

Paper:

Neurophysiological and Dynamical Control Principles Underlying Variable and Stereotyped Movement Patterns During Motor Skill Acquisition

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While novices who are unfamiliar to a new motor skill typically show variable and unstable movements, highly skilled experts show a stable and accurate performance. These distinct differences in motor control between experts and novices have led researchers to hypothesize that neuromotor noise is reduced in the process of motor skill acquisition. On the other hand, it should be noted that novices' movements have other characteristics; they are habituated and stereotyped. In this review, we discuss the principles governing spatiotemporal organization of movements in novices and experts while solving specific motor problems under varied conditions, by introducing experimental and theoretical studies that use neurophysiological techniques such as electromyography, functional magnetic resonance imaging, and transcranial magnetic stimulation, and mathematical models such as stochastic and dynamical models. On the basis of the findings from a variety of perceptual-motor skills (e.g., ball-throwing, badminton smash, long-distance running, piano and drum performance, street dance, a popular hand game of rock-paper-scissors, and temporal order judgement task), we argue that the novices' characteristic movement patterns were organized under specific constraints and typical strategy, without which the variability would increase even more, while experts' movements were organized with functional and compensatory variability that can drive out erroneous noise variability. We also showed that in a particular type of interlimb coordination, skilled and unskilled movement patterns could be seamlessly described as the time evolution of nonlinear and self-organized dynamical systems, suggesting that the dynamical systems approach is a major candidate for understanding the principle underlying organization of experts' and novices' movements.

Keywords: human motor skill, learning, neuroscience, dynamical systems approach, novices and experts

1. Introduction

Highly skilled athletes, musicians, or craftspersons who have acquired specific perceptual-motor skills through long-term practice can show stable, precise, and accurate performances that even cutting-edge artificial intelligent machines or robots cannot do. For example, top-level golfers can perform an approach shot directed to land the ball on the green from various distances and under various conditions (e.g., on rainy or windy days, from hazard areas such as bunker or rough). On the other hand, novices who are quite unfamiliar with a new motor skill typically show highly unstable, variable, and erroneous performances that seem to be clumsy. For example, beginners of golf can rarely hit a ball with a golf club, and even if the club happens to strike the ball, it almost always flies or rolls in an unintended direction.

These distinct differences in motor control between experts and novices have led researchers to hypothesize that neuromotor noise arising from random firing in the sensorimotor pathways, including the central and peripheral nervous systems, should be reduced for motor skill acquisition [1, 2]. However, it should be noted that the movements of novices are characterized as not only unstable, variable, and erroneous but also consistent, habituated, and stereotyped. For example, Bernstein [3] pointed out that during cycling, when the bicycle inclines to the left, a beginner typically and instinctively turns the handlebars to the right (i.e., wrong and opposite direction). Novices of street dance have difficulty in producing variable and flexible movement patterns, that is, the coordination of joint movements are fixed [4]. On the other hand, experts



can perform variable and flexible movements depending on the context or task requirements. In addition, theoretical development for analyzing and interpreting variable and complex time-series has enabled researchers to reveal the critical role of variability in motor control and learning [5,6]. Therefore, one of the fundamental challenges in the study of human motor control and learning is to understand the principles that govern the spatiotemporal organization of movements in novices and experts while trying to solve specific motor problems under variable conditions. In this review, we addressed this issue by introducing a variety of perceptual-motor skills including ball-throwing, badminton smash, long-distance running, piano and drum performance, street dance, a popular hand game of rock-paper-scissors (RPS), and temporal order judgement (TOJ) task.

In Section 2, we show the characteristics of skilled and unskilled movements from a classical point of view (i.e., motor learning for noise reduction). In Section 3, we show typical electromyographic (EMG) patterns of co-contraction of antagonistic muscle pairs of novices whose performance was more variable and erroneous than those of experts. In Section 4, we introduced studies demonstrating that stable and accurate performances can be produced by functional and compensatory organization of variable executing parameters. In Section 5, we introduced a statistical estimation, Bayesian integration, in which variability plays a critical role in estimating the optimal dependence on prior knowledge (i.e., memory) and sensory information. In Section 6, we showed an example in which skilled athletes who have played a specific-type of sport have superior ability to inhibit typical responses. We also discussed the neural correlates of response inhibition. In Section 7, we argue that the possibility that a nonlinear dynamical approach can describe the spatiotemporal organization of movements in novices and experts as the time evolution of self-organized systems.

2. Reduced Variability in Performance and Movements During Skill Acquisition

Novices who are unfamiliar with a novel motor skill typically show more variable performances, movements, and movement-related parameters such as EMG activities in a variety of motor skills than experts do. For example, Sakurai and Ohtsuki [7] examined the characteristics of muscle activities in the forearm, upper arm, and back (trunk) muscles, and performance accuracy of skilled and unskilled individuals during badminton smash and found that the novices showed less constant time from peak EMG amplitude to impact and more variable performances. Using analysis of covariance, Nakayama et al. [8] found that long-distance runners attained higher running speed and smaller variability in stride intervals than non-runners. Fujii et al. [9,10] reported that in repetitive rapid tapping task with a drumstick, professional drummers showed less variable performance, measured in terms of inter-tapping intervals, and a lower level of

muscle co-contraction than non-drummers. Miura et al. [4] reported that in the case of a whole-body sensorimotor synchronization task with knee flexion and extension movements in a standing position to a metronome beat with various beat rates, expert street dancers showed more stable coordination pattern than non-dancers.

The characteristics found in the above studies have been confirmed by not only cross-sectional studies (i.e., expert–novice comparison studies) but also longitudinal studies in which changes in learning-related parameters within the same individuals in the process of motor skill acquisition were examined. Sakurai and Ohtsuki [7] examined the effect of practice on performance and muscle activities for badminton smash and found that the peak amplitude of the wrist flexor EMG tended to appear before the time of impact, which was typically observed in skilled badminton players. In addition, a number of studies have suggested that movement outcomes and patterns become more consistent with practice for a variety of skills such as reaching [11], tracking [12], typing [13], slalom-like skiing task [14], and ball-throwing [15].

3. Stereotyped Co-Contraction of Antagonistic EMGs in Movements Performed by Novices or Under Physical/Psychological Perturbations

Novices' performances are variable on one hand, but the underlying motor control strategy can be consistent and stereotyped on the other hand. For example, previous researches assessing EMG activities have consistently indicated that compared to skilled individuals, novices are likely to show higher levels of co-contraction of antagonistic arm muscles during the execution of unfamiliar motor tasks such as piano performance [16] and drumming performance [9,10]. An experiment employing reaching movement tasks [17] also demonstrated that motor skill learning led to gradual decreases in co-contraction levels of both the arm and shoulder muscles, which were highly correlated with measured joint stiffness. Importantly, although at the very beginning of learning the participants of this experiment revealed torque profiles that were variable from trial to trial, they soon achieved occasionally successful trials. Osu et al. [17] attributed the reason for this finding to increased muscle co-contraction levels, insisting that it is an effective strategy used by the central nervous system (CNS) early during learning to improve movement accuracy, even in the absence of a fully formed internal model of the effector, by increasing the viscoelastic resistance of the musculoskeletal system. Moreover, a simulation study by using a driven damped oscillator [18] indicated that viscoelastic resistance led to an output signal that is tightly coupled to the input, helping the CNS to tame the perturbing effects of non-muscular forces.

We may also apply this view to particular circumstances in which motor outputs can be variable. It is generally known that the co-contraction levels increase

in expectation of a physical perturbation. Interestingly, previous experimental studies demonstrated that psychological stress exerts the same effects as that by physical perturbation using situations that accompany extra cognitive load [19], increased precision demands [20,21], or social-evaluative threats [22,23]. These sources of psychological stress could provide a condition where a new perceptual-motor solution has to be found [24] due to increased neuromotor noise [19], which possibly stems from an altered state of the motor system (e.g., increased corticospinal tract excitability [25–27] during early stages of learning. Whether during movements at early stages of learning or those under physical/psychological perturbations, stereotyped muscle co-contraction can be an adaptive strategy to stabilize movements by freezing the excessive biomechanical degrees of freedom [28] and mitigating the adverse effects of various sources of noise on motor performance.

4. Variability as a Result of Compensatory Coordination

To organize spatiotemporal pattern of movements as the solution for motor problems, humans have to deal with huge degrees of freedom in each element of the motor system (e.g., joints, muscles, neurons, synapses) [28,29]. Because the individual degrees of freedom are subject to variation, for example, fluctuation in the activation level in α -motoneuron pool in the spinal cord, human movements inevitably become variable. Statistically, when individual degrees of freedom vary randomly, the whole variance equals the sum of the individual variance. Therefore, even if the individual degrees of freedom have only a small variance, the whole system with huge degrees of freedom is obliged to show large variability.

The number of degrees of freedom in human motor system is not only very huge but also highly redundant. This means that when the individual degrees of freedom are coordinated to compensate one another, variability of the whole system can be smaller than the sum of variability of the individual degrees of freedom. Recent development of mathematical/statistical methods has made it possible to quantify functional or task-related structure of variability [15,30–32]. For example, Kudo et al. [15] showed that the compensatory coordination among executing parameters improves the process of motor skill acquisition by using a statistical method to evaluate this particular type of coordination. In their experiment, the participants practiced a ball-throwing task aimed at a stationary target for 150 times with the non-dominant hand. The results showed that the mean absolute error (i.e., mean absolute distance from the ball landing point to the target) reduced with practice, and the compensatory relationship among the release parameters (i.e., ball-release point, and orientation and magnitude of velocity vector of the ball at the release point) improved. Similar functional organization of variability has been observed in reaching [20], force production with fingers [33], and aiming [34] tasks, all of

which required accuracy. These studies suggest that noise variability in novices changes into flexible and adaptive variability in experts during motor skill acquisition.

5. Bayesian Integration: Variability Plays a Critical Role in the Integration of Prior Knowledge with Sensory Information

Experienced golf professionals who calculatingly play in The Open Championship know a lot about Links courses (e.g., slope of the green, grain of grass, and direction and force of the wind). Without prior knowledge, the players could not select the optimal direction and strength of stroke in various situations. This example implies that expert athletes or players should have an appropriate knowledge about the tasks or environments through previous experiences. However, trial-by-trial variations often arise in the tasks and environments. When the variation is considerable, too much dependence on prior knowledge may bring fatal erroneous judgements or actions. In this case, experts should perform based on current information that they sense on site by giving less priority to prior knowledge. Taken together, experts should appropriately integrate prior knowledge with current sensory information. The Bayesian integration model [35–39] gives us an optimal solution for integration in a probabilistic manner.

Recent psychophysical studies have shown that Bayesian integration is implemented in various human behaviors such as reaching [40,41], reproducing forces [35], and timing [42–45]. In this review, we introduce data regarding the perceptual task requiring TOJ of two tactile stimuli, one delivered to each hand.

The stimulus onset asynchrony (SOA) of the two stimuli is defined as that which are truly delivered to the hands (T_{true}) and that which are represented in the early stage of sensory processing (T_{sensed}). These parameters can be formulated using the Bayesian theorem as follows:

$$p(T_{\text{true}}|T_{\text{sensed}}) = \frac{1}{a} p(T_{\text{true}}) p(T_{\text{sensed}}|T_{\text{true}}), \quad \dots \quad (1)$$

where a is the normalization constant, $p(T_{\text{true}})$ is the prior of T_{true} , $p(T_{\text{sensed}}|T_{\text{true}})$ is the likelihood of T_{sensed} when T_{true} is given, and $p(T_{\text{true}}|T_{\text{sensed}})$ is the posterior of T_{true} when the CNS perceives T_{sensed} .

Miyazaki et al. [45] experimentally imposed biased Gaussian distributions on trial-by-trial variability of the true SOA between the two stimuli (**Fig. 1A**). Here, we assumed that the participants can learn the biased Gaussian distribution as the prior and that the likelihood also had a Gaussian distribution. Then, we can calculate the optimal estimate for the SOA, $T_{\text{estimated}}$ (for details, see Kording et al. [40] as follows:

$$T_{\text{estimated}} = (1 - k)\mu_{\text{prior}} + kT_{\text{sensed}}, \quad \dots \quad (2)$$

where

$$k = \frac{\sigma_{\text{prior}}^2}{\sigma_{\text{prior}}^2 + \sigma_{\text{sensed}}^2} \quad \dots \quad (3)$$

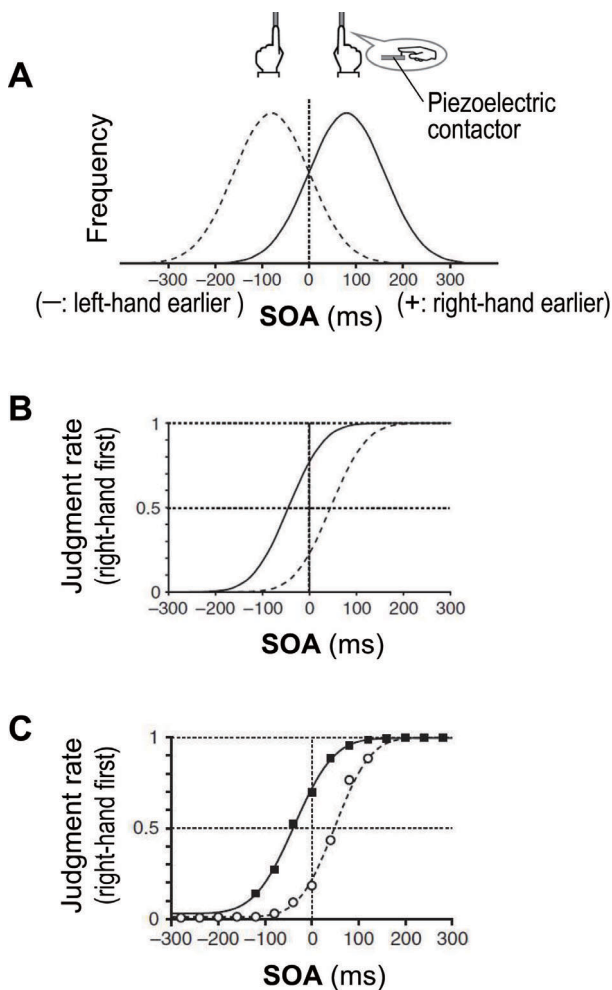


Fig. 1. Bayesian integration in temporal order judgement (TOJ) of two tactile stimuli, one delivered to each hand [45]. **A:** Prior distribution of the stimulus-onset asynchrony (SOA) of the two stimuli. On the x-axis, the positive values of the SOA signify that the right hand was stimulated earlier than the left, and the negative values signify the left hand was stimulated earlier. The y-axis is the frequency of the SOA. The solid Gaussian has a mean (μ_{prior}) of 80 ms and a standard deviation (SD; σ_{prior}) of 80 ms. Given this prior, participants were exposed to stimulus pairs with the right hand being stimulated earlier in $\approx 84\%$ of the trials. Conversely, given the dashed Gaussian ($\mu_{\text{prior}} = -80$ ms, $\sigma_{\text{prior}} = 80$ ms), participants were exposed to stimulus pairs with the left hand earlier in $\approx 84\%$ of trials. **B:** Predictions of TOJ responses by Bayesian integration model (Eq. (4)). The psychometric functions shift away from peaks of the prior distributions. **C:** Experimental observation for tactile TOJ. The psychometric functions of the participants' responses were in accordance with the Bayesian integration model. The opposing effect of lag adaptation has been observed in the multi-sensory [79–81] and multi-feature [82] integrative tasks. Bayesian models predict that lag adaptation occurs at the stage of likelihood (i.e., early sensory processing) [83] and that the prior-dependent Bayesian effects cannot be observed under strong lag adaptation [45]. In the tactile TOJ between the hands, lag adaptation should not occur and a Bayesian shift appears.

μ_{prior} and σ_{prior} denote the mean and standard deviation (SD) of the prior distributions, respectively. The σ_{sensed} denotes SD of the likelihood, that is, the size of the sensory uncertainty (i.e., inverse of sensory resolution) regarding the SOA. As shown in Eq. (3), the optimal estimate $T_{\text{estimated}}$ is obtained as a weighted sum of μ_{prior} and T_{sensed} .

The Bayesian integration model predicts the TOJ response as follows (for details, see Miyazaki et al. [45]):

$$d_u = - \left(\frac{\sigma_{\text{sensed}}}{\sigma_{\text{prior}}} \right)^2 \mu_{\text{prior}}, \quad \dots \quad (4)$$

where d_u denotes the horizontal transition of the psychometric function of TOJ according to the prior distribution. The Bayesian model predicts that the psychometric function shifts away from the peaks of the prior distributions (**Figs. 1A, B**). Such a psychometric shift was observed in the tactile TOJ (**Fig. 1C**). The psychometric shift implies that the participant's TOJ was biased toward the order that they had previously and most frequently experienced. For example, after the participants frequently experienced stimulus pairs with the right hand stimulated earlier than the left (solid lines **Fig. 1A**), their judgement rate of the right-hand-first increased (solid lines **Figs. 1B, C**). Thus, Bayesian integration induces the temporal order estimation depending on prior experience.

The dependency on the prior experience is determined in the size of the variability (Eq. (4)). When the variability of σ_{prior} is smaller (i.e., reliability of prior information is higher), the Bayesian estimate depends more on the prior experience. Conversely, when the σ_{prior} is larger, the estimate depends less on the prior but more on the current sensory information. Theoretically, the Bayesian strategy minimizes the mean square error (MSE) of the estimate from the actual target state. The MSE can be expressed as follows [40]:

$$MSE = k \sigma_{\text{sensed}}^2 \cdot \dots \quad (5)$$

Note that the coefficient k (Eq. (3)) is always smaller than 1. This implies that Bayesian integration inevitably reduces the effect of sensory noise that is inherent to our nervous system.

Here, we should also note the side effects of Bayesian integration. For example (solid lines **Fig. 1C**), after the participants frequently experienced the stimulus pairs with the right hand stimulated earlier, they tended to judge even the stimulus pairs in which the left hand was stimulated slightly earlier (e.g., $\text{SOA} = -20$ ms) as right-hand-first. Such a judgement is an illusory or erroneous response. Thus, Bayesian integration can increase our success rate by depending on a stereotyped event in prior experience, but it can also lead to erroneous behavior or evaluations with infrequent or unfamiliar events. These effects can explain the reason why players in sport games are often faked or tricked by unfamiliar events. Experts at faking opponents would cleverly inculcate the prior into the opponents in the context of the games. Moreover, players skillful at avoiding the fakes may be able to in-

hibit the responses biased to the stereotyped event in the prior experience.

6. Neural Mechanisms Related to Response Inhibition

In baseball, a batter has to decide to swing or not to swing within a fraction of a second after the pitcher throws the ball. For better batting performance, the batter has to rapidly inhibit their ongoing swing when they judge the ball thrown out of the strike zone. However, novices in baseball batting usually have difficulty in stopping their swing movement once they start to swing the bat.

In the area of experimental psychology and neurophysiology, this type of motor inhibition has been studied by using Go/NoGo task [46–48] or stop signal paradigm [49–51], in which rapid inhibition of planned or ongoing movement is required. In addition, recent neuroimaging studies using functional magnetic resonance imaging (fMRI) have shown that the neural networks associated with inhibitory processing, including the dorsolateral and ventrolateral prefrontal cortices (DLPFC and VLPFC, respectively), supplementary motor area (SMA), anterior cingulate cortex (ACC), and temporal and parietal lobes [52, 53].

While comparing athletes and non-athletes, Kida et al. [54] reported that skilled baseball players show shorter Go/NoGo reaction times than tennis players and non-athletes, although there were no differences in the simple reaction time in players either for sports experience or skill levels. Their longitudinal study of high school baseball players also showed that an intensive two years of baseball practice improved the Go/NoGo reaction time, while the simple reaction time remained constant. Nakamoto and Mori [55], used event-related potentials (ERPs) obtained by time-locked averaging electroencephalography (EEG) and found that the amplitudes of P300 in NoGo trials, which have been interpreted as the strength of response inhibition, were larger in baseball players than in controls at frontal electrodes when the stimulus–response mapping was similar to that used in baseball batting. They suggested that baseball players have stronger brain inhibitory functions that can stop movements as quickly as possible. Similar findings using ERPs during Go/NoGo tasks were also reported in fencers [56]. These studies indicate that neural plastic changes found in Go/NoGo tasks are related to the acquisition and execution of motor skills during extensive daily physical and cognitive training that requires quick Go or NoGo decision making.

Kadota et al. focused on the modified RPS task [57, 58]. The RPS gestures are in a three-sided impasse (i.e., rock wins over scissors, but loses to paper; paper wins over rock, but loses to scissors; and scissors wins over paper, but loses to rock). This game is frequently used in daily life, and the responses are well-learned behaviors. In the modified RPS task, participants respond quickly to a presented gesture signifying rock, paper, or scissors. Be-

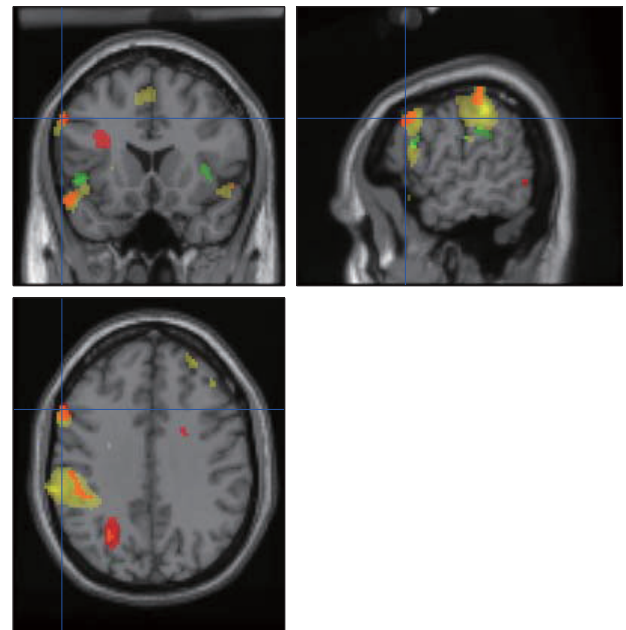


Fig. 2. Targeting of the left middle frontal gyrus for transcranial magnetic stimulation (TMS). A: Spatial overlap between activation areas during modified rock-paper-scissors (RPS) task. Red significant areas activated in the lose compared with the win group. Yellow significant activation in the lose group. Green significant activation in the win group. All regions shown are significant activation areas, $P < 0.001$ uncorrected. B: Illustration of the TMS experiment for a participant using the system that can precisely control stimulus location on the brain [58].

cause losing is more difficult than winning, it is thought that the win response is the stereotyped response in the modified RPS task and that the difficulty in making positive attempts to lose reflects a malfunction of stereotyped response inhibition [59]. Recent fMRI studies have shown that the prefrontal cortex is activated when healthy participants attempt to purposefully lose [57, 58, 60], suggesting that the prefrontal cortex is involved in an attempt to lose and may play a role in the inhibition of stereotyped behavior.

However, while the results derived from fMRI studies can show brain activities relating to the task, they cannot show the specific functions of the activated brain regions. Kadota et al. [58] therefore investigated the causal relationship between the brain area detected by fMRI and the behavior of participants by single-pulse transcranial magnetic stimulation (TMS) that is used as a momentary interference technique in a stimulated brain area. To examine the critical time interval during which the cortical area was involved in the inhibition of the stereotyped response during the modified RPS task, we applied single-pulse TMS at various times (ranging from -500 ms before the onset of the visual stimulus to $+300$ ms after the onset of the visual stimulus). From the fMRI data, participants in the lose condition showed higher activation of the left DLPFC as compared to those in the win condition (**Fig. 2**). If the left DLPFC was essential for the inhibi-

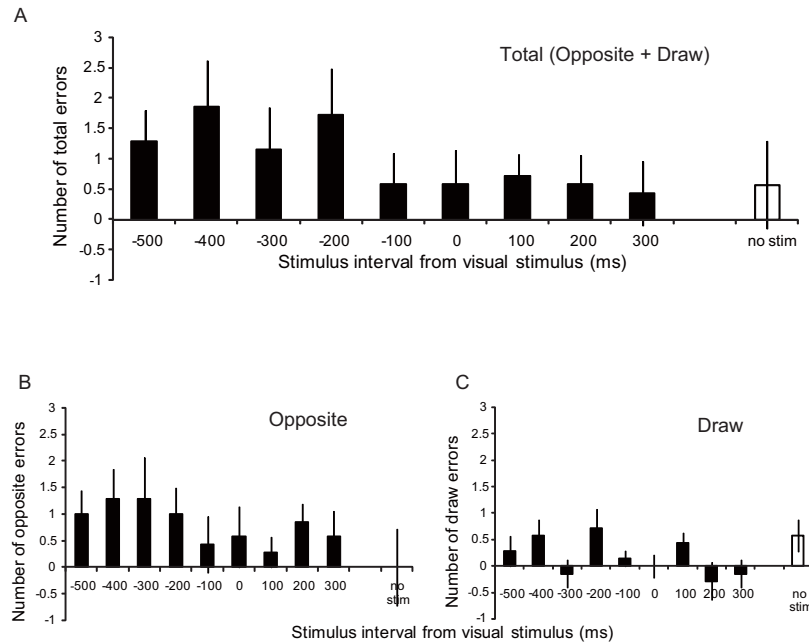


Fig. 3. The increase in the number of errors from the win to the lose condition (mean \pm standard error [SE]) following TMS at each stimulus interval (black bar) and with no stimulus (open bar). A: Total number of response errors, B: opposite-type errors, C: draw-type errors [58].

tion of stereotyped responses, the correct responses would decrease following single-pulse TMS of this area during the lose task. We delivered TMS over the left DLPFC when participants were trying to win or lose and compared the effect of TMS. The number of response errors, which was calculated from subtraction of the error numbers in the win condition from the numbers in the lose condition, increased when TMS was delivered at around -200 ms stimulus interval in comparison with no stimulation (**Fig. 3**). In particular, participants tended to show an increased number of opposite-type errors (i.e., to win erroneously in the lose condition). Taken together, these results indicated that the left DLPFC is an essential neural substrate for the inhibition of stereotyped responses.

These studies may indicate a neurophysiological mechanisms underlying stereotyped and nonstereotyped behavior (i.e., flexible and context-dependent behaviors), which characterize the novices' and experts' movement patterns. Because deactivation of a certain brain structure was also reported necessary to produce context-dependent response (i.e., timing and reaction time response to identical visual stimulus) [61], characteristics of brain activities of experts (and novices) should be investigated more extensively in a variety of perceptual-motor skills to understand the neurophysiological principles of skill acquisition.

7. Dynamical Principles of Motor Skill Acquisition

Novices become experts after long-term intensive and deliberate practice [62]. The process of motor skill acquisition is neither smooth nor linear, but rather discontinu-

ous and nonlinear. There are several characteristic stages in skill acquisition [3, 63], and diverse phenomena, such as sudden improvement of performance, temporary deterioration in a once-acquired skill, or qualitative change in motor control called automatization, can be observed during the course of skill acquisition. The dynamical systems model that was originally introduced by Haken [64], has been suggested to have the potential to describe such diverse and complex phenomena on variability of motor performance during the process of motor skill acquisition [5], because nonlinear dynamical systems can show complex behavior as it evolves in time.

Recently, Fujii et al. [65] showed that stable bimanual coordination pattern exists in professional drummers compared to non-drummers during rapid and rhythmic drumming movements. In their experiment, participants were asked to hold a drumstick in each hand and perform bimanual tapping in an anti-phase pattern as fast and as accurately as possible for 10 s (**Fig. 4A**). A clear difference was observed between professional drummers and non-drummers in the relative phase patterns (ϕ , the phase difference between the right hand and the left hand movements when they are plotted on a phase plane consisting of position and velocity) (**Fig. 4B**). That is, while the relative phase of non-drummers showed continuous wrapping or wandering in the interval between 0° to 360° , that of the professional drummers showed no such phase wrapping or wandering pattern. This occurred because the non-drummers erroneously tapped in succession with the same hand (i.e., L-R-R-L) although they were asked to tap in an anti-phase pattern (i.e., L-R-L-R) (**Fig. 4C**). Correspondingly, the non-drummers showed a more variable ϕ pattern than the drummers.

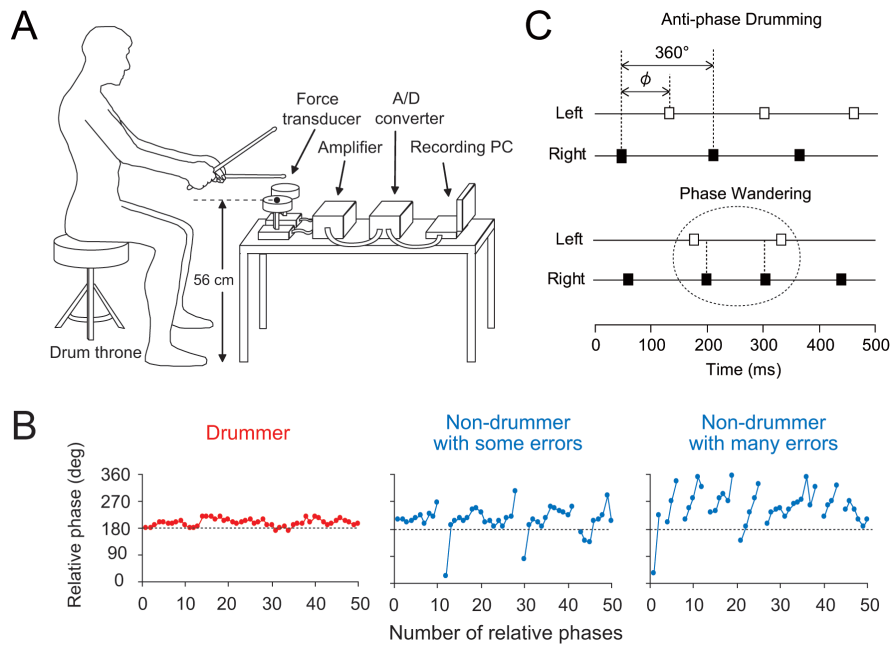


Fig. 4. Experimental setting. B: Schematic diagrams of correct anti-phase drumming pattern (upper) and erroneous phase wandering pattern (lower). Left and right hand taps are shown by open and filled squares, respectively. More than one taps of the same hand appearing in succession (e.g., L-R-R-L) considered an error and as phase wandering. C: Typical examples of relative phase (ϕ) patterns observed in a professional drummer (red) and non-drummers (blue) during bimanual anti-phase drumming.

What principles govern over the organization of rhythmic bimanual movements in professional drummers and non-drummers? To theoretically describe the observed bimanual coordination pattern in experts and novices, we formulated a dynamical model by extending Haken-Kelso-Bunz [66] model as follows:

$$\begin{aligned} \dot{\phi} = & -a \sin \phi - 2b \sin 2\phi - c \sin(\phi - \psi) \\ & + \Delta\omega + d \cos \phi + \sqrt{Q}\xi_t, \quad \dots \dots (6) \end{aligned}$$

where the overdot indicates the derivative of the *order parameter* ϕ with respect to time and ξ_t denotes a Gaussian white noise that functions as stochastic force of strength Q [67]. The terms $-a \sin \phi$ and $-2b \sin 2\phi$ are referred to as *intrinsic dynamics* [5] (i.e., spontaneous coordination tendencies in human bimanual coordination). The terms $-c \sin(\phi - \psi)$ and $d \cos \phi$ are referred to as *behavioral information* that have a specific parametric influence on the order parameter dynamics [5, 68–71].

The term $\Delta\omega$ is a *symmetry breaking parameter* that represents a difference in uncoupled frequency of the individual system components (e.g., asymmetry in maximum tapping frequency between hands) [65, 72]. An increase of $\Delta\omega$ breaks the symmetry of the potential function and causes an appearance of running solution or a phase wandering pattern. Accordingly, the bimanual coordination patterns for both professional drummers and non-drummers were successfully modeled by a nonspecific change in the symmetry breaking parameter, or *intrinsic constraint of asymmetry* $\Delta\omega$ (Figs. 5A, B).

The detailed simulation of Eq. (6) revealed an interesting relationship between the parameter $\Delta\omega$ and the variability of relative phase ($SD \phi$). The change in the parameter $\Delta\omega$ induced the *S-shaped* change in the *intra-trial* variability (Fig. 5C) and the *inverted U-shaped* change in the *inter-trial* variability (Fig. 5D). These nonlinear changes in the variability of relative phase result from a *saddle node bifurcation*, a mechanism by which the *attractor layout* changes in dynamical systems [73].

Miura et al. [4] also found phase transition phenomena in street dance movements. In street dance, basic knee-bending movements are divided into two patterns: down and up movements. Down movement flexes the knees on the beat, while up movement extends the knees on the beat. Both skilled street dancers and non-dancers, who had not had the experience of street dance, could perform relatively stable down movement over a wide range of movement frequencies. However, when the non-dancers were instructed to perform up movement at high movement frequencies such as beyond 120 beats per minute, unintentional phase transition from up to down movement occurred. That is, although the non-dancers tried to perform the up movement (knee extension on the beat), they performed the down movement (knee flexion on the beat) unintentionally during high movement frequency. On the contrary, skilled street dancers could resist such unintentional phase transition, and could perform more stable up movement than in non-dancers. These results suggest that intrinsically stable and relatively unstable action-

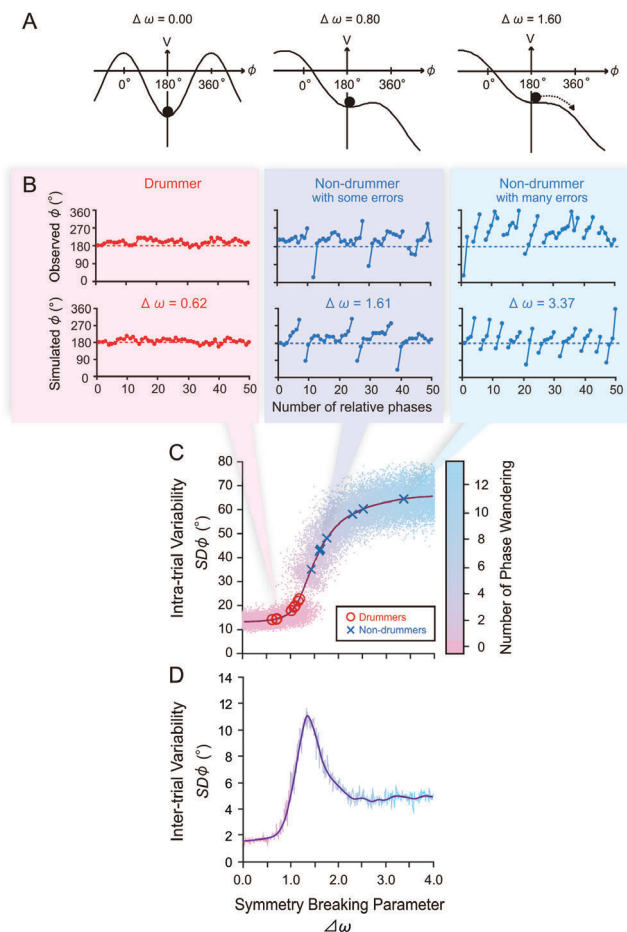


Fig. 5. A: Schematic diagrams of evolving potential functions of Eq. (6) ($a = 1$, $b = 0$, $c = 2$, $\psi = 180^\circ$, and $\Delta\omega = 0.00, 0.80$, and 1.60). B: Typical example of observed and simulated time evolution of relative phase (ϕ) for a drummer (red) and non-drummers (blue). C: Intra-trial variability ($SD\phi$) as a function of $\Delta\omega$ simulated by Eq. (6). ($a = 1$, $b = 0$, $c = 2$, $\psi = 180^\circ$, $d = 0.8\Delta\omega$, $\sqrt{Q} = 20^\circ$, and $\Delta\omega$ is changed from 0.00 to 4.00 by 0.01 .) The observed intra-trial $SD\phi$ s for drummers ($N = 8$, red) and non-drummers ($N = 8$, blue) are plotted on the simulated line. The color of each point corresponds to the number of phase wanderings. D: Inter-trial variability ($SD\phi$) as a function of $\Delta\omega$ simulated in Equation 6. Intra-trial variability shows S-shaped function while inter-trial variability shows inverted U-shaped function.

perception coordination pattern exists as constraints over the formation of movement patterns, and the intrinsic dynamics is modified, that is, the intrinsically unstable coordination pattern (up movement) become stable in street dancers by long-term practice over the years.

These studies show that the dynamical systems approach can contribute to understanding the mathematical principles underlying skill acquisition and also suggest that human motor control and learning can be described as time-evolution or self-organization of dynamical systems (Kudo et al. [74] and Ohgane et al. [75]).

8. Conclusions

In the series of our studies examining the difference between experts and novices we have found that experts' functional variability or coordination of the executing parameters can drive out erroneous variability typically observed in performance by novices. These results indicate that experts do not use a unique or single set of parameters for the tasks, suggesting the necessity of practicing under varying conditions and requiring varying solutions. We would like to emphasize the importance of practice for expertization, because growing evidence has suggested that a lot of characteristics in an expert's brain was formed through practice or acquired, rather than innate [76, 77].

We also found that stereotyped response (i.e., typical EMG co-contraction or typical responses based on probability distribution of particular events) can be produced from motor control strategies to reduce the final output errors under variable conditions, and activation of particular brain structures are necessary to inhibit stereotyped responses. In addition, we introduced the dynamical systems approach to describe the process of skill acquisition. This approach should be a promising candidate to understand the principles that govern spatiotemporal organization of movements in novices and experts, because characteristic movement patterns specific to novices (i.e., phase wandering in drumming and phase transition in street dancing) and experts (i.e., stable movement patterns) can be seamlessly described as the time evolution of nonlinear and self-organized dynamical systems.

Since motor skill acquisition in humans is a complex phenomena including the change in performance, movement, and neurophysiological variables such as electromyographic and brain activities [78], interdisciplinary approach consisting of experimental and theoretical methods are needed to not only understand human motor skill but also develop an effective practice methods for motor skill acquisition.

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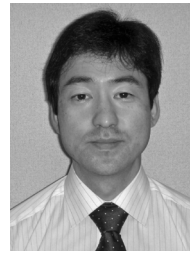
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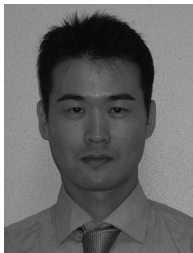
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