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Nonlinear attractor dynamics in the fundamental and extended prism adaptation paradigm

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ABSTRACT

Adaptation and re-adaptation processes are studied in terms of dynamic attractors that evolve and devolve. In doing so, a theoretical account is given for the fundamental observation that adaptation and re-adaptation processes do not exhibit one-trial learning. Moreover, the emergence of the latent aftereffect in the extended prism paradigm is addressed.

1. Introduction

Nonlinear physics provides us with powerful concepts to explore the fundamental laws of biological systems. For example, it has been shown that the dynamics of predator–prey systems is determined by limit cycle attractors while the competition between and cooperation among species is governed by the interplay between stable and unstable fixed point attractors [1]. In view of the general applicability of nonlinear physics concepts, it does not come as a surprise that in a variety of studies they have been applied to perception–action phenomena as well [2–7]. However, relatively little attention has been devoted to approach the plasticity of perception–action systems from the nonlinear physics perspective. Although it has been demonstrated that learning of perception–action tasks involves the emergence of attractors and self-organized states [8–13], to the best of our knowledge a nonlinear physics account for the fundamental and clinically relevant prism adaptation paradigm has not been developed so far.

Prism adaptation is a striking and much-researched example of a self-organized behavioral and cognitive re-organization process [14–17] that features clinically relevant bio-markers [18]. As such, prism adaptation is a fundamental form of learning that involves the visuo-motor system. It is believed that such motor learning processes involve changing synaptic connections κ_i of neural networks [19], where κ_i may be decomposed into a fixed part $\kappa_{i,0}$ and a variable part $d_i(t)$: $\kappa_i(t) = \kappa_{i,0} + d_i(t)$. Synaptic connections κ_i are believed to change due to appropriate excitations. In our context, feedback signals x on the behavioral level can be regarded as sources of such excitations. However, changes in κ_i affect motor behavior and in doing so change the aforementioned feedback signals. Consequently, adaptation involves a circular causality loop that involves both behavioral, environmental, and neural levels. Motor performance and feedback result in changes of the connectivity matrix of neural networks. The changing connectivity matrix results in changes of motor performance and feedback.

The fundamental prism adaptation paradigm not only consists of the adaptation process but typically involves three types of processes: the baseline process, the adaptation process when subjects are wearing prisms and adapt to the perturbed perception–action system, and the re-adaptation process when subjects have normal vision again (prisms off) but experience the aftereffect of the adaptation process, see Fig. 1. Adaptation and re-adaptation processes can be monitored on the basis of performance measures. Wearing prisms perturbs the perception–action system such that performance errors occur. For example, when participants attempt to throw a ball to a target, a systematic performance error occurs.

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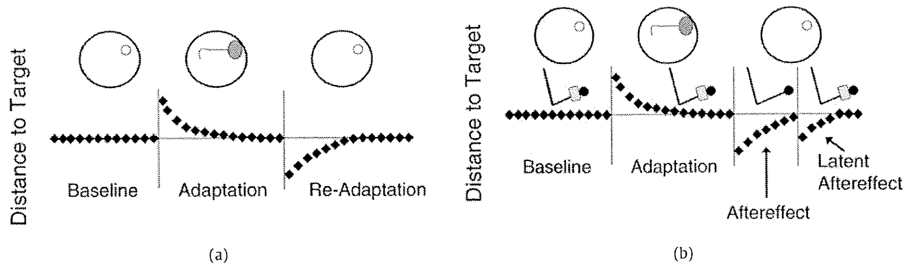


Fig. 1. (a) Illustration of baseline, adaptation and re-adaptation processes studied in the fundamental prism adaptation paradigm. (b) Two kinds of re-adaption processes occur when the context is changed across adaptation and re-adaptation phases. Context changes may be realized by attaching and detaching weights on the throwing arm [21].[1]

This performance error vanishes during the adaptation process. When participants remove the prisms, the perception–action system is still adapted to the perturbed conditions which implies a further systematic performance error. This aftereffect error is in the direction opposite to the direction of the first encountered performance error (see Fig. 1 again).

Using an extended prism adaptation paradigm, it has been shown that re-adaptation processes are context-dependent [20,21]. When experimental conditions are changed across adaptation and re-adaptation processes (i.e., when the context under which the re-adaptation occurs differs from the context under which the adaptation occurred), then re-adaptation is only partial, see Fig. 1 panel (b). During this partial (or primary) re-adaptation process the performance error vanishes. However, when experimental conditions are reinstated, the performance error occurs again and another (secondary) re-adaptation process is triggered.

As we will show next it is worthwhile to discuss the secondary aftereffect in the context of memory phenomena. A number of experimental results have suggested that a parallel should be drawn between aftereffects of prism adaptation and memory phenomena (e.g., [22]). The parallel is most particularly evident in respect to long-term priming or implicit memory, a kind of priming/memory observed under conditions in which incidental study is followed by an indirect test. Study or training is incidental in a memory experiment when conditions (typically instructions) orient attention to an information-processing goal different from that of remembering the presented materials. A memory test is indirect in an experiment when conditions orient attention to a current activity involving (surreptitiously) the material at study without drawing attention to the prior incidence of study. In prism adaptation, the learning in training (the adaptation) is incidental to trying to perform an act successfully. The test (for the adaptation) is indirect in that it simply has the person attempt to perform, again, the specified act successfully. One major view of long-term priming or implicit memory is that its magnitude depends on the kinds of processes and conditions shared between the original experiencing of an event (call it 'study') and the subsequent testing of the memory for that event (e.g., [23–26]). The central thesis is that whether a given condition of study/training leads to good or poor memory performance depends on the type of test. Experiments suggest that memory performance is maximal when study and test are fully symmetric, that is, when for a given event or fact study and test engage the same mental operations in the same circumstances. Conversely, memory performance is less than maximal when there is an asymmetry between study and test. A simple change in format from incidental study to indirect test suffices to reduce memory performance, for example, in the case of words, from upper to lower case [24], from typed to handwritten [23], from normally transcribed to transcribed backwards [27]. For the most general case, memory performance declines to the degree that the interaction (I) between one's intention and the stimulus situation at study (e.g., the task one has to do with items of a particular type presented in a particular way) differs from the interaction between one's intention and the stimulus situation at test [25]. If the interactions are the same, that is, $\Delta I = 0$, memory is intact; if the interactions are not the same, that is, $\Delta I \neq 0$, memory is impaired. In a phrase, forgetting occurs when the study-test symmetry is broken.

A prism adaptation experiment of Kitazawa et al. [20] provides a relevant parallel to the implicit memory results. At study or training, adaptation to prisms was established for a reaching-to-target task that was conducted at one of four speeds. At test, the reaching-to-target task was performed at the training speed or at one of the other speeds. Transfer as indexed by the aftereffect was maximal when training and test speeds were the same (Δspeed $= 0$), and decreased systematically with the size of the difference between them. Whether the training led to large ('good') or small ('poor') adaptation ('memory'), depended on the similarity of test to training. An overview of the prism adaptation literature suggests that cases of complete, incomplete or zero generalization of adaptation from training to test are analogous to the cases in the implicit memory literature. No single mechanism can be identified. Differences in limbs, movement directions, and movement parameters all matter, singly or in combination. For adaptation, as for long-term priming (implicit memory), the governing dynamics seem to require a δ term that respects the training-test symmetry.

In Sections 2.1 and 2.2, we will discuss the fundamental and the extended prism paradigm from the nonlinear physics perspective. In doing so, we will identify dynamic attractors that putatively determine adaptation and re-adaptation processes. In Section 2.3, we briefly comment on implications of our model for prism adaptation experiments involving non-stationary experimental conditions. Our basic model will be presented in Section 2.

2. Attractor dynamics for prism adaptation

Let $\mathbf{x} \in \mathbb{R}$ denote the performance error of subjects participating in a prism adaptation experiment. For example, we may think of an experiment in which subjects are asked to throw a ball to a target. Then x would correspond to the distance of the ball from the target and serves as the feedback signal mentioned in Section 1. The performance error x as a function of time t is assumed to satisfy a first-order dynamical evolution equation of the form

[1] In the study by Fernández-Ruiz et al. [21] the influences of the prism and attached weight on throwing can be considered to be orthogonal, e.g., whereas prism deflects throws leftward or rightward, the attached weight does not deflects throws in left–right directions (it might deflect throws inward, closer to the thrower). The dynamics described are for the leftward–rightward changes in throwing.

$$\frac{d}{dt}x = f(x,t). \quad (1)$$

The function f is composed of several terms that reflect different contributions to the error dynamics. First of all, f involves a function f_0 which describes the baseline performance and a function f_A that accounts for the adaptation process. Second, since the error dynamics in general depends on changes of experimental conditions (see Introduction), we assume that f consists of a set of functions Z_i with $i = 1, 2, 3, \ldots$ that represent the impacts of these conditions (right versus left-hand throwing, throwing speed,...). In sum, we have $f = f_0 + f_A + \sum_i Z_i$. Since the decomposition of f into f_0 and the functions Z_i is not unique we define f_0 and the functions Z_i such that under baseline performance we have $\sum_i Z_i = 0$. In fact, the term $\sum_i Z_i$ can be neglected in the context of the fundamental prism paradigm when experimental conditions other than that of putting on and off prisms are not varied. In contrast, as we will show below for the extended prism paradigm the term $\sum_i Z_i$ is of crucial importance.

The function f_0 depends on the performance error and corresponds to the force of an intrinsic attractor with potential $V_0(x) = -\int^x f_0(x')\,dx'$, where both x and x' denote performance errors. We assume that the intrinsic attractor is attractive with $f_0(0) = 0$ and $df_0/dx < 0$. When participants put on prisms, the reference frame for perceiving and acting is shifted in a particular direction and by a particular amount. Therefore, in general we write $f_0(x - s)$, where $s \in \mathbb{R}$ denotes the prismatic shift. For $s \neq 0$ the fixed point of the attractor is shifted to $x = s$. Of course, under baseline conditions we have $s = 0$.

In line with the dynamic systems approach to learning [8–10], we assume that f_A reflects a new attractor that emerges during the adaptation process. This adaptation attractor will be described in terms of the potential $f_A = -\partial V_A/\partial x$. For the sake of simplicity, we describe the intrinsic attractor and the adaptation attractor in the same coordinate system. Consequently, V_A depends in general on $x - s$. In addition, V_A depends on t because the potential reflects a dynamic attractor that changes with time such that $V_A = V_A(x - s, t)$. Taking all the aforementioned considerations into account, we see that Eq. (1) becomes

$$\frac{d}{dt}x = f_0(x - s) - \frac{\partial}{\partial x}V_A(x - s, t) + \sum_i Z_i. \quad (2)$$

Note that above and in what follows we use the continuous time variable t to develop and analyze our model for prism adaptation. Taking a conceptual point of view, however, t is assumed to be closely related to behavioral activity (for example, in the figures presented below we will calibrate t to the number of throws that a participant performs during adaptation and re-adaptation). That is, although we make extensive use of the time variable t, we do not claim that time as such drives adaptation and re-adaptation processes. Eq. (2) is a top-down approach to model the system constituted by the agent, the environment, and the task involved in the prism adaptation. The terms in Eq. (2) reflect the neural network with its connections κ_i as well as the perception–action system in general and environmental properties (e.g. target and ball). That is, the evolution equation for the error dynamics accounts for the agent–environment–task system in its entity including the neural network mentioned in Section 1 as a special part. The fixed connectivity parameters $\kappa_{i,0}$ are represented in Eq. (2) by the baseline function f_0. They are assumed to be context-dependent which implies that $\kappa_{i,0}$ are also related to the experimental constraints expressed in terms of the parameters Z_i. The variable synaptic connectivity parts $d_i(t)$ are expressed in the top-down modeling approach (2) in terms of adaptation potential V_A. However, as mentioned already, the terms V_A, Z_i, and f_0 do not refer exclusively to neural network properties but to the agent–environment–task system.

Returning to Eq. (2), we decompose the attractor force $-dV_A/dx$ into its amplitude $\beta(t) \geqslant 0$, a prototype force h_A that exhibits a fixed shape and a time-dependent tuning parameter $\alpha(t) \in \mathbb{R}$. We assume that the prototype force corresponds to a fixed point attractor with $h_A(0) = 0$ and $dh_A(x)/dx < 0$. The tuning parameter shifts the fixed point of the adaptation attractor such that $-dV_A(x - s, t)/dx = \beta(t)h_A(x - s - \alpha(t))$. Substituting this expression into Eq. (2) yields

$$\frac{d}{dt}x = f_0(x - s) + \beta(t)h_A\big(x - s - \alpha(t)\big) + \sum_i Z_i. \quad (3)$$

We further assume that $\beta(t)$ increases during the adaptation process according to $d\beta/dt = g(x, \alpha, \beta)$. Likewise α changes during the adaptation process in the manner $d\alpha/dt = G(x, \alpha, \beta)$. That is, we assume that we are dealing with autonomous processes that do not depend explicitly on time. In order to guide our modeling approach by analytical results, we neglect the β-dynamics to a certain extent and put $\beta = c|\alpha|$. Note that other choices for which β increases monotonically as a function of $|\alpha|$ (e.g. $\beta \propto \alpha^2$) could alternatively be used and would not affect the fundamental properties of our model. Absorbing the parameter c into the function h_A, we can simply write $\beta = |\alpha|$. This gives us

$$\frac{d}{dt}x = f_0(x - s) + \big|\alpha(t)\big|h_A\big(x - s - \alpha(t)\big) + \sum_i Z_i. \quad (4)$$

Moreover, we will assume that G depends only on the performance error x,

$$\frac{d}{dt}\alpha = G(x), \quad (5)$$

and that the adaptation attractor becomes stationary when the error vanishes: $G(0) = 0$. The parameter α must counteract the performance error x. Therefore, we require $dG(x)/dx < 0$. That is, α increases for negative errors and decreases for positive errors. Moreover, G may involve a saturation threshold (e.g. we may use $G(x) = -\kappa \arctan(x)$ with $\kappa > 0$). Finally, note that it is plausible to assume that in general there is a time delay τ between the occurrence of the performance error x at time t and the utilization of x to control the dynamics of α. That is, the argument of the function $G(x)$ in Eq. (5) will be retarded like $G(x(t - \tau))$. A detailed analysis of the time-delayed dynamic system composed of Eqs. (4) and (5) is beyond the scope of the present study, which is the reason why we will put in what follows $\tau = 0$. However, we will return to potential implications of a finite delay $\tau > 0$ in the Conclusions.

Eqs. (4) and (5) describe the evolution of the attractor potential $V_A(x, t)$ during adaptation. Note that Eqs. (4) and (5) describe a set of nonlinear evolution equations even if the function f_0, h_A and G are linear functions. This is because of the nonlinear coupling between the amplitude dynamics and the dynamics of the fixed point shift represented by the expression $|\alpha(t)|h_A(x - s - \alpha(t))$. We will return to this issue briefly in the conclusions. When participants remove the prisms, their perception–action capabilities have to re-adapt. In line with our dynamic systems approach, we see that during the re-adaptation process the adaptation attractor weakens and eventually disappears. We will assume that the laws that govern the emergence of the adaptation attractor also determine its progressive weakening. That is, the re-adaptation process is described by the evolution equations (4) and (5) again. However, we have $s = 0$. As we will see in the following sections, Eq. (4) with $s = 0$ describes indeed the evolution of the aftereffect.

As mentioned in the introduction, a change of the experimental conditions across adaptation and re-adaptation processes induces the emergence of a partial re-adaptation process that might be followed by a secondary re-adaptation process. In particular, the similarity of test and training conditions affects the ability to recall studied items (see Introduction). If test and training conditions

Table 1
Nonlinear dynamic processes as discussed in Section 2 and defined by Eqs. (4) and (5).

	Fundamental case	Extended case
Baseline performance (Prism off)	$s=0$, $\sum_i Z_i=0$	$s=0$, $\sum_i Z_i=0$
Adaptation process A (Prism on)	$s\neq 0$, $\sum_i Z_i=0$	$s\neq 0$, $\sum_i Z_i=0$
Re-adaptation process R (Aftereffect)	$s=0$, $\sum_i Z_i=0$	–
Primary re-adaptation R_1 (Experimental conditions changed)	–	$s=0$, $\sum_i Z_i=\delta\neq 0$
Secondary re-adaptation R_2 (Experimental conditions reinstated)	–	$s=0$, $\sum_i Z_i=0$

differ recall performance becomes worse. Likewise, in studies on bimanual coordination, evidence has been found that the degree of symmetry of the experimental setup affects performance [2, 28–30]. For example, when human subjects swing two pendulums simultaneously with their right and left hands, then motor performance depends crucially on the symmetry of the experimental setup. That is, the motor performance of subjects who hold pendulums in a symmetric fashion (both pendulums point downwards) differs from the performance of subjects with one ordinary and one inverted pendulum (one pendulum points upwards; the other downwards). The evidence provided in the aforementioned studies can be summarized in a phenomenological law. Accordingly, breaking the similarity or symmetry in experiments on memory, motor performance, and adaptation induces forces that affect the dynamic processes underlying memory retrieval, motor coordination, and adaptation. That is, we will consider next forces that emerge due a mismatch or asymmetry in experimental conditions. The most fundamental force in this context is a constant force [2]. We assume that in this case the expression $\sum_i Z_i$ can approximately be regarded as a constant force term $\sum_i Z_i=\delta$. Accordingly, we assume that the force term $\sum_i Z_i=\delta$ varies when experimental conditions across adaptation and re-adaptation processes vary.

Note that in general this asymmetry-induced force can depend on state variables [30] and in particular on the performance error x. For the purpose of our analysis, however, the crucial issue is to assume that $\sum_i Z_i$ is different from zero in the case of the extended prism paradigm (as it is depicted in Fig. 1) without identifying precisely how it is different from zero. The functional relationship between $\sum_i Z_i$ and x is an interesting issue, of course, but at the present stage of our modeling effort of secondary importance. In short, Eqs. (4) and (5) with $s=0$ and $\sum_i Z_i=\delta$ describe primary re-adaptation processes under changed experimental conditions. If experimental conditions of the adaptation process are reinstated, then the asymmetry-induced force vanishes: $\delta=0$. Consequently, the secondary re-adaptation process (latent aftereffect) is described by Eqs. (4) and (5) for $s=0$ and $\sum_i Z_i=0$. Table 1 summarizes the nonlinear dynamics of adaptation attractors emerging in the fundamental and extended prism adaptation paradigm in line with the consideration that we made so far. In addition, to the cases listed in Table 1 one may consider an experimental condition for which test conditions during the primary re-adaptation process and adaptation process are held constant ($s=0$, $\sum_i Z_i=0$) but differ during the secondary re-adaptation process ($s=0$, $\sum_i Z_i\neq 0$). This condition could serve as a control condition for the experimental realization of the extended prism paradigm as described in Table 1. In the following sections, we will discuss these cases for linear forces f_0 and h_A.

2.1. Fundamental prism adaptation paradigm

Let us discuss how the performance error in general or the distance to the target in ball throwing tasks changes as a function of time provided that we are dealing with attractors that feature approximately linear forces. Let f_0 and h_A denote linear functions $f_0(x)=-x/T_0$ and $h_A(x)=-x/T_A$, respectively, where T_0 and T_A are constants. Then Eqs. (4) and (5) become

$$\frac{d}{dt}x=-\frac{1}{T_0}(x-s)-\frac{|\alpha(t)|}{T_A}\big(x-s-\alpha(t)\big),$$
$$\frac{d}{dt}\alpha=G(x). \tag{6}$$

The adaptation process A involves the initial conditions $x(0)=s$ and $\alpha(0)=0$. The dynamic system (6) exhibits a single fixed point or stationary point $(x_{st},\alpha_{st,\text{prism on}})$ at $x_{st}=0$ and

$$\alpha_{st,\text{prism on}}=-\frac{s}{2}\left(1+\sqrt{1+\frac{4D}{T_0}}\right). \tag{7}$$

Note that in what follows the subindex 'st' refers to stationary. Note also that above and in what follows we will frequently use the rescaled time constant D defined by $D=T_A/|s|$. If s is positive (negative) we find that $\alpha_{st,\text{prism on}}$ is negative (positive). Roughly speaking, the tuning parameter α shifts the reference frame of the perception–action system back in the direction of the original (unperturbed) reference frame. Note that the inequality $|\alpha_{st}|>|s|$ holds. The reason for this is that the force of the adaptation attractor has to compensate for the impact of the intrinsic force f_0. That is, for $\alpha=-s$ the adaptation attractor has a fixed point at the origin such that the performance error would converge to zero under the exclusive impact of the adaptation attractor. Due to the impact of the intrinsic force f_0, however, the adaptation process has not reached stationarity at $\alpha=-s$. Stationarity is only established at $\alpha=\alpha_{st,\text{prism on}}$ given by Eq. (7). Linear stability analysis of the fixed point reveals that for small values of x we have

$$\frac{d^2}{dt^2}x+B\frac{d}{dt}x+\gamma Cx=0 \tag{8}$$

with $B=1/T_0+|\alpha_{st,\text{prism on}}|/T_A>0$, $\gamma=-dG(0)/dx>0$, and $C=(2|\alpha_{st,\text{prism on}}|-|s|)/T_A>0$. Consequently, we have a stable fixed point and the adaptation process converges from $(x,\alpha)=(s,0)$ to $(x,\alpha)=(0,\alpha_{st,\text{prism on}})$ for any prismatic shift s. From the damped oscillator equation (8), it follows that for $B^2>4\gamma C$ we have a stable node at $(0,\alpha_{st,\text{prism on}})$. Close to the fixed point the adaptation process A corresponds to an overdamped dynamics. In contrast, for $B^2<4\gamma C$ we have a stable focus and the adaptation process exhibits an oscillatory damped behavior. Using the explicit solution (7), we obtain

$$\left[\frac{1}{T_0}+\frac{1}{2D}\left(1+\sqrt{1+\frac{4D}{T_0}}\right)\right]^2\lessgtr -4\frac{dG(0)}{dx}\sqrt{1+\frac{4D}{T_0}}. \tag{9}$$

Let us consider B as independent parameter and $D(B)$ as dependent parameter. In this case, the separation line between oscillatory damped and non-oscillatory behavior in the parameter space spanned by B/γ and $T_0\gamma^2$ is given by

$$\frac{B}{\gamma}=4\left(1\pm\sqrt{1-\frac{1}{16T_0\gamma^2}}\right). \tag{10}$$

Fig. 2 illustrates the parameters domains for which damped oscillatory and overdamped (non-oscillatory) dynamic patterns can be found.

When subjects take off their prisms, the re-adaptation dynamics R satisfies the evolution equations (4) and (5) with $s=0$ which in the case of linear attractor forces read

$$\frac{\mathrm{d}}{\mathrm{d}t}x = -\frac{x}{T_0} - \frac{|\alpha(t)|(x - \alpha(t))}{T_A},$$
$$\frac{\mathrm{d}}{\mathrm{d}t}\alpha = G(x). \tag{11}$$

The aftereffect typically is smaller in the amount than the prismatic shift (see e.g. [31]). The deviation between prismatic shift and aftereffect depends on experimental details. For example, the duration of the break between the adaptation and re-adaption condition affects the magnitude of the aftereffect [32]. Consequently, the initial conditions $x(0)$ and $\alpha(0)$ for the prism off phase in general will depend on experimental details and we would need to model these details by a separate set of evolution equations. If the between-phases dynamics can be neglected we are dealing with some kind of idealized case (which will be illustrated in Fig. 3; see below). In this case, the initial state of the perception–action systems in the prism off phase corresponds to the final state of the system of the preceding prism on phase. Accordingly, the initial conditions are $x(0) = -s$ and $\alpha(0) = \alpha_{\mathrm{st,prism\,on}}$ as defined by Eq. (7) (note again that alternative initial condition such as $|x(0)| = |s| - \epsilon$ with $\epsilon > 0$ can be used as well; this does not affect the following discussion).

The re-adaptation dynamics exhibits the fixed point $(x_{\mathrm{st}}, \alpha_{\mathrm{st}}) = (0, 0)$. Eq. (11) can equivalently be expressed in terms of the nonlinear oscillator equation

$$\frac{\mathrm{d}^2}{\mathrm{d}t^2}\alpha = -\left(\frac{1}{T_0} - |\alpha|\left[\frac{\mathrm{d}G(\gamma^{-1}\mathrm{d}\alpha/\mathrm{d}t)}{\mathrm{d}x}\right]^{-1}\right)\frac{\mathrm{d}}{\mathrm{d}t}\alpha - \frac{|\alpha|}{T_A}\alpha. \tag{12}$$

Note that the expression $-[\mathrm{d}G/\mathrm{d}x]^{-1}$ is larger than zero in any case. Consequently, the damping coefficient is positive in any case. Likewise, the force $-T_A^{-1}|\alpha|\alpha$ is attractive. Therefore, the point $(\alpha, \mathrm{d}\alpha/\mathrm{d}t) = (0, 0)$ is a stable fixed point and the re-adaptation dynamics R converges from $(x, \alpha) = (-s, \alpha_{\mathrm{st,prism\,on}})$ to $(x, \alpha) = (0, 0)$. Simulations of adaptation and re-adaptation processes A and R, respectively, are shown in Figs. 3 and 4. Panel (a) in Fig. 3 illustrates the vanishing of the performance error in the case of a overdamped non-oscillatory adaptation process related to a stable node (i.e. the upper sign in Eq. (9) holds). Panel (a) in Fig. 4 depicts the corresponding re-adaptation process R. That is, Fig. 4(a) illustrates the aftereffect of the adaptation dynamics shown in Fig. 3(a). For these parameters the re-adaptation dynamics is a overdamped non-oscillatory process. Panel (b) in Fig. 3 illustrates the prism adaptation process A for a perception–action system involving a stable focus (i.e. the lower sign in Eq. (9) holds). In this case the corresponding re-adaptation process R exhibits an oscillatory damped pattern as well, see Fig. 4(b).

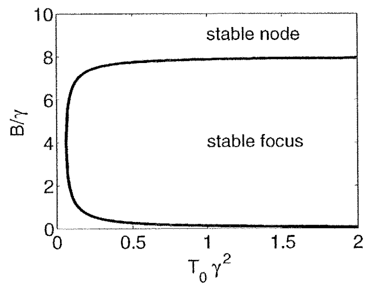


Fig. 2. Separation line computed from Eq. (10) separating two parameter domains for which adaptation is governed by qualitatively different types of attractors (nodes versus foci).

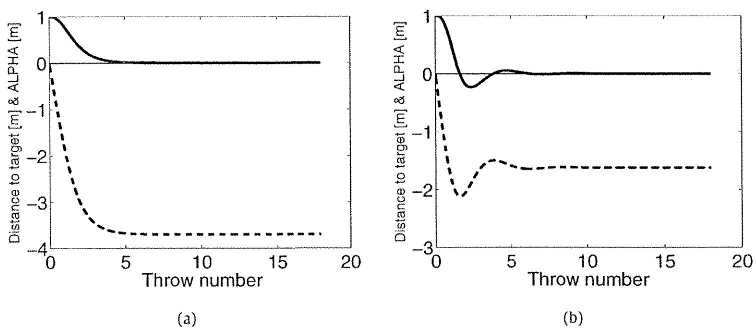


Fig. 3. Illustration of adaptation dynamics as computed from Eq. (6). Performance error is here and in the following figures regarded as the distance to target in a throwing task. $x(t)$ (solid line) and $\alpha(t)$ (dashed line) versus rescaled time given in units of throws. (a) Non-oscillatory case for $s = 1$ m, $T_0 = 1$ min, $D = 1$ min ($\Rightarrow T_A = 1$ min m), $G = -\kappa \arctan(x)$, $\kappa = 4$ min^{-1}, time rescaling: 2 throws/min. (b) Oscillatory case; parameters as for panel (a) but with $T_0 = 0.1$ min instead of $T_0 = 1.0$ min. Numerics: Eq. (6) was solved iteratively using an Euler forward scheme with time step $\Delta t = 0.01$ min.

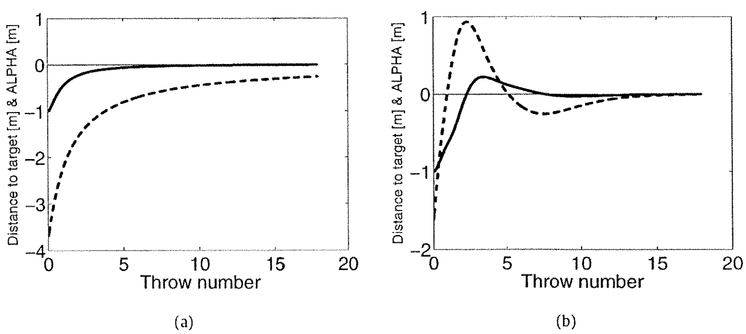
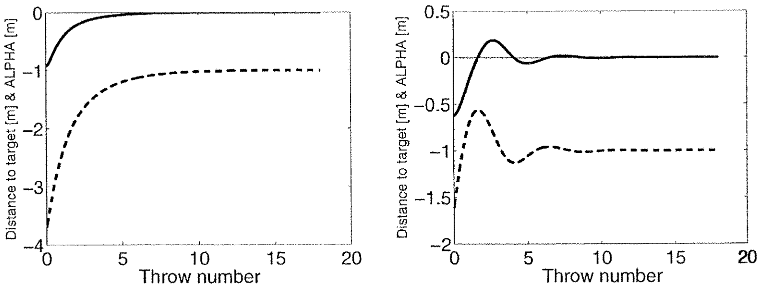
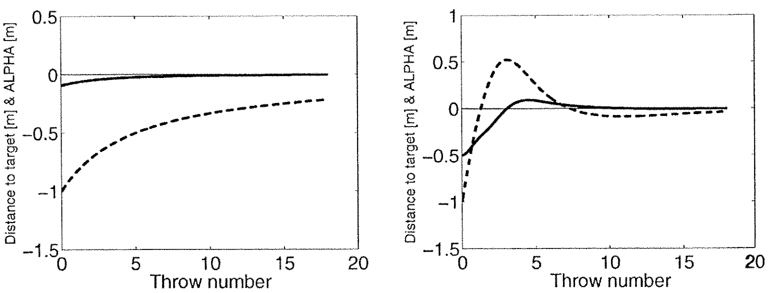


Fig. 4. Re-adaptation dynamics computed from Eq. (11). $x(t)$ (solid line) and $\alpha(t)$ (dashed line) versus rescaled time. (a) Non-oscillatory case. (b) Oscillatory case. Parameters and numerics as in Fig. 3.



(a) (b)

Fig. 5. Illustration of primary (partial) re-adaptation dynamics as computed from Eq. (13). $x(t)$ (solid line) and $\alpha(t)$ (dashed line) versus rescaled time. (a) Non-oscillatory case for $s = 1$ m, $\delta = 1$ m/min, $T_0 = 0.1$ min, $D = 1$ min ($\Rightarrow T_A = 1$ min m), $G = -\kappa \arctan(x)$, $\kappa = 4$ min^{-1}, time rescaling: 2 throws/min. (b) Oscillatory case; parameters as in panel (a) but with $T_0 = 1.0$ min instead of $T_0 = 0.1$ min. Numerics: Eq. (13) was solved iteratively using an Euler forward scheme with time step $\Delta t = 0.01$ min.



(a) (b)

Fig. 6. Secondary re-adaptation dynamics computed from Eq. (11). $x(t)$ (solid line) and $\alpha(t)$ (dashed line) versus rescaled time. (a) Non-oscillatory case. (b) Oscillatory case. Parameters and numerics as in Fig. 5.

2.2. *Extended prism adaptation paradigm*

Let us consider next the extended prism adaptation paradigm featuring the re-adaptation processes R_1 and R_2. The primary re-adaptation process R_1 is described by Eqs. (4) and (5) with $s = 0$ and $\sum_i Z_i = \delta \neq 0$. When subsequent to R_1 the original experimental conditions are reinstated, the secondary adaptation process R_2 occurs that is described by Eqs. (4), (5) with $s = 0$ and $\sum_i Z_i = 0$ (see also Table 1). To begin with, Eqs. (4), (5) for the primary process R_1 can be cast for linear attractor forces f_0 and h_A into the form

$$\frac{d}{dt}x = \delta - \frac{x}{T_0} - \frac{|\alpha(t)|(x - \alpha(t))}{T_A},$$
$$\frac{d}{dt}\alpha = G(x). \tag{13}$$

In line with our discussion in the preceding section on the magnitude of the aftereffect relative to the magnitude of the prismatic shift, we mention that we may consider the idealized case in which the re-adaption process involves the initial conditions $x(0) = -s$ and $\alpha(0) = \alpha_{\text{st,prism on}}$. However, Eq. (13) can also be solved for alternative initial conditions. For example, we may assume that the initial error $x(0)$ is given by the fixed point of Eq. (13) when α is regarded as a constant defined by the final parameter value of the preceding prism on phase. In this latter case, we obtain $x(0) = -s + \delta/(1/T_0 + |\alpha_{\text{st,prism on}}|/T_A)$ which for appropriately chosen system parameters results in $|x(0)| < |s|$.

The fixed point of the re-adaptation dynamics R_1 is given by $x_{st} = 0$ and

$$\alpha_{st,\delta} = -\operatorname{sgn}(\delta)\sqrt{|\delta| T_A}, \tag{14}$$

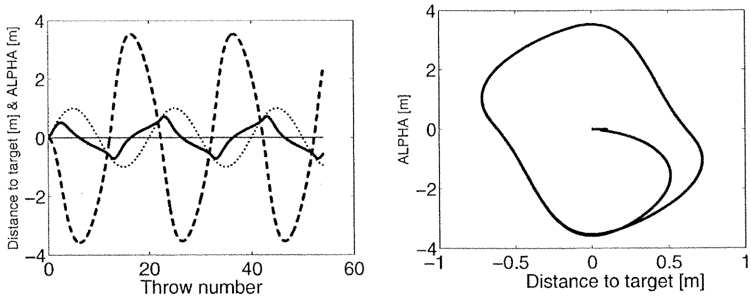
where $\operatorname{sgn}(z)$ is the sign operator with $\operatorname{sgn}(z) = 1$ for $z > 0$ and $\operatorname{sgn}(z) = -1$ for $z < 0$. Using linear stability analysis, we can show that small perturbations x satisfy the oscillator equation

$$\frac{d^2}{dt^2}x + B\frac{d}{dt}x + \gamma C x = 0 \tag{15}$$

with $B = 1/T_0 + |\alpha_{st,\delta}|/T_A > 0$, $\gamma = -dG(0)/dx > 0$, and $C = 2|\alpha_{st,\delta}|/T_A > 0$. We see that we are dealing again with a damped oscillator and a stable fixed point. Moreover, we can distinguish between a stable node and a stable focus. Using the approach of the previous section, we obtain the inequalities

$$\left[\frac{1}{T_0} + \sqrt{\frac{|\delta|}{T_A}}\right]^2 \gtrless -4\frac{dG(0)}{dx}\sqrt{\frac{|\delta|}{T_0}}. \tag{16}$$

If the upper (lower) sign holds, we are dealing with a stable node (stable focus). The secondary adaptation process R_2 is defined Eqs. (4), (5) with $s = 0$ and $\sum_i Z_i = 0$ which for the special case of linear forces f_0 and h_A correspond to Eq. (11). In the context of the extended prism paradigm, Eq. (11) describes the latent aftereffect. We have discussed solutions of Eq. (11) in detail in Section 2.1. For the re-adaptation process R_2, we need to consider the initial condition $\alpha(0) = \alpha_{st,\delta} = -\operatorname{sgn}(\delta)\sqrt{|\delta| T_A}$. The initial performance error $x(0)$ corresponds to the fixed point of the error dynamics when $\alpha = \alpha(0)$ is considered to be constant. Thus, we obtain the initial condition $x(0) = -\delta/(1/T_0 + \sqrt{|\delta|/T_A})$. Since from the experiment it is known that the sign of $x(0)$ is opposite to the sign of the prismatic shift s, we see that the sign of δ is fixed by the sign of s: $s\delta > 1$. Figs. 5 and 6 illustrate typical primary and secondary aftereffects R_1 and R_2 as predicted by our model using the initial conditions $x(0) = -s + \delta/(1/T_0 + |\alpha_{\text{st,prism on}}|/T_A)$ and $x(0) = -\delta/(1/T_0 + \sqrt{|\delta|/T_A})$, respectively. Fig. 5 depicts the evo-



(a) (b)

Fig. 7. Adaptation dynamics as computed from Eq. (6) with s replaced by a time-dependent prismatic shift $s(t) = s_0 \sin(2\pi t/T_{\text{drive}})$. (a) $x(t)$ (solid line), $\alpha(t)$ (dashed line), and $s(t)$ (dotted line) versus rescaled time. (b) Trajectory in the phase space (x, α). Parameters and numerics as in Fig. 3; $T_{\text{drive}} = 10$ min, $s_0 = 1$ m.

lution of the performance error during the primary re-adaptation process R_1 under changed experimental conditions. For the graph shown in panel (a) the parameters are chosen such that the upper sign in Eq. (16) holds. That is, we are dealing with an attractor defined by a stable node. Fig. 6(a) depicts the latent aftereffect R_2 following the primary aftereffect shown in Fig. 5(b). Fig. 5(b) exemplifies a primary re-adaptation process R_1 for the oscillatory damped case discussed above (i.e. the lower sign in Eq. (16) holds). According to our numerical simulation, the secondary re-adaptation process R_2 shows in this case an oscillatory damped pattern as well, see Fig. 6(b).

2.3. Prism adaptation under non-stationary experimental conditions

Our dynamic model may be used to explore from a theoretical perspective adaptation processes under non-stationary experimental conditions. Non-stationary conditions occur, for example, when participants have to adapt to a sequence of gradual manipulations [33]. In the context of prism adaption, we may assume that the prismatic shift s during the adaptation process is changed periodically like $s(t) = s_0 \sin(\Omega t)$. In this case, Eqs. (4) and (5) describe a periodically driven second-order dynamical system. In general, such systems can exhibit various dynamic patterns and a thorough analysis of this case is beyond the scope of our present effort. However, we carried out a numerical analysis and showed that the adaptation process under such a non-stationary condition can settle down in a periodic behavior with an oscillation period equal to the period of the driving force, see Fig. 7. Panel (a) shows the oscillatory prismatic shift $s(t)$ as well as the response of the adaptation dynamics in terms of performance error $x(t)$ and attractor amplitude $\alpha(t)$. Panels (a) and (b) indicate that the adaptation dynamics approaches, after a transient period (of about 5 throws for the parameters used in Fig. 7), a periodic solution in the phase space spanned by x and α. It is clear that both theoretical and experimental future efforts are needed to obtain a more comprehensive understanding for adaptation dynamics in such non-stationary experimental paradigms.

3. Conclusion

Prism adaptation does not exhibit one-trial learning. Likewise, re-adaptation processes do not exhibit one-trial learning. The performance error during adaptation and re-adaptation gradually decreases [14–18]. That is, there is empirical evidence that participants of a prism adaptation experiment do not use an explicit strategy to compensate for the performance errors that they experience. Even for participants who attempted to use a volitional strategy, gradually evolving adaptation processes have been observed in prism adaptation experiments [22]. We developed a theoretical account for this observation. Accordingly, adaptation and re-adaptation processes involve a dynamic attractor that evolves and devolves as a function of time related to the performance of some kind of behavioral activity (e.g. throwing a ball to a target). Consequently, adaptation and re-adaptation are *dynamic* processes. In such a conceptual framework learning consists of a sequence of differential improvements and one-trial learning is impossible.

Our approach takes the context-dependency of adaptation processes into account. When the context changes between the adaptation and the re-adaptation processes then only a partial re-adaptation process occurs. As soon as the context is reinstated a latent re-adaptation process occurs. Context changes were regarded as asymmetry-induced forces. The inequality (16) indicates that the nature of the attractors that govern the re-adaptation dynamics crucially depends on such forces.

In Section 2, we have discussed our proposed model from the dynamic systems perspective of learning [8–10]. This perspective in general and Eqs. (4) and (5) in particular are to a certain extent consistent with alternative approaches to learning. For example, we may re-interpret the adaptation potential V_A as a weighted combination of basis function ϕ_i related to motor primitives r_i [34, 35]. In this case, we decompose V_A like $V_A(z,t) = \sum_i w_i(t)\phi_i(z)$, where $w_i(t)$ are weights that change during adaptation and re-adaptation processes. If we use a set of bi-orthogonal functions ϕ_i and ϕ_i^+ (i.e. we have $\int \phi_i^+(z)\phi_k(z)\,dz = \delta_{ik}$) we can compute the evolution of the weight factors w_i from $w_i(t) = \int \phi_i^+(z) V_A(z,t)\,dz$. As far as the latent aftereffect is concerned, we note that the context change addressed in Section 2.2 would imply a shift from a motor primitive set $\{r_i\}$ to another set $\{r_i'\}$ which in turn would imply a basis function shift $\phi_i \to \phi_i'$. Assuming that the shifted basis functions ϕ_i' can approximately we written like $\phi_i' = \phi_i + \Delta_i$, where Δ_i measures the function mismatch, then the functions Z_i in Eq. (4) could be interpreted as $Z_i = w_i \Delta_i$. That is, the parameter $\delta = \sum_i Z_i \neq 0$ occurring in the context of the extended prism paradigm could be interpreted as the weighted mismatch between motor primitives (or basis functions) available in different contexts.

As discussed in Section 2.2, the parameter δ may be used to determine the magnitude of initial aftereffects in the extended prism paradigm. Accordingly, we have $x(0) = -s + \delta/(1/T_0 + |\alpha_{\text{st, prism on}}|/T_A)$ and $x(0) = -\delta/(1/T_0 + \sqrt{|\delta|/T_A})$ for R_1 and R_2, respectively. In this case, our considerations suggest a reciprocal relationship between the magnitudes of the aftereffects: for R_1 we see that $|x(0)|$ decreases with $|\delta|$ (i.e. we have $d|x(0)|/d|\delta| < 0$); for R_2 we see that $|x(0)|$ increases with $|\delta|$ (i.e. we have $d|x(0)|/d|\delta| > 0$), see Fig. 8. This reciprocal relationship (the smaller the primary initial aftereffect, the larger the latent initial aftereffect) has indeed been found in the experiment by Fernandez-Ruiz et al. [21]. Note that in the special case $1/T_0 \gg |\alpha_{\text{st, prism on}}|/T_A$ and $1/T_0 \gg \sqrt{|\delta|/T_A}$ we see that the magnitudes of the aftereffects simply add

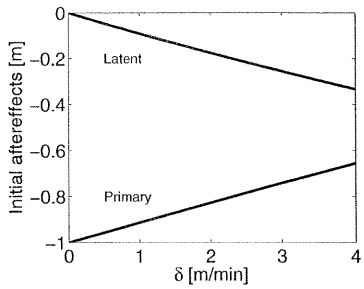


Fig. 8. Magnitudes of primary and latent initial aftereffects computed from $x(0) = -s + \delta/(1/T_0 + |\alpha_{\text{st, prism on}}|/T_A)$ and $x(0) = -\delta/(1/T_0 + \sqrt{|\delta|/T_A})$ and Eq. (7). Parameters (as in Figs. 5 and 6 for the non-oscillatory case): $s = 1$ m, $T_0 = 0.1$ min, $T_A = 1$ min m.

up to the magnitude of the prismatic shift: $x_{R_1}(0) + x_{R_2}(0) = -s$. In the literature there is so far only one study available in which the relationship between $x_{R_1}(0)$ and $x_{R_2}(0)$ has been addressed (Fernandez-Ruiz et al. [21]). However, the focus of [21] was not on exploring this relationship in detail. Therefore, future experimental work is needed to clarify the functional dependencies between the primary and latent aftereffects and to see to what extent they are related to the aforementioned predictions of our dynamic systems approach to prism adaptation.

Our proposed model is nonlinear even if the functions f_0, h_A and G are linear functions. This is because of the nonlinear coupling between the amplitude dynamics and the dynamics of fixed point shift (e.g. see the expression $|\alpha(t)|h_A(x - s - \alpha(t))$ in Eq. (4) as well as the term $\beta(t)h_A(x - s - \alpha(t))$ in Eq. (3) for the more general case).

The attractor dynamics satisfies a coupled set of evolution equations in which the performance error is coupled to the amplitude and shift parameter of the adaptation attractor. This results in the emergence of second-order dynamical processes. In particular, the adaptation and re-adaptation processes are determined by attractors given in terms of stable nodes and stable foci. Consequently, our analysis highlights the need to distinguish in the context of the prism adaptation paradigm between overdamped non-oscillatory processes and oscillatory damped processes. While clinical studies have pointed out the need to explore quantitatively the properties of prism adaptation processes [18], to the best of our knowledge empirical research has not yet been devoted to identify quantitatively the nature of adaptation attractors. Our nonlinear physics approach to adaptation processes provides a sound basis for future research in this direction.

As mentioned above, our model effectively corresponds to a second-order dynamical system although the error dynamics is assumed to satisfy a first-order dynamical evolution equation, see Eq. (1). The first order dynamics in Eq. (1) may be motivated by the observation that performance errors initially decay in a monotonic fashion (as illustrated schematically in Fig. 1). Such a monotonic decay is a characteristic feature of first-order dynamical systems. However, higher-order dynamic systems can produce monotonically decaying functions as well. Consequently, in general, we may consider a more general model for prism adaptation processes as defined by

$$\sum_{k=1}^{N} c_k \frac{d^k}{dt^k} x = f_0(x - s) + |\alpha(t)| h_A\big(x - s - \alpha(t)\big) + \sum_i Z_i,$$
$$\frac{d}{dt}\alpha = G(x) \qquad (17)$$

with $c_N = 1$. In this case, the error $x(t)$ satisfies a differential equation of order N and the total coupled dynamical system represents a differential equation of the order $N + 1$. A linear stability analysis for such higher order dynamical systems can in principle be carried out but becomes mathematically more involved for $N > 1$ than for $N = 1$. The case $N = 1$ discussed in Section 2 does not admit for chaotic solutions, whereas for $N > 1$ it might be the case that such solutions exist. Consequently, if experimental evidence for chaotic adaptation dynamics could be found, then this would speak in favor for a higher order adaptation dynamics as described by Eq. (17) with $N > 1$. Alternatively, chaotic behavior could indicate that we need to take a time delay into consideration – as briefly addressed at the beginning of Section 2.

As mentioned at the beginning of Section 2, it is plausible to replace $G(x)$ in Eq. (17) by a time-delayed feedback function of the form $G(x(t - \tau))$. In general, it is known that a time delay τ in a dynamic system with a fixed point can destabilize the system such that is becomes oscillatory [36,37] or chaotic [38]. Future work has to explore whether the adaptation model (17) with $G = G(x(t - \tau))$ exhibits such delay-induced oscillatory and chaotic solutions and under which conditions they occur. If such solutions exist it would be useful to distinguish between solutions with low and high amplitudes. In the low amplitude case, the oscillatory or chaotic behavior could be interpreted as some kind of dynamic noise. In this case, the model would predict that the performance variability of participants is on a relatively high level but nevertheless participants were able to adapt and readapt successfully to experimental manipulations. In the high amplitude case, we would identify the oscillatory and chaotic processes as non-stationary behavioral patterns. The model would predict a failure of both the adaptation process and the re-adaptation process in the sense that these processes would no longer be able to reduce performance errors towards stable stationary levels close to zero.

References

[1] F. Verhulst, Nonlinear Differential Equations and Dynamical Systems, second ed., Springer, Berlin, 1996.
[2] J.A.S. Kelso, Dynamic Patterns – The Self-Organization of Brain and Behavior, MIT Press, Cambridge, 1995.
[3] H. Haken, Principles of Brain Functioning, Springer, Berlin, 1996.
[4] V.K. Jirsa, J.A.S. Kelso, Coordination Dynamics: Issues and Trends, Springer, Berlin, 2004.
[5] T.D. Frank, A. Daffertshofer, C.E. Peper, P.J. Beek, H. Haken, Physica D 144 (2000) 62.
[6] T.D. Frank, A. Daffertshofer, P.J. Beek, Phys. Rev. E 63 (2001) 011905.
[7] T.D. Frank, R. Friedrich, P.J. Beek, Phys. Rev. E 74 (2006) 051905.
[8] G.S. Schöner, J.A.S. Kelso, Biol. Cybern. 58 (1988) 71.
[9] G.S. Schöner, J.A.S. Kelso, Biol. Cybern. 58 (1988) 81.
[10] G.S. Schöner, Biol. Cybern. 62 (1989) 39.
[11] E.L. Saltzman, K.G. Munhall, J. Motor Behav. 24 (1992) 49.
[12] D. Corbetta, B. Vereijken, Int. J. Sport Psychol. 30 (1999) 507.
[13] T.D. Frank, M. Michelbrink, H. Beckmann, W.I. Schöllhorn, Biol. Cybern. 98 (2008) 19.
[14] C.S. Harris, Psychol. Rev. 72 (1965) 419.
[15] R.B. Welch, Perception 3 (1974) 367.
[16] A.S. Kornheiser, Psychol. Bull. 83 (1976) 783.
[17] G.M. Redding, Y. Rossetti, B. Wallace, Neurosci Behav. Rev. 29 (2005) 431.
[18] R.L. Brookes, R.I. Nicolson, A.J. Fawcett, Neurophysiologica 45 (2007) 1921.
[19] B. Kolb, Brain Plasticity and Behavior, Erlbaum, New Jersey, 1995.
[20] S. Kitazawa, T. Kimura, T. Uka, J. Neurosci. 17 (4) (1997) 1481.
[21] J. Fernández-Ruiz, C. Hall-Haro, R. Diaz, J. Mischner, P. Vergara, J.C. Lopez-Garcia, Learning Memory 7 (2000) 193.
[22] T.A. Martin, J.G. Keatin, H.P. Goodkin, A.J. Bastian, W.T. Thach, Brain 119 (1996) 1199.
[23] H.L. Roediger III, T.A. Blaxton, Memory Cognit. 15 (1987) 379.
[24] T.A. Blaxton, J. Exp. Psychol. – Learning Memory Cognit. 15 (1989) 657.
[25] J.J. Franks, C.W. Bilbrey, K.G. Lien, T.P. McNamara, Memory Cognit. 28 (2001) 1140.
[26] G. Lukatela, T. Eaton, M.A. Moreno, M.T. Turvey, Memory Cognit. 35 (2007) 781.
[27] P. Graf, L. Ryan, J. Exp. Psychol. – Learning Memory Cognit. 16 (1990) 978.
[28] D. Sternad, D. Collins, M.T. Turvey, Biol. Cybern. 73 (1995) 27.
[29] E.L. Amazeen, P.G. Amazeen, P.J. Treffner, M.T. Turvey, J. Exp. Psychol. – Hum. Percept. Perform. 23 (1997) 1552.

[30] H. Park, M.T. Turvey, in: A. Fuchs, V.K. Jirsa (Eds.), Coordination: Neural, Behavioral and Social Dynamics, Springer, Berlin, 2008.
[31] J. Fernández-Ruiz, R. Diaz, Learning Memory 6 (1999) 47.
[32] J. Fernández-Ruiz, R. Diaz, C. Aguilar, C. Hall-Haro, Cognitive Brain Res. 20 (2004) 92.
[33] K. Yamamoto, D.S. Hoffman, P.L. Strick, J. Neurophysiol. 329 (2006) 268.
[34] F.A. Mussa-Ivaldi, S.F. Giszter, E. Bizzi, Proc. Natl. Acad. Sci. USA 91 (1996) 7534.
[35] K.A. Thoroughman, R. Shadmehr, Nature 407 (2000) 742.
[36] M.C. Mackey, L. Glass, Science 197 (1977) 287.
[37] A. Longtin, J.G. Milton, J.E. Bos, M.C. Mackey, Phys. Rev. A 41 (1990) 6992.
[38] K. Ikeda, H. Daido, O. Akimoto, Phys. Rev. Lett. 45 (1980) 709.