equivalent to the mathematical framework of decision theory (Trommershäuser, Gepshtein, Maloney, Landy, & Banks, 2005), we demonstrated that subjects did not plan in terms of a single solution but took a family of solutions into account defined by adjacent values of execution variables. In sum, this study demonstrated that actors take their variability into account when selecting motor strategies.

There is always noise in performance, even after extensive practice. In Experiment 2, we showed that skilled subjects further decreased their motor noise benefiting from the enhanced sensory error information via the mechanism of SR. More importantly, when the enhanced information was eliminated, improved performance was retained. The results suggested that the CNS had the potential to further decrease its intrinsic noise and increase its movement accuracy via external manipulation, i.e., enhancing the sensory error information by adding noise or lowering the error signaling threshold. Importantly, improved performance can persist even after removal of external manipulations. The results have implications for the design of intervention protocols in rehabilitation.
As a follow up study, Experiment 3 demonstrated that the magnitude of the noise added to the system is an important variable and the control of movement only benefits from optimally enhanced sensory information. Comparison of the effectiveness of four different levels of error-dependent noise revealed that, consistent with the framework of stochastic resonance, the effect of noise on performance significantly depended on the noise amplitude. The results indicated that an optimal level of noise stimulated further improvement of the control of skilled movements.

**Adaptation and After-Effects**

Motor commands that generate motor outcome are generated by the CNS by taking into account the state of the limb and the state of the environment. When experiencing a novel environment, the actual performance typically deviates from the desired performance. During practice, motor commands are modified based on the discrepancy between the actual and desired motor output and a new sensorimotor map is formed (Shadmehr & Mussa-Ivaldi, 1994; Flanagan & Rao, 1995). For example, learning to adapt to novel forces in one direction of the reaching movement resulted in the generalization to other directions even though this generalization decreased with the angular distance (Sainburg, Ghez, & Kalakanis, 1999). Random perturbations such as induced by randomly changing gains of the force field, were also applied to characterize the adaptation to a randomly varying environment (Takahashi, Scheidt, & Reinkensmeyer, 2001). The results suggested that the CNS adopted a dual strategy, i.e., both the internal model was updated and the arm impedance was increased to resist the variations of the force field.
A similar study conducted by Burdet and colleagues (Burdet, Osu, Franklin, Milner, & Kawato, 2001) showed that subjects used impedance control to stabilize arm movement in a destabilizing force field (i.e. the force direction was perpendicular to the hand velocity and its magnitude was proportional to the deviation of the hand from a straight line). The results in Experiments 2 and 3 apparently did not support this idea of increasing muscle stiffness. The possible reason is that we did not apply a mechanical but a perceptual manipulation. Our results suggested that the improved performance was due to the enhanced error feedback via the mechanism of SR. Further, if the strategy of impedance control was adopted, in Experiment 3 the group who experienced the largest noise magnitude should have the largest improvement in performance, which is not the case in our results. Hence these augments do not apply to our results. Rather, the fact that adaptations did not scale with noise magnitude is a sign that stochastic resonance is a more likely candidate for explanation.

**Augmented Information Feedback**

Actors require information in order to learn a new task. Intrinsic information, predominantly from proprioception, plays an important role for the improvement in performance. Extrinsic or augmented information provides supplementary information to learners. In the skittles task, the change of target color signaling success or failure of the trial is essentially augmented information feedback. One important type of augmented information feedback is knowledge of result (KR) which refers to verbalizable extrinsic information about the performance outcome. Almost 100 years ago Thorndike (1927) asked blindfolded subjects to draw lines of different lengths and contrasted conditions where he presented or withdrew verbal KR. As to be expected subjects’ performance was
significantly better with KR than without KR (i.e., experimenter said ‘right’ if the length was within a tolerance band around the correct length, otherwise providing a ‘wrong’ signal). Although it was also shown that learning could happen without augmented feedback, it was necessary that subjects received a reference-of-correctness that enabled them to evaluate performance themselves (Zelaznik, Shapiro, & Newell 1978). Our results in Experiments 2 and 3 suggested that manipulating augmented information feedback (i.e. enhancing error information) could further improve skilled performance. Especially the results in Experiment 3 indicated that the amount of error information mattered for performance improvement.

It was shown that the relative frequency of KR is crucial for learning. Relative frequency refers to the percentage of trials after which KR is provided (Schmidt, 1988). Salmoni and colleagues concluded that decreasing the relative frequency of KR increased learning (Salmoni, Schmidt, & Walter, 1984). Although Swinnen (1984) found that subjects performed best with the highest relative frequency of KR, it appears that reducing the relative frequency of KR can be also detrimental or beneficial to performance. In Experiment 3 the relative error information was manipulated. Relative error information refers to the rate between success and failure trials. Our results in Experiments 3 suggested that the relative error information of KR rather than the frequency of KR was crucial for learning. Too high or low relative error information is of less benefit to the performance than the optimal one. Therefore, it is possible that the relative error information of KR could interpret the discrepancy between the above two studies.
Retention

In Experiment 2, one primary result was that subjects retained their improved performance over a relatively long interval. Importantly, performance improvement is only regarded as learning if the improved performance is retained. Otherwise, the observed changes are only short-term adaptations. Examples such as riding a bicycle and driving a car are motor skills that are never forgotten. There are also examples from laboratory studies that showed retention after long intervals. Typewriting is a motor skill where decreasing the time between key strokes is usually set as the task goal. Towne (1922) found long retention of typing skills over intervals of months. Fleishman and Parker (1962) used a three-dimensional tracking task and showed that motor skills could be retained over years without further practice. In Experiment 2, we showed retention over five days (i.e. 1200 throws in total) after the removal of enhanced error information, which supported the previous results.

On the other hand, the retention results in Experiment 2 were seemingly inconsistent with many recent studies that studied adaptations under manipulations of the external force field or visual motor rotation during a reaching movement (Shadmehr & Mussa-Ivaldi, 1994; Flanagan & Rao, 1995). When these manipulations are removed subjects return to the initial conditions within several trials. However, there are significant differences between these manipulations and the ones used in the present experiment. When the force field or visual motor rotations were removed, the adapted motor commands induced substantial deviations from the desired performance in the workspace without additional forces. Therefore, the errors drove the updating of sensorimotor map and the system adapted back to the initial performance. In contrast, in Experiments 2 and
3 subjects experienced even less error compared to the first 2 blocks after noise was removed or the threshold was reset to normal. Therefore, maintaining their adapted performance did not result in an increased error that would necessitate a change or even reversal in the adaptations. There are studies that showed prolonged retention by eliminating the kinematic errors after removing the perturbing forces (Scheidt et al., 2000). More specifically, when the force field was removed and the limb trajectory error was prevented simultaneously, subjects persisted in generating large forces even though they were unnecessary to perform an accurate reach. The control group that was shown kinematic error adapted back at a faster rate than the experimental group. Similarly, when the after-effect (i.e. curved hand path) of the force field perturbation ensembled the desired movement, subjects persisted to perform the same motor pattern (Patton & Mussa-Ivaldi, 2004). Therefore, the significantly decreased error feedback after removal of the intervention manipulations and the success reward feedback potentially prevented the reversal of adaptations.

Taken together, the current thesis provided insight on how the CNS selects control strategies in the presence of sensorimotor noise and noise from the environment. It extended our understanding on the role of intrinsic and extrinsic variability during the control of movement. It suggested potential intervention manipulations for motor learning and rehabilitation.
REFERENCES


