Specific Aspects in the Adaptation of Human Eye-Hand-Coordination

DISSERTATION

Zur Erlangung des akademischen Grades
Doctor rerum naturalium (Dr. rer. nat.)

Vorgelegt dem
Fachbereich 2 (Biologie/Chemie)
der Universität Bremen

von
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Bremen, 2011

Datum der Verteidigung:	14.12.2011

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List of Publications

List of Publications in temporal order. All publications used in this cumulative dissertation are marked with *.

Articles in Referenced Journals

Bornschlegl, M. A., Fahle, M., & Redding, G. M. (submitted). The role of movement synchronization with an auditory signal in producing visual prism adaptation. *Perception*. *

Bornschlegl, M. A., Spang, K., Hochstein, L., Ackermann, L. & Fahle, M. (submitted). The influence of prism adaptation on proprioception: Answers from generalisation. *PLoS ONE*. *

Bornschlegl, M. A., Arévalo, O., Eberhardt, S. & Fahle, M. (submitted). Rapid dual-adaptation with learning to learn. *PLoS ONE*. *

Arévalo, O. J., **Bornschlegl, M. A.**, Ernst, U., Fahle, M. & Pawelzik, K. R. (submitted). Dynamics of dual prism adaptation: Relating experimental results to a minimalistic neural model. *PLoS ONE*.

Conference Talks and Poster Presentations

Patzelt, F., **Schaumlöffel, M. A.**, Pawelzik, K., Fahle, M. (2007). Adaptation in eye-hand coordination. *Midterm Evaluation of the German National Network for Computational Neuroscience*, Berlin, Germany. *

Arévalo, O., Hochstein, L. & **Bornschlegl, M. A.**, Ernst, U. & Fahle, M. (2008). Spatial transfer in prism adaptation. *International Workshop: Aspects of Adaptive Cortex Dynamics*, Hanse Institut for Advanced Study, Delmenhorst, Germany. *

Arévalo, O., Hochstein, L., **Bornschlegl, M. A.**, Ernst, U., Pawelzik, K. R. & Fahle, M. (2008). Spatial transfer in prism adaptation. *Frontiers in computational neuroscience, 4th Bernstein Symposium, Munich 2008, Germany*. *

Bornschlegl, M. A. & Fahle, M. (2009). Repeated Phase Changes induce Learning of Visuomotor Adaptation. *51. Tagung experimentell arbeitender Psycholog|innen*, Jena 29.03 - 01.04.2009. *

Bornschlegl, M. A., Redding, G., & Fahle, M. (2009). Prism adaptation: The visual system adapts only with additional auditory spatial information. *Summer School 2009: Two Eyes, two Ears, one System?*, Bad Bederkesa 13.09. - 18.09.2009. *

Bornschlegl, M. A., Arévalo, O. J., Ernst, U., Pawelzik, K. R., & Fahle, M. (2009). Learning of Visuomotor Adaptation: Insights from Experiments and Simulations. In *Frontiers in Computational Neuroscience Conference Abstract: Bernstein Symposium 2009*. *

Arévalo, O. J., **Bornschlegl, M. A.**, Ernst, U., Pawelzik, K. R., & Fahle, M. (2010). Predicting the dynamics of dual prism adaptation with a biophysically plausible neural model. In *Frontiers in Computational Neuroscienc. Conference Abstract: Bernstein Conference on Computational Neuroscience*.

Bornschlegl, M. A. & Fahle, M. (2011). Rapid learning to learn during adaptation of eye-hand coordination. *Bernstein Cluster D Symposium: Multisensory perception and action*, Tübingen 28.09. - 29.09.2011. *

Table of Content

Theoretical Outline

1 Sensorimotor Control

In everyday life pointing towards a street sign or grasping an object like a cup of tea seems to be utterly simple. Only when seeing how sensorimotor control slowly develops in a child or when the system is disturbed through illness or experimentally, e.g. through shifting prisms, one can grasp the complexity of processes needed to accomplish such seemingly easy tasks. As the term “sensorimotor control” implies, information from one or more sensory systems is used to generate a command in the motor system. Usually the sensory systems will be vision and audition since these senses allow the localization of interesting objects both within but also beyond our range of grasp. But also proprioception which is the position and motion sense of our body parts (especially arms/hands and legs/feet, but also orientation of e.g. head to trunk) serves as input to sensorimotor control. The essential part of sensorimotor control is that information from different sensory modalities is integrated. In the fully developed and healthy system this leads to a coherent representation of action space which allows for better performance than a mono-sensory system would (Rowland, Quessy, Stanford, & Stein, 2007). By introducing a specific spatial disturbance to one of the systems we are able to study not only how the system normally functions but also how it adapts to changes and thus maintains its ability to perform with high precision.

1.1 Multisensory integration

Only if two inputs have the same cause it is reasonable to establish a multisensory representation of them. The best guess a system can obtain from sensory data alone about whether or not two inputs should be integrated into a single percept is their spatial and temporal proximity. So this is the basis for multisensory integration. If, for example, one can see a cup and simultaneously hears a "cloncking" sound from approximately that direction while one moves the hand towards the cup it is sensible to integrate these separate sensory inputs into a multisensory perception of the hand bumping into the cup (see Fig. 1). Early in sensory processing, in superior colliculus, separate coordinate systems are present for each of the sensory systems involved in sensorimotor control. It has been shown that even at this very early stage multisensory integration enhances signal detection and localization (Rowland et al., 2007). On a cortical level, in parietal cortex, sensory input is integrated from retina and the relative position of eye to head via gain fields (Andersen, Essick, & Siegel, 1985), as well as head position and orientation relative to the trunc (Snyder, Grieve, Brotchie, & Andersen, 1998). This multisensory integration ultimately results in a world-centered (allocentric) coordinate system which allows the efficient planning of eye and head movements towards “interesting targets” but also enables efficient planning of hand movements. As intermediate stages of the integration of monosensory visual and proprioceptive (egocentric) reference frames different multisensory egocentric coordinate systems are represented from eye-centered over head-centered and body-centered to world-centered coordinates (Andersen, Snyder, Bradley, & Xing, 1997). This plurality of mappings is used for different tasks: visual tracking for instance can be achieved best starting from eye-centered coordinates but grasping an object with the hand requires body- and world-centered coordinates.

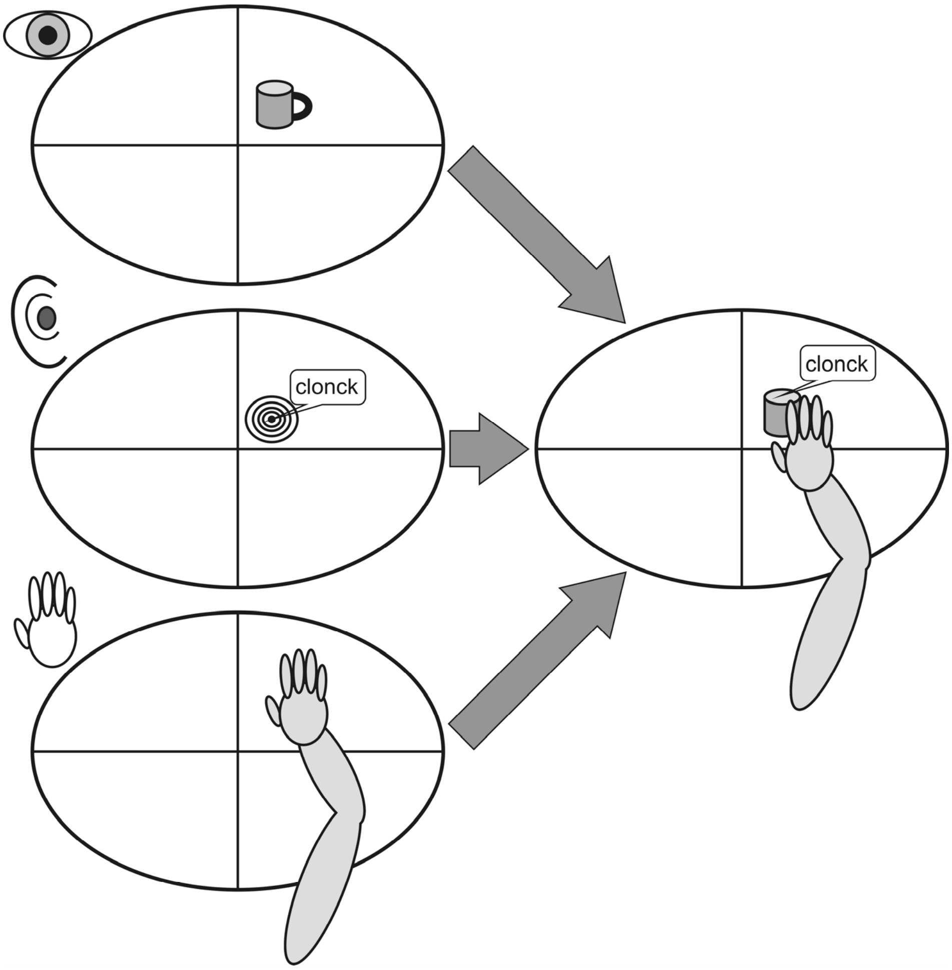

Figure 1. Multisensory Integration. Separate monosensory information from visual, auditory, and proprioceptive coordinate systems is integrated into a coherent multisensory representation of a single event.

1.2 Control loops and sensory feedback

Before a movement towards a visible object can be executed several conceptual steps are necessary. Let's assume the simplest case first: an object is seen and its localization is represented in different coordinate systems, a movement is planned towards this location and subsequently the motor plan is executed resulting in a movement of the hand towards the object. Since this simplified case only relies on a feedforward control of the movement, no sensory feedback is included to control the movement path: it is an open-loop (see Fig. 3a). In everyday life, complete lack of feedback seldom occurs for sufficiently slow movements (while it is the rule for fast, ballistic movements), but it can be produced experimentally by occluding visual feedback of the moving limb (Redding & Wallace, 1988b) (see Fig. 3a) and disturbing proprioceptive feedback of limb position and movement by applying a vibrating stimulus on a specific part of the respective muscle (Bernier, Chua, Inglis, & Franks, 2007). While the lack of visual feedback can be overcome by some practice (e.g. you can learn to tie a ribbon or knot behind your back) sensorimotor control is easier and more accurate with visual feedback to guide your movements.

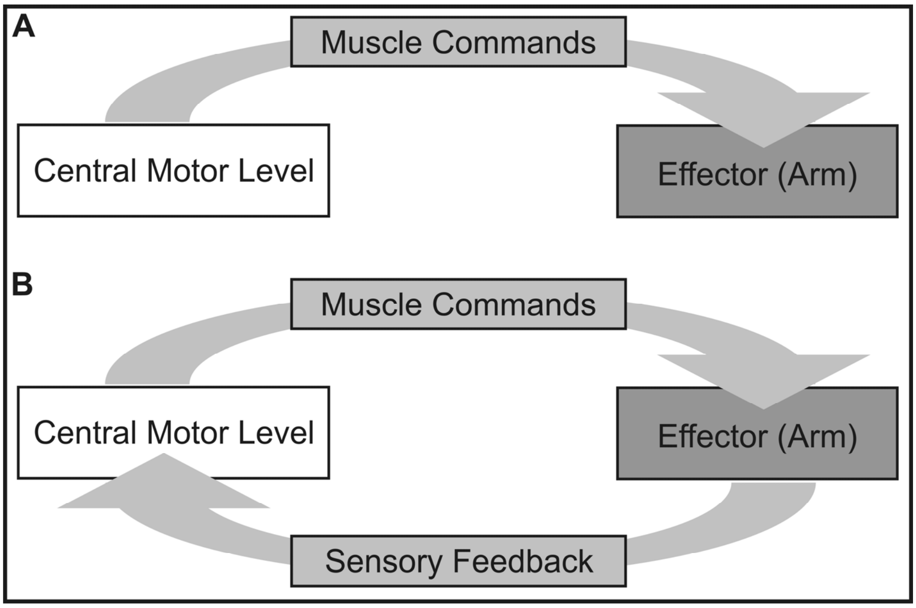

Figure 2. Control Loops. Two different control loops in sensorimotor control for a) open-loop control consisting only of a feedforward control and b) closed-loop control including sensory feedback from the effector to the central motor level. Figure based on Elsner and Prinz (2006).

Whenever sensory feedback is used to control and possibly correct a movement this control system is referred to as closed-loop control (Adams, 1971;

Schmidt, 1975). In such a system, the expected position of the effector (e.g. the hand) is stored with an efference copy (Andersen et al., 1997) and compared to the actual position. If a difference is detected the new sensory information is fed back into the control loop and a slightly altered motor command is issued. So in this latter case the control loop is closed in a sense that the information "goes in circles" until the intended movement is completed (see Fig. 2b). When sensory feedback is available like in concurrent feedback this comparison of intended and achieved limb position is active throughout the movement (Lee & van Donkelaar, 2006). An intermediate use of feedback between open- and closed-loop control can be found in situations where visual feedback is delayed until (close to) the endpoint of the intended movement. For proprioception the feedback loop is closed throughout the movement but visual feedback cannot be used to control and correct the movement until the endpoint is reached. So the feedback loop is essentially closed but the visual feedback can only be used as a measure of success for a subsequent movement. This is the case in experimental conditions referred to as "terminal feedback" (see Fig. 3b).

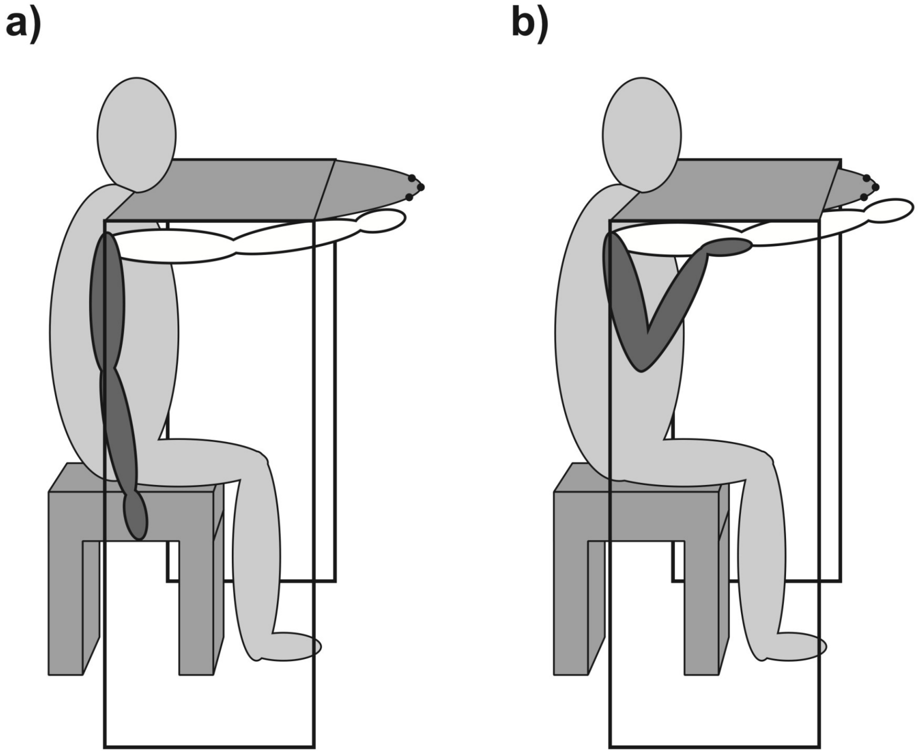

Figure 3. Adaptation Table with Two Different Feedback Conditions. Subject sitting at the adaptation table; both starting position (arm in dark grey) and movement endpoint (arm in white) are shown for a) a lower starting position with long top surface occluding visual feedback (no feedback) and b) upper starting position with short top surface providing visual feedback (terminal feedback).

2 Basics in Adaptation of Eye-Hand Coordination

Sensorimotor control relies on a fairly complex control system. Nonetheless, it alone would not enable us to maintain accurate performance throughout our life and in differing environmental settings and under differing demands. Adapting to changes in the relation between sensory signals and motor output is the key to flexible and accurate (motor) performance. In the past century horizontally shifting prism glasses were extensively used for studying the adaptation mechanisms of eye-hand coordination (Bailey, 1951; Helmholtz, 1867; Kornheiser, 1976; Redding, Rossetti, & Wallace, 2005).

2.1 Phenomenal description of prism adaptation

At first glance prism adaptation seems utterly simple (see Fig. 4). Horizontally shifting prisms introduce a mismatch between visual and proprioceptive coordinates. Executing a pointing movement towards a visual target with the hand unseen results in a pointing error: the target is missed in the direction of the shift (direct effect). Subsequent pointing movements reduce the pointing error until the adaptation is complete. After the prism glasses are removed the adapted subject shows a pointing error in the opposite direction (aftereffect). Subsequent pointing movements again reduce the pointing error until the subject is re-adapted to the normal sensorimotor conditions.

Of course this is just the simplest case of a single adaptation. By varying specific aspects of the task or experimental procedure the basic pattern can be systematically altered. Many studies use the sizes of direct effect and aftereffect as measurements of transfer to different conditions or strength or retention of a previous adaptation. The speed of error reduction expressed as the adaptation rate is a measure of efficiency of the adaptation process. But additional measurements (apart from pointing precision) can be taken into account. For instance, measurements of the orientation of the subjective sensory coordinate systems (i.e. subjective straight ahead in the visual and proprioceptive system) have revealed important insights in the relative weight of visual and proprioceptive adaptation.

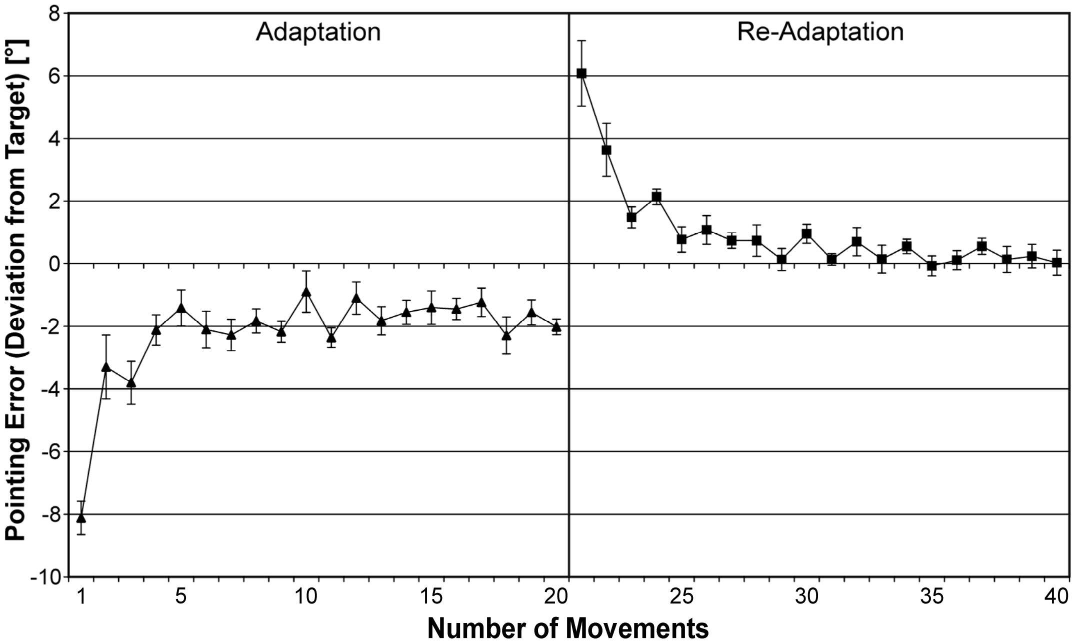

Figure 4. Time Course of Prism Adaptation. Temporal course of the pointing error during prism adaptation to 17° leftwards shift shown as a function of the number of pointing movements executed. Deviations from a central target are shown for the adaptation with leftwards pointing errors and for the re-adaptation with rightwards pointing errors. Data are taken from my second manuscript (generalization). Group averages for 9 subjects are shown, error bars denote Standard Error of the Mean.

2.2 Methods in investigating the adaptation of eye-hand coordination

In research of eye-hand coordination different methods have been used to study sensorimotor adaptation processes. Methodological differences are found for the type of sensorimotor distortion, the adaptation task, and the type of experimental setup.

2.2.1 Sensorimotor distortions

To study adaptation the default sensorimotor mapping has to be altered. For visuomotor control (e.g. pointing movements) this distortion can be introduced in either the visual or the proprioceptive system. Common visual distortions include a change in visual gain (e.g. looking through magnifying glasses) (Heuer & Hegele, 2008), a shift of the visual image either vertically or horizontally (e.g. with prism glasses) (Redding et al., 2005), and a rotation of visual feedback (van den Dobbelsteen, Brenner, & Smeets, 2004). Proprioceptive distortions include muscle vibration either to reduce signal reliability or to introduce a specific proprioceptive shift (e.g. neck muscle vibration: Karnath, 1994) and force fields of various types which can be generated using a robotic manipulandum (Bays, Flanagan, & Wolpert, 2005). As I was interested in basic processes of sensorimotor adaptation I chose horizontal visual shifts as experimental disturbance in all my experiments/studies.

2.2.2 Adaptation tasks

As sensorimotor control comprises every goal-directed movement many different movement types can be used for studying adaptation. Depending on the type of sensorimotor distortion and experimental hypothesis to be tested different movement types are more appropriate. For instance, pointing movements only require a short execution time and thus allow many repetitions in a short testing time (Redding et al., 2005). Grasping movements, on the other hand, additionally involve the shaping of fingers to the target object (aperture) and orientation of the hand (Perenin & Vighetto, 1988). Tracking movements of a continuously moving target allow the investigation of rapid online corrections during adaptation (Abeele & Bock, 2001). Throwing movements (Martin, Keating, Goodkin, Bastian, & Thach, 1996) are yet another movement type which allows studying of adaptations in the extrapersonal space (beyond grasping range).

2.2.3 Experimental setups

Corresponding to the diversity of adaptation tasks different experimental setups are best suited to address different hypotheses. For instance the classical table with visual occluders is a good combination with horizontally shifting prisms (Redding & Wallace, 2006b). With some additions in the setup the straight ahead orientation of visual and proprioceptive coordinate systems can easily be tested in addition to pointing performance. Also the length of visual occluders in the table top can be varied easily allowing for different amounts of visual feedback during the movements (Fig. 3). The experimental setup of my first and second study is shown in Figure 3 as an example of such an adaptation table. Subjects sit at this table with their head in a chin and head rest at the same level as the table top. The length of this table top can be varied allowing for different visual feedback conditions (Fig. 3a: no feedback, b: terminal feedback). But naturally, a different task such as throwing a ball requires a quite different setup than pointing movements. At a throwing wall (Martin et al., 1996) one or more targets can be mounted in extrapersonal space and throwing performance can be recorded. More complex sensorimotor distortions such as a rotation of the visual feedback or a force field require a virtual reality as experimental setup (Vetter, Goodbody, & Wolpert, 1999). As an example the virtual reality setup used in my third study is shown in Figure 5. The subject sits at a table looking down at the natural space for hand movements. Direct vision of the hand is occluded by a mirror. Instead the subject sees the projection of a computer screen where pointing targets and a realistic virtual hand are presented. Hand positions are recorded using a high precision, low friction robotic manipulandum (Phantom Premium 1.5 HF). A virtual reality usually significantly simplifies visual feedback in comparison to real world feedback. In some studies visual feedback of hand position was even reduced to a cursor representing the hand. Such sparse feedback tends to trigger cognitive adaptation strategies whereas realistic visual feedback of a pointing hand also incorporates automatic adaptation processes (Clower & Boussaoud, 2000).

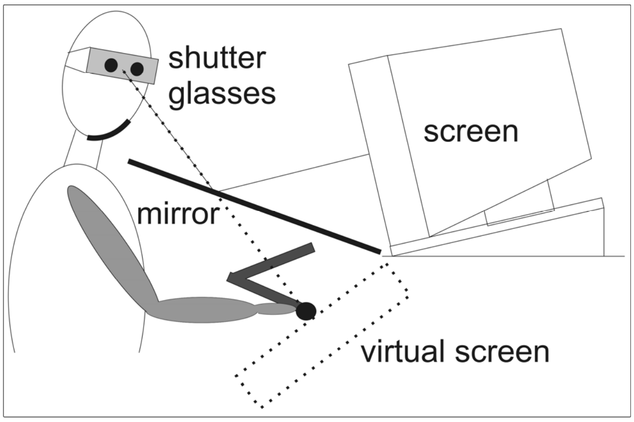

Figure 5. Virtual Reality Setup. Subject sitting at a virtual reality setup viewing a computer screen via a mirror. The virtual screen appears in natural hand working space. Three-dimensional scenes are created with shutter glasses.

3 Specific Aspects of the Adaptation of Eye-Hand Coordination

In my dissertation I describe three specific aspects of the adaptation of eye-hand coordination: i) the relative weight of visual and proprioceptive adaptation, ii) the generalization of prism adaptation, and iii) dual-adaptation and learning to learn. These aspects are introduced in the following sections and I describe and discuss them in more detail in my three manuscripts.

3.1 Relative weight of visual and proprioceptive adaptation

Redding et al. (2005) formulated a comprehensive theory of prism adaptation based on two main adaptive processes (recalibration and realignment) and a supportive process (postural adjustments). Postural adjustments are considered a relatively “low level” process. For asymmetrical postures held or exercised for a prolonged time a new equilibrium point between the involved pair of (proprioceptive) receptors is found such that the new straight ahead is changed towards the exercised direction. The first main adaptive process is recalibration which is a fast strategic error reduction. Realignment as the second main adaptive process achieves a comparatively slow error reduction through an adaptive change in the alignment of sensory maps underlying sensorimotor control (vision and proprioception). For a change of the relative orientation (or relative position of coordinate origins) the direction of control and guidance between the competing sensory inputs is an important aspect. In most cases both sensory maps will be partly adjusted, but one of the systems is chosen to guide the adaptation of the second sensory system resulting in a greater change in this second system.

3.1.1 Feedback delay and duration

Redding and Wallace (1990) found two main factors influencing this direction of control: feedback delay and feedback duration. Feedback delay is the time span from movement onset until visual feedback is available. This can be either instant, like with concurrent visual feedback where the pointing hand is visible throughout the whole movement, or it can be delayed until later during the movement with the hand hidden during a part or even the whole movement as with terminal feedback (Fig. 3b). In several studies Redding and Wallace (1990, 1993, 2006b) found that short visual feedback delays are linked to proprioceptive adaptation under visual guidance whereas long feedback delays lead to visual adaptation under proprioceptive guidance. Linked to but partly independent from feedback delay is the second factor: feedback duration. It is a measure of the time spent with the moving hand visible and thus visual feedback available to sensorimotor control. When both visual and proprioceptive feedback are available spatial discordance between the coordinate systems can be detected. With terminal feedback a long feedback duration in the endpoint of the movement provides enough time to switch from (default) visual to proprioceptive guidance, leading to visual adaptation (Redding & Wallace, 1993). In summary, feedback delay and duration are linked to the feedback conditions terminal versus concurrent feedback which are leading to visual versus proprioceptive adaptation, respectively.

3.1.2 Signal reliability

Varying the certainty of sensory feedback and thus the reliability of sensory inputs Ernst and Banks (2002) showed how multisensory integration is influenced during sensorimotor control. Signal reliability proved to be the key in determining the locus of control: during adaptations the sensory coordinate systems were altered according to Bayesian estimations. While high precision of visual feedback lead to proprioceptive adaptation (i.e. visual guidance) artificially introduced visual noise (blur) produced visual adaptation (i.e. proprioceptive guidance). More precisely, Ernst and Banks (2002) showed that the estimated target position was the result of a weighted average of the discordant visual and proprioceptive feedback based on the Bayesian estimation incorporating signal reliability (see Fig. 6).

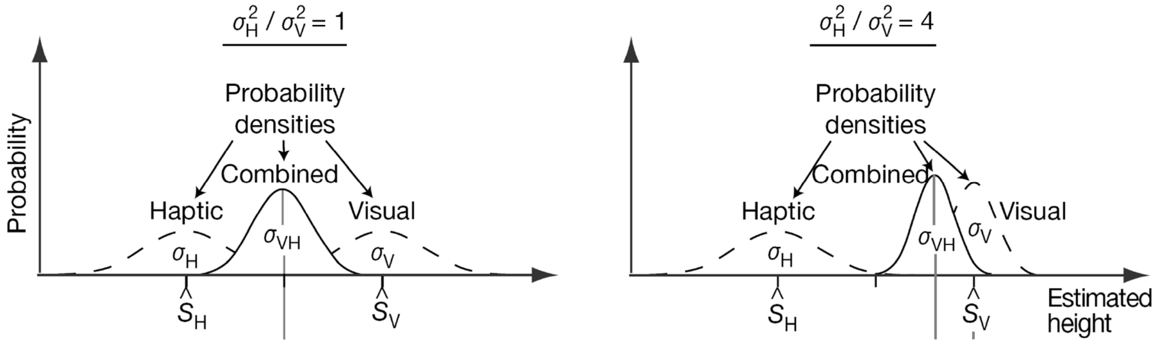

Figure 6. Weighted Average based on Bayesian Estimates. A Bayesian estimate is computed for different signal reliabilities (i.e. probability densities) in the visual signal. When signal reliability is equal for haptic and visual signals both inputs are weighted equally for the combined representation. But when the visual signal shows a better signal reliability the visual input is weighted stronger and the resulting combined representation is closer to the visual representation. Figure adapted from Ernst and Banks (2002).

3.1.3 Influence of an auditory pacing signal

In my first manuscript, I showed that there is at least one other factor influencing this balance namely an auditory pacing signal. Subjects who adapted while pointing regularly in rhythm with an unseen metronome so that each movement began and ended simultaneously with a tone showed visual adaptation. In contrast, subjects who heard the metronome but did not successfully point in rhythm with it or subjects pointing without an auditory pacing signal primarily showed proprioceptive adaptation. The question is how and why does an auditory signal influence the relative adaptation of visual and proprioceptive coordinates but only if it is heard during movement start and endpoint? An auditory pacing signal might influence sensorimotor control and adaptation in several ways: i) Paced movements are executed with a regular speed across trials and thus feedback delay and duration are also similar between trials. In addition, regular pointing movements might allow a better and easier transfer of “insights” from one to another movement. ii) Pacing the movement speed with a rhythmic auditory signal should facilitate the activation of the distributed neural adaptation network (Pollok, Gross, Müller, Aschersleben, & Schnitzler, 2005). iii) Perceiving a stationary auditory signal simultaneously with visual and proprioceptive feedback might serve as a spatial anchor point for multisensory integration. This three-way comparison allows the easy localization of the origin of disturbance in the visual system which is leading to visual adaptation.

3.2 Generalization of prism adaptation

Another important aspect of adaptation is how an adaptation generalizes from the training conditions to different test conditions. Different aspects of generalization have been considered in previous studies: transfer between arms (Redding & Wallace, 2008; van den Dobbelsteen et al., 2004), generalization to different arm postures and movement types (Martin et al., 1996), generalization to different sensorimotor mappings or different strengths of the same disturbance (Bingham & Romack, 1999; Welch, Bridgeman, Anand, & Browman, 1993), and spatial generalization (Bedford, 1989; Ghahramani, Wolpert, & Jordan, 1996; Redding & Wallace, 2006b). In the latter case, an adaptation is acquired for a specific spatial location (i.e. target) and subsequently the generalization across space is tested at different locations.

3.2.1 Hypothetical generalization patterns

Bedford (1989) formulated three hypotheses on the nature of such spatial generalizations and how visual and proprioceptive coordinates can be linked together: minimum constraint, maximum constraint, and intermediate linear constraint. In the minimum constraint hypothesis theoretically any link between visual and proprioceptive coordinates is possible. Regarded more practically this hypothesis predicts most transfer (e.g. aftereffect) of an adaptation at the training location and close to it with decreasing transfer for increasing distances. This results in a Gaussian distribution of transfer with the maximum at the training location. In contrast, the maximum constraint hypothesis allows only a change of complete coordinate systems. As a result it predicts a constant shift between visual and proprioceptive mappings with the same size of aftereffect at each location. The third hypothesis, intermediate linear constraint, is less strict: as the name implies transformations of the coordinate systems are limited to linear changes. In addition to a shift between mappings, like in the maximum constraint hypothesis, also the scaling between the two mappings can be altered. This results in a straight line as a generalization pattern with more transfer on one side of space as compared to the opposite side.

3.2.2 Experimental results on generalization patterns

Bedford (1989) herself found generalization patterns according to the linear constraint hypothesis for (automatic) adaptations to horizontal shifts. But she also showed that an instruction for conscious corrections resulted in a change between mappings according to the minimum constraint hypothesis (Bedford, 1993a). Using adaptations in a virtual reality Gharahmani et al. (1996) tested generalization of an adaptation in a two-dimensional array. They found a nonlinear decay of transfer according to the minimum constraint hypothesis. Given the artificial nature of their task and adaptation environment it is plausible to assume strategic corrections, i.e. recalibration (Redding et al., 2005), underlying the adaptation in their study. Later, Redding and Wallace (2006b) explicitly tested the generalization patterns of recalibration and realignment combined with the influence of visual and proprioceptive adaptation. For recalibration they found a Gaussian distribution of aftereffect according to the minimum constraint hypothesis whereas for realignment they found a straight line as generalization pattern according to the intermediate linear constraint.

3.2.3 Asymmetric generalization

Most interestingly, Redding and Wallace (2006b) found opposite slopes of the generalization pattern between visual and proprioceptive adaptation. Although they only tested the generalization after adaptations at a central target they interpreted the different slopes as a result of a laterally perceived adaptation target due to a shift of coordinate systems during adaptations. Since the direction of change is opposite for visual and proprioceptive adaptation, after an adaptation to rightward shifting prisms, the perceived target position for visual adaptation would be on the left side and on the right side for proprioceptive adaptation. As a consequence most transfer would be found on the trained side. But I find a logical gap in this explanation. First of all, for rightwards shifting prisms the adaptive direction of change in the visual system (visual shift, VS) is to the right, while in the proprioceptive system (proprioceptive shift, PS) it is to the left. As a result, during proprioceptive adaptation an interpretation of the target position in the adapting coordinate system results in a training target always on the right side. This is in accordance with Redding and Wallace's (2006b) explanation. But during visual adaptation (in visual coordinates) at first the target is located on the right and during the course of adaptation the perceived eccentricity is reduced. It is not however perceived as a training target on the left side since this would require a visual shift larger than the horizontal shift introduced by the prisms.

3.2.4 Underestimation of change

In my second study I addressed the question how lateral adaptation targets influence the generalization pattern and whether the maximum of transfer lies on the training side as suggested by previous research (Redding & Wallace, 2006b). Although I found the same direction of the generalization gradient as Redding and Wallace (2006b) with proprioceptive adaptation, my results clearly falsify the hypothesis of most transfer on the training side. Instead I found an alternative explanation for the asymmetrical transfer. All previous results for asymmetrical transfer of an adaptation can be explained by an underestimation of change in the localizing signal (i.e. guiding system). For example in proprioceptive adaptation the visual system guides the adaptation and localizes the target. When looking from a central adaptation target to a test target on the left side the eccentricity of the lateral target is underestimated and a movement plan is formulated for this (false) assumed target position. For a rightwards shift the aftereffect is to the left of a target. So when mathematically adding the "normal" size of aftereffect to the (false) assumed target position the measured pointing error (distance between real target and pointing finger) is reduced. The underestimation has the opposite effect for a target in the right side where a reduced eccentricity of target position adds to the size of measured aftereffect. In my study, I could also show that this effect of underestimation is not limited to spatial generalization but seems to be a more general principal in sensorimotor adaptation which is also present in proprioceptive generalization (i.e. between different head to body orientations).

3.3 Dual-adaptation and learning to learn

One key aspect distinguishing sensorimotor adaptation (e.g. prism adaptation) from ordinary cognitive learning (e.g. memorizing vocabulary) is that once a new sensorimotor mapping has been acquired with an adaptation the default mapping is “lost”. So when testing in the normal setting (e.g. without prisms) an aftereffect occurs and the default sensorimotor mapping has to be re-acquired with another adaptation. While the presence of this aftereffect allows us to study adaptation presumably without strategic control (Redding et al., 2005) altering the size of the aftereffect, this is a major drawback of adaptation processes in everyday life. Fortunately, alternative sensorimotor mappings can be learnt with enough training and experience in both mappings which eventually allows instant access to both of these mappings. Usually many repetitions of adaptation and re-adaptation are needed and the initial pointing errors are gradually reduced during this process. This acquisition phase as well as the final state is referred to as “dual-adaptation” (Welch et al., 1993). Sometimes during dual-adaptation the adaptation rate of individual adaptations increases, a phenomenon first described by Harlow (1949) as “learning to learn”.

3.3.1 Involvement of learning to learn

One of the first studies systematically describing dual-adaptation with human subjects was published by McGonigle and Flook (1978). They described the basic aspects of dual-adaptation: over the course of several adaptations and re-adaptations distributed over five days, pointing errors in all mappings were reduced. Coupled with this dual-adaptation they also found faster adaptations in the later experimental blocks indicating the involvement of learning to learn. In later dual-adaptation studies learning to learn was not always found for adaptation rates. Bingham and Romack (1999) reported dual-adaptation with constant rates whereas Welch et al. (1993) found dual-adaptation with increasing adaptation rates. In my third study I addressed this debated aspect of dual-adaptation finding a linear acceleration of adaptation rates during dual-adaptation. Thus I confirmed the involvement of learning to learn in the acquisition of alternate sensorimotor processes. The complexity of sensorimotor disturbance (e.g. horizontal shift versus visual rotation) and of the adaptation task (e.g. pointing versus throwing) may contribute to the involvement of learning to learn. As a prerequisite for the presence of learning to learn I discuss temporal closeness/proximity of single trials as well as of repeated adaptations. In summary, the presence of learning to learn is an important indicator for an efficient dual-adaptation process.

3.3.2 Efficiency of dual-adaptation

In general, the temporal aspect and efficiency of dual-adaptation has been neglected in all previous studies. While pursuing other hypotheses previous investigations all employed prolonged experimental schedules with several hours of adaptations which stretched over several days or even months (Bingham & Romack, 1999; Cunningham & Welch, 1994; Martin et al., 1996; McGonigle & Flook, 1978; Welch et al., 1993). In these schedules there are two extremes published: rapid and random switching between opposing sensorimotor mappings (Cunningham & Welch, 1994; Osu, Hirai, Yoshioka, & Kawato, 2004) versus blocked adaptation schedules with many subsequent trials in the same mapping (Martin et al., 1996; Shadmehr & Brashers-Krug, 1997). Some studies showed the first adaptation strategy as superior because it allowed the acquisition of opposing visuomotor rotations that were otherwise not learnable (Osu et al., 2004). Other studies showed that for blocked adaptations breaks of several hours are needed between sessions with alternate sensorimotor mappings to allow dual-adaptation (Shadmehr & Brashers-Krug, 1997). But it has also been shown that long adaptations contribute essentially to a well established and robust representation of a new sensorimotor mapping (Fernández-Ruiz & Díaz, 1999) which could be a good basis for dual-adaptation. I found an effective way of acquiring alternative sensorimotor mappings by varying the length of adaptations as well as the number of adaptation and re-adaptation blocks. Although previous studies showed different dual-adaptation results for frequent changes between mappings and blocked adaptation I found dual-adaptation for all adaptation lengths and block numbers. Even the efficiency of the dual-adaptation process was similar between the different schedules as it only depended on the number of trials in each mapping. So in summary, in my third study I prove that one hour with an effective adaptation procedure is sufficient to acquire dual-adaptations.

4 Summary

Sensorimotor control enables us to interact with our environment. When separate sensory inputs seem to have the same origin a multisensory percept is formed. Shaped by our intentions, sensory information is used to create motor plans. Two different control modes exist: open-loop control relying only on a feedforward movement plan and closed-loop control including sensory feedback of the moving limb during the movement.

While the basic phenomenon of an adaptation of eye-hand coordination like prism adaptation appears to be a simple error reduction, at a closer look it becomes clear that several distinct processes are involved. This complex system has been studied with a wide variety of methods with different sensorimotor distortions, both visual and proprioceptive, different adaptation tasks such as pointing or tracking, and different experimental setups with the main distinction between real world and virtual reality setups. In my dissertation I describe and discuss three specific aspects of adaptation: 1) the relative weight of visual and proprioceptive adaptation, 2) spatial and proprioceptive generalization of adaptation, and 3) acquisition of alternative mappings with repeated adaptations.

An important aspect of sensorimotor adaptation is how the ambiguous mismatch between visual and proprioceptive coordinate systems is resolved. While the source of the distortion is located in the visual system for horizontally shifting prism adaptation, different experimental factors have been found to affect the relative weight of visual and proprioceptive adaptation. Redding and Wallace (2000) showed that a minimum of both feedback delay and feedback duration is required for visual adaptation. A different aspect was found by Ernst and Banks (2002) who showed that signal reliability is included by means of a Bayesian estimate. In my experiment I showed that an auditory pacing signal is another factor facilitating visual adaptation.

As a second aspect of adaptation in my dissertation I examined the generalization of prism adaptation over space. Three hypothetical generalization patterns have been suggested: minimum constraint with a nonlinear spatial generalization, maximum constraint with a flat generalization, and intermediate linear constraint with a straight line as generalization. Experimental results showed nonlinear generalization for recalibration (or conscious corrections) and straight lines as generalization for realignment. In addition, asymmetric generalization was found for realignment with opposite slopes in the generalization after visual and proprioceptive adaptation. While the original explanation was based on a flawed logic, based on my results from spatial and proprioceptive generalization I can explain all previous results as an underestimation of change in the guiding system.

The third aspect of adaptation I address in my dissertation is the acquisition of alternate sensorimotor mappings (dual-adaptation) with the associated process learning to learn. Previous studies showed that opposing mappings can be learnt with enough practice but that some sensorimotor distortions required specific experimental procedures like random switching between mappings or breaks of several hours between mappings. Additionally, previous research was ambiguous about the involvement of learning to learn, a process increasing the efficiency of single adaptations by accelerating the adaptation rates. Testing repeated adaptations in different experimental schedules I showed the involvement of learning to learn. I also found that the efficiency of dual-adaptation only depends on the number of trials in each sensorimotor mapping irrespective of their segmentation in blocks of differing lengths.

5 Zusammenfassung

Sensomotorische Kontrolle ermöglicht es uns mit unserer Umgebung zu interagieren und diese zu beeinflussen. Dafür werden Signale aus unterschiedlichen sensorischen Systemen zu einer kohärenten multisensorischen Repräsentation zusammengefasst. Angepasst an unsere Intentionen werden die sensorischen Informationen verwendet, um zielgerichtete Bewegungspläne zu erstellen. Dabei wurden zwei Arten der Bewegungskontrolle beschrieben: open-loop und closed-loop Kontrolle. Ersteres ist ein reiner „Feedforward"-Prozess, basiert also rein auf einem anfangs erstellten Bewegungsplan, wohingegen zweiteres auch einen Rückmeldungs-Prozess („Feedback") enthält. Während der Bewegungsausführung wir der Bewegungsfortschritt kontinuierlich mit einer vorhergesagten Position verglichen und gegebenenfalls korrigiert.

Betrachtet man die Adaptation der Auge-Hand Koordination nur oberflächlich, dann gleicht diese zunächst nur einer einfachen Fehlerreduktion. Untersucht man diesen grundlegenden Prozess allerdings genauer, wird offensichtlich, dass es sich hierbei vielmehr um eine komplexe Kombination mehrerer Teilprozesse handelt. Um das Ausmaß der Komplexität zu erfassen, wurde in vergangenen Studien eine Vielzahl an Methoden eingesetzt. Dabei wurden verschiedene Störungen der sensomotorischen Kontrolle eingesetzt, die entweder das visuelle oder das propriozeptive System beeinflussen, und verschiedene Adaptationsaufgaben, etwa Zeigen oder Folgebewegungen, wurden in unterschiedlichen Typen von Versuchaufbauten verwendet, deren grundlegende Unterscheidung in der Verwendung von realem Feedback oder einer virtuellen Realität bestand. In meiner Dissertation gehe ich auf drei spezifische Aspekte der Adaptation ein: 1) die relative Ausprägung der Adaptation in entweder dem visuellen oder dem propriozeptiven System, 2) räumliche und propriozeptive Generalisierung und 3) das Lernen alternativer sensomotorischer Karten durch wiederholte Adaptationen.

Ein erster wichtiger Aspekt sensomotorischer Adaptation ist, wie der mehrdeutige sensorische Konflikt zwischen visueller und propriozeptiver räumlicher Repräsentation gelöst wird. Obwohl bei der Adaptation auf einen horizontalen Versatz durch eine Prismenbrille die eigentliche Störung im visuellen System vorliegt, haben verschiedene experimentelle Faktoren einen Einfluss darauf, welches der beiden sensorischen Systeme durch eine Adaptation an das andere angepasst wird.

Redding und Wallace (2000) konnten hierzu zeigen, dass sowohl ein Minimum an Zeit am Anfang der Bewegung ohne visuelles Feedback („feedback delay") benötigt wird, als auch dass am Ende der Bewegung eine minimale Zeitspanne mit visuellem Feedback („feedback duration") erforderlich ist. Ein weiterer Faktor wurde von Ernst und Banks (2002) beschrieben. Sie konnten zeigen, dass die relative Sicherheit einer sensorischen Modalität mit einer Bayes'schen Schätzung in die Wahl des zu adaptierenden Systems einbezogen wird. In meinem Experiment konnte ich zeigen, dass zusätzlich auch ein rhythmisches auditives Signal zur Kontrolle der Bewegungsgeschwindigkeit eine Adaptation des visuellen Systems begünstigt.

Der zweite Aspekt einer Adaptation, den ich in meiner Dissertation untersucht habe, ist die räumliche Generalisierung von Prismenadaptation. In der Literatur wurden dazu drei hypothetische Generalisierungsmuster vorgeschlagen: „minimum constraint" mit einer nichtlinearen (normalverteilten) Generalisierung, „maximum constraint" mit einer konstanten Generalisierung und „intermediate linear constraint" mit einer Generalisierung, die durch eine Gerade beschrieben werden kann. Bisherige experimentelle Ergebnisse zeigten nichtlineare Generalisierung für Rekalibrierungsprozesse (bzw. kognitive Kontrolle) und eine Gerade als Generalisierungsmuster für Realignment-Prozesse. Es wurde für Realignment außerdem eine asymmetrische Generalisierung gefunden mit entgegen gesetzten Steigungen für visuelle und propriozeptive Adaptationen. Die ursprüngliche Erklärung für diese Asymmetrie beinhaltete eine logische Lücke. Allerdings konnte ich durch die Ergebnisse meiner Experimente zu räumlicher und propriozeptiver Generalisierung eine neue Erklärung finden: die Unterschätzung von Veränderungen des leitenden sensorischen Systems.

Der dritte Aspekt einer Adaptation, auf den ich in meiner Dissertation eingehe, ist der Erwerb alternativer sensomotorischer Karten durch wiederholte Adaptationen („dual-adaptation") mit dem assoziierten Prozess „learning to learn". Frühere Studien zeigten, dass mit ausreichend Übung entgegen gesetzte sensomotorische Karten gelernt werden können, wenn dafür spezifische Anforderungen an die experimentelle Durchführung erfüllt sind wie etwa zufällige Wechsel zwischen den alternativen Karten oder mehrstündige Pausen zwischen den Adaptationen zu den einzelnen Karten. Zusätzlich war in früheren Untersuchungen nicht eindeutig geworden ob oder unter welchen Bedingungen „learning to learn", ein Prozess zur Erhöhung der Effektivität einzelner Adaptationen, an dieser dualen Adaptation beteiligt ist. Durch die Untersuchung von wiederholten Adaptationen in unterschiedlichen experimentellen Zeitplänen zeigte ich die Beteiligung von „learning to learn“ mit einer Beschleunigung der Adaptationsraten im Verlauf des Experimentes. Ich konnte außerdem zeigen, dass die Effizienz einer dualen Adaptation im Sinne einer Lerngeschwindigkeit nur von der Anzahl der ausgeführten Bewegungen abhängt, ganz unabhängig davon, in wie viele und wie lang dauernde einzelne Adaptationsblöcke diese aufgeteilt waren.

Manuscripts

Running head: PRISM ADAPTATION

The Role of Movement Synchronization with an Auditory Signal in Producing Prism Adaptation

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Key words: prism adaptation; motor control; spatial mapping; spatial alignment; rhythmic sound

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Abstract

The prism adaptation procedure is often used to study the plasticity of eye-hand coordination to misalignment of the visual and proprioceptive spatial maps. Misalignment can be resolved by adaptive change in spatial maps of either the eyes or hand or both. In this procedure pacing pointing movements with a rhythmic auditory signal is usually employed to control movement speed, but the role of the auditory signal itself in producing adaptation has not been examined. The present experiment addressed this issue by testing three conditions: (1) exposure pointing was self-paced without an auditory signal, (2) exposure pointing was paced by an auditory signal without synchronization, and (3) exposure pointing was synchronized with the auditory signal. The first condition produced primarily proprioceptive adaptation. The second condition also produced primarily proprioceptive adaptation, but visual adaptation was also present. The third condition produced primarily visual adaptation. Results are discussed in terms of two possible roles for the auditory signal: (1) a rhythmic auditory signal may enhance overall activation of the adaptive neural network and (2) movement synchronization with a rhythmic auditory signal may enable multisensory integration including auditory spatial information that selects the more reliable proprioceptive signal for movement control with consequential detection of misalignment in and realignment of the visual system.

The Role of Movement Synchronization with an Auditory Signal in Producing Prism Adaptation

Exposure to prisms that displace the visual field, for example, in the rightward direction initially disrupts behavior, for example, in visual guided reaching. Recovery of accurate behavior involves at least two very different and dissociable adaptive processes; ordinary error correction and extraordinary spatial realignment (Bedford, 1989, 1993a, 1993b, 1999; Redding & Wallace, 1985a, 1985b, 1993, 1996, 2001, 2002, 2006b; see also Newport & Jackson, 2006; Redding, Clark, & Wallace, 1985; Redding et al., 2005; Redding & Wallace, 1997b; Simani, McGuire, & Sabes, 2007; Weiner, Hallett, & Funkenstein, 1983). Error correction produces rapid adaptation, while spatial realignment occurs more slowly. Error reduction processes that persist in the face of developing realignment of visual and motor spatial maps may produce over compensation for the optical displacement, appearing as non-adaptive behavior. Spatial realignment may be experimentally isolated from error correction by measuring the aftereffects of prism exposure under conditions where error correction strategies are no longer applied (see Redding & Wallace, 2006b, 2011).

The misalignment between spatial maps for the eyes and hand introduced by prismatic displacement is reduced by adaptive change in either the visual map or the proprioceptive map or both (Cohen, 1967; Craske, 1967; Harris, 1963, 1965; Hay & Pick, Jr, 1966; Redding & Wallace, 1988a, 1988b; Rock & Harris, 1967). Visual adaptation occurs when slow pointing movements are made during exposure and visual feedback is delayed until the terminus of the pointing movement (Canon, 1970; Cohen, 1967; Kelso, Cook, Olson, & Epstein, 1975; Redding & Wallace, 1990, 1992, 1994, 2000; Uhlarik, 1973; Uhlarik & Canon, 1971), while conversely proprioceptive adaptation predominates with fast pointing and early visual feedback (Choe & Welch, 1974; Redding & Wallace, 1990, 1992, 1994). Intermediate conditions in pointing speed and feedback delay may produce both visual and proprioceptive adaptation, which algebraically sum to equal the total adaptation in the eye-hand coordination loop (Hay & Pick, Jr, 1966; McLaughlin & Webster, 1967; Templeton, Howard, & Wilkinson, 1974; Wallace, 1977; Wilkinson, 1971).

Feedback delay arguably motivates the conditions necessary for visual adaptation. Limb movement is initiated by a control signal coding the position of the visual target sent to the limb, but during the following period when the limb is not visible the visual system tracks the proprioceptive signal from the moving limb

(Stritzke & Trommershäuser, 2007); that is, the direction of control is reversed from the initial eyes-to-hand, becoming hand-to-eye control. When the hand becomes visible at the end of the pointing movement, it does not appear in the expected position because of the optical displacement. This spatial discordance between expected and achieved visual position signals a misalignment of the map of visual space with the map of proprioceptive space. Realignment occurs for the visual map because the misalignment is detected in the visual system, changing the mapping constant toward agreement with the proprioceptive map. When visual feedback is available early in the pointing movement the direction of control remains eye-to-hand with consequential discordance detection and realignment in the proprioceptive system.

The present research was concerned with another possible factor at a higher order level of processing that may influence direction of control and the locus of spatial realignment; namely, synchronization of exposure pointing movements with a rhythmic auditory signal. In so far as we are aware, all investigations of visual adaptation have employed a regular auditory signal to cue pointing movements. In none of these studies was the source of the auditory signal visible and, therefore, could not be a direct source of spatial discordance and consequential adaptation (cf. Bedford, 2007). Nevertheless, a rhythmic auditory signal is a confounded factor and might contribute to localization of adaptation. In this paper we develop and test hypotheses about how this might occur.

In these previous experiments the task workspace is defined in terms of visual, proprioceptive, and auditory reference frames. Each element of the task, target, hand, and sound is coded not only in its own reference frame, but also in the other two reference frames. When the hand becomes visible its visual position differs from its position in both proprioceptive and auditory reference frames. Put another way, only the visual position of the hand has changed and not its position in the proprioceptive or auditory reference frames. This inter-sensory evidence suggests that visual position is unreliable and favors selection of the proprioceptive system for guiding visual-motor behavior. Consequently, spatial discordance and spatial realignment occurs in the guided visual system.

Such inter-sensory evaluation is most likely to occur when visual feedback is delayed until the terminus of the movement and when movement is synchronized with the auditory signal. With early visual feedback immediate visual dominance of the hand position precludes the three-way comparison among sensory reference frames. When the auditory signal is not synchronous with movement termination any three-way comparison cannot be made, except perhaps from memory. Therefore, synchronous auditory signals may contribute to localization of spatial discordance and consequently realignment in the visual system.

Moreover, the system default may be visual guidance of the proprioceptive system. Vision is more accurate in the frontal-parallel dimensions affected by prismatic displacement, while proprioception is more accurate in the sagittal or depth dimension (van Beers, Wolpert, & Haggard, 2002). Therefore, visual dominance/control may be the natural default selection in adaptation to horizontal prismatic displacement with early visual feedback and when movements are not synchronized with the auditory signal or when there is no auditory signal.

A third possibility is that rhythmic sound alone might have a general alerting effect. Sensory-motor learning and spatial realignment likely involves neural activity in a spatially distributed neural network (e.g. Scheidt et al., 2012). Such a neural network likely includes (1) the cerebellum where realignment may occur, (2) premotor cortical areas responsible for coordinative linking of sensory-motor systems, and (3) the motor cortex where the spatial discordance signal may originate. Pollok et al. (2005) using neural imaging have demonstrated that an auditory pacing signal for finger movements establishes just such a distributed oscillatory network. Therefore, a rhythmic auditory signal during prism exposure might enhance activity of the adaptive network responsible for spatial realignment, the consequence of which would be an increased level of adaptation for the components otherwise favored by the exposure conditions.

We tested three exposure conditions with delayed (terminal) visual feedback designed to assess each of these three hypotheses about the possible effects of a rhythmic auditory signal on the kind and magnitude of prism adaptation: (1) Exposure pointing was self-paced by the subject without an auditory signal (No Sound, NS group). This condition tested the hypothesis that visual dominance/control is the natural default selection in adaptation to horizontal prismatic displacement even when feedback is delayed. Proprioceptive adaptation was expected, but not visual adaptation. (2) Exposure pointing was performed in the presence of a rhythmic auditory signal, but instructions did not emphasize synchronization of movements with the auditory signal (Sound Only, SO group). This condition tested the hypothesis that rhythmic background sound has a general alerting effect, enhancing activation of the distributed adaptive network. The level of adaptation was expect to increase, especially proprioceptive adaptation because exposure conditions, namely, auditory asynchrony of pointing movements, otherwise favored visual dominance and control of pointing movements. (3) Exposure pointing was performed in the presence of a rhythmic auditory signal with explicit instructions to pace movements to the auditory signal. This condition tested the hypothesis that synchronizing movements with a rhythmic auditory signal enables detection of the unreliable nature of the visual reference frame and selection of the proprioceptive frame to control pointing movements. Visual adaptation was expected to be substantial, but not proprioceptive adaptation. In each condition visual and proprioceptive adaptation were evaluated against zero to test the hypothesized selection of the dominant controlling reference frame.

Movement kinematics were recorded and used to assess how well movements were synchronized with the auditory signal. In addition to visual and proprioceptive aftereffect tests, the total aftereffect in the eye-hand coordination loop was tested to assess additivity of the components aftereffects. Deviation from additivity would suggest that error correction strategies transferred to the aftereffect tests. Finally, direct effects of prismatic displacement during exposure were recorded for comparison with the usual time course of adaptation.

Method

Participants

The 42 subjects (16 male) were right-handed volunteers, mostly students at Bremen University, aged 20 to 30 years (*M* = 23.45, *SD* = 3.14). All subjects had normal or corrected to normal visual acuity (Snellen: 20/20) and ‘normal’ stereoscopic vision (≤ 550’’); they were also naïve to prism adaptation. Subjects were assigned randomly to one of the three experimental groups (14 subjects each). The number of male subjects was almost equal across groups: four, six, and six for groups No Sound, Sound Only, and Sound Paced, respectively. Subjects were treated in accordance with the Declaration of Helsinki (2008) and gave written informed consent prior to the experiment. Each subject was paid 8 € for their participation.

Apparatus

Subjects sat at a table-like apparatus with the top at chin-level, as illustrated in Figure 7. A chinrest restricting head rotation was mounted on the subject's side of and centered on the apparatus. The opposite side of the top surface was curved to allow approximately the same amount of visual feedback for different lateral hand positions at the endpoint of movement. By varying the width in the sagittal plane of the top surface of the apparatus terminal visual feedback of hand position was either completely occluded (Figure 7a) or the terminal 4 cm of the pointing finger was visible (Figure 7b). Three targets were attached at the curved front of the apparatus' top surface. One target was fixed at the center (0°) directly in front of the subject; the other targets were positioned at 10° to the left and right of the middle target: target positions were adjusted for each subject to compensate for the width of the apparatus required for terminal visual feedback. A sound source was fixed on a shelf to the right and behind the subject and not visible to the subject during the experiment and produced short beats at a rate of 40 bpm. For the adaptation procedure, two wedge prisms mounted in a spectacles frame with base left were used. The power of these prisms was 15 prism diopters and introduced a visual displacement to the right of approximately 8.5 deg of visual angle.

Measurements of hand movements in three dimensions were taken with a computer-controlled ultrasound measuring system operating with high spatial (< 1 mm) and temporal resolution (13 ms) based on the travelling time of ultrasound pulses (Zebris Medical, Isny/Germany). Small transmitters were mounted on the top of the pointing finger and on the back of each of the three targets: left, central, and right positions. Finger and target positions were recorded in three dimensions, calibrated on the central target position. Movement endpoint was identified from the recordings as the first relative maximum in depth (z-coordinate) after movement onset, indicating full arm extension. Movement endpoint coordinates were then compared to the central target coordinates to determine the difference in the horizontal dimension. These difference values were then expressed in degrees of visual angle deviation left or right from the central target and submitted to analysis.

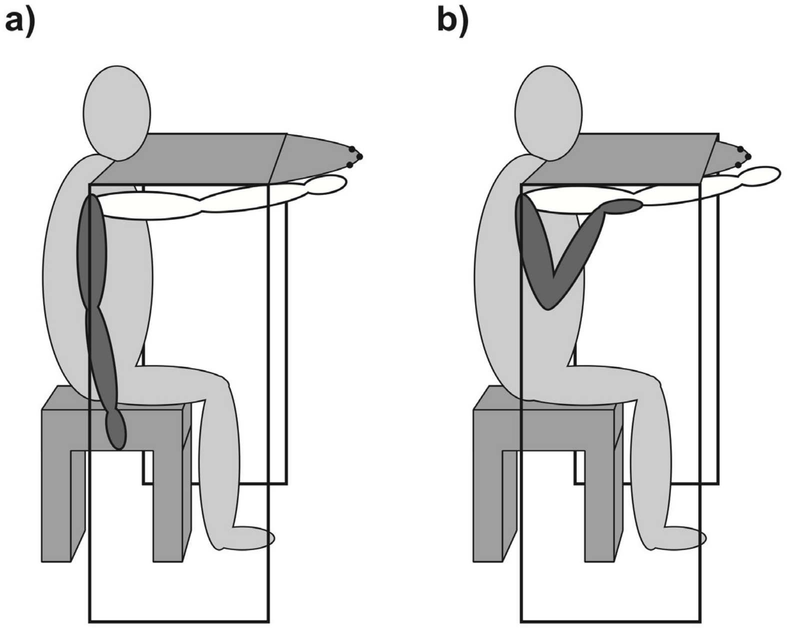

Figure 7. Adaptation Table. Subject sitting at the apparatus; both starting position (arm in dark grey) and movement endpoint (arm in white) are shown for a) lower starting position with wide top surface occluding visual feedback and b) upper starting position with narrow top surface providing visual feedback.

Subjects performed pointing movements with the extended index finger of their right hand below the top plane of the apparatus from two different starting positions. The lower position was with extended arm hanging down from the shoulder (see Figure 7a). The straightened arm was then moved up to just below the target and then back down to the starting position, resulting in a smooth up-down cyclical movement. The upper position required the subject to start each movement from a tactile position marked on the under surface of the apparatus approximately 28 cm directly in front of the subject (see Figure 7b). Subjects then straightened their arm toward the target and returned to the starting position, resulting in a smooth cyclical out and back sagittal movement with little change in pointing altitude. These different lower and upper starting positions were used for aftereffect measures and exposure pointing, respectively, to minimize any generalization of error corrective strategies developed during exposure to the aftereffect measures (Redding & Wallace, 2006b).

Procedure

All subjects received visual feedback only at the terminus of exposure pointing movements (i.e., delayed feedback) where only approximately 4 cm of the fingertip was visible. Subjects were randomly assigned to one of three treatment groups.

Subjects in the Sound-Paced (SP) group were instructed to carefully synchronize their movements to the auditory signal occurring every 1.5 s, leaving the starting position on one beat, arriving at the target on the next beat, returning to the starting position on the third beat, and so on for the entire experiment. They were encouraged to end each outward and backward segment of their movements exactly on one of the beats, so that at the end of the outward movement they could see their finger during the acoustic signal. Additionally, these subjects also had a training phase consisting of 20 pointing movements without prismatic displacement both from the lower and upper starting position with visual feedback at the end of each movement. Movements were directed to the central target. During the training phase, the Experimenter continued to stress the importance of the rhythm, demonstrated the timing of pointing movements, and corrected the subject's performance if necessary.

Subjects in the Sound-Only groups (SO) received instructions similar to those of the Sound-Paced group, except that synchrony with the auditory signal was not stressed and they received no training in synchronizing movements to the auditory signal.

Subjects in the No-Sound (NS) group pointed without the auditory signal. They were instructed to point slowly and regularly to the target trying to keep the same pointing speed throughout the experiment.

Following the instruction phase, the experimental procedure was the same for all three groups: pre-exposure tasks, prism exposure, post-exposure tasks, and re-adaptation. Upon arrival in the laboratory, each subject was informed of the general aim of the study, but the description of their participation was limited so that they only knew they were participating in a study of eye-hand-coordination and therefore had to perform different kinds of rhythmic pointing movements. Before the experiment, subjects were tested regarding visual acuity by means of the Freiburg visual acuity test (Bach, 1996) and stereoscopic vision (Lang Stereo Test, Western Ophthalmics Corp). Each subject was informed of the exact procedure of each task they were going to perform. Instructions were given according to the group of the subject (see above). The subject was then seated in a chair before the apparatus with head positioned in the chinrest.

Subjects were first asked to perform the pre-exposure tasks. Before each task, subjects had to close their eyes and the experimenter gave a short reminder of the procedure of the next task, including lower starting position with the associated movement and target for the movement.

The three pre-exposure tasks were similar to the pre-exposure baseline tests obtained by Redding and Wallace (2006b) and consisted of a visual shift test, a proprioceptive shift test, and a total shift test without visual feedback (see Figure 7a). The test order was pseudo-randomized between subjects in a group; each group had the same set of pseudo- random test orders. Performance on each test was recorded as lateral distance from the specified target position in degrees of visual angle.

Visual Shift. The visual shift test involved no pointing movements but instead required the subjects to judge whether a small point of light was straight ahead of them. For this, the laboratory was completely darkened and a small point of light via a custom laser pointer was projected onto a white surface 125 cm in front of the subject. The experimenter slowly moved the light from a lateral starting position towards the other side and the subject verbally indicated when it appeared to be straight ahead. Performance was stored as a photograph made by a fixed camera fixed in a known position relative to objective straight ahead. Afterwards the pointer was turned off and moved to a starting position on the other side; then the next trial started, up to a total of 10 trials. The first trial always began on the right side, with alternating starting sides for subsequent trials. Lateral eccentricity of starting position was randomly varied for each trial. The stored photographs of pointer position were later examined to determine pointer position relative to objective straight ahead expressed in degrees of visual angle along the horizontal dimension using previously established calibration. Results of the visual shift test can be taken as measurement of the straight ahead in the visual system, thus representing the current orientation of the visual straight ahead relative to the objective straight ahead.

Proprioceptive Shift. In the proprioceptive shift test subjects performed 10 pointing movements starting from the lower position. The eyes of the subjects were closed during these pointing movements to ensure planning of the movement based on proprioception. They were instructed to point so that at the end of each movement their hand was straight ahead of their nose. With the head as frame of reference this can be assumed to be a measure of straight ahead in the proprioceptive system.

Total Shift. The total shift test required 10 pointing movements to each of the three targets but without visual feedback of finger position. All movements started from the lower position. A random sequence of targets was verbally given to each subject, one target at a time whenever the subject was in the starting position. Performance in this test can be interpreted as the result of both visual and proprioceptive movement planning.

Following the pre-exposure tasks, subjects performed the prism exposure task. The apparatus was set to provide terminal visual feedback (see Figure 7b). The experimenter then placed the prism glasses on the subject. In this task, subjects were asked to point 30 times to the central target starting from the upper position. Terminal lateral error from the target was recorded in degrees of visual angle for each exposure pointing trial.

Following exposure the apparatus was set to occlude visual feedback (see Figure 7a), the prism glasses were removed, and the subjects were asked to perform the same tasks as in pre-exposure again, now as post-exposure tasks. The median of a subject’s performance in each post-exposure task was compared to the respective median of performance in pre-exposure. Any difference was interpreted as an aftereffect in the respective system: visual shift (VS), proprioceptive shift (PS), and total shift (TS) in eye-hand coordination. The adaptive direction of change is in the direction of the rightward displacement for the VS measure, but opposite the direction of the displacement for the PS and TS measures (Redding & Wallace, 1998, 2000; Welch, 1978).

To conclude the experiment subjects pointed 20 times to each of the three exposure targets with visual feedback and without prismatic displacement. This final phase was included to ensure re-adaptation to normal eye-hand-coordination and the data are not reported here.

Results

Aftereffects of exposure and direct effects in terms of terminal error in pointing during exposure were analyzed for three groups receiving no sound (NS) during exposure pointing, rhythmic sound only (SO) during exposure pointing, and exposure pointing movements paced (SP) to the rhythmic sound. The results, given in detail in the following sections, included: (1) synchrony of movements with the auditory signals was greater for the SP conditions than for the SO condition, (2) for the NS condition only proprioceptive adaptation was statistically significant, (3) for the SO condition both visual and proprioceptive adaptation were significant, (4) for the SP condition only visual adaptation was statistically significant, (5) additivity of visual and proprioceptive shifts to equal the total shift was present, and (6) direct effects during exposure rapidly decreased, but adaptation leveled off short of target achievement.

Timing Performance Manipulation Check

To check for the effectiveness of the experimental manipulation timing performance of each subject in the groups with rhythmic sound (SO and SP) was measured during the exposure task. Asynchrony between movements and rhythmic sound was computed based on the difference between time spent between sequential outward and backward movements and the expected time span (3 s). These differences were squared to remove the algebraic sign, the squared values were summed and divided by the number of movements, and the square root was used as a measure of asynchrony expressed in seconds. This index of asynchrony expresses the average deviation from expected movement time in seconds. A zero value for this index would mean perfect synchrony.

Comparison between the two sound groups showed higher values of asynchrony for the group with only rhythmic sound (SO), *M* = 0.275 s, *SEM* = 0.030, as compared to the group with movements paced to the rhythmic sound (SP), *M* = 0.168 s, *SEM* = 0.007, *t*(26) = 3.48, *p* = .002 (two-tailed). Although synchrony was not perfect for the Sound-Paced group, it was significantly better than for the Sound-Only group. This confirms the effectiveness of experimental manipulation.

Adaptive Components

The data for visual shift (VS) and proprioceptive shift (PS) as a function of sound treatment group are displayed in Figure 8. To evaluate the hypotheses planned comparisons against zero were performed on the component aftereffects.

For the No-Sound (NS) group proprioceptive adaptation, 1.6 deg ± SEM = 0.6 was statistically greater than zero, *t*(13) = 2.60, *p* = .011, but visual adaptation was not statistically different from zero, 0.7 deg ± *SEM* = 0.8, *t*(13) = 0.86, *p* = .204. As expected, self-paced pointing without rhythmic sound produced primarily proprioceptive adaptation.

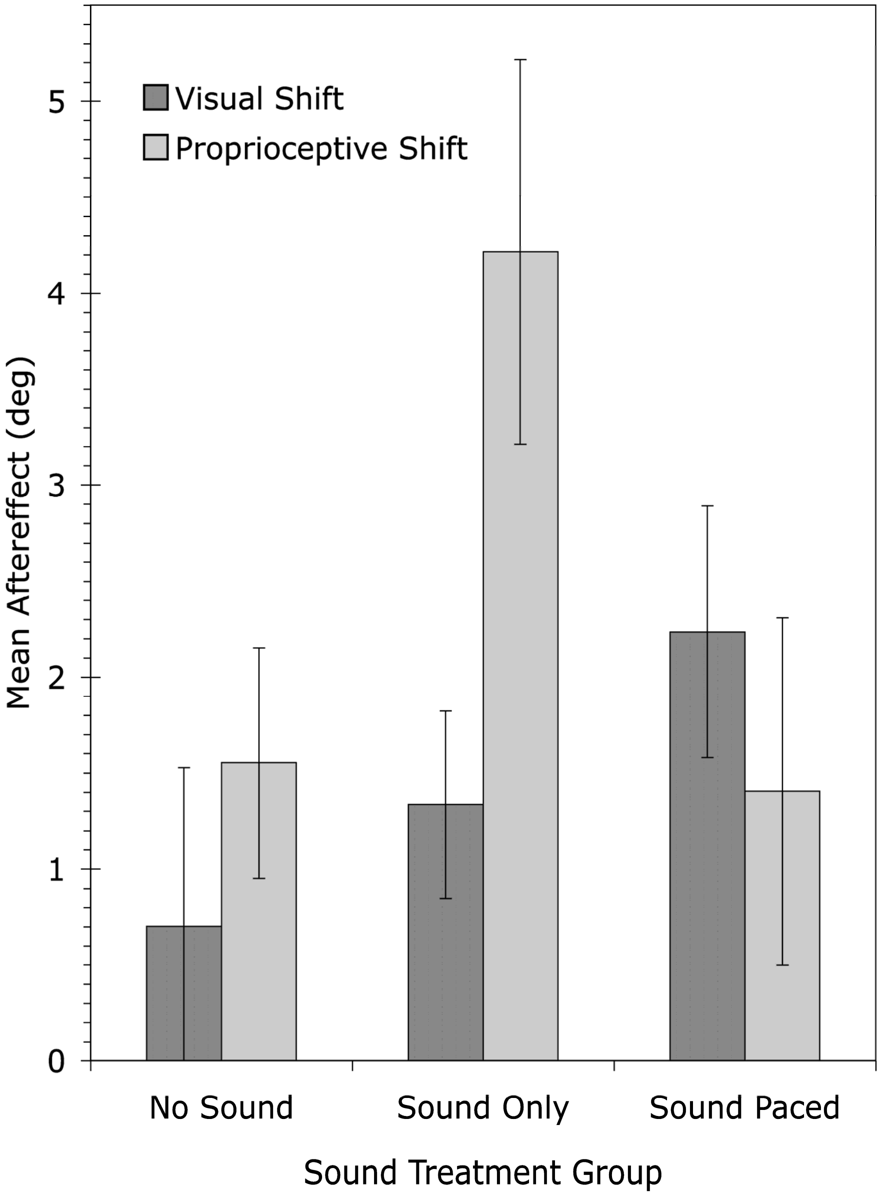

Figure 8. Adaptive Components. Visual and proprioceptive aftereffects are shown as a function of sound treatment group. Error bars denote Standard Error of the Mean.

For the Sound-Only (SO) group proprioceptive adaptation, 4.2 deg ± *SEM* = 1.0, was statistically greater than zero, *t*(13) = 4.20, *p* < .001, as was visual adaptation, 1.3 deg ± *SEM* = 0.5, *t*(13) = 2.73, *p* = .008. As expected, rhythmic sound alone produced an overall increase in adaptation, particular for proprioceptive adaptation.

For the Sound-Paced (SP) group visual adaptation, 2.2 deg ± *SEM* = 0.7, was statistically greater than zero, *t*(13) = 3.41, *p* = .002, but proprioceptive adaptation was not statistically different from zero, 1.4 deg ± *SEM* = 0.9, *t*(13) = 1.55, *p* = .072. As expected, exposure pointing synchronized with the auditory signal favored visual adaptation, but not proprioceptive adaptation.

An ANOVA with repeated measures computed with adaptive components (VS, PS) as the within subjects factor and group (SO, SP) as the between subjects factor confirmed the interactive effect of the experimental manipulation on adaptive components. The main effect of Components was not statistically significant, *F*(1, 26) = 1.69, *p* = 0.205, and neither was the main effect of Group, *F*(1, 26) = 1.75, *p* = 0.198, but the interaction of Component by Group was significant, *F*(1, 26) = 6.11, *p* = .020.

Component Additivity

The total shift (TS) was compared to the sum of components (VS + PS) to assess the contribution of ordinary sensory-motor learning to the realignment aftereffects. An ANOVA with repeated measures was computed with the component measure (TS, VS + PS) as the within subjects factor and group (NS, SO, SP) as the between subjects factor. There were no statistically reliable sources of variance in this analysis, *p* > .05. On average, the sum VS + PS, 3.8 deg ± *SEM* = 0.7, was numerically larger than TS, 3.0 deg ± *SEM* = 0.3. However, there is no reason to believe that deviation from additivity was substantial in the data or that ordinary sensory-motor error correction transferred largely to the aftereffect tests.

Exposure Performance

Equipment failure resulted in the loss of terminal error data for some subjects on some trials. In the SO group four subjects were missing data on the last exposure trial, another subject was missing data on the last two trials, and another subject was missing data on the last three trials. In the SP group data were lost for one subject after the first eleven exposure trials. The group mean was substituted for these missing data. This augmented data set was subjected to an ANOVA with repeated measures, which revealed statistical significance for the main effect of Exposure Trial, *F*(29, 1131) = 65.33, *p* < .001, and the interaction of Group by Exposure Trial, *F*(58, 1131) = 1.64, *p* = .002. The main effect of Groups was not significant, *F*(2, 39) = 0.57, *p* = .571.

For ease of interpretation, terminal error was averaged over successive blocks of six exposure trials. These data are displayed in Figure 9. As can be seen, terminal error was reduced more rapidly for the SP group in initial exposure trials, but then tended to level off at about 0.8 deg. In contrast, terminal error continued to decrease for the other two groups until apparently leveling off at about 0.3 deg for the NS group and 0.7 deg for the SO group. Overall, terminal error remained at about 0.6

deg for the last two exposure blocks. The rapid initial decrease in terminal error is typical of prism adaptation (for a review, see Redding & Wallace, 2011) and the failure to achieve the target has previously been found when competition between visual and proprioceptive control interferes with ordinary error correction (Redding & Wallace, 1993; Wischhusen & Fahle, 2006). Thus, direct effects were consistent with previous findings in prism adaptation.

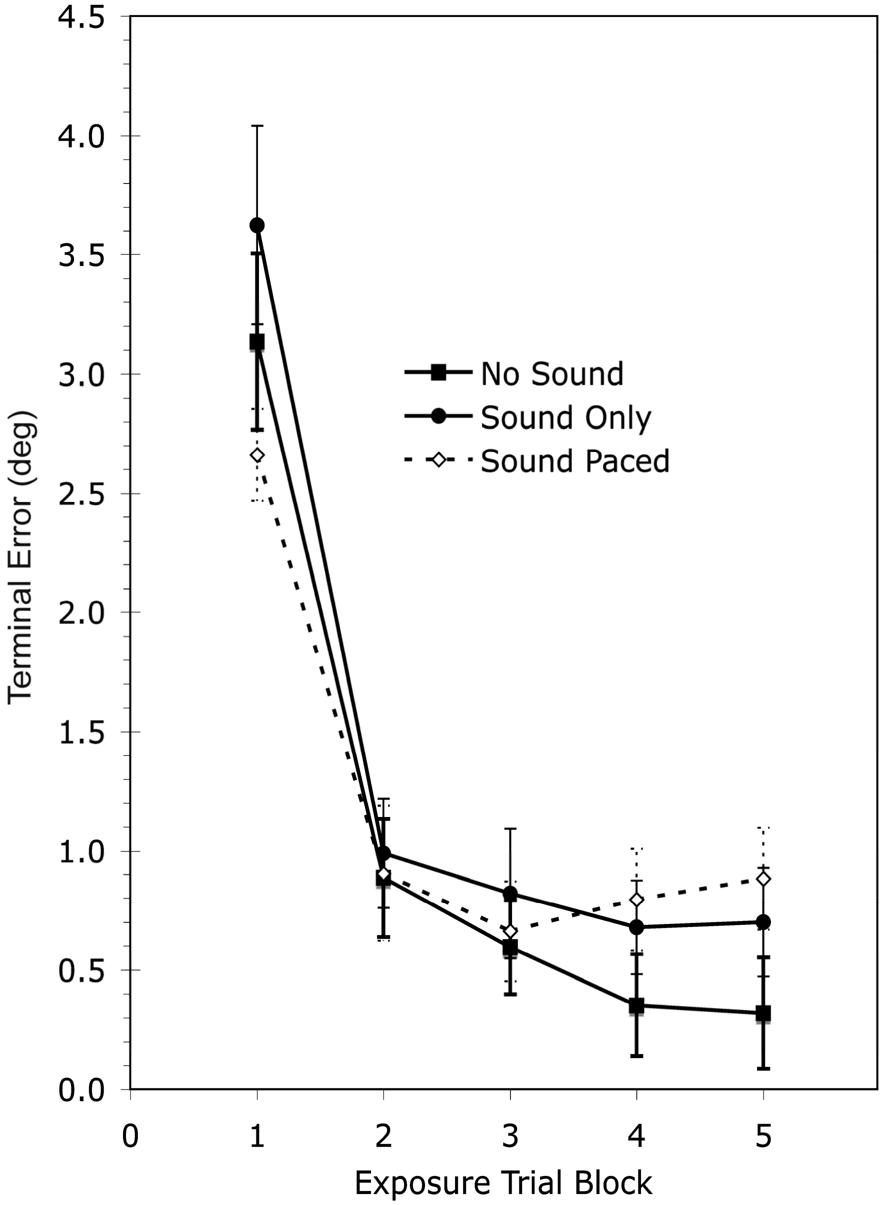

Figure 9. Analysis of Terminal Error. Terminal Error is shown as a function of blocks of six exposure trials for each of the sound treatment groups. Error bars denote Standard Error of the Mean.

Discussion

These results suggest that three higher-level processes are involved in determining the visual and proprioceptive locus of prism adaptation: (1) Evaluation of the movement task and selection of the most reliable source of information for movement control (Ernst & Banks, 2002): Without the third, auditory reference frame eye-hand coordination defaults to the more reliable visual reference frame for movement control in frontal-parallel dimensions with consequential locus of adaptation in the proprioceptive reference frame.

(2) Augmented activation of the appropriate distributed adaptive neural network: Adding the auditory reference frame to the task, but without strict instructions to use the auditory signal in task performance produces an overall alerting effect that enhances adaptation, particularly in the proprioceptive reference frame: guidance by the more accurate visual reference frame continues to be the dominant process, while the presence of activity in the auditory reference frame serves to more strongly activate the distributed adaptive network (Pollok et al., 2005).

(3) Inter-sensory comparison of available reference frames to select the more reliable reference frame for movement control: Requiring active use of the auditory reference frame in the task by instructions to synchronize movements with the rhythmic auditory signal encourages a three-way comparison among reference frames which favors proprioceptive movement control, with consequential increase in visual adaptation and reduction in proprioceptive adaptation. Synchronization of movement with the auditory signal may be particular critical for inter-sensory comparison because the audio-visual integration interval appears to be very short (Meredith, Nemitz, & Stein, 1987; Senkowski, Talsma, Grigutsch, Herrmann, & Woldorff, 2007). Therefore, even slight deviations from synchrony may reduce the three-way comparison among visual, auditory, and proprioceptive reference frames critical for visual adaptation.

It is important to note that these processes operate to influence the direction and activation of control between eyes and hand. Spatial realignment then occurs in the controlled or guided sensory-motor system by a process of comparing the expected (feedforward) consequence with the (feedback) outcome to detect misalignment (spatial discordance) and activate the realignment process (Redding & Wallace, 1996, 1997a, 2006b). However, the present results also suggest that delayed visual feedback may be a necessary, but not sufficient condition for visual adaptation: delayed visual feedback without an auditory signal produced primarily proprioceptive adaptation. On the other hand, synchronization of movement with an auditory signal may also be a necessary, but not a sufficient condition for visual adaptation: proprioceptive adaptation predominates even when pointing movements are synchronized with the auditory signal if visual feedback is available early in the pointing movement (Redding & Wallace, 2008). In summary, the present results suggest that delayed visual feedback and auditory synchronization of movements together are necessary and sufficient conditions for visual adaptation and that proprioceptive adaptation predominates when either condition is not present.

A cautionary note is suggested by the incomplete exposure adaptation. It appears that the adaptive system may have not settled on one direction of control, but oscillated between visual and proprioceptive guidance, which produced interference with ordinary error correction, especially for the Sound-Paced condition (see Figure 9). There may be yet another necessary factor involved in selection of the direction of control between visual and proprioceptive systems. For example, it might be that the demands of synchronization of movements to an auditory signal limit the ability to exercise ordinary adaptive motor control. Further research is needed to completely establish the role of movement synchronization with an auditory signal in producing prism adaptation.

Finally, the implications of the present results for the application of prism adaptation should be stressed (Redding & Wallace, 2006a; Redding et al., 2005). We now know an additional procedure to more reliably produce visual adaptation: pointing during exposure should be performed at regular, relatively long intervals paced by a sound signal. We have shown that the synchronicity of movements necessary for visual adaptation can be easily achieved by (1) pre-experiment instructions that emphasize the importance of pacing each movement to the rhythmic sound and (2) a pre-experimental training phase. Allowing subjects to point ad lib may produce prism adaptation, but that adaptation will be primarily in the proprioceptive hand-head sensory-motor system. Indeed, prism adaptation may also be used as a diagnostic procedure by manipulating the locus of adaptation and observing which condition produces the greatest amelioration of the symptomatology.

Acknowledgments

Supported by the BMBF (Bernstein initiative) and the German Research Council (DFG). We would like to thank Annika Thüns for assistance in data collection.

Running head: Influence of Prism Adaptation on Proprioception

The Influence of Prism Adaptation on Proprioception: Answers from Generalisation

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Abstract

The spatial generalisation pattern of prism adaptation in eye-hand coordination can indicate the neuronal mechanisms solving intersensory conflicts. We tested the generalisation pattern of adaptation eye-hand-coordination using a pointing task and a 17° prism shift with a classical (spatial generalisation) and a new (proprioceptive generalisation) paradigm. In this novel approach generalisation of adaptation is studied for different head to body orientations for the first time. In Experiment 1 spatial generalisation was tested over a wide spatial range of targets. To determine the spatial location of a target subjects have to exclusively rely on the orientation of their eyes relative to their head. The task was to adapt to a specific target, the aftereffect was then tested either at the same or a different location. Varying the angle between head and trunk in Experiment 2 tested the influence of the neck muscle proprioception on the generalisation of adaptation. The pointing target was kept constant but subjects were rotated to the left or right by varying distances between two adaptation periods. We measured the relative amount of adaptation in the visual and proprioceptive system indicating a primarily proprioceptive adaptation in both experiments. While we found almost complete linear generalisation for spatial generalisation, the generalisation pattern in Experiment 2 was strongly modulated by the amount of body rotation. In both experiments the modulation of generalisation patterns can be explained by an underestimation of the proprioceptive change in the visual localising system. We summarize this new model in a box and arrow model of eye-hand coordination incorporating the underestimation of signals in the guiding subsystem. Our model can explain previously found opposite generalisation patterns for visual as compared to proprioceptive adaptation and overcome limitations of previous explanations.

The Influence of Prism Adaptation on Proprioception: Answers from Generalisation

Prism adaptation is a phenomenon that has been studied since Helmholtz (1867). Starting in the middle of the 20th century (e.g. Bailey, 1951) a new effort was made in understanding the deceptively simple process of prism adaptation. It has gradually become clear how complicated the neuronal processes underlying prism adaptation are (for reviews at different points in time see: Kornheiser, 1976; Redding et al., 2005). Martin et al. (1996) suggested three criteria defining (motor) adaptation, (1) the movement itself is preserved and only modified in its parameters, (2) it is changed only with iterations, (3) afterwards (without prisms) the original behaviour cannot be accessed directly, it has to be changed back again gradually. Because of the automatic nature of the aftereffect, the strength of adaptation and also its generalisation are typically measured by the amount of aftereffect found in a particular condition. Alternatively the direct effect of a second or following adaptation can be taken as an indicator for the transfer or persistence of an adaptation (Bock, Schneider, & Bloomberg, 2001; Davidson & Wolpert, 2004; Donchin, Sawaki, Madupu, Cohen, & Shadmehr, 2002; Martin et al., 1996).

Redding et al. (2005) established a model for prism adaptation based on three independent processes: postural adjustments, strategic control, and spatial realignment. Postural adjustments occur whenever asymmetrical postures (looking or pointing to one side) are required over a prolonged period of time. This process modifies the coordinate system of the part of the body involved by biasing its direction of straight ahead towards the lateral posture (Ebenholtz, 1974, 1976; Paap & Ebenholtz, 1976). Consequently postural adjustment produces a visual or proprioceptive shift when the eye or the arm, respectively, is exercised asymmetrically. The second process, strategic control or recalibration, occurs when an adaptation is (partly) achieved by cognitive strategies, such as deliberately pointing sideways. Welch (1978) described it as a kind of associative learning. It generalises depending on the amount of similarity to the training condition, so transfer decreases with increasing difference between experimental situations. Realignment is the third process. Whenever there is discordance between two spatial maps realignment automatically and gradually aligns these maps with each other. As claimed by Redding et al. (2005) this process is unique to prism exposure. It is a kind of non-associative learning (Bedford, 1993a; Guigon & Baraduc, 2002; Redding

& Wallace, 1997b) and therefore generalises to the whole workspace provided that the adapted system is used. Although Redding et al. (2005) propose three processes, they discuss prism adaptation mainly as a result of recalibration and realignment. Furthermore, they entitle only realignment as “true” adaptation.

Irrespective of the individual processes underlying the adaptation, theoretically different patterns of generalisation are possible. For prism adaptation, Bedford (1989) introduced three different hypotheses how the relation between the visual and proprioceptive system might be changed: minimum constraint hypothesis, maximum constraint hypothesis, and the intermediate linear constraint. These hypotheses describe the possible theoretical limitations for links between visual and proprioceptive coordinates. In the minimum constraint hypothesis arbitrary combinations between points in the visual and proprioceptive space are possible. But the pattern most likely to result for training at a single location is a nonlinear change with its maximum at the training point and decreasing change with increasing distance to that point. The resulting pattern of generalisation resembles that often found for associative learning. On the other extreme, in the maximum constraint hypothesis only adaptations of equal size are allowed for all points of the visual-proprioceptive relation. This hypothesis predicts a pattern of generalisation with a constant shift for all locations even with a single training point. The last hypothesis, the intermediate linear constraint, is a mixture between the first two hypotheses. In addition to a shift in the pattern of generalisation, also the scaling between the two spaces can be adjusted so that the resulting relation is the best linear fit for all visual and proprioceptive points. For lateral training positions most transfer (and therefore aftereffect) is expected on the trained side resulting in patterns of generalisation with slopes descending from the training side to the contralateral side.

These three hypotheses show a good congruency with the theoretical constructs of Redding and Wallace (2006b). Whenever cognitive control is strongly involved in adaptation the generalisation pattern resembles that of associative learning with most transfer at the training point and less with decreasing similarity (e.g. increasing spatial distance or increasing difference in proprioceptive input) to the training condition. This pattern is predicted both by the minimum constraint hypothesis and the recalibration process. In many situations where the human visuo-motor system more or less automatically adapts corresponding to a realignment process, the coupling between vision and proprioception changes according to the maximum constraint or intermediate linear constraint hypothesis. The resulting pattern of generalisation either is a constant shift or - more interestingly - a shift and a change of scaling between the two dimensions. Depending on the spatial location of the training point a rescaling can occur which can either minimize or maximize one dimension in relation to the other (Bedford, 1989). More generally, for the intermediate linear constraint hypothesis Bedford (1989) found generalisation patterns of the aftereffect with either positive or negative slopes.

Especially studying these kinds of generalisation patterns allows a better understanding of the processes involved in prism adaptation. It is reasonable to assume that the brain chooses the most easy or efficient way to solve sensory conflicts. So the experimentally observed generalisation patterns are an indicator for what is an easy solution for the nervous system. This again allows for conclusions on the functional architecture of the sensory-motor system. Bedford (1989) and Ghahramani et al. (1996) as well as Redding and Wallace (2006b) used spatial generalisation, investigating the transfer of an adaptation to untrained target locations, to study adaptation mechanisms. While Bedford’s (1989) linear generalisation patterns indicated a realignment and rescaling of the sensory maps involved, Ghahramani (1996) found nonlinear generalisation indicating an associative learning based process: decreasing transfer with increasing distance. Redding and Wallace (2006b) then showed that different neuronal mechanisms result in different generalisation patterns and that both linear and nonlinear generalisation are possible for prism adaptation because there are two distinct processes involved: realignment and recalibration.

Based on this previous work, there are two different aspects of generalisation that we will discuss in this article. The first one is the generalisation along the spatial dimension as it was studied previously. It is tested by adapting at one point and testing the aftereffect at a different spatial location. Previous studies were limited to either adaptation at a central target (Redding & Wallace, 2006b) or to adaptations in a small range of spatial locations (Bedford, 1989; Ghahramani et al., 1996). Extending the adaptation process to more adaptation and test locations enabled us to study the adaptation process in depth showing an effect obscured before. The second aspect of generalisation is the generalisation along the proprioceptive rather than spatial dimension. For this innovative concept we induced an experimentally controlled change in proprioception of a specific part of the body between adaptation and testing condition. We chose to vary neck muscle proprioception by different head-to-body angles. This procedure allows for transfer of predictions from purely spatial generalisation to another dimension clarifying underlying neuronal mechanisms. Thus both, spatial and proprioceptive generalisation, are important aspects of generalisation that help distinguishing the specific underlying processes of prism adaptation.

Experiment 1

The classical way of studying the transfer of prism adaptation is either to change the task (different starting positions or different movement types (e.g. throwing vs. pointing)) or to change the test situation (e.g. different target locations). The latter example is a test for the spatial generalisation and allows differentiating between the processes involved in prism adaptation (Redding & Wallace, 2006b).

Using rightward shifting prisms for the adaptation at a central target, Redding and Wallace (2006b) found a difference in generalisation patterns of total realignment aftereffects between different amounts of visual feedback during the adaptation phase. They compared the two extreme conditions of visual feedback: limiting the visual feedback to the endpoint of each movement (terminal feedback) and not restricting the amount of feedback at all (concurrent feedback). While for terminal feedback they had the biggest aftereffect at the left target and the smallest at the right target, they found the inverse pattern for concurrent feedback. They interpreted this finding as resulting from different systems that had been adapted in the two conditions: terminal feedback provokes adaptation in the visual system, concurrent feedback leads to adaptation of the proprioceptive system. Although the training position was physically straight ahead of the subject in both conditions, for the adapted system due to a shift in straight ahead it appears laterally displaced. The direction of this displacement is opposite for the proprioceptive and the visual system and therefore the patterns of generalisation also show slopes in opposite directions.

For our experiment we transfer the results of Redding and Wallace (2006b) to leftward shifting prisms and terminal feedback. We expect a generalisation pattern with positive slope because the type and amount of feedback should elicit adaptation in the visual system resulting in a leftward visual shift. In adapted visual coordinates the trained target appears shifted to the right, therefore, following the logic of Redding and Wallace (2006b), the maximum aftereffect is expected at the right target and the minimum at the left target. We tested this prediction in a spatial generalisation experiment. Our refined experimental design allowed the testing of generalisation in a broad range of locations including lateral training targets and with only little influence of recalibration expected.

Methods

Ethics Statement

Procedures of all reported experiments were approved of by the Bremen University ethics committee. The guidelines in the declaration of Helsinki (2008) were strictly followed throughout all reported experiments.

Subjects

In experiment 1, nine right-handed volunteers participated, aged 19 to 29 years (*M* = 23.88, *SE* = 1.24), four male subjects. All subjects had normal or corrected to normal visual acuity (Snellen: 20/20) and normal stereoscopic vision (≤ 60’’). Only subjects with an interpupillary distance corresponding to the prism glasses (64 ± 5 mm) were included. Before the start of the experiment, subjects were briefed about the experimental procedure and gave their informed consent.

Apparatus

Subjects sat at a table with the table top at chin-level, the table’s length was adjustable to the subject’s arm length. A chinrest with head fixation was mounted on the centre of one side of the table top, restricting head rotation. The opposite side of the table top was curved to limit the visual feedback for different hand positions in the endpoint of movements by the same amount (see Figure 10). Four targets were attached at the curved front of the table. One target was fixed at the centre (0°) directly in front of the subject, the other targets had variable positions at the table. After adjusting the length of the table top to the individual subject (approximately 50 cm, 1° ≈ 0.9 cm), these targets were placed at -17°, 17°, and 34° from the subject’s straight ahead where minus means leftwards and plus indicates rightwards (see Figure 10). For the adaptation procedures, wedge prisms with base right were used. These prisms had 30 prism dioptres and therefore introduced a visual shift to the left of approximately 17° of visual angle. The custom made glasses were mounted with lateral occluders to limit the visual field to the size of the glasses (binocular field of view: 105° horizontally, 100° vertically).

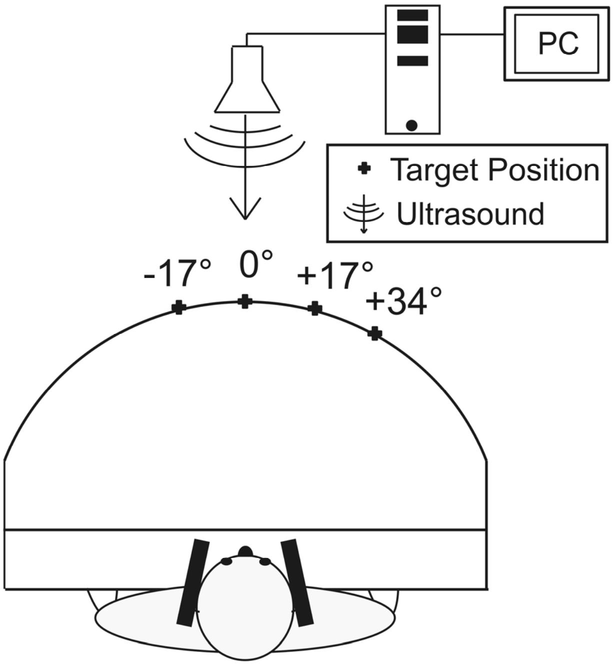

Figure 10. Apparatus for spatial generalisation. Subject sitting at the apparatus with head rotation restricted by lateral cheek cushions fixed at a chinrest. Four targets are mounted on the curved front of the table top with ultrasound microphones recording the position of each target as well as the top of the index finger and the chin rest.

Procedure

Throughout all experiments lateral deviations from a target were measured automatically at the endpoint of each movement and stored as pointing errors. Movement data were recorded using a computer controlled ultrasound based system (Zebris Medizintechnik, Isny, Germany). Ultrasound microphones were fixed at each target as well as directly in front of the chinrest and on a thimble which was mounted on the subject’s right index finger. Recorded movements were analysed using custom made software: Movement endpoints were automatically identified as the point in time with the first relative maximum in movement height after movement onset. Coordinates of movement endpoints were then processed in MatLab R2008B and Excel 2003 to compute pointing errors in degrees of visual angle. In all phases of the experiment, subjects conducted 20 quick ballistic pointing movements to the target. Visual feedback of hand position was always restricted to the endpoints of movements (terminal feedback, c.f. apparatus).

The experiment began with baseline measurements consisting of 20 fast pointing movements to each of the four targets: left (L), centre (C), right (R1), and far right (R2). Each of these blocks was followed by a measurement of the subjective straight ahead (SSA): the subject pointed in the direction of their nose with eyes closed and held the position for 5 sec. The median position of the finger was taken as the SSA measurement for the corresponding target. These measurements were subsequently treated as baseline performances and the median of pointing performance for each target was used to correct all following pointing movements. Similarly the SSA baselines were used to correct the respective SSAs in the later experiment. Baseline correction was included to cancel any pre-existing pointing biases in normal performance, especially measurements of SSA were taken after each target baseline to counteract possible shifts in proprioceptive straight ahead due to simple postural adjustments.

The baseline test was followed by nine experimental blocks, consisting of an adaptation (with prism glasses) and a readaptation phase (without prism glasses) of 20 pointing movements each. After each adaptation SSA was measured. The blocks consisted of a complete combination of three possible targets for each phase. The targets during adaptation were C, R1, and R2, whereas the readaptation targets were L, C, and R1. Thus, because of the prism glasses applied during adaptation the targets appeared at -17°, 0°, and 17° in both adaptation and readaptation phase. This allowed us to study the transfer for a difference in apparent target positions ranging from -34° to 34° (c.f. table 1 for an overview of target combinations and the resulting differences in eye position/apparent target position). The order of blocks was balanced between subjects and subjects were assigned randomly to these sequences.

Table 1. Combination of targets during adaptation and aftereffect with the respective eye position at each target and the change in eye position between phases.

	Aftereffect Target (Eye Position)		
Adaptation Target (Eye Position)	**L (-17°)**	**C (0°)**	**R1 (17°)**
C (-17°)	0°	17°	34°
R1 (0°)	-17°	0°	17°
R2 (17°)	-34°	-17°	0°

L: left target, C: central target, R1: right target, R2: far right target

Results

The primary hypothesis concerning the generalisation pattern was evaluated by comparison of size of aftereffects as a function of combination of targets in adaptation and aftereffect. In general, pointing errors for the first movement during exposure to prisms (direct effects) of each block were about 52.1% of the prismatic shift (*M* = -8.71°, *SE* = 0.41). The average size of aftereffect defined as pointing error for the first movement in the readaptation phase of each block was about 39.5% of the prismatic shift (*M* = 6.59°, *SE* = 0.22) but showed a medium interindividual variability (min = 5.27°, max = 7.61°). Therefore, for further analysis all aftereffect measurements were corrected by the respective individual average aftereffect (ipsative norm). A one-way ANOVA was computed with target Combinations (centre-left, centre-centre, centre-right, right-left, right-centre, right-right, far right-left, far right-centre, far right-right) as the within subjects factor. The main effect of Combinations was not statistically reliable, *F*(8, 64) = 2.06, *p* = .053, but showed a trend. A comparison of extreme values between maximal change in eye position to the left (far right-left, -34°) and right (centre-right, 34°) supported this statistical trend: with an average difference of -2.28° (*SE* = 0.980) the comparison was statistically reliable (*p* = .048).

The results described above suggest that the size of aftereffect might depend on the combination of adaptation and aftereffect targets. To further investigate this hypothesis we assigned the respective difference in eye position between exposure and test to the different combinations of targets. We submitted the data to a linear regression analysis of size of aftereffect predicted by difference in eye position. These data are displayed in Figure 11. Difference in eye position statistically reliable predicted size of aftereffect, Beta = -.304, *T* = -2.84, *p* = .006. Difference in eye position also explained a small proportion of variance in the size of aftereffect, R^2 = .093, *F*(1, 79) = 8.05, *p* = .006. Thus, the size of aftereffect increased for an increasing change in eye position to the left and decreased for an increasing change to the right resulting in a generalisation pattern with negative slope.

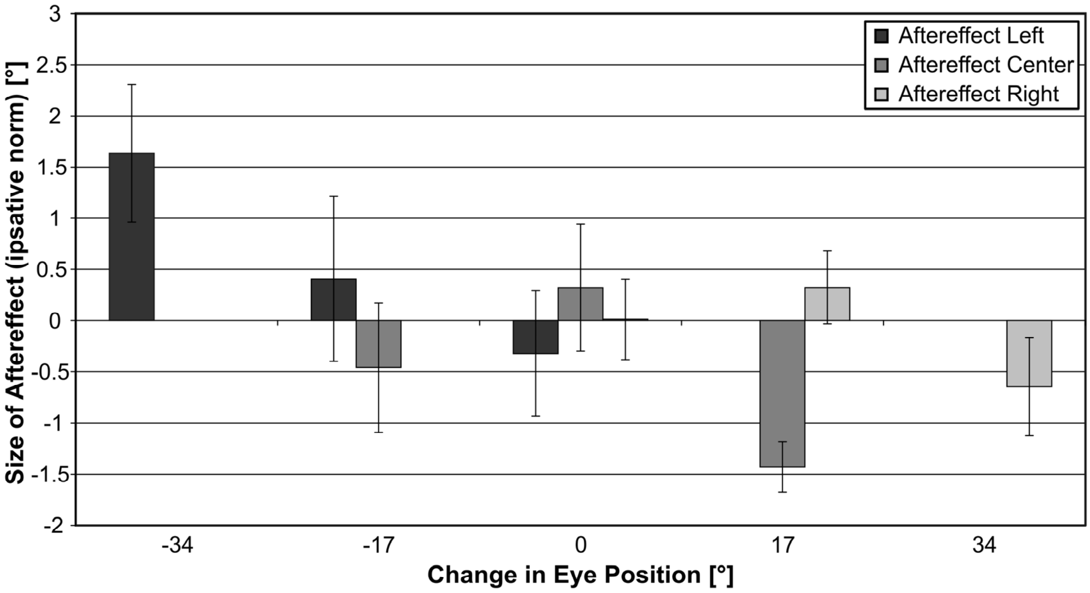

Figure 11. Aftereffect in spatial generalisation. Size of aftereffect in spatial generalisation is shown as a function of change in eye position between adaptation and aftereffect testing, group averages of ipsative norm shown. Error bars denote Standard Error of the Mean.

Testing our secondary hypothesis we computed the group average of all measurements of proprioceptive straight ahead to identify whether the visual or proprioceptive system was adapted. Surprisingly, we found a proprioceptive shift to the left (*M* = -2.86°, *SE* = 0.46). Visual inspection showed an increasing shift to the left in proprioceptive straight ahead during the course of the experiment (see Figure 12). This was confirmed by a linear regression of proprioceptive straight ahead as a function of adaptation target (centre, right, far right) and test order (position 1 to 9). Both Target (Beta = -.276, *T* = -2.63, *p* = .010) and Test Order (Beta = -.251, *T* = -2.39, *p* = .019) statistically reliable predicted the size of proprioceptive straight ahead. The factors also explained a medium proportion of variance in proprioceptive straight ahead, R^2 = .139, *F*(2, 78) = 6.31, *p* = .003. So, a proprioceptive shift to the left occurred increasingly from left to right adaptation targets. This trend was intensified by test order: later measurements of proprioceptive straight ahead showed a stronger deviation to the left as compared to early measurements during the experiment. The effect of test order is summarized in Figure 12.

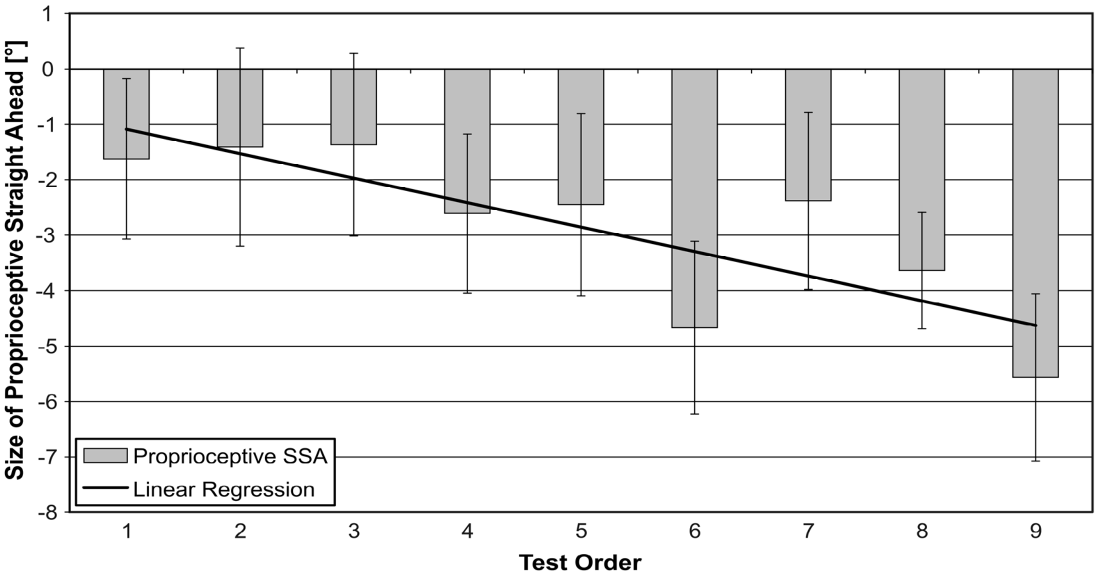

Figure 12. Test order effect in proprioceptive straight ahead. Average proprioceptive straight ahead is shown for each position in test order and as a linear function of test order (time spent during experiment, irrespective of target combinations). Error bars denote Standard Error of the Mean.

Discussion

Our primary hypothesis concerned the spatial generalisation pattern found for adaptations at different spatial locations. As expected, we found a linear generalisation pattern depending on the spatial location of adaptation and test targets although with negative slope (Figure 11). The direction of slope can be explained when taking into account the adapted system evaluated in the secondary hypothesis. Here we predicted visual adaptation after adapting by pointing with terminal visual feedback. We could not confirm this hypothesis but found an unpredicted shift in the proprioceptive system with an unexpected change of straight ahead to the left.

Looking more generally at our data, we found the valid basic pattern expected for prism adaptation in all experimental blocks with direct effects of about 52 % of optical shift at the beginning of each adaptation phase and with an average aftereffect of about 39.5% of optical shift at the beginning of readaptation phases. This is in agreement with previous studies (Fernández-Ruiz & Díaz, 1999; Redding et al., 2005).

Our main interest concerned the pattern of generalisation. We found linear generalisation of the adaptation in the horizontal dimension. The highest aftereffect values were measured at the left target whereas the lowest values were measured at the right target. This clearly contradicts the expected pattern for visual adaptation but instead matches the pattern Redding and Wallace (2006b) expected for proprioceptive adaptation. However our data clearly falsify their hypothesis of strongest transfer on the trained side. Instead we find an almost complete generalisation to different target positions with largest aftereffects on the left side although most adaptation targets were on the right side. So we indeed find a modulation into a linear generalisation by a change in scaling between proprioceptive and visual coordinate systems (Bedford, 1989). We account this modulation to a small (2%) underestimation of change in the localising system (eye to head rotation). In the most extreme case when subjects are adapting at the far right target (i.e. R2, at 34°) due to the prisms the eyes are directed to 17° during the adaptation. Subsequently, the aftereffect is tested at the left target so the eyes are directed to –17° corresponding to a change in eye position of 34° to the left. If this change is underestimated by 2% the target will be mislocalised at ~33° and therefore pointing movements are planned for this wrong target location. As a consequence the measured aftereffect is artificially increased by ~1° (see Figure 13). Interestingly, eye movements to the left which is the same direction as the prismatic shift show a larger effect of underestimation of change.

Measurements of the subjective straight ahead in the proprioceptive system showed an unexpected shift to the left which increased over the course of the experiment. This result was not expected for two reasons. First, the reduced amount of visual feedback during the experiment, especially during the adaptation phases, should produce visual adaptation (Redding & Wallace, 2000). As a result, no change in proprioceptive straight ahead would occur. But one can argue that the movement speed was too fast so that the feedback duration in the endpoint of a movement was not sufficient for the required switch to proprioceptive guidance (Redding & Wallace, 2000). Also, movements were not regularly paced by an acoustic signal which has recently been shown to be involved in producing visual adaptation (Bornschlegl, Fahle, & Redding, submitted). Second, if adaptation of the visuo-motor system to a prismatic shift to the left is achieved by a change in the (arm) proprioceptive system, the direction of change should be opposite to the direction of the shift (in this case to the right) to successfully reduce pointing errors (Redding et al., 2005).

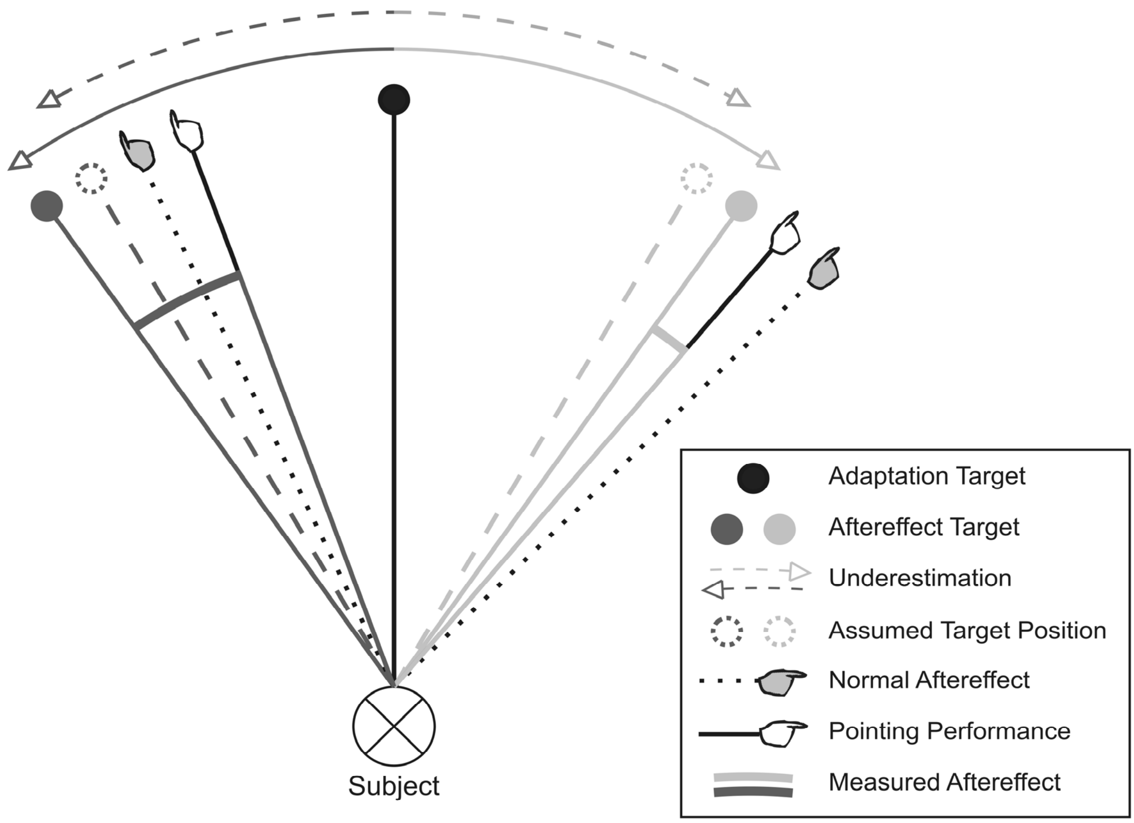

Figure 13. Underestimation mechanism for visual localisation. Following an adaptation to leftwards shifting prisms (displayed as black circle at central position) the aftereffect is tested at a different location either on the left side (dark grey circle) or on the right side (light grey circle). The required change in eye position for target foveation (curved continuous arrow) is underestimated (curved broken arrow). As a consequence the target position is assumed at a lesser eccentricity (circles with broken lines), subsequent movements are planned for and aimed at this assumed position while still being subjected to the normal aftereffect. Pointing performance is displayed for the first movement (white hand with continuous black line) with the measured angular aftereffect (thick curved line). Due to underestimation, the size of measured aftereffect is increased relative to normal aftereffect (grey hand with broken line) for testing on the left side whereas it is decreased on the right side.

A possible explanation for the unusual proprioceptive shift in the same direction as the prismatic shift to the left is an adaptation of neck muscle proprioception resulting in a change of perceived angular head position. If this were the case, the head which is actually fixed in a straight ahead position would feel turned towards the right side (or the body would feel turned to the left side). Now, if subjects take this felt change into account during pointing straight ahead and thus correct for the nonexistent rotation of head to body, the measured proprioceptive straight ahead seems shifted towards the left. When subjects are free to move their head during adaptation like in hallway exposure (Redding & Wallace, 1985b, 1987) it is very likely that at least part of the prismatic shift is compensated by a head rotation in the direction of the shift. This enables subjects to centre their eyes in the head when fixating a target straight ahead thus allowing eye movements of equal size to the left and right side. Also, the rotation of the head is the natural response to encounter the asymmetrical depth shift produced by prisms (objects in the direction of shift seem nearer to the observer, objects in the opposite direction seem further away) because this phenomenon normally occurs when looking sideways or turning the head sideways with eyes centred in the head. Such asymmetrical posture of the head would result in postural adjustments (Redding et al., 2005) at least if it is kept for a prolonged time. This explanation can be excluded since the subjects in our experiment had their head fixed in the apparatus so that an asymmetrical head posture during the adaptation phases could be prevented. But Seizova-Cajic and Azzi (2010) recently showed the cognitive influence on a change in proprioception. It may therefore be that a felt head rotation due to the asymmetrical depth shift is sufficient to produce postural adjustments. Preliminary data (unpublished) show that in both cases with head rotation restricted or head free to move during adaptation neck muscle proprioception can be adapted. Together with the adaptation in the visual and proprioceptive system it adds up to the amount of total shift (conventional aftereffect). If this was the case in our experiment it is plausible that this adaptation strengthens during the course of the experiment thus explaining the strong effect of temporal order because postural adjustments are considered a slow process which builds up over time (Redding & Wallace, 2004).

Experiment 2

Finding unexpected results in the spatial generalisation pattern in Experiment 1 encouraged us to further explore generalisation. So we wanted to test whether a different localising system would show the same pattern as found in Experiment 1. We transferred the prediction for spatial generalisation to an experimental setting based on Harris' (1965) explanation for prism adaptation as consisting of a change in the position sense or proprioceptive change. He suggests three different loci of adaptation: position of the arm relative to the head or body (arm-to-head or arm-to-body relation), head orientation relative to the body (head-to-body relation), and eye orientation relative to the head (eye-to-head relation). Although the locus of adaptation is crucial for the generalisation in space, to different postures, or even different tasks, this aspect only plays a minor role in later explanations for prism adaptation (c.f. Redding et al., 2005: proprioceptive vs. visual system). In addition to retinal coordinates and the relative orientation of eyes to the head, the orientation of head to body is an important source of information to localise objects visually. Perceived head rotation can be experimentally changed. It has been shown that neck muscle proprioception can be disturbed like any other proprioception by vibration leading to a sensation of head movement (Karnath, 1994; McIntyre & Seizova-Cajic, 2007). More easily, the importance of neck muscle proprioception can be examined by actual rotations of head relative to body. Studying the transfer of an adaptation to different head to body angles allows an insight into how this signal is involved in adapting eye-hand coordination.

While the test for spatial generalisation (Experiment 1) varied the location of the target and thus both the required eye-to-head and arm-to-head relations, the new experimental setting maintains the location of the target and thus the required eye-to-head and arm-to-head relation. In this experiment subjects adapt twice always pointing to the same target but in between these phases their body is rotated relative to the head. The only change therefore introduced during the experiment is in the head-to-body relation influencing the hand-to-body relation. This procedure also avoids the change between adaptation and test conditions normally introduced by removing the prism glasses. With terminal feedback, adaptation would be expected predominantly in the visual system (Redding & Wallace, 2006b), so to speak in the eye-to-head relation. But the commonly observable visual shift can also result from a change in the head-to-body relation (Ebenholtz, 1976; Harris, 1965) decreasing the required change in the eye-to-head relation. In addition, Bornschlegl et al. (submitted) found that the guiding system during adaptation is not simply selected based on feedback type (terminal or concurrent) and feedback duration. Other factors like an acoustic pacing signal have to be taken into account.

In this experimental setting a body rotation to the left corresponds to testing for a target on the right side and vice versa, thus the predictions for the slopes of generalisation are reversed as compared to the spatial generalisation. In this very different scenario the same direction of slope is predicted when testing the initial pointing error at a different body orientation not for the aftereffect but during a second adaptation phase. This, too, is reversing the prediction for the slopes because maximal transfer produces no initial pointing error whereas minimal transfer produces high values of initial pointing error. So with terminal feedback and visual adaptation and leftwards shifting prisms, body rotations to the left should result in less initial pointing error than body rotations to the right corresponding to a generalisation pattern with a positive slope of absolute values. We tested these predictions in a proprioceptive generalisation experiment for a broad range of head-to-body orientations and with leftwards and rightward shifting prisms. This enabled us to further clarify the stronger effect found for a change in eye position in the same direction as the prismatic shift.

Methods

Subjects

In experiment 2, twenty right-handed volunteers participated, aged 19 to 27 years (*M* = 22.5, *SE* = 0.52), seven male subjects. All subjects were selected according to the same criteria as in experiment 1. The subjects were assigned randomly to one of two groups, each group comprised ten subjects. Both groups were treated identically except that one group adapted to leftward shifting prisms (left shift group) and the other to rightward shifting prisms (right shift group). Before the start of the experiment, subjects were briefed about the experimental procedure and gave their informed consent.

Apparatus

The same apparatus as in experiment 1 was used with some slight changes. Only the central target was required, the other targets were removed from the table. Subjects now sat on a chair which could be rotated to one of five different orientations by the experimenter. This apparatus allowed manipulating the subject’s relative orientation of head to body while keeping the target position and its relation to the subject’s head fixed at 0°. A sketch of the apparatus is shown in Figure 14.

For the adaptation procedures, wedge prisms were used with different orientations of the bases for two groups: base right for the left shift group, resulting in an optical shift to the left, and base left for the right shift group, introducing a rightwards shift. These prisms had 30 prism dioptres and therefore introduced a shift of approximately 17° of visual angle.

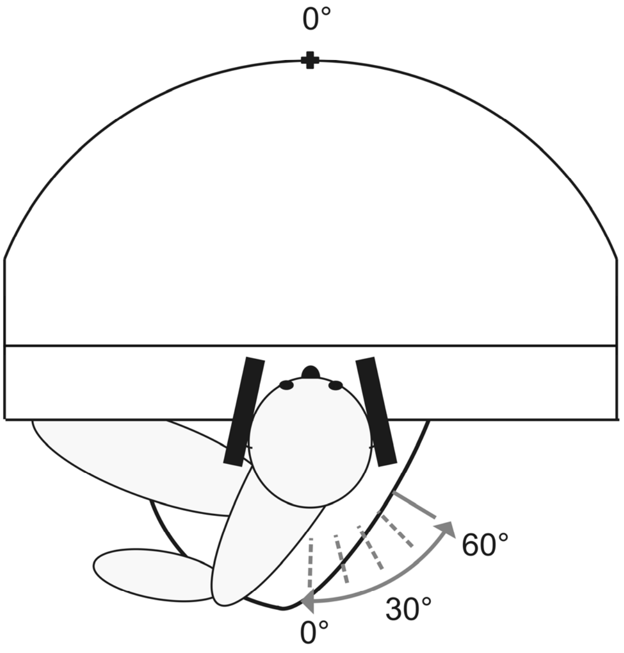

Figure 14. Apparatus for proprioceptive generalisation. Subject sitting at the apparatus with chair rotatable to five different angles (0°, 15°, 30°, 45°, 60°), maximum head-to-body rotation shown. Head rotation was restricted by lateral cheek cushions fixing the head in a position aligned with the target straight ahead.

Procedure

At the beginning of the experiment, baseline performances were recorded for two starting orientations: for body rotations to the left at 0° (S1) and for relative rotations to the right at -60° (S2). The median of each baseline was used to correct the individual results in the subsequent experiment. Each subject was tested at five rotations to the left (0°, -15°, -30°, -45°, -60°) and five rotations to the right (0°, 15°, 30°, 45°, 60°). To control for possible carryover effects one half of the subjects were first tested at the rotations to the left and afterwards at the rotations to the right. Test order was inversed for the other half of the subjects. In addition, the test order of rotations was balanced over all subjects. Each rotation was measured in a separate block consisting of three phases. In the first phase (A1), with prism glasses the subject adapted at the starting orientation. Subsequently, in the second phase (A2), the experimenter rotated the chair to the test orientation given in the individual protocol and the subject adapted again. In the third phase (RA), the prism glasses were removed and the chair was rotated back to the start orientation. Again the subject pointed to the target, now readapting.

In total, subjects pointed 20 times to the target in 2 phases during the baseline and 10 * 3 phases during the main experiment, resulting in 640 pointing movements. This experimental procedure required approximately 35 to 40 minutes per subject.

Results

All subjects adapted and readapted as expected with initial pointing errors that were gradually reduced during the following pointing movements. The temporal course of the experimental block with most change in head-to-body orientation (0°, -60°, 0°) for both groups is shown in Figure 15. The initial performance in A2 varied between subjects, blocks, and groups.

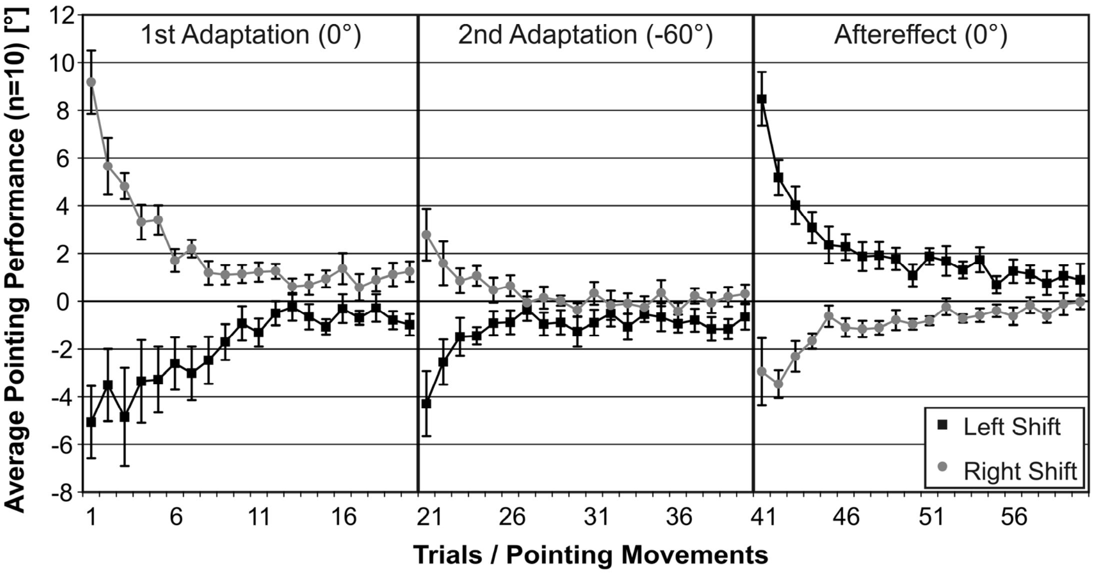

Figure 15. Temporal course of experimental block -60° rotation, left shift and right shift. Average pointing performance is shown as a function of trials for the experimental block with –60° of body rotation after first adaptation. Experimental phases are indicated by heading and group is marked by colour and symbol (left shift: black square; right shift: grey circle). Error bars denote Standard Error of the Mean.

For statistical data analysis both groups were jointly analysed. To achieve best comparability between groups the data were transformed. In the left shift group the sign of all data points was inversed so that all expected initial errors during the adaptations had positive values, whereas in the right shift group the sign of all body rotations was inversed. The latter abolished the mirror-inverted (left - right) predictions for the different direction of prismatic shift during adaptation.

Separate ANOVAs with repeated measures were computed for A2, and for control reasons also for A1 and RA. All ANOVAs had body rotation (for rotations to the left and right each: 0°, 15°, 30°, 45°, 60°) as within-subject factor and group (left shift, right shift) as between subject factor. Dependent variable always was the performance of the initial pointing movement of the corresponding phase. Degrees of freedom were Greenhouse-Geisser corrected when necessary (Maulchy-test: $p < .01$). In the second adaptation (A2), with an alpha level of .05, the effect of body rotation was statistically significant, $F(5.39, 96.92) = 12.35$, $p < .01$. Within-subject contrasts showed a significant linear ($F(1, 18) = 48.98$, $p < .01$), quadratic ($F(1, 18) = 9.50$, $p < .01$), and cubic ($F(1, 18) = 7.29$, $p = .015$) component of this effect. There was no significant effect of the following body rotation on initial performance in A1 ($F(9, 162) = 1.15$, $p = .33$) but in RA ($F(9, 162) = 2.56$, $p < .01$). In both ANOVAs for the adaptation phases a significant difference between groups was found (A2: $F(1, 18) = 16.69$, $p < .01$; A1: $F(1, 18) = 14.98$, $p < .01$) with larger errors for the right shift group. The difference between groups was not significant for the readaptation phase (RA: $F(1, 18) = 3.31$, $p = .09$).

For further analysis of the influence of body rotation on A2, the sizes of the direct effect were regressed on body rotations between adaptations. In the simple linear regression, this predictor accounted for a small proportion of the variance in pointing performance ($R^2 = .17$), which was highly significant, $F(1, 198) = 39.37$, $p < .01$. The body rotation (b = -.034, p < .01) demonstrated a significant effect on the direct effects. In the cubic model, the predictor accounted for a slightly increased proportion of the variance ($R^2 = .20$), which was highly significant, $F(3, 196) = 16.41$, $p < .01$. In this model, the body rotation demonstrated a significant effect on the direct effects but the quadratic and cubic influence was comparably small (b1 = -.013, b2 < .001, b3 < -.001).

As can be seen in Figure 16a, pointing error in A2 was smallest for a body rotation 60° to the right and the highest direct effect was observed for a body rotation 60° to the left. For the right shift group this finding is mirror-inverted for the direction of rotation (Figure 16b) because of the data transformation. Visual inspection of the data indicates a steeper gradient for rotations in the direction of the prismatic shift.

In summary, our results show a generalisation gradient for size of pointing error across different head-to-body orientations with a negative slope for the left shift group and a positive slope for the right shift group.

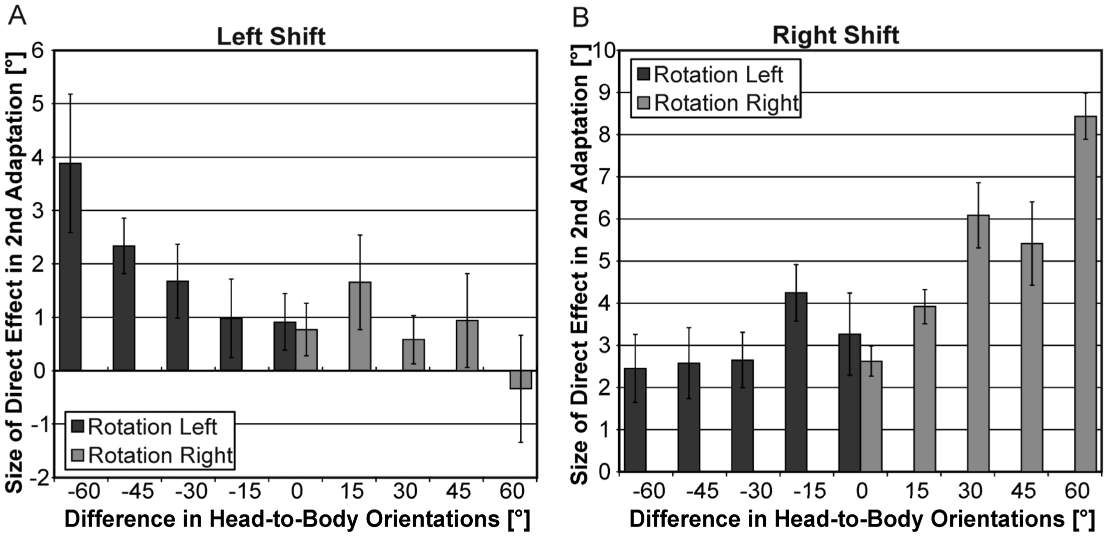

Figure 16. Generalisation to different head-to-body orientations, left shift and right shift. Second adaptation is shown as a function of difference in head-to-body orientations between first and second adaptation both for a) left shift group and b) right shift group with the expected direction of errors as positive values. Rotations to the left are shown in dark grey, rotations to the right in light grey. Error bars denote Standard Error of the Mean.

Discussion

As for the spatial generalisation in Experiment 1 we found a linear pattern of generalisation for different head to body rotations with a strong modulation of the direct effect in the second adaptation by the amount of change. This modulation was slightly more pronounced in the direction of the shift. We found an effect of the direction of prismatic shift. Over all, direct effects in the second adaptation were larger in the group tested with a rightwards shift. Also, as expected, the direction of the linear generalisation was inverted between groups with increasing errors for rotations to the left in the left shift group and increasing errors for rotations to the right in the right shift group.

The slope of generalisation patterns we found was mirror-inverted to that predicted for a visual adaptation by the theory of Redding and Wallace (2006b) and Bedford (1989). Instead, the pattern can be explained by a complete generalisation of the first adaptation plus an underestimation of change (2%) of the neck muscle proprioception. Similar to the spatial generalisation, this underestimation of change leads to a mislocalisation of the target relative to the body with the effect that the pointing arm does not compensate sufficiently for the body rotation (see Figure 17).

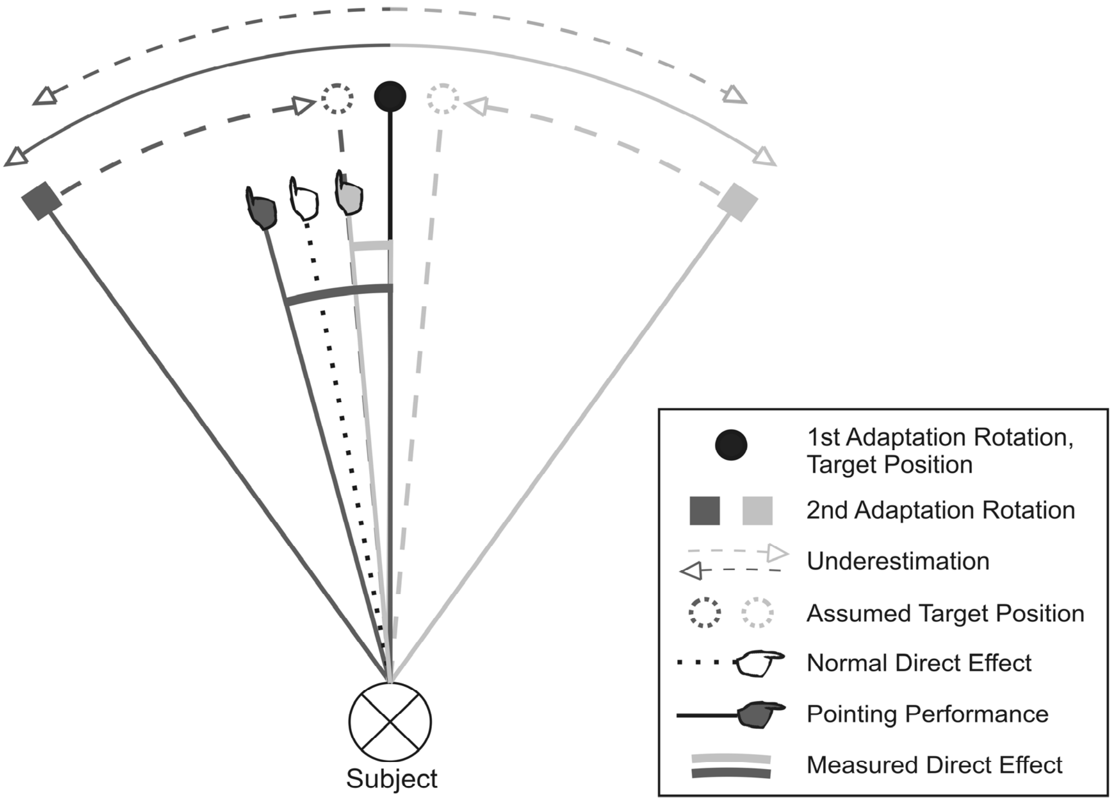

Figure 17. Underestimation of change in head-to-body orientations. Following an adaptation to leftwards shifting prisms (displayed as filled black circle at central position) a second adaptation is tested with a different head-to-body orientation with either a rotation to the left (dark grey square) or to the right (light grey square). The induced proprioceptive change (curved continuous arrow) is underestimated (curved broken arrows). As a consequence the subject does not compensate for enough rotation and the target position is assumed at a slightly displaced position (circles with broken lines), subsequent movements are planned for and aimed at this assumed position while still being subjected to the normal aftereffect. Pointing performance is displayed for the first movement (dark grey and light grey hand with continuous black line) with the measured angular direct effect (thick curved line). Due to underestimation, the size of measured direct effect is increased relative to normal direct effect (white hand with broken line) for testing rotations to the left side whereas it is decreased for rotations to the right side.

On top of the linear generalisation we found a slightly curved component. Most likely, this is the result of recalibration in addition to the realignment process which is responsible for the nearly complete generalisation. The involvement of recalibration in Experiment 2 is quite plausible because the two adaptation phases were kept as similar as possible. Subjects were still wearing prisms and pointed to the same target, the only change between training and test condition was the rotation of the body relative to the head. We can also strengthen this claim with a computational model reported elsewhere in detail (Redding & Wallace, 1988a). This model shows that the simple combination of a nonlinear generalisation (like recalibration) and a linear regression with a slope (like realignment) leads to an overall generalisation pattern most easily described by two straight lines with a steep slope on the side of direction of shift and a flat slope on the opposite side.

Control Experiment / Experiment 3

Both Experiment 1 and 2 showed that the size of adaptation measures depends on the amount of change (between tests) in a specific proprioceptor involved in the eye-hand coordination. But these experiments did not allow a final conclusion whether the visual or the proprioceptive part of the coordination system adapted (c.f. VS and PS, Redding & Wallace, 1988a). Especially for the interpretation of results in Experiment 2 the locus of adaptation is important. Therefore we conducted an additional experiment with two groups, one for each main experiment, in which we measured the size of VS and PS in the course of the experiment in addition to the size of direct effect and aftereffect.

Methods

Subjects

Twelve healthy right-handed subjects, six in each group, aged 19 to 27 (*M* = 23.91, *SE* = 0.97), four males, participated in the control experiment,. All subjects had normal visual acuity (Snellen 20/20) or corrected to normal acuity with contact lenses and gave their informed consent prior to the experiment.

Apparatus

For group 1 the same apparatus was used as in Experiment 1 (see Figure 10) and for group 2 the apparatus described for Experiment 2 was employed (see Figure 14). For measurements of VS the apparatus was enhanced by a white projection screen 2m in front of the subject and a laserpointer mounted behind the screen. The pointer projected a small red light point which could be moved horizontally on the screen. Measurements of VS were taken with a photograph (camera: Canon PowerShot A40). The position of visual straight ahead was later computed in Matlab R2008B using a previously recorded calibration. Both groups were tested with the leftwards shifting prisms (17°) used in Experiment 1 and 2.

Procedure

Experimental procedure was kept as close to the corresponding main experiment as possible. The major difference to the previous experiments was the additional testing of VS and PS in both baseline and the experimental blocks. The procedure for VS was the following: in the completely darkened room the subject watched a small red light point on a white projection screen. The point was moved slowly by the experimenter starting from the right side of the screen towards the left side. The subject verbally indicated when the point was directly straight ahead and the experimenter documented the location of the light point with a photograph. Then the light point was turned off, moved to the left side of the screen, and turned on again so that the next measure of VS could be taken. The testing of VS always consisted of 10 measures alternately starting from the right and left side of the projection screen. The eccentricity in starting position was varied unsystematically by the experimenter. For the measurement of PS, subjects had to close their eyes and then point straight ahead of their nose. They were instructed to move as fast as in all other phases and to perform 10 consecutive pointing movements.

The number of experimental blocks was reduced in both groups in order to prevent exhaustion; the resulting testing time including pre-tests was approximately 60 minutes for each subject. In the following the exact experimental procedure for both groups will be described.

The experimental procedure for group 1 started with the measurement of baseline performance in pointing at all four targets (L, C, R1, R2) and in visual (VS) and proprioceptive (PS) straight ahead. Subsequently five experimental blocks were measured, each consisting of four phases: adaptation (AD), visual (VS) and proprioceptive (PS) straight ahead, and aftereffect (AE). The target combinations for AD and AE were: C-R1, R1-L, R1-C, R1-R1, R2-L, resulting in a difference in eye position ranging from 34° to the left to 34° to the right like in Experiment 1 but with each difference tested only once.

For group 2 the experimental procedure started with the measurement of baseline performance in pointing at 0° body rotation, visual (VS) and proprioceptive (PS) straight ahead. Thereafter three experimental blocks were measured, each consisting of five phases: first adaptation (AD1), second adaptation (AD2), VS, PS, and aftereffect (AE). All measurements of AD1, VS, PS, and AE were taken at 0°

body rotation, for AD2 the subjects were rotated either to 0°, -30°, or -60°, resulting in a difference between head-to-body rotations from 60° to the left to 0°. In both groups the order of blocks was balanced across subjects and subjects were assigned randomly to the test-orders.

Results

For both groups one-tailed t-tests against zero were computed separately for VS and PS. In group 1 we found a small visual shift ($M = -1.31$, $SD = 1.36$), $t(29) = -5.26$, $p < 0.001$ and a larger proprioceptive shift ($M = 4.72$, $SD = 3.00$), $t(29) = 8.63$, $p < 0.001$. In group 2 a similar pattern was found with both a visual ($M = -2.24$, $SD = 2.04$), $t(17) = -4.64$, $p < 0.001$ and proprioceptive shift ($M = 3.99$, $SD = 5.52$), $t(16) = 2.98$, $p = 0.004$. The size of adapted components is summarized in Figure 18 with the expected direction of change as positive values.

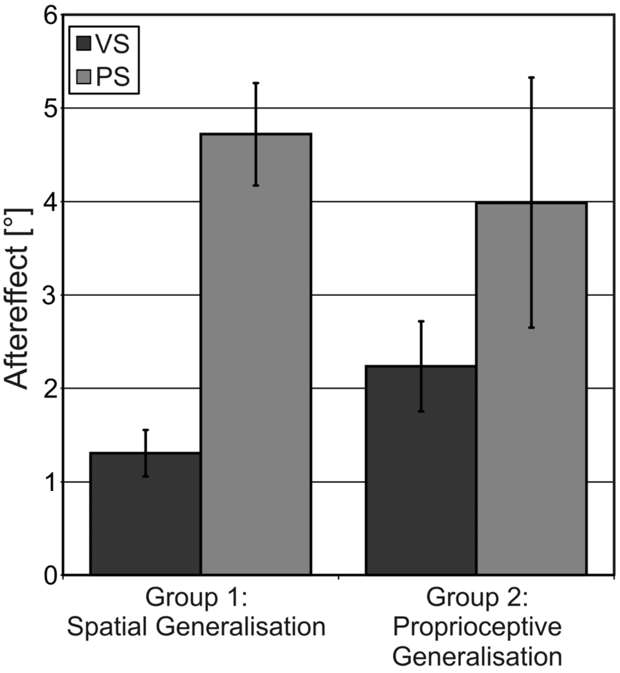

Figure 18. Comparison of adapted components. Comparison of adapted components (VS: dark grey, PS: light grey) between groups (spatial generalisation, proprioceptive generalisation), group averages are shown with the expected direction of change as positive values. Error bars denote Standard Error of the Mean.

For control reasons the regression analyses of the corresponding previous experiment were repeated for both control groups. Although the patterns of generalisation are in accordance with the previous findings (see Figure 13 a, b) neither the regression for group 1 (*b* = -0.10, *t*(28) = -0.54, *p* = 0.59) nor for group 2 (*b* = 0.39, *t*(16) = 1.69, *p* = 0.11) were statistically significant while still pointing in the same direction as in the previous experiments (see Figure 19). This may be due to a lack of statistical power (group 1: 1 – β = 0.78; group 2: 1 – β = 0.86) caused by the small sample size (n = 6) and the reduced number of experimental blocks in the control groups.

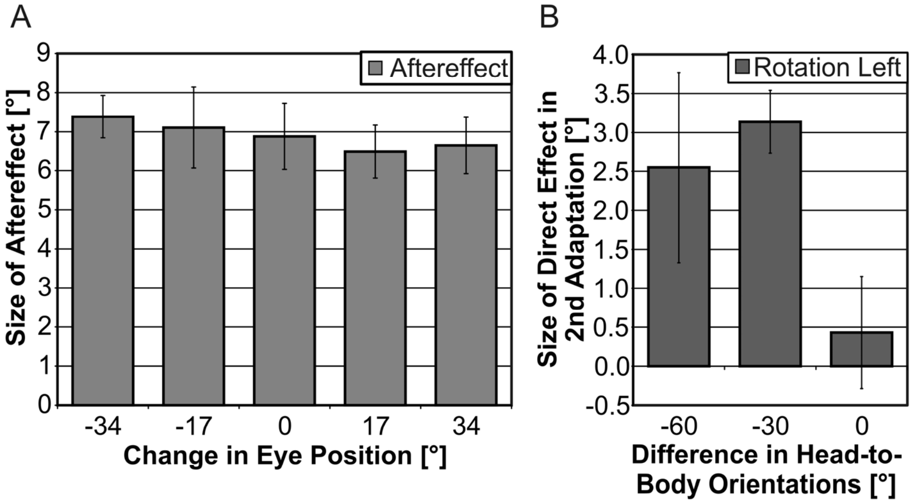

Figure 19. Generalisation patterns in the control experiment. Generalisation patterns for a) the aftereffect in spatial generalisation and b) the direct effect for a second adaptation in proprioceptive generalisation, group averages are shown with the expected direction of pointing errors as positive values. Error bars denote Standard Error of the Mean.

Discussion

In both groups we found visual as well as proprioceptive adaptation with a small bias towards proprioceptive adaptation. By restricting visual feedback to the endpoint of movements we expected to find primarily visual adaptation (Redding & Wallace, 2006b). But the movement speed and type (quick ballistic movements) may have prevented a stronger visual adaptation. As Redding and Wallace (2000) found out earlier, a sufficiently long feedback duration in the endpoint of movements is required to switch from visual to proprioceptive guidance. This feedback duration automatically decreases with increasing movement speed and might therefore have been too short in our experiments.

During the course of Experiment 1 subjects showed a shift in proprioceptive straight ahead to the left (in the same direction as prism shift) which increased in size during the experiment. This result could not be replicated in either of the groups in the Control Experiment. The reasons may be found in the slightly changed experimental protocol to enable measurement of both proprioceptive and visual straight ahead. Procedure in Experiment 1 required the subject to repeatedly change rapidly between adaptation and readaptation phases. Each adaptation and the following test of aftereffect were separated only by the short measurement of proprioceptive straight ahead by holding a straight ahead arm posture while eyes closed. This experimental procedure might well have led to an adaptation in perceived head rotation. In the control experiment fewer adaptations were required and adaptation phases were separated more clearly from the testing of aftereffect by measuring both visual and proprioceptive straight ahead in between adaptation and testing of aftereffect. Thus the temporal distance between target pointing movements with and without prisms prevented the direct sensory comparison between those conditions eliminating the possible effect of felt head rotation. We have to conclude that the exact experimental conditions are of utmost importance for any analysis of prism adaptation.

General Discussion

We found generalisation patterns that resembled linear generalisation. These patterns correspond to the findings of Redding and Wallace (2006b) and the intermediate linear constraint proposed by Bedford (1989). Using two different generalisation approaches we can interpret our results as complete generalisation with modified appearance of the generalisation pattern by an underestimation of the signals from the sensory subsystem localising the target.

Our results show a major difference to previously published studies on the generalisation of prism adaptation. While Redding and Wallace (2006b) and Bedford (1989) found most transfer of an adaptation on the spatial side of the point trained (adaptation target), we find exactly the opposite sign in the gradient of our generalisation pattern. Our control measurement for the adapted components (VS and PS) revealed a primarily proprioceptive adaptation, although we expected to find adaptation in the visual system (cf. Redding & Wallace, 2006b, but see Bornschlegl et al., submitted for further discussion). Based on these premises, the direction of generalisation matches the prediction for proprioceptive adaptation (Redding

& Wallace, 2006b). But it has to be noted that these authors only tested spatial generalisation for an adaptation at a central target. They recorded opposite signs of the generalisation gradient for proprioceptive and visual adaptation. Their interpretation for this is that the position of the central target is perceived as shifted slightly to the side. Using rightwards shifting prisms with a proprioceptive adaptation the objectively straight ahead target would appear slightly to the right, while with a visual adaptation it would appear shifted to the opposite side. Following Redding and Wallace (2006b) and Bedford (1989) a lateral position of the adaptation target results in a linear generalisation pattern with most transfer on the training side.

We tested this theory using adaptation both at lateral and central targets at a wide range of locations using the maximal possible difference in adaptation and test targets. After adaptation at a target clearly lying on the **right** side (34°), we find the biggest aftereffect at a target on the **left** side (-17°). This contradicts the conclusions of Redding and Wallace (2006b) and Bedford (1989). Instead, we propose that the adaptation generalises completely (over the whole workspace) and that the measured deviations from this pattern result from an underestimation of the proprioceptive signal in the localising system. For our case of spatial generalisation with fixed head position this would be an underestimation of the change in eye position relative to the head. This is remarkable because we consistently find this in spite of the natural bias of overestimating target eccentricity when presented in the visual periphery even if it is subsequently fixated (Henriques, Klier, Smith, Lowy, & Crawford, 1998; Vaziri, Diedrichsen, & Shadmehr, 2006).

Our conclusion of underestimation is strongly supported by the results of Experiment 2 on proprioceptive generalisation. We can exclude the influence of a lateral target on the generalisation pattern because the target was always the same and also always straight ahead of the subject’s head. In fact, we clearly find a strong modulation of the complete generalisation by the amount of body rotation introduced. Similar to spatial generalisation the modulation can be interpreted as the result of an underestimation of proprioceptive change in the localising system, which in this case is the neck muscle proprioception coding the relative orientation of head to body. Although Redding et al. (2005) count neck muscle proprioception as part of the proprioceptive (hand-head) system we see it more fit to be part of the visual system. We base this suggestion on two arguments: 1) Head rotation relative to the body is a crucial factor for inferring the spatial location of a visual target (in addition to retinal coordinates and orientation of eyes relative to the head). It is known that in parietal cortex object locations are represented in different coordinate systems: retinal maps, head centred, and hand centred coordinates (Pesaran, Nelson, & Andersen, 2006; for review see Andersen & Cui, 2009). Therefore, this subsystem (although proprioceptive in nature) is part of the visual system since it serves to visually localize targets. 2) The direction of an adaptive change of felt head rotation is always in the same direction as the prismatic shift. Since this is true for all measurements of visual adaptation (Redding et al., 2005: VS) but not for measurements of proprioceptive adaptation (Redding et al., 2005: PS) it is only natural to assume neck muscle proprioception as part of the visual system.

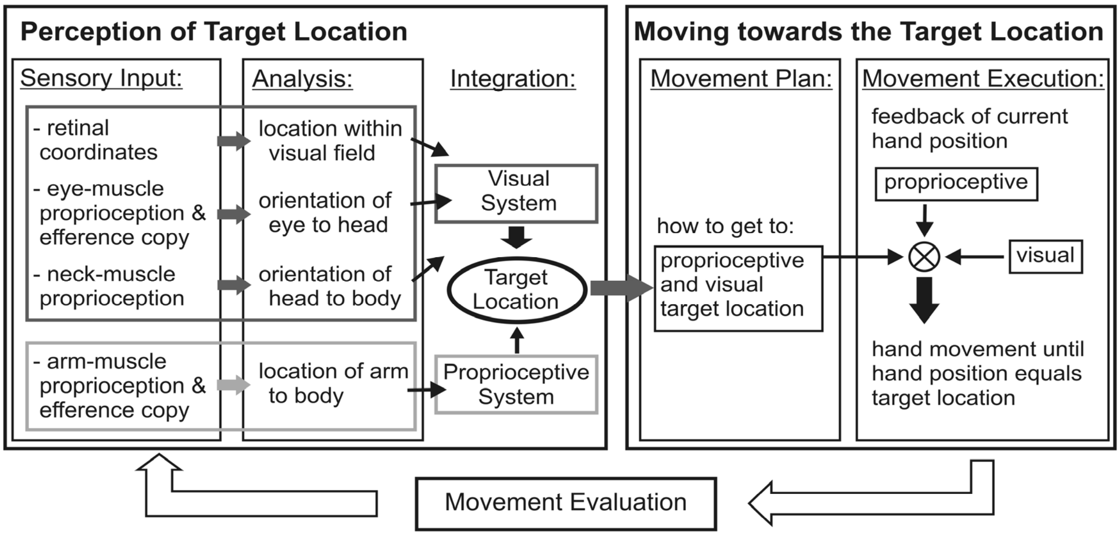

Figure 20. Model of eye-hand-coordination. Two stages of eye-hand-coordination are assumed: stage 1 – perception of target location, stage 2 – movement towards the target. During the first stage sensory input is analysed and integrated into the visual and proprioceptive subsystems and the target position is derived. In the second stage a movement is planned for the derived target position and the movement is executed until the available proprioceptive and visual feedback of hand position matches the derived target position. Subsequently, the movement and sensory feedback are evaluated and fed back into the first stage.

We formalised the idea of underestimation of the localising system as a key process in generalisation of prism adaptation in a simplified model of eye-hand coordination (Figure 20). It consists of two processing stages: perception of target location and moving to the target. In the first stage, sensory input is gathered from visual and proprioceptive signals, namely retinal coordinates (location within the visual field), eye-muscle proprioception and efference copy (orientation of eye to head), neck-muscle proprioception (orientation of head to body), and arm-muscle proprioception and efference copy (location of arm relative to body). All sensory input is analysed and combined to extract the location of a target at this stage. The result is used as input to the second stage in which a movement plan is created and executed. Normally, both visual and proprioceptive information about hand position are used in a closed-loop control to correct the movement path if necessary. In the special case of terminal feedback visual information about the hand path is prevented during the movement so only proprioceptive information can be used for the closed-loop control. With conflicting input signals according to the situation one of the signals is chosen to guide the other(s) (cf. Redding & Wallace, 2006b) and to localise the target. In the case of visual guidance the relevant input (e.g. eye muscle efference copy) is used to infer the position of the target in the visual coordinate system which is then transformed into proprioceptive coordinates. Afterwards it is fed into the second stage for movement planning. If as a consequence of adaptation the spatial input signal to the localising system, in this case visual, is underestimated the error occurs early at the first processing stage. Consequently a movement plan to a wrong location will be created and executed. The resulting movement would not point to a sufficiently large eccentricity. In contrast, in the case of proprioceptive guidance the target position is acquired correctly. But the error is introduced in the second stage: proprioceptive input from the arm is underestimated during the proprioceptive closed-loop control of movement execution. This leads to the interpretation that the movement did not go far enough (to the side) and erroneously provokes an online correction of the movement path. The resulting movement would point to a too large eccentricity. So, on this very simple assumption our model predicts opposite slopes in generalisation patterns of an adaptation for visual versus proprioceptive guidance.

A first and easy way to test the model’s validity is to apply it to previously published results. The important question is: can we interpret the results of Redding and Wallace (2006b) as underestimation of change in die localising subsystem? They found opposing generalisation gradients for proprioceptive and visual adaptation which can be explained completely by an underestimation of the signals within the guiding system! In the case of proprioceptive adaptation, like in our Experiment 1, movements are guided by the visual system. An underestimation of the visual localising signal leads to assumed lateral target positions at less eccentricity for movement planning. Due to the adapted state of the visuo-motor system the normal size of aftereffect has to be added to these assumed target positions. As a consequence, after adaptation with rightwards shifting prisms (aftereffect to the left of the target) a stronger aftereffect occurs at the right target and a smaller one at the left target. In the case of visual adaptation Redding and Wallace (2006b) found the opposite generalisation pattern. With proprioceptive guidance we predict an underestimation of the proprioceptive signal during movement execution. The closed-loop control of movement path then initiates online corrections for the seemingly inert arm. Due to this (over)compensation the resulting movement reaches to a too large eccentricity (see Figure 21). Again, the normal aftereffect has to be added to this error in movement execution so more aftereffect can be measured at the left target and less at the right target.

Like Redding and Wallace (2006b) and Bedford (1989) we tested generalisation only in one dimension. It is difficult to conclude and predict from measurements in just one dimension how a complex system with two sensory modalities (vision and proprioception) with a complete three dimensional representation of space each adapts. So, in part, this criticism of Ghahramani et al. (1996) can be applied to our experiments, too. At least we tested generalisation in this one dimension very carefully with different training locations and both absolute and relative changes to the left and right side. Testing generalisation in a two dimensional target array Ghahramani et al. (1996) found decreasing transfer of an adaptation to targets with increasing distance. This is the expected generalisation pattern for a recalibration process. From the methods employed in their study it is very likely that they were indeed measuring the generalisation of an adaptation achieved by recalibration. The artificial feedback of hand position with a cursor on a screen might not be enough information to identify and accept it as veridical visual feedback of hand position which would be necessary for a realignment of visual and proprioceptive coordinates. In our experiments, we used real feedback of hand position and most likely measured the generalisation patterns of a realignment process. This assumption is further supported by the complete generalisation that we find only modified by the underestimation of the localising signal. Supposedly, when measuring the generalisation of a realignment process in a two-dimensional array we would also find complete generalisation modified by an underestimation of change.

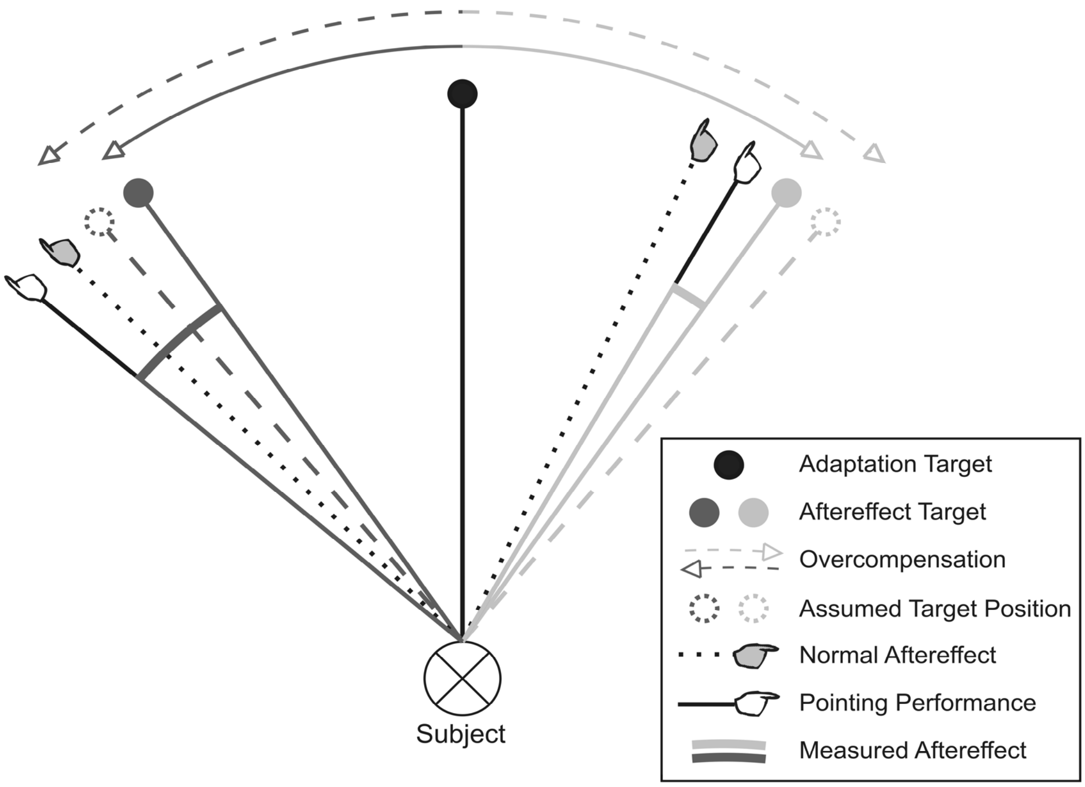

Figure 21. Overcompensation due to underestimation of proprioceptive input during movement execution. Following an adaptation to rightwards shifting prisms (displayed as black circle at central position) the aftereffect is tested at a different location either on the left side (dark grey circle) or on the right side (light grey circle). While pointing to the target the arm proprioceptive input is underestimated and due to a closed-loop control of movement the normally required change in movement path (curved continuous arrow) is overcompensated for (curved broken arrow). As a consequence a target position at a larger eccentricity is headed for (circles with broken lines) while still being subjected to the normal aftereffect. Pointing performance is displayed for the first movement (white hand with continuous black line) with the measured angular aftereffect (thick curved line). Due to underestimation, the size of measured aftereffect is increased relative to normal aftereffect (grey hand with broken line) for testing on the left side whereas it is decreased on the right side.

Repeated adaptation and readaptation like in our experiments repeatedly confronts the subject with pointing errors that can be interpreted as a continuous mislocalisation of targets. This significantly reduces signal reliability of the localising system. As a consequence the perceived target eccentricity is reduced. As Ernst and Banks (2002) showed reduced signal reliability changes the multisensory integration: subjects rely less on a signal when (artificial) noise is introduced selectively in this sensory modality. Independent of signal reliability, Sober and Sabes (2005) found an astonishing flexibility in eye-hand coordination regarding how the input signals are weighted for a movement plan. They concluded that vision and proprioception are weighted to minimize necessary coordinate transformations because this process is prone to introduce noise in the system. We can experimentally confirm that the specific form of adaptation in eye-hand coordination depends strongly on the (experimental) conditions.

In summary, we found linear generalisation for spatial as well as proprioceptive generalisation. We explain this pattern with an assumed complete generalisation modulated by an underestimation of the (proprioceptive) signal of the target localising subsystem (i.e. eye to head orientation or head to body orientation).

Acknowledgments

We would like to thank Annika Thüns for assistance in data collection.

Running head: RAPID DUAL-ADAPTATION

Rapid Dual-Adaptation with Learning to Learn

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Abstract

When subjected to environments with two different sensorimotor demands humans can acquire alternative sensorimotor mappings through dual-adaptation. Previous studies suggested that prolonged training schedules stretching over several days were required to acquire dual-adaptation. We aimed to find effective dual-adaptation in a continuum of training schedules ranging from single re-mappings (e.g. many movements in an adaptation to the same mapping) to frequent changes between mappings (e.g. many switches of adaptation situations). Moreover, we analysed whether an efficient dual-adaptation additionally involves an acceleration of adaptation rates (learning to learn). We tested repeated blocks of adaptation and re-adaptation to a prism-like visual shift in a virtual reality setup using a massed training schedule (one session of 1200 trials with 600 movements in each mapping). Between experimental groups we varied the number of blocks associated with differing block lengths ranging from few long blocks to many short blocks, both with a large and small angular visual shift. We found dual-adaptation in all groups with a gradual reduction of initial pointing errors (direct effects, aftereffects) over the course of the experiment. Amount of error reduction per movement was similar between groups irrespective of number of blocks. Initial error reduction proved to be independent of both the size of shift and experimental phase (adaptation, re-adaptation). Adaptation and re-adaptation rates increased during the experiment indicating learning to learn. Similar to dual-adaptation this process can be described as a function of the number of movements whereas the number of blocks as well as the size of shift proved irrelevant. We conclude that dual-adaptation (i.e. the reduction in initial errors), as well as the associated process learning to learn (i.e. acceleration of adaptations), rely on the number of interactions with the new and old mapping, irrespective of schedule within the training session, at least under our experimental conditions.

Rapid Dual-Adaptation with Learning to Learn

Eye-hand coordination is a key ability for successful human behaviour. It balances performance on a continuum between flexibility and stability and allows skillfull behaviour and adaptive performance in varying environments. Thus it enables us to be as precise and variable as possible at the same time. In this context, adaptation gives us the ability to quickly adjust fine motor skills (e.g. pointing movements) to environmental changes. This process ensures high flexibility: eye-hand coordination can be adjusted easily to a new condition (e.g. pointing when wearing horizontal prisms). A major drawback of adaptation processes is that each change, even back to the original condition, requires an active adaptation process. But it has been shown that, under certain circumstances, multiple sensorimotor mappings can be learnt instead of only adapted to and subsequently accessed instantly without (or at least with less) negative transfer (aftereffects) (Cunningham & Welch, 1994; Flook & McGonigle, 1977, McGonigle & Flook, 1978; Welch et al., 1993). This ability/process has previously been addressed to as “dual-adaptation” although this process would be described more appropriately as a *dual-learning*. A change which can be going along with dual-adaptation is a process called “learning to learn” (Harlow, 1949): during the course of repeated changes between two (or multiple) sensorimotor mappings the balance between flexibility and stability of performance is tipped/changed towards flexibility. A more appropriate label for this process would be *learning to adapt*. For historical reasons and to avoid further confusion of these two aspects of repeated adaptations, we will use the established terms “dual-adaptation” and “learning to learn”.

The joint effects of dual-adaptation and learning to learn can be measured both in performance (reduced initial pointing errors, increase in adaptation rates McGonigle & Flook, 1978) and in a difference in neural activation for new/fresh adaptations and well established/learnt mappings (Shadmehr & Holcomb, 1997). These authors located the essence of an established adaptation in a reduction of activation in sensorimotor cortex and putamen. In a different approach Debas et al. (2010) compared the neural activation patterns in motor sequence learning and motor adaptation during the fresh state and after a consolidation period of 12 hours, either over the day or including a night’s sleep. In contrast to motor sequence learning, the authors found no consolidation through sleep for motor adaptation but a retention of some (about one third) of the previous adaptation irrespective of time of day during consolidation. For the initial activation they found activation bilaterally in M1, SMA, cerebellum, S1, basal ganglia, and thalamus. During the retention of a previous adaptation after the consolidation period, additional activation was found in the right cerebellum in lobule VI.

So far, dual-adaptation was studied over the course of several days or even weeks possibly confounding dual-adaptation with learning to learn. One of the first studies reporting dual-adaptation with repeated adaptations was (McGonigle & Flook, 1978). Using 5 short adaptation blocks of 40 trials each and adaptation days separated by 3 days break they found some retention of the previous adaptations and thus showed the ability of learning different adaptations (10 * 3 conditions (prisms with base left, base right, and plain glass) á 10 trials). Several years later, Welch et al. (1993) picked up the idea of dual-adaptation again. On two days, separated by 48 hours, their subjects repeatedly adapted and re-adapted with 12 dual-adaptation cycles consisting of 30 pointing trials with and without prisms each. During these three hours of adaptation, the mean target pointing error of each cycle linearly decreased from about 3° down to about 2° indicating dual-adaptation. In the following years, repeated adaptations were studied with varying schedules stretched over several days (Bingham & Romack, 1999; Cunningham & Welch, 1994) or even several weeks (Martin et al., 1996). In an extensive adaptation schedule (Martin et al., 1996), two subjects adapted and re-adapted alternately to horizontally shifting prisms while throwing a ball back and forth between each other. Over the course of six weeks, with five adaptation sessions per week, the subjects were instantly able to switch between normal and prism-shifted sensorimotor mapping without the typical initial pointing errors (direct effect and aftereffect).

While a reduced initial pointing error is widely accepted as the defining characteristic of dual-adaptation, the involvement of a change in adaptation rates is debated. Welch et al. (1993) reported increasing adaptation rates for later adaptation cycles. Using movement time (in a peg in hole task) as the performance measure, Bingham and Romack (1999) found dual-adaptation with constant adaptation rates. Thus, it currently remains unclear how a change/increase of adaptation rates is linked to dual-adaptation and learning to learn. We addressed this important aspect of repeated adaptations, analysing adaptation rates in differing experimental conditions.

Astonishingly, another aspect of dual-adaptation has been widely ignored. Although in different studies a huge variety of procedures was employed, the influence of experimental procedure on learning rates has never been isolated. Evaluating the current literature revealed two extremes of experimental procedure: a) very short adaptation cycles paired with many changes between (opposing) sensorimotor mappings and b) long adaptation cycles paired with few changes. As an example of the first extreme, Cunningham and Welch (1994) studied dual-adaptation using adaptation phases of (at most) seven subsequent movements in the same mapping, and even experimental blocks with pseudorandom order of mappings were employed. These procedures imply short adaptations and many changes between the mappings. They found that an alternative sensorimotor mapping (rotation of the visual input) could be learnt for a tracking task. Another example of this procedure was used by Osu et al. (2004), who found that rapid and random switching allows for a dual-adaptation of opposing sensorimotor mappings. They tested rotations and force fields which cannot be learnt simultaneously otherwise. On the other extreme, Shadmehr and Brashers-Krug (1997) used a procedure with long adaptation phases and few changes between mappings. By testing the influence of time delays between adaptations, they also found that opposing mappings can be learnt but only with a delay/pause of at least five hours between adaptations. It has been concluded (Shadmehr, Brashers-Krug, & Mussa-Ivaldi, 1995; Tong, Wolpert, & Flanagan, 2002) that different (opposing) mappings interfere with each other because the learning of each mapping requires the same processes/resources. A different conclusion is that only one internal model can be represented in motor working memory at a time (Wigmore, Tong, & Flanagan, 2002). However, Fernández-Ruiz and Díaz (1999) showed that the strength of a single adaptation depends on the number of interactions after successful error reduction: With increasing numbers of extra interactions the adaptation got more persistent. In the same line of argumentation, Paz, Natan, Boraud, Bergman, and Vaadia (2005) underlined the special properties of the plateau-phase of an adaptation. They found a change of activation in M1 only during late adaptations when performance reached a plateau. A robust representation of one mapping resulting from long adaptations may well lead to effective learning and consequently to a fast dual-adaptation.

Although results are available separately for both extremes (long adaptations with few changes and short adaptations with many changes), a direct comparison of the learning efficiency between different phase lengths and number of changes is missing. We addressed the question after the best learning conditions for dual-adaptation by testing both, short and long adaptations, as well as intermediate phase lengths while keeping the total number of movements constant. This way we can evaluate which parameters of the schedule enable the learning process: the number of *interactions* with a new mapping (movements) or the number of *switchings* between mappings.

We hypothesize that the number of interactions with a new sensorimotor mapping is most important for dual-adaptation, and thus for the acquisition of alternative mappings. Hence, we expect equal learning rates per movement between groups with differing phase lengths and different learning rates per block between the groups. We also expect to find learning to learn with accelerated adaptation rates in the later adaptation blocks. With our experiment, we confirmed both hypotheses finding dual-adaptation as a function of movements, as well as finding an acceleration of adaptation rates as a function of number of movements.

Method

Ethics Statement

All experiments were approved of by the Bremen University ethics committee. Prior to the experiment, subjects were briefed about the experimental procedure and gave their written informed consent. The guidelines in the declaration of Helsinki (2008) were strictly followed throughout the experiment.

Participants

The 50 subjects (21 male) were right-handed volunteers, mostly students at Bremen University, aged 20 to 30 years (*M* = 24.14, *SD* = 3.21). All subjects had normal or corrected to normal visual acuity (Snellen: 20/20) and ‘normal’ stereoscopic vision (≤ 550’’); they were also naïve to prism adaptation. Each subject was paid 8 € per hour for their participation.

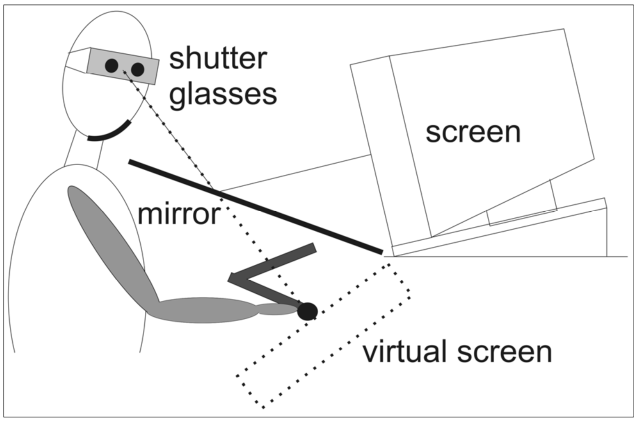

Figure 22. Virtual reality setup. Subject sitting at a virtual reality setup viewing a computer screen via a mirror. The virtual screen appeared in natural hand working space. Three-dimensional scenes were created with shutter glasses.

Apparatus

Subjects sat at a virtual reality (VR) setup with a monitor viewed via a mirror (see Fig. 22). Shutter glasses were used to create a 3D visual VR. In the setup, the subject was looking down at the working area hidden behind the mirror which is designed to coincide with natural hand movement space. The virtual screen appeared perpendicular to the viewing axis (47 cm in front of the subject). The target position was shown in the VR approximately 6 cm behind the screen. A surrounding rectangular frame (16.5 * 25 cm size) was shown at zero disparity horizontally centered around the target to allow easy and successful fusion in the VR. The target was presented at one of two possible positions: on the right side of the screen (see Fig. 23) for the original mapping and on left side for the shifted mapping. Subjects were pointing at the target with a virtual hand shown on the screen. The virtual hand was created with Cinema4D and is shown in a pointing posture holding a stick. It is based on an open source 3D model of the human body (Open3DProject, 2005). A screenshot of the virtual reality with the target and frame as well as the virtual hand is shown in Figure 23. When using the original mapping, the position of the virtual hand matched that of the real hand. When using the shifted mapping, the position of target and virtual hand were shifted by ~17° (i.e. 16.7°) or 8° to the left with respect to their real (original, proprioceptive) position. To successfully reach the target while in shifted mapping mode, the subject had to point to the position of the target in the original mapping (real hand pointing to the right target (not shown at that time), virtual hand pointing to the left target). The target was presented for the whole trial (until movement completion), whenever a button located on the starting position was pressed. Hand movements were recorded by a manipulandum (Phantom Premium 1.5 HF) with six degrees of freedom (3 spatial, 3 rotational) and used in real time for controlling the position and rotation of a virtual hand on the screen.

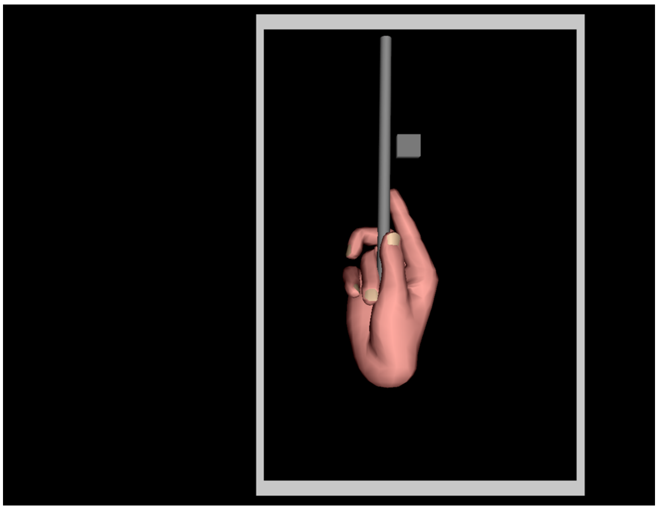

Figure 23. Screenshot of Virtual Reality. A screenshot of the virtual reality is shown, as it appeared with target, rectangular frame and virtual hand in the endpoint of each pointing movement. The virtual hand is pointing at the target with a small leftwards error. Subjects tried to reach the target with the fingertip of the index finger.

Procedure

The experimental task was the same for all subjects throughout the whole experiment: pointing at a visually presented virtual target. Subjects held the manipulandum handle in their right hand with the extended index finger touching the handle, thus matching the hand and finger posture of the virtual hand (see Fig. 23). Before each movement, subjects placed their hand on a small box directly in front of them (starting position) automatically pressing a hidden button with the side of their hand. Movements began at the starting position and ended where the subject localized the virtual target (see below). Subjects were instructed to move smoothly to the target with no online error corrections, and to try to reach the target with the tip of their right index finger. They were told that the virtual hand was at exactly the same position as their own hand and they did not expect any changes in this mapping of real and virtual coordinates. Visual feedback of hand position (virtual hand shown on screen) was provided only at the endpoint of each movement (terminal feedback) for a short duration of time (300 ms). The endpoint of a movement was determined by movement speed decreasing below a threshold of 1 cm/s. After receiving feedback, subjects moved back to the starting position where the next movement started with the button press.

Each subject carried out 1215 movements in total: 15 in a familiarization phase prior to experimental blocks, 600 with shifted mapping, and 600 with original mapping. During the familiarization phase, subjects had time to get used to the apparatus and task while pointing in the original mapping. In the subsequent experimental blocks the different mappings were used alternately in an adaptation (shifted mapping) and re-adaptation (original mapping) phase. The number of blocks and phase lengths were varied between experimental groups, ranging from 5 blocks á 120 movements each in adaptation and re-adaptation phases to 120 blocks á 5 movements in both phases (see table 1 for the complete combination of number of blocks and phase lengths). Short breaks were included in the procedure every 300 movements, resulting in three breaks for all groups except for the group with 5 blocks of 120 movements per phase. This group had a break after each block (every 240 movements), resulting in a total of four breaks. Subjects were allowed to stand up and move around during the breaks but stayed within the laboratory room. Each break usually lasted only for a short time (~1 minute), but the subjects were free to continue whenever they felt ready. Each combination of number of blocks and phase lengths was tested in separate groups with both, a large (17°) and a small (8°) visual shift. In total, 10 experimental groups of five subjects each were tested.

Results

In the adaptation of the first block we find typical adaptation behaviour with decreasing pointing errors within both adaptation and re-adaptation phases. On average, subjects initially pointed to -11.95° ± 1.13 SE and -5.34° ± 0.54 SE during adaptation to 17° and 8°, respectively (direct effect), and to 5.48° ± 0.76 SE and 4.18° ± 0.51 SE during re-adaptation to 17° and 8°, respectively (aftereffect). These initial pointing errors were statistically different for the direct effect ($t(24) = -5.83$, $p < .001$) but not for the aftereffect ($t(24) = 1.63$, $p = .116$) between subjects with 17° and 8° of shift. In the subsequent adaptation blocks we found a gradual reduction of initial errors and increasing adaptation rates. These findings will be described in more detail in the following paragraphs.

Analysis of adaptation and re-adaptation rates. For the analysis of adaptation and re-adaptation rates we created chunks of 60 movements separately for adaptation and re-adaptation. Movements of subsequent blocks of the respective phase were averaged at each position within the block (all first movements of the block sequence were averaged yielding the first average movement, average of all second movements yielded the second average movement, and so on). Thus subsequent blocks were combined to an average chunk cycle with the normal phase length of the respective group, but based on 60 movements. Exponential fits $y = a_1 \exp(a_2 x) + a_3$ were computed for each chunk cycle of adaptation and re-adaptation. The fitting parameter a_2 was used for further analysis; it represents an estimate of adaptation rate. Since it is based on an exponential decay, all values are negative. High negative numbers represent fast decays and thus fast adaptation rates. Since not all exponential fits were successful, these outliers in fitting parameters were identified as $M \pm 2SD$ and treated as missing values. These missing values were replaced by values computed with the linear trend of the individual data-set. The number of replacements was relatively small in adaptation, with 16 subjects which had only few replacements (M = 2.19, SD = 1.47). In re-adaptation only 14 subjects required a few replacements (M = 2.93, SD = 2.13), but 2 subjects had to be excluded entirely. Separate analyses were computed for adaptation and re-adaptation rates each.

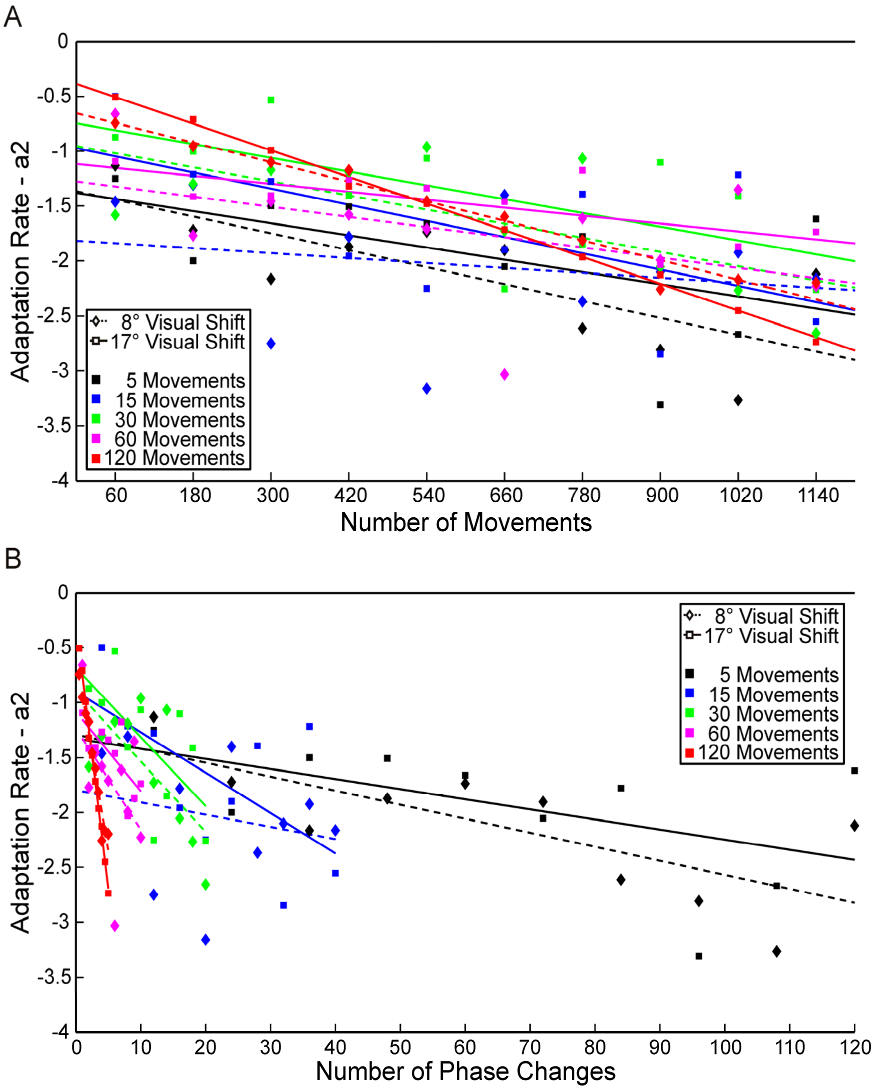

Figure 24. Development of adaptation rates during the experiment. Adaptation rates were computed for average chunks of 60 movements each and are shown as a function of a) the number of movements and b) the number of blocks. Group averages shown with linear regression.

As shown in Figure 24, values of the fit parameter a_2 became more negative during the experiment indicating an increase in adaptation rates. This acceleration of adaptation rates was similar between groups when analysed as a function of movements (Fig. 24a), and differed between groups when analysed as a function of blocks (Fig. 24b).

In a first step, we analysed *adaptation rates as a function of movements* by means of an ANOVA with repeated measures with movements (average chunks of 60 movements each: 60, 120, 180, 240, 300, 360, 420, 480, 540, 600) as within subjects factor and size of visual shift (8° and 17°) and number of movements per adaptation cycle (5, 15, 30, 60, 120) as between subjects factors. We found a significant main effect for Movements: *F*(9, 360) = 7.23, $p < 0.001$. Helmert contrasts for Movements showed a significant difference to the later levels for the first five Movement Chunks (see table 2), indicating faster adaptation rates in later blocks. No significant effects were found for between subjects factors or their interactions ($p > .373$; for interactions Movements x between subjects factors, $p > .173$).

Table 2. Statistics of Helmert contrasts for adaptation rates, main effect of Movements.

Level	**df**	**df error**	**F**	***p***
Level 1	1	40	31.83	< .001
Level 2	1	40	11.06	.002
Level 3	1	40	11.46	.002
Level 4	1	40	8.43	.006
Level 5	1	40	5.37	.026

Since we found a significant increase in adaptation rates per movement during the experiment (more negative values of a_2), we analysed the change in adaptation rates per phase change using linear fits ($y = a\,x + b$) for each subject. We computed a univariate ANOVA for the fit parameter a (slope) with Size of Shift and Number of Movements as between subjects factors. The main effect for Movements was statistically significant (*F*(4, 40) = 6271.47, $p < 0.001$). The main effect for Size of Shift and the interaction of Movements and Shift were not statistically significant ($p > .864$). Post-hoc tests revealed significant differences between all groups ($p < .001$) except for the comparison between the groups with 5 and 15 movements per phase ($p = .054$). Change in adaptation rates per phase monotonically increased with increasing number of movements per phase (decreasing number of phase changes).

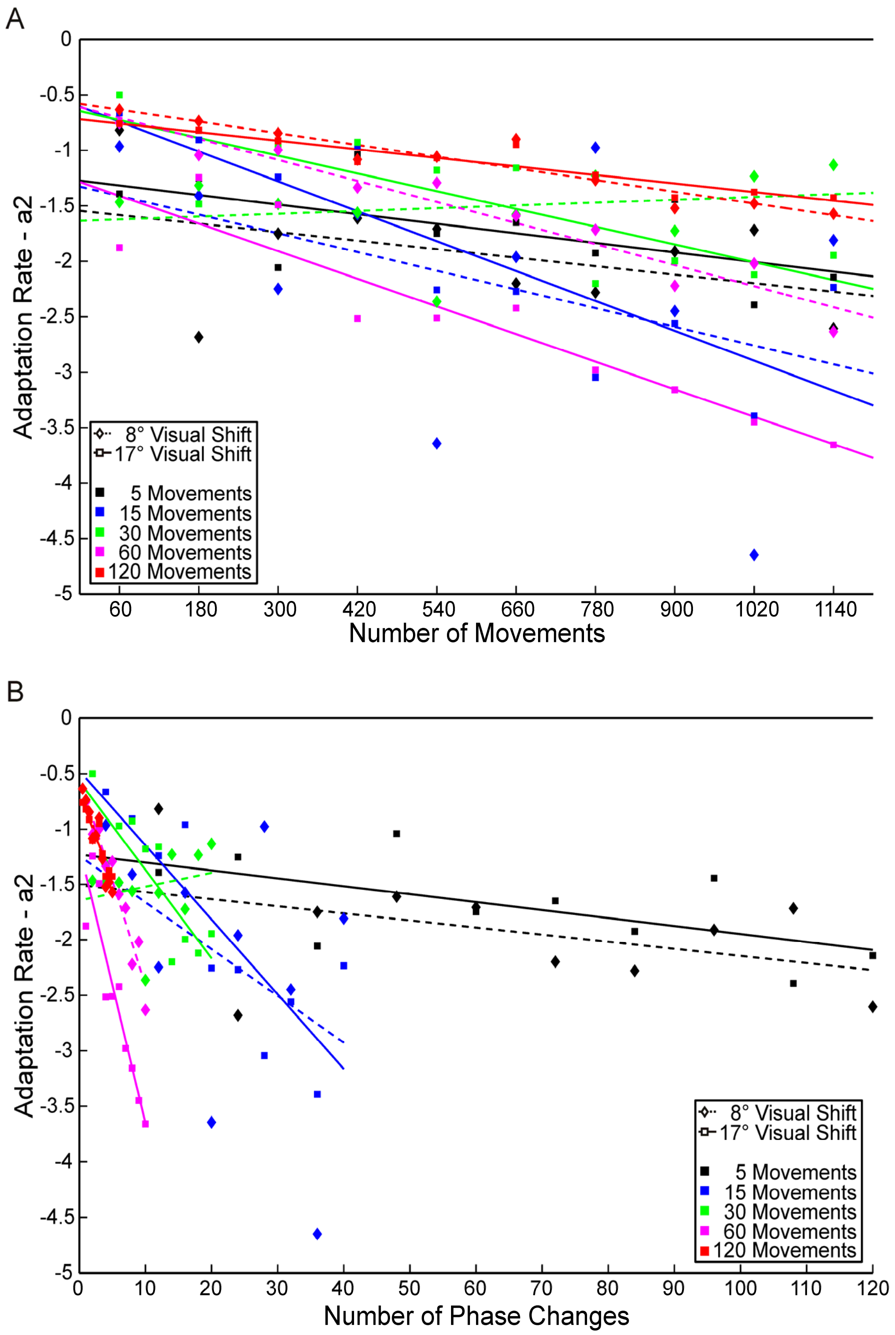

Figure 25. Development of re-adaptation rates during the experiment. Re-adaptation rates were computed for average chunks of 60 movements each and are shown as a function of a) the number of movements and b) the number of blocks. Group averages shown with linear regression.

As shown in Figure 25, values of the fit parameter a_2 became more negative during the experiment indicating an increase in re-adaptation rates. As seen for the adaptation rates, this acceleration of re-adaptation rates was similar between groups when analysed as a function of movements (Fig. 25a), and differed between groups when analysed as a function of blocks (Fig. 25b).

For the analysis of re-adaptation rates, the same statistical analyses for re-adaptation rates was repeated, as done before for adaptation rates. We found a significant main effect for Movements, F(9, 342) = 6.44, p < 0.001. Helmert contrasts for Movements showed a significant difference to the later levels for the first four Movement Chunks (see table 3) indicating faster re-adaptation rates in later blocks. No significant effects were found for between subjects factors or their interactions (p > .104; for interactions Movements x between subjects factors, p > .180).

Table 3. Statistics of Helmert contrasts for re-adaptation rates, main effect of Movements.

Level	df	df error	F	p
Level 1	1	38	26.30	< .001
Level 2	1	38	7.68	.009
Level 3	1	38	6.74	.013
Level 4	1	38	18.45	< .001

Since we also found a significant increase in re-adaptation rates during the experiment (more negative values of a_2), we repeated the same analysis done for adaptation rates (see above), but this time for the change in re-adaptation rates per phase change using linear fits ($y = a\,x + b$) for each subject. We computed a univariate ANOVA for the fit parameter “a” (slope) with Size of Shift and Number of Movements as between subjects factors. Main effect for Movements was statistically significant ($F(4, 38) = 9957.58$, $p < 0.001$). The main effect for Size of Shift and the interaction of Movements and Shift were not statistically significant ($p > .560$). Post-hoc tests revealed significant differences between all groups ($p < .002$). Change in re-adaptation rates per phase monotonically increased with increasing number of movements per phase (decreasing number of phase changes).

Analysis of learning parameters. In order to allow a comparison between the importance of number of movements versus number of phase changes for the learning to learn aspect, two exponential fits ($y = a_1 \exp(a_2 x) + a_3$) were computed for each learning curve consisting of the initial performances of all adaptation cycles. The first fit was for number of movements as the independent variable x, the second fit was for number of phase changes as independent variable. In all further analyses, the parameters of these fits were used to assess the initial performance level / initial error (a_1+a_3), learning rate (a_2), and final offset / remaining error (a_3). Since not all fits were successful, outliers in the fit-parameters were identified separately for both sizes of visual shift. This was done iteratively, based on the fit parameter a_1, whenever its value outreached M ± 2SD and until no more outliers were found (5 iterations). Subjects with outliers in the learning fit parameters were excluded from further statistical analysis (13 direct effect, 13 aftereffect).

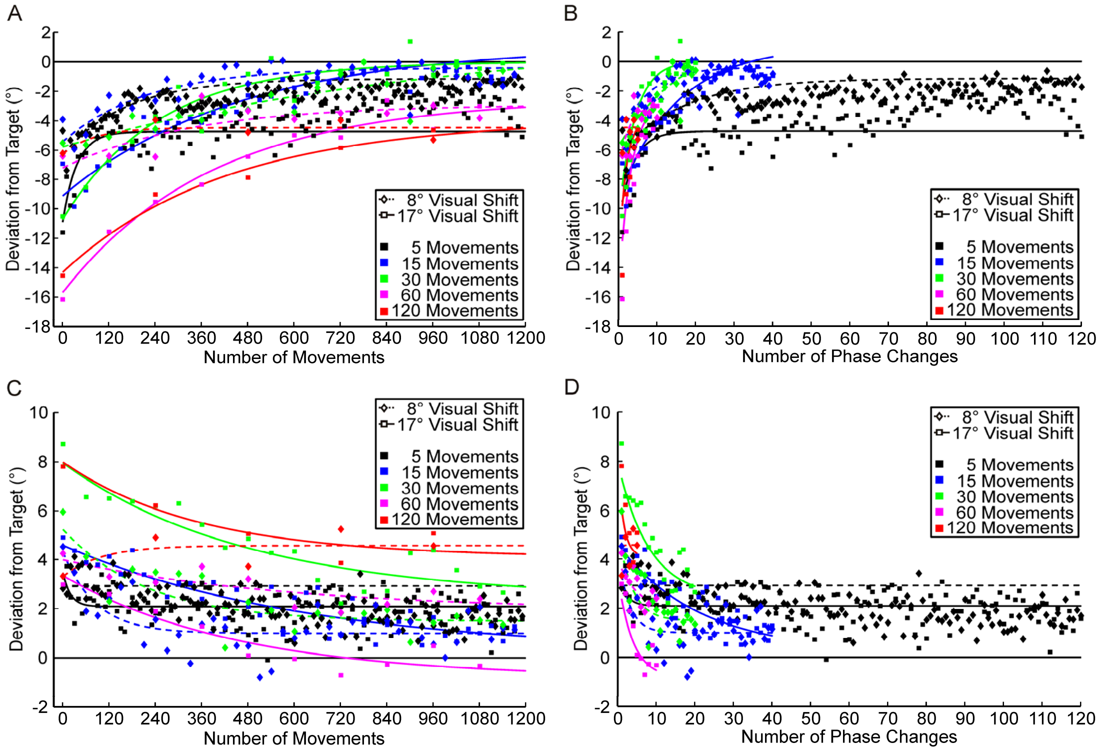

Figure 26. Time course of dual-adaptation. Development of initial pointing errors during the experiment for adaptations (a,b) and re-adaptations (c,d). Data are shown as a function of a,c) the number of movements and b,d) the number of blocks. Group averages shown with exponential fit.

Visual inspection reveals an overall reduction of initial pointing errors (direct effect and aftereffect) during the course of the experiment (Fig. 26). Learning curves are most similar between groups when analysed as a function of number of movements between blocks. When analysed as a function of blocks, the learning curves for blocks with many movements show a faster learning as compared to blocks with few movements. This is the case for both, direct effect and aftereffect.

We analysed **learning rates**, **initial error**, and **remaining error** as a function of change per **phase** by computing a MANOVA for these variables with Phase (adaptation, re-adaptation) as within subjects factor and Size of Visual Shift and Phase Length as between subjects factors. Corrected models for the initial error ($F(19, 54) = 34.07$, $p < .001$, $R^2 = .923$), as well as for the remaining error ($F(19, 54)$

= 2.20, *p* = .012, R^2 = .436), significantly predicted the experimental data. In contrast, the corrected model for learning rates (*F*(19, 54) = 0.85, *p* = .643, R^2 = .230) did not significantly predict the experimental data. Further analysing the influence of experimental phase, size of visual shift and phase length, separate one-way ANOVAs were computed for initial error and remaining error. Phase, Size of Visual Shift and Phase Length were each included as between subjects factors. All factors significantly influenced the size of **initial pointing error**: the main effect of Phase was statistically significant, *F*(1, 54) = 475.48, *p* < .001, indicating negative values for adaptation and positive values for re-adaptation. The main effect of Size of Visual Shift was also statistically significant, *F*(1, 54) = 14.90, *p* < .001, with an initial pointing error of more than twice the size for the groups with 17° shift as compared to the groups with 8° shift. Also the main effect of Phase Length was statistically significant, *F*(4, 54) = 2.78, *p* = .036. Pairwise post-hoc comparisons showed that our groups with 30 movements per phase differed statistically significant from our groups with 5 (*p* = .007) and 60 (*p* = .007) movements per phase, with less initial error during adaptation and more during re-adaptation. The interaction of Phase and Size of Visual Shift was also significant, *F*(1, 54) = 32.47, *p* < .001, which is explained by an expected difference (initial error of about twice the size) to be found between 17° and 8° shift for adaptation, but not for re-adaptation (initial errors of about the same size). All remaining interactions were not significant (*p* > .307). For the **remaining error,** only the main effect of Phase was significant, *F*(1, 54) = 11.85, *p* = .001, explained by a negative value remaining for adaptation and a positive for re-adaptation. The main effects of Size of Visual Shift (*p* = .309) and Phase Length (*p* = .581) were not statistically significant. Only the interaction of Phase and Phase Length significantly influenced the size of remaining error, *F*(4, 54) = 2.74, *p* = .038. All other interactions were not significant (*p* > .152).

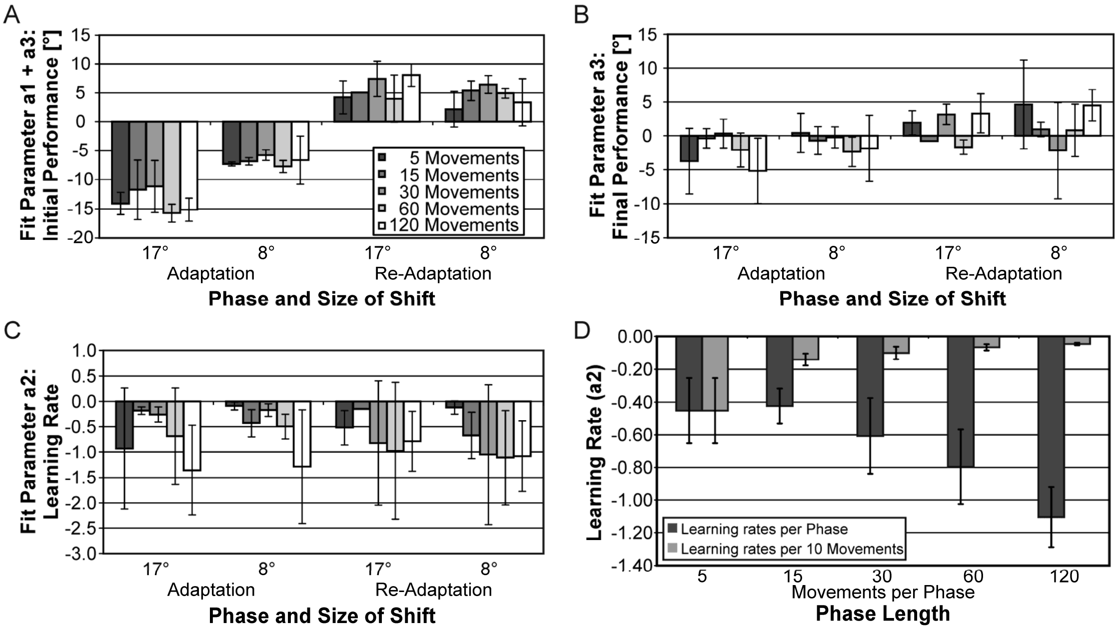

Figure 27. Values of fit parameters for the exponential fits of the dual-adaptation learning curves. Fit parameters are shown separately for all groups (5 to 120 movements per phase) and phases (adaptation and re-adaptation) in a) for the initial error a_1+a_2, b) the remaining offset a_3, and c) the learning rate a_2. A comparison of learning rates a_2 per movement and per phase is displayed in d). Group averages with error bars denoting Standard Error of the Mean.

To further analyse the dependency of **learning rates** on Phase Length (5, 15, 30, 60, 120; and the number of phase changes), Phase (adaptation, aftereffect), and Size of Shift (17°, 8°), separate linear regressions were computed for learning rates depending on the number of movements and depending on the number of blocks underlying the learning process. These data are displayed in Figure 27d. For learning rates per movements between initial pointing movements (number of movements between data points differing between groups), the regression was not statistically significant (*F*(3, 70) = 2.56, *p* = .062), but it showed a statistical trend. It only explained a small proportion of variance in learning rates, R² = .099. Nevertheless, Phase Length statistically reliably predicted the size of learning rate, Beta = .284, *T* = 2.50, *p* = .015. Thus, the learning per movement marginally slowed down with increasing phase lengths (and decreasing number of phase changes). This trend can be explained as an artefact of the exponential fitting procedure: exponential fits for sparse data (e.g. our group with 120 movements per phase and only 5 datapoints) underestimate the underlying learning rate of the exponential fit. Both, Phase and Size of Shift, did not statistically reliably predict the size of learning rate (*p* > .217). In the second linear regression, the same analysis was repeated for learning rates per block between initial pointing movements (subsequent data points in each group). The linear regression was statistically significant explaining a small proportion of variance in learning rates, $R^2 = .109$, $F(3, 70) = 2.85$, $p = .044$. Phase Length statistically reliably predicted the size of learning rate, Beta = -.309, $T = -2.73$, $p = .008$. Thus, the learning per phase significantly sped up with increasing phase lengths. Both Phase and Size of Shift did not predict size of learning rate in a statistically reliable way ($p > .389$).

Discussion

Comparing repeated adaptations under different conditions we found clear evidence of a learning process (learning to learn) revealed by increasing adaptation rates in addition to decreasing initial pointing errors and aftereffects (dual-adaptation). Adaptation and re-adaptation rates increased at similar rates per movement between groups with differing phase lengths, and consequently the rate of change per phase differed strongly between groups with faster increase of adaptation rates for increasing number of movements per phase. Moreover, we found no difference in adaptation rates between groups with big versus small visual shift. The initial performance level in our dual-adaptation experiment and the final offset of learning curves depend on the size of both, visual shift and phase length. While the influence of visual shift was as expected (at least qualitatively), we did not expect an influence of phase length on the size of the initial performance level. Since the experimental procedure was exactly the same for all subjects up to the first adaptation pointing movements, this difference between groups has to originate from pre-existing differences between subjects, which did not average out because of our small number of subjects per group.

When precisely analysing learning rates, we addressed the question of the relative importance of the number of consecutive movements within one condition and the number of changes between conditions. While finding constant learning rates per movement between groups, we found increasing learning rates per change between conditions with increasing phase lengths. Our results lead us to the conclusion that during the dual-adaptation process the number of interactions (e.g. movements) in both mappings (old and new) is the most important. The learning rate increases only marginally with an increasing number of changes between mappings, as indicated by a statistical trend which can be explained as an artefact of exponential fitting.

In contrast to Bingham & Romack (1999) we find dual-adaptation (reduced initial pointing errors) coupled with an increase in adaptation rates in later adaptation cycles. This is in agreement with previous findings by Welch et al. (1993). The fact that an acceleration of adaptation rates was not found in all studies suggests multiple processes (potentially) involved in the acquisition of dual-adaptation. The primary process (dual-adaptation) enables the acquisition of an alternate sensorimotor mapping, while maintaining the normal/usual mapping. The secondary process (learning to learn) enhances the general flexibility of sensorimotor control, allowing faster adaptations to new sensorimotor mappings. This is (at least partly) achieved by an increased contribution of the viscoelasticity of the musculoskeletal system to sensorimotor control at the beginning of a learning (or dual-adaptation) process (Osu et al., 2004). When the alternative internal model is well established, and thus dual-adaptation has been achieved, the contribution of viscoelasticity is reduced in favour of the internal model (Osu et al., 2004).

Coming back to explain why Bingham and Romack (1999) found no change in adaptation rates: Their experimental procedure was based on the measurement of movement times during a peg in a hole task. Subjects adapted until three subsequent trials were within baseline performance. Thereafter, the mapping was changed and the same procedure was repeated until 6 blocks of adaptation and re-adaptation were completed on the first day. Less blocks were tested on the following 2 days. The critical point in this procedure is that the adaptation to each mapping was stopped once the baseline performance in movement time was reached. This may be problematic for triggering learning to learn for two reasons: First, movement times within baseline level cannot ensure straight and smooth movement paths. Instead, completion times at baseline level could simply indicate faster but still distorted movements. Therefore, by relying only on movement times to stop learning, the adaptation to a new sensorimotor mapping may not have been completed before the change of mappings. Second, if the adaptation process is stopped whenever the adaptation process is just completed (or not even fully so), there is no time to strengthen the new sensorimotor mapping (Fernández-Ruiz & Díaz, 1999). On a neural basis, this may prevent the activation of the neural network for established sensorimotor mappings (Debas et al., 2010; Sakai et al., 1998; Shadmehr

& Holcomb, 1997). Thus, by ending the adaptation when it seems complete, the new mapping cannot enter a more solid memory state which could be the basis for the learning to learn process per se. But it has to be noted that, in our procedure with rapid repetitions, five subsequent movements seem to suffice if subsequently many such rapid changes between the alternative mappings are presented.

The hypothesis of the existence of two possible underlying processes in dual-adaptation can be addressed in further experiments. A test for simple dual-adaptation should be the retention of both sensorimotor mappings after a prolonged period of time (e.g. Martin et al., 1996). The second process could be tested by two approaches (apart from analysis of adaptation rates): a) analysing general pointing/motor variability after successful dual-adaptation and b) comparing adaptation rates in a new sensorimotor challenge between subjects with dual-adaptation and naive subjects. The latter test for learning to learn could be either comprised of an adaptation of the same kind (but different direction and/or size of displacement), of a different kind but within the same modality (rotation of visual feedback), or of a different kind in another modality (proprioceptive: force field). It would be of scientific interest to test the specificity and duration/time scale of an increased flexibility due to the learning to learn process, as Bock et al. (2001) partly did by showing a facilitation of the adaptation process with a previous adaptation to an unrelated discordance.

One of the key aspects of our study in comparison to previous studies was the time scale of dual-adaptation. In previous studies (Bingham & Romack, 1999; Cunningham & Welch, 1994; Martin et al., 1996; McGonigle & Flook, 1978; Welch et al., 1993), it seemed to require very long training phases compared to single adaptations. Experimental procedures stretched over days or even weeks or including breaks of several hours between adaptations. Our experimental results prove that neither outstretched experimental procedures nor long breaks between adaptations are required for dual-adaptation. In fact, the contrary seems to be the case: Temporal closeness of the opposing sensorimotor mappings coupled with intense training seems to enable a superordinate learning process (learning to learn) supporting the dual-adaptation. At least this can be assumed if sufficient time is spent with each mapping and sufficient changes between mappings occur. Compared to our learning rates, Martin et al. (1996) found very slow learning although they used a procedure with many throwing trials in total (900 with prisms and 1075 without prisms per week over the course of six weeks). They also provided sufficient time spent in each mapping to successfully adapt to the displacement (50 throws), coupled with several changes between mappings (4 blocks per day). The question about why they found comparably ineffective learning still remains. The first reason might be linked to the experimental procedure: in spite of their overall large number of trials they only had 200 throws with prisms per day. In our procedure we had 600 movements with visual shift in one session. This leads us to the conclusion that dual-adaptation is best achieved with massed training to ensure effective usage of the learning to learn process. The second set of reasons is related to the task: throwing between two subjects who are alternately wearing prisms. This task might slow down dual-adaptation because a) it provides no precise error feedback such as a static target with performance representation does (e.g. the thrown ball attached to the target wall), b) dual-adaptation in the single subject is confounded with the aftereffect of the second subject (second subject has to catch the ball and throw it back), and c) throwing per se is slower in adaptations as compared to adapting while pointing (presumably because the target for throwing is located in extrapersonal space).

Some implications can be derived from our experiment for future studies concerning sensorimotor adaptation. First of all, we showed strong effects of dual-adaptation including learning to learn altering both the size of errors in adaptation and re-adaptation (i.e. aftereffect). Thus, multiple adaptations within the same subject should be avoided whenever it is possible, unless the learning aspects of adaptation are the goal of the study. But if multiple adaptations within subjects are needed, the experimental design should carefully balance out possible effects of test order. A related second implication concerns the acceleration of adaptations due to the involvement of learning to learn. Since we found similar acceleration per interaction throughout the experiment for all groups, we conclude that it is sufficient to rapidly act within a new sensorimotor mapping for triggering learning to learn. A key aspect might be the temporal closeness of single interactions, but also of the alternate sensorimotor mappings. Another aspect might be related to the similarity of test situations since in our experiment the only observable difference between the mappings was the target position. In classical prism adaptation experiments, another difference is obviously the presence and absence of the glasses holding the prisms, in addition to any visual distortions despite the intended shift. Hence, to avoid learning to learn and its accelerating effect on adaptation rates, we would advise temporal distance between single adaptations (best on separate days) and an adaptation procedure relying on other methods than rapid subsequent pointing movements (e.g. throwing).

In recent years, an increasing number of academic but also commercial and medical applications of virtual reality have emerged (Alaraj et al., 2011; Riva, 1998; Stone, 2001). A new sensorimotor mapping between proprioception and vision has to be acquired for efficient performance in most virtual realities (Groen & Werkhoven, 1998). For the learning of the specific sensorimotor requirements in a virtual reality environment, we can deduce two guidelines for efficient training from our experiment: i) For initial training, the single interactions should be as simple as possible (i.e. short reaching movements) and with realistic feedback (i.e. a virtual hand instead of a cursor). ii) Many subsequent repetitions of basic tasks should be allowed in the virtual reality, alternating in blocks with an equivalent of the task within the normal sensorimotor mapping and within at least an hour of training. This duration may need to be extended for more complex tasks and a new sensorimotor mapping more complex than a horizontal shift.

In summary, we found that both dual-adaptation and learning to learn depend on the total number of interactions with the alternative sensorimotor mappings. The speed of acquisition of the new mapping as well as the acceleration of adaptations does not depend on the specific experimental schedule (number of blocks and block length) as long as enough interactions are available for both old and new mapping.

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Anhang

Acknowledgment / Danksagung

This dissertation would not have been possible if not for the support of many people in my scientific and private life; I would like to thank you all! Since I communicated with some of you in English and others in German, I will write my acknowledgment in mixed language, depending on whom I thank, in either English or German.

Allen voran danke ich Herrn Prof. Dr. Manfred Fahle für die Gelegenheit und Möglichkeit hier im Institut für Human-Neurobiologie und als Mitglied der Bernstein-Gruppe zu promovieren. Ich bedanke mich für Ihre Unterstützung bei all meinen Forschungs-Vorhaben und dafür, dass Sie mir jede gewünschte Fortbildung ermöglicht haben. Sie haben mir in der Zeit der Promotion stets viel Freiheit gelassen und Vertrauen entgegengebracht, dafür danke ich Ihnen.

My very special thanks I wish to direct to Prof. Gordon Redding for his interest and trust in me as a young researcher. Starting a collaboration with you turned out to be one of the most important milestones in my time as a PhD student. Our collaboration was not only fruitful and effective; I also learned so many important things from you! Although for most of the time we were on separate sides of the earth, I'd like to think of you as my "honorary supervisor". Your guidance from a "psychology" point of view with your huge experience with prism adaptation supported me in ways nobody else could have! I am most honored that you agreed to act as second reviewer of my dissertation.

Ich möchte auch der gesamten derzeitigen Arbeitsgruppe der Human-Neurobiologie und auch den ehemaligen Mitgliedern, die ich kennen gelernt habe, für diese angenehme Arbeitsumgebung danken. Insbesondere danke ich Frau Dr. Cathleen Grimsen, ohne Dich läuft hier glaube ich überhaupt nichts mehr, und Herrn Dr. Sirko Straube für viele hilfreiche Diskussionen. Auch Frau Daniela Gledhill möchte ich ganz herzlich danken, der Austausch mit Dir und unsere vielen gemeinsamen Mittagspausen haben viele Ärgernisse des Alltags in ein erträglicheres

Licht gerückt. Du bist mir in der Zeit hier eine liebe Freundin geworden und ich danke Dir von ganzem Herzen für Deine Unterstützung auf ganz vielen Ebenen! Als meine (ehemaligen) Zimmerkollegen haben natürlich auch Herr Marc Schipper und Frau Maren Praß ein ganz dickes Dankeschön verdient. Die „Werkstatt“-Zeit wird mir wohl für immer in Erinnerung bleiben. Ich bin auch besonders froh über die schöne geteilte Zeit in 1130 im Cognium mit Dir, Maren. Vielen Dank auch für die diversen gemeinsamen Leckereien! Ein großes Danke auch für Herrn Sven Eberhardt, ohne Dich hätte ich bestimmt nicht so eine tolle Virtual Reality bekommen, Dein Engagement dafür war einfach einmalig und ganz großartig! Frau Dr. Karoline Spang danke ich für die hilfreiche Unterstützung im Manuskript überarbeiten, ich habe dabei eine Menge von Dir gelernt. In meiner Zeit als Doktorandin durfte ich auch vier Studentinnen in ihren Abschlussarbeiten betreuen: Frau Lena Hochstein, Frau Leena Ackermann, Frau Angela Neumann und Frau Klaudia Pochopien. Ich danke euch allen für diese unglaublich wichtige und tolle Erfahrung! Besonders Dir, Lena, danke ich für lange und intensive Diskussionen und den wissenschaftlichen Austausch, ich habe dabei unschätzbar viel gelernt.

Als Mitglied der Bernstein Gruppe hatte ich die Möglichkeit auch im interdisziplinären Austausch meinen wissenschaftlichen Horizont zu erweitern, vielen Dank! I’d also like to thank Orlando Arévalo as my colleague on the „physics“ side of the project. You taught me a lot of what I know of modelling and networks. Ein ganz besonderer Dank gilt auch Frau Manuela Jagemann und Frau Agnes Jansen, ohne Euer organisatorisches Zauberwerk würde hier sicher einiges nicht mehr so glatt ablaufen.

Ein wichtiger Teil meiner Doktorandenzeit war meine Teilnahme am Mentoring-Programm planM. Ich habe dabei viel über mich selbst und unsere Wissenschaftsstruktur gelernt, dafür möchte ich besonders Frau Susanne Abeld, Frau Anneliese Niehoff und Frau Ose Leendertz als Organisatorinnen danken. Frau Prof. Dr. Prisca Stenneken danke ich für ihre unerschütterliche Unterstützung („eine der Schnecken wird das Rennen schon machen“), ich wünsche Dir alles Liebe und Gute! Das ganze Mentoring wurde aber erst durch meine Mit-Mentees besonders wertvoll, ich danke euch allen ganz herzlich für diese schöne gemeinsame Zeit!

Immer in anstrengenden und herausfordernden Zeiten ist der private Rückhalt besonders wichtig. Ich danke Dir, Ciarán, dass ich mich letztendlich immer auf Dich verlassen kann und für Deine unendlich wichtige Unterstützung. Ohne Deine Mithilfe wäre aus der Dissertation so nichts geworden. Ein Dankeschön habe ich auch für meinen kleinen Sonnenschein Lisa, Du hast mir auch in den beruflich stressigsten Zeiten zu einer unvergleichlichen Balance verholfen. Mein Dank gilt auch meiner Mutter Barbara Vetter, Deine Unterstützung ist einfach unendlich wertvoll, vielen Dank auch für die vielen Freupakete! Ich danke auch meinem Vater Klaus Schaumlöffel für all die wichtigen kleinen Dinge. Auch meinem Schwiegervater Rudolf Bornschlegl danke ich für die vielseitige Unterstützung. Du hast immer an mich geglaubt, danke, dass wir uns auch in schwierigen Zeiten keine Sorgen machen mussten!

Eigenständigkeitserklärung

Hiermit versichere ich, dass ich die vorliegende Arbeit selbständig und nur mit den angegebenen Hilfsmitteln angefertigt habe, und dass ich alle Stellen, die dem Wortlaut oder dem Sinn nach anderen Werken, auch elektronischen Medien, entnommen sind, durch Angabe der Quellen als Entlehnung kenntlich gemacht habe.

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