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Review

Applications of prism adaptation: a tutorial in theory and method

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Abstract

Data and theory from prism adaptation are reviewed for the purpose of identifying control methods in applications of the procedure. Prism exposure evokes three kinds of adaptive or compensatory processes: postural adjustments (visual capture and muscle potentiation), strategic control (including recalibration of target position), and spatial realignment of various sensory-motor reference frames. Muscle potentiation, recalibration, and realignment can all produce prism exposure aftereffects and can all contribute to adaptive performance during prism exposure. Control over these adaptive responses can be achieved by manipulating the locus of asymmetric exercise during exposure (muscle potentiation), the similarity between exposure and post-exposure tasks (calibration), and the timing of visual feedback availability during exposure (realignment).

Keywords: Prism adaptation; Realignment; Recalibration; Visual capture; Unilateral neglect; Sensory-motor transfer

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The recent resurgence of interest in application of prism adaptation methodology promises to increase our understanding of both normal perceptual-motor control (e.g. Fernández-Ruiz et al., 2000; Kitazawa et al., 1995; Kitazawa et al., 1997; Martin et al., 1996a; Martin et al., 2002; Roller et al., 2001) and neuropathology (e.g. Berberovic et al., 2004; Farnè et al., 2002; Ferber et al., 2003; Frassinetti et al., 2002; Maravita et al., 2003; Pisella et al., 2002; Rode et al., 1998/1999; Rossetti et al., 1998; Tilikete et al., 2001). Adaptation to prismatic displacement is particularly suited for application because its incremental nature permits examination over relatively short time periods, in contrast to prismatic distortions like left-right or up-down reversal of the visual field that involve discrete, all-or-none adaptive states and require extended exposure for adaptation to occur (e.g. Sekiyama et al., 2000; Stratton, 1897a; Stratton, 1897b; Taylor, 1962). However, recent application has not always taken into consideration the long history (e.g. Held and Hein, 1958; Helmholtz, 1909; Kohler, 1951) and complexity of prism adaptation (Redding and Wallace, 1993, 1997a, 2002, 2003a). Consequently, the promise of application has not been fully realized. Here, we sketch the current state of knowledge in prism adaptation and the methodology needed for maximal benefit from its application. We will show that prism adaptation is not a simple process and, while the procedure can be used for many different applications, certain minimal methodological standards should be met before the procedure is developed for a specific application.

We begin by listing the primary empirical characteristics of prism adaptation. Then we impose order on the empirical facts by identifying the various processes of prism adaptation that must be methodologically segregated. Next, we sketch the perceptual-motor organization supporting the various adaptive processes, especially how they are interrelated. Then we critique some examples of application of the prism adaptation procedure. Finally, we conclude with methodological recommendations that should permit optimal use of the procedure in application.

1. Empirical observations

When a person first looks through wedge prisms that optically displace the visual field, for example 10° in the rightward direction, the person may have little feeling that anything is out of the ordinary, but then he/she experiences surprising difficulty in perceptual-motor tasks (i.e. direct effects of prism exposure). For example, pointing toward a visual target produces error to the right of target position, where the target is seen to be located. Performance error is gradually reduced to pre-exposure levels as the person makes repeated attempts at target pointing (error reduction phase). Adaptation to the prismatic displacement occurs. And, when the prisms are removed the person experiences surprising errors in the opposite direction, to the left of the target! This negative aftereffect of prism exposure demonstrates a persistence of adaptation acquired during exposure. Thus, the basic prism adaptation procedure simply involves (1) pre-exposure baseline measurement of performance, (2) active exposure to prismatic displacement to produce adaptation, and (3) post-exposure compensatory aftereffect measurement of adaptation persistence. Is this all there is to prism adaptation? Prism adaptation is deceptively simple. In fact, there are many nuances of prism adaptation in both method and results.

First, the initial direct effect of the prisms at the beginning of exposure is not directly predictable by the magnitude of prismatic displacement. While direct effects are in the direction of displacement and roughly proportional to the displacement, the amount of direct effect may not even nearly match the magnitude of displacement. For example, objects in a well-structured visual field appear to be displaced only about 40 percent of the prismatic displacement even though participants remain stationary and see no part of their body: there is an immediate correction effect (Rock et al., 1966). Another modulation of direct effect is the straight-ahead shift (Harris, 1974) where cognitive judgment of straight ahead tends to be centered in the optically displaced structured visual field such that straight ahead objects tend to be judged closer to straight ahead than they appear in spite of the optical displacement.

A third initial factor affecting direct effect is visual capture (Hay et al., 1965; Tastevin, 1937) where the stationary hand tends to be felt to be located near where it looks to be located. A final factor affecting direct effect is first trial ‘adaptation’ (Redding and Wallace, 2003b, 2004a). The effect of the prisms on the first exposure trial is usually much less than would be expected by the amount of prismatic displacement, even if the pointing hand is only visible at the end of movement and cannot be visually guided to the target. For example, error in target pointing may be only 4 deg to the right for a 10 deg rightward prismatic displacement: only 40 percent of the displacement. Thus, the immediate direct effect of prismatic displacement on experience and performance is surprisingly complex.

Second, the time course of error reduction, adaptation during prism exposure, is also complex. In general, target pointing error at the terminus of movement (terminal error) decreases, approaching pretest values in as few as about 15 trials: that is, subjects increasingly point toward the actual rather than virtual target (Redding and Wallace, 1993; Rossetti et al., 1993). However, direct effect (terminal error) reduction varies, depending upon exposure condition (Redding and Wallace, 1993; Uhlarik and Canon, 1971). If the pointing limb is visible over the distal part of the pointing movement, target achievement occurs in fewer trials than if only the finger tip is visible at the end of the pointing movement, at least when the hand movement is not too fast (Rossetti et al., 1993). (These conditions have been called concurrent and terminal exposure, respectively, because both visual and proprioceptive feedback is available concurrently with movement or only at the terminus of the movement). If exposure pointing is continued beyond target achievement (zero terminal error), overcompensation may appear in which error occurs opposite the direction of the prismatic displacement, especially with terminal exposure (Redding and Wallace, 1993, 1990, 1992, 1994).

If the full movement path from starting to target positions is visible, no direct effect of the prismatic displacement is observed: that is, terminal error is near zero on the first trial and remains so throughout exposure (Redding and Wallace, 1996, 1997b). Similarly, if concurrent exposure and very slow movements toward the target is used, direct effects may not appear (personal observation). Direct effects may also be undetectable with small prismatic displacement or gradually introduced displacement such that subjects are not aware of the target displacement and do not make noticeable errors during exposure (Dewar, 1971; Howard et al., 1974; Jakobson and Goodale, 1989; Templeton et al., 1974; Uhlarik, 1973).

Third, aftereffects of prism adaptation are perhaps most complex. Aftereffect magnitude may show more generalization when exposure (training) and post-exposure (test) conditions are similar, for example, in movement speed (Kitazawa et al., 1997) or movement posture (Martin et al., 1996a). Simultaneous dual adaptation can even occur where different exposure conditions (e.g. directions of prismatic displacement) elicit different aftereffects when post-exposure test conditions are differentially similar to exposure conditions (Martin et al., 1996a; Redding and Wallace, 2003a; Bingham and Romack, 1999; Prablanc et al., 1975; Welch et al., 1993). On the other hand, aftereffects may show complete generalization for all points in a spatial reference frame implicated in exposure (Redding and Wallace, 1997a; Bedford, 1993a; Guigon and Baraduc, 2002).

Local aftereffects may appear in different sensory-motor systems and their associated reference frames (e.g. visual eye–head and proprioceptive hand–head) that show additivity for an inclusive (e.g. eye–hand) coordination loop involved in exposure (Redding and Wallace, 1993; Templeton et al., 1974; Hay and Pick, 1966; Hay, 1970; Hay and Brouchon, 1972; Redding and Wallace, 1976, 1978; Wilkinson, 1971). Muscle potentiation aftereffects may also occur when an effector is asymmetrically exercised during prism exposure (Ebenholtz, 1974, 1976; Paap and Ebenholtz, 1976); for example, asymmetric fixation of a prismatically displaced target may produce visual aftereffects.

Aftereffects and direct effects are not simply related. Among the initial reduction in the direct effects of prism exposure, only the straight-ahead shift seems to be accompanied by aftereffects under certain conditions (Redding and Wallace, 1978). The immediate correction effect does not seem to produce reliable aftereffects of prism exposure (Wallace et al., 1973). Visual capture does not produce reliable aftereffects (Welch, 1978, 1986; Welch and Warren, 1980, 1986; Welch et al., 1979). First trial 'adaptation' is also unrelated to aftereffects of prism exposure (Redding and Wallace, 2004a).

Reduction in the direct effect of terminal error over the exposure period and resultant aftereffects are more complexly related. Direct effect compensation for the prismatic displacement usually reaches 100 percent, but aftereffects typically show only about 40 percent compensation (Redding and Wallace, 1993). Overcompensation during exposure is related to aftereffect magnitude (Redding and Wallace, 1993, 1990, 1992, 1994). Visibility of the entire movement path does not produce direct effects or aftereffects (Redding and Wallace, 1996, 1997b, 2001), but if only starting and target positions are visible, both kinds of effects occur (Redding and Wallace, 2001). However, aftereffects do appear even if the prismatic displacement is so small or introduced gradually such that error during exposure (direct effects) is undetectable (Dewar, 1971; Howard et al., 1974; Jakobson and Goodale, 1989; Templeton et al., 1974; Uhlarik, 1973). Aftereffects even appear larger when awareness of the visual displacement is prevented (Michel, 2003; Michel and Rossetti, 2004). Aftereffects can appear without direct effects and vice versa (Weiner et al., 1983).

From these empirical findings it is easy to see that prism adaptation is not as simple as it may appear. Indeed, it seems confusingly complex! In Section 2, we impose order on the above empirical observations by identifying the primary adaptive processes evoked by prism adaptation.

2. Adaptive processes

Prism exposure evokes all the mechanisms of adaptive perceptual-motor performance in all their complexity (Redding and Wallace, 1997a). At least three classes of adaptive processes are elicited by prism exposure: postural adjustments, strategic control, and spatial realignment (or 'true' adaptation). All of these classes of processes can affect performance during prism exposure where performance feedback is available (direct effects) and performance after prism exposure where performance feedback is not available (aftereffects).

Sensory-motor asymmetry introduced by prismatic displacement can produce change in perceived and/or actual posture of body parts. The classic demonstration of change in perceived posture is visual capture, for example, where the visible limb is felt to be positioned where it looks to be (Hay et al., 1965; Tastevin, 1937). Visual capture is only one example of the more general class of inter-sensory bias effects (Welch and Warren, 1986). For example, the asymmetry in the visual field produced by prismatic displacement can induce a change in felt head position (Redding and Wallace, 2003b, 2004a). Inter-sensory bias does not itself produce aftereffects (Welch and Warren, 1980; Welch et al., 1979), but it can reduce the direct effect of prismatic displacement on performance during prism exposure, producing the appearance of adaptation: for example, felt rotation of the (un-rotated) head opposite the direction of prismatic displacement during exposure reduces effective prismatic displacement and, therefore, target-pointing error in the direction of displacement (Redding and Wallace, 2003b, 2004a).

Asymmetric motor exercise during prism exposure can modify the reference set point of an effector and thereby its actual resting position (Ebenholtz, 1974; Ebenholtz, 1976; Ebenholtz and Fisher, 1982). For example, the asymmetric eye posture required to fixate an objectively straight-ahead target during prism exposure biases the straight-ahead eye position in the direction of the prismatic displacement. Similarly, if the visual target is objectively positioned so as to avoid asymmetric exercise of the eyes, then the limb is asymmetrically exercised in target pointing during prism exposure with consequential bias of the straight-ahead limb position opposite the direction of the prismatic displacement (Redding and Wallace, 1978, 1988a). Such muscle-potentiation produces aftereffects that match the direction of other prism adaptation aftereffects (Paap and Ebenholtz, 1976), as well as affecting direct effects by reducing the effective spatial misalignment. However, muscle-potentiation cannot be the sole source of aftereffects because they can occur in the absence of asymmetric exercise (Craske and Crawshaw, 1975; Craske and Crawshaw, 1978; Crawshaw and Craske, 1974; Redding and Wallace, 1987, 1988b).

The performance errors induced by prismatic displacement recruit all of the strategic control processes that normally produce everyday adaptive behavior. Traditionally, error correction has been recognized as ‘conscious correction’ (Welch, 1978; Welch, 1986), but this term depreciates the complexity and pre-conscious nature of motor control (Redding and Wallace, 1993, 1997a). Strategic control includes the selection, modification, or learning of movement plans appropriate to the task at hand and movement plans consist largely of feedforward control elements that anticipate perturbation errors before they can occur or before they can become large (Redding and Wallace, 1997a).

When a movement plan fails to achieve its goal performance, as happens during prism exposure, online feedback control may serve to correct the performance error if sufficient time is available (i.e. for relatively slow movements) or knowledge of results from early trials may recalibrate target position for the movement plan, thereby improving exposure performance on following trials. Recalibration is a kind of associative learning (Welch, 1978), specific to points or regions of a reference frame, but it may generalize to post prism exposure performance provided conditions are sufficiently similar, thereby producing prism exposure aftereffects (Redding and Wallace, 2002, 2003a, 2001, 2004b). However, recalibration also cannot be the sole cause of prism exposure aftereffects, if only because they can appear in the absence of performance errors (Dewar, 1971; Howard et al., 1974; Jakobson and Goodale, 1989; Templeton et al., 1974; Uhlarik, 1973).

The source of aftereffects unique to prism exposure is spatial realignment (Redding and Wallace, 1993, 1997a, 2002, 2003a, 2001). The registered difference between the goal-performance expected from a feedforward movement plan and the performance achieved under feedback control (reafference) signals a spatial discordance between spatial maps and produces incremental realignment that improves exposure performance. The most dramatic empirical evidence that the expected-achieved position difference is necessary for realignment is the absence of prism exposure aftereffects when limb movement is slow enough to be entirely under visual feedback control, such that no error signal is generated (Redding and Wallace, 1996, 1997b).

Spatial realignment depends upon active strategic control for detection spatial discordance, but recalibration can interfere with realignment by reducing the detected spatial discordance: substitution of a virtual target for movement initiation that reduces target pointing error (direct effects) on previous exposure trials (i.e. side pointing) can eliminate or at least reduce the expected-achieved position discordance (Redding and Wallace, 1993, 1997a; see also Rossetti et al., 1993; Rossetti and Koga, 1994). Spatial realignment is a kind of non-associative learning (Redding and Wallace, 1997a; Bedford, 1993a; Guigon and Baraduc, 2002) that generalizes to entire reference frames whenever a performance task involves the realigned spatial map(s), thereby producing prism exposure aftereffects.

Postural adjustment, strategic recalibration, and spatial realignment can all produce prism exposure aftereffects, but for different reasons. Moreover, they can all contribute to adaptive performance during prism exposure (Redding and Wallace, 1993, 2003b, 2004a). The relationship between strategic control (including calibration) and spatial alignment is particularly complex. In Section 3, we elaborate this relationship.

3. Strategic control and spatial alignment

High-level strategic control and low-level spatial alignment are separable, but interdependent. We begin by providing a behavioral definition of the two concepts, we then outline the perceptual-motor organization that supports the two adaptive functions, and finally we consider the manner in which they interact and generalize for the particular exposure task.

3.1. Behavioral definition

Strategic control refers to ordinary, everyday adaptive behavior: a person sees a coffee cup, codes its location in the visual-motor reference frame, and sends the cup location to the hand as a reaching-grasping command. The command not only specifies the cup location, but also the general region of extrapersonal space relevant to the task: that is, the focus of the proprioceptive-motor reference frame is shifted from, for example, the computer keyboard, to the desk top where the cup is located. We say that the proprioceptive-motor reference frame is 'cali-calibrated' for the new task. A person may choose to visual guide the hand to the cup or depend upon highly practiced, 'automatic' behavior in a familiar environment. We call these 'feedback' and 'feedforward' strategies. When a person misses the coffee cup, the cup location is re-evaluated and a modified command is issued to the hand. We call this process 'recalibration'. Of course, feedforward and feedback strategies may be temporally coordinated in control of the initial and terminal parts, respectively, of the hand movement. And recalibration may take the form of coding a target position to the side of the cup so as to reduce previous error.

Now, alignment refers to the missing step in the above sketch of strategic control: the transformation of visual-motor coordinates into proprioceptive-motor coordinates. The visual-motor reference frame is centered on the head, but the proprioceptive-motor reference frame may be centered on the shoulder: that is, the distance between head and shoulder separates the centers of the two coordinate systems. If reaching–grasping behavior is to be accurate, head-centered location commands must be transformed into shoulder-centered locations. When the spatial relationship between visual-motor and proprioceptive-motor reference frames is changed, as it is when prisms displace the visual-motor reference frame, realignment is necessary to realign the two reference frames.

Alignment and realignment are possible because the transformation involves constant parameters. Calibration and recalibration take into account shifts in reference frames arising, for example, from head and shoulder movements, and the remaining constants are transparently embodied in the alignment transformations. In everyday perceptual-motor performance alignment is a completely automatic and transparent process. Only when misalignment (arising from experimental manipulation, growth, or pathology) occurs does the realignment process become apparent.

3.2. Reference frames and sensory-motor systems

In this section, we review evidence for the sensory-motor systems and associated reference frames involved in strategic control and alignment. Behavioral data from prism adaptation research (Redding and Wallace, 1997a, 2002) suggests that basic sensory-motor systems are linked through a noetic nexus (Redding and Wallace, 1997a, 2002, 1988c), a switching point between component sensory-motor systems (e.g. visual eye–head and proprioceptive hand–head systems) that form coordinative structures (synergies; e.g. eye–hand coordination) and that utilize different reference frames[1]. The spatial transformations of the noetic nexus ultimately establish a common origin and orientation for the various coordinate systems, but there may be no single, unitary representation of perceptual-motor space; alignment of coordinate systems is in the transformations, not necessarily in a unitary spatial map[2]. Coordinative structures are strategic control functions created by hierarchical planning that varies from general to task specific movement plans (Redding and Wallace, 1997a).

Algorithms specific to the representations recruited for a specific task perform transformations between coordinate systems. Strategically recruited linkages are generally assumed to be sensory-motor, perception-action systems (Milner and Goodale, 1995), may be egocentric or allocentric, and are modulated by higher cognitive functions, including attention (see also, Redding et al., 1985, 1992; Redding and Wallace, 1985; Welch and Sampanes, 2004).

Behavioral evidence for this view is provided by the local nature and additivity of realignment aftereffects. Depending upon exposure conditions, realignment aftereffects of prism exposure may appear in different amounts in the component reference frames implicated by the exposure task (Redding and Wallace, 1997a, 1990). For example, with a sagittal target pointing exposure task, aftereffects change from being primarily proprioceptive in nature to being primarily visual in nature as sight of the pointing limb is delayed from early to late (concurrent to terminal exposure) in the pointing movement (e.g. Redding and Wallace, 1990). And the total aftereffect for the exposure task is equal to the sum

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[1] The noetic nexus also serves transformations between sensory and motor reference frames within a sensory-motor system (Redding and Wallace, 1997a; de Graaf et al., 1995), but discussion of this function is beyond the present scope.

[2] Neurophysiological investigations (for reviews see Andersen et al. (1997), Colby and Goldberg (1999) and Stein (1992)) have challenged the traditional view of a single, unitary reference frame (e.g. Mountcastle et al., 1975; Ventre et al., 1984), primarily because no such topographic map has been found in the brain (see also the work of Farnè et al. (1998)). The present view is neutral with respect to this controversy.

of aftereffects in the component reference frames[3]. Thus, sensory-motor systems, including their spatial representations, are independent, although they are strategically combined to form coordinative structures for particular tasks (see also the work of Bard et al. (1995)).

3.3. Calibration versus alignment

Redding and Wallace (1997a) and (2002) distinguished different levels of spatial representation for calibration and alignment (see also the works of Weiner et al. (1983), Clower and Boussaoud (2000) and Welch and Sampanes (2004))[4]. Calibration provides a regional description of a task-work space (including position of targets and obstacles) within the larger perceptual-motor space, thereby increasing the precision and efficiency of task performance (Redding and Wallace, 2003a)[5]. Calibration may be egocentric or allocentric. A regional egocentric (self-centered) reference frame may be mapped onto (calibrated for) an allocentric (externally-centered) reference frame (Redding and Wallace, 2002, 2003a). Calibration is intentional (invoking endogenous spatial attention) and perceptual-motor (identifying targets and obstacles and recruiting effectors), and is a function of strategic control (evaluating, selecting, and developing movement plans).

Calibration of a region of perceptual-motor space, however, presupposes alignment of the origins and axes of the coordinate systems for the sensory-motor systems recruited for a particular task. If we subtract out the variable differences between origins of coordinate systems due to ordinary range of movement, 'a constant remains for the intact, adult organism; that constant reflects the long-term, steady-state difference between coordinate system origins, as distinct from ordinary variability. Such constants set parameters for the transformations and do not have to be computed for calibration purposes' (Redding and Wallace, 2002, p. 129). Indeed, alignment is transparent for calibration and misalignment appears to be calibration errors. By 'transparent' we mean alignment is 'hidden' from calibration, that calibration does not 'see' the present state of alignment, and that alignment does not have to be computed by calibration. At the level of strategic control (including calibration) the state of alignment is not 'known' and not accessible. On the other hand, we do not mean to imply that all parts of strategic control are consciously available.

The most direct empirical evidence of the calibration-alignment distinction comes from comparison of visual and proprioceptive calibration under prismatic misalignment for a target-pointing task (Redding and Wallace, 2001). Visual calibration with sight of the limb in the starting position reduced variable error compared to proprioceptive calibration when the limb was not seen (see also the works of Bowditch and Southard (1880) and Rossetti et al. (1994)). However, transparent misalignment under visual calibration increased constant error compared to proprioceptive calibration[6].

Additional evidence comes from comparison of direct effects of prismatic displacement during exposure with aftereffects obtained after prism exposure (e.g. Redding and Wallace, 1993). With repeated exposure trials exposure performance errors (direct effects) quickly disappeared, but aftereffects increased more slowly and did not achieve a level of complete compensation for the prismatic displacement. Moreover, in later trials direct effects tended to show overcompensation, error opposite the initial direction induced by the displacement. This pattern of data suggests at least two adaptive processes operating during prism exposure: rapid recalibration of target position to quickly reduce performance error and slowly developing realignment to bring coordinate system origins into correspondence. Overcompensation arises from the double correction of recalibration and transparent realignment.

The calibration-alignment processing distinction may correspond to localization of function in cerebrum and cerebellum, respectively (Jeannerod and Rossetti, 1993). The ability to adapt to prismatic displacement remains with intact cerebellum but damaged posterior parietal cortex (Pisella et al., 2004), while prism adaptation is lost with damaged cerebellum, but intact posterior parietal cortex (Weiner et al., 1983; Pisella et al., submitted; Baizer et al., 1999; Martin et al., 1996b)[7].

It is particularly noteworthy that Weiner et al. (Weiner et al., 1983) found significant adaptive performance during

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[3] There are many instances of additivity (e.g. Redding and Wallace, 1993; Templeton et al., 1974; Hay and Pick, 1966; Hay, 1970; Hay and Brouchon, 1972; Redding and Wallace, 1976, 1978; Wilkinson, 1971; Mikaelian, 1970; Mikaelian, 1972; Mikaelian, 1974; Redding, 1978; Wallace and Garrett, 1975; Wallace and Redding, 1979).

[4] Clower and Boussaoud (2000) and Welch and Sampanes (2004) use the terms 'skill acquisition' and 'recalibration' where we use 'calibration' and 'alignment', respectively. Although confusing, we believe that the present terminology is more appropriate. Calibration and recalibration refer to the specific aspect of skill acquisition immediately affected by prism exposure, while alignment and realignment refer to the slower remapping of spatial reference frames (Redding and Wallace, 1997a, 2002).

[5] A regional task-work space might be thought of as the focus of spatial attention, but we prefer a description in terms of task parameters, with minimal invocation of endogenous processes.

[6] To ensure that realignment occurred the movement path between visible starting position and target was occluded (cf. Redding and Wallace, 1996, 1997b).

[7] Clower et al. (1996) detected activity in the posterior parietal cortex, but not in the cerebellum under prism exposure conditions where realignment would not be expected to occur: namely, alternated direction of optical displacement every four target-pointing trials. Spatial realignment is a slow process, requiring consistent, long-term misalignment to be activated (Redding and Wallace, 1997a, 2002). The 'aftereffects' found by Clower et al. (Clower et al., 1996) therefore likely reflect strategic recalibrations contingent upon exposure conditions (Redding and Wallace, 2003a) and localized in posterior parietal cortex: a more precise localization is difficult to extract from their paper because there was a discrepancy between the main text and their figure's Talairach coordinates (see also the works of Andersen et al., 1997; Pisella et al., 2004; Berberovic and Mattingley, 2002).

prism exposure (direct effects) for cerebellar patients, but no aftereffects of prism exposure. Thus, strategic recalibration localized in the intact parietal cortex could be deployed to compensate for erroneous calibration arising from the prismatic displacement, but realignment localized in the damaged cerebellum could not occur. Conversely, Pisella et al. (2004) found aftereffects of prism exposure for parietal patients, but slowed adaptive performance during exposure. Thus, exposure performance may have reflected slowly developing realignment without the benefit of strategic recalibration[8].

3.4. Generalization of recalibration and realignment

Recalibration and realignment produced by prism exposure both generalize beyond the exposure conditions, but in different ways. In general, recalibration follows the associative generalization gradient (Welch, 1978, 1986), while realignment shows complete dimensional generalization for all coordinates in a reference frame and for all tasks that implicate the realigned sensory-motor reference frames (Redding and Wallace, 1997a; Bedford, 1993a; Guigon and Baraduc, 2002; Redding and Wallace, 2004b).

Recalibration shows transfer of training effects, depending upon the similarity between training (exposure) conditions and test (post-exposure) conditions (Redding and Wallace, 2003a). For example, if the same target-pointing task is used for both training and test (exposure and post-exposure) and recalibration is deployed to reduce performance error during exposure (direct effects), transfer to post-exposure (aftereffect) will occur in the form of performance opposite the direction of prismatic displacement employed during exposure. Further, transfer will be maximal for test targets that have the same position as training targets and will decline for test target positions that are incrementally different from training target positions (Bedford, 1993a, 1989, 1993b). The primary interest in transfer of training is the relationship between transfer and similarity of training and test conditions.

Realignment is localized in the transformation that links a sensory-motor system to all other sensory-motor systems and will generalize to any task that implicates the realigned components of the coordinative structure exercised during prism exposure, separately or in combination with other sensory-motor systems. For example, adaptation to a target-pointing exposure task with prismatic displacement usually involves change in origin alignment of the coordinate reference frames for both eye–head visual sensory-motor system and the head–hand proprioceptive sensory-motor system. During prism exposure, such realignment contributes to reduction in direct effects of prismatic displacement. After prism exposure, realignment will produce change in target pointing opposite the direction of the prismatic displacement: the same direction as for transfer of training (recalibration). However, in contrast to recalibration, with realignment pointing straight ahead without vision will also change opposite the direction of displacement and non-manual (e.g. verbal) production of visual straight ahead will change in the direction of displacement. Moreover, these aftereffects will extend equally to all coordinates in the realigned visual or proprioceptive reference frames.

Therefore, recalibration generalization depends upon similarity of conditions, while realignment generalization depends upon the involved reference frames (Redding and Wallace, 2003a, 2004b). If the coordinative structures exercised during exposure and post-exposure are the same or highly similar (e.g. target pointing that requires coordination of eyes and hand), recalibration and realignment both predict the same directional aftereffect. However, if post-exposure tasks involve the separate component systems (e.g. head–hand and eye–head setting of straight ahead), then only realignment predicts aftereffects. Aftereffects may show associative generalization along task dimensions, but at the same time show dimensional generalization for implicated reference frames (Redding and Wallace, 2003a, 2004b).

4. Critique of selected applications

In this section, we illustrate with selected, representative applications of prism adaptation the need for more adequate control procedures. We first consider applications where the primary interest was in illuminating the nature of ordinary perceptual-motor control. Then, we examine applications where the interest was in neuropathology, especially unilateral neglect.

Kitazawa et al. (1997) employed the prism adaptation procedure to study the relationship between the kinematics and dynamics of visual-motor control. Ten subjects performed target-touching movements during pre-exposure, prism exposure, and post-exposure, with view of the limb only after target touching but in all three phases. Different conditions examined transfer of prism exposure training with slow (or rapid) pointing to post-exposure slow-to-rapid pointing movements (i.e. average movement times of 5.0, 2.0, 0.8, and less than 0.3 s, respectively). Subjects were trained to produce the required movement speed on demand and were necessarily alerted before each block of trials about the selected movement speed. Proper aftereffects were measured by taking only the first post-exposure response: that is, before subsequent visual feedback could influence the aftereffects. Aftereffects were largest when movement velocity (82, 206, 515, 1374 mm/s) matched for exposure and post-exposure and incrementally declined as the velocity difference increased. Because velocity contingent aftereffects imply force modulation, Kitazawa et al. concluded that

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[8] For additional evidence for posterior parietal localization of strategic calibration see investigations of optic ataxia (Milner et al., 2001; Perenin and Vighetto, 1983; Pisella et al., 2000).

contingent adaptation involves the dynamics, as well as kinematics of movement control[9].

In the present context, two aspects of Kitazawa et al.'s methodology are important. First, the fact that exposure and post-exposure tasks were identical except for the manipulated similarity in movement velocity makes this study a paradigmatic example of transfer of training. Moreover, the 15 s inter-trial interval was conducive of strategic recalibration and differential transfer was aided by the necessary alert when the required movement speed changed. Also, the extreme terminal feedback (only after target touching) was optimal for producing strategic recalibration: 'a mediated off-line visual guidance strategy (side pointing)' (Redding and Wallace, 2000, p. 95). Second, objective displacement of the visual stimulus array by an amount equal to and opposite the prismatic displacement reduced the possibility that eye-muscle potentiation confounded the study. However, the consequential asymmetric limb exercise may have produced confounding arm-muscle potentiation.

In agreement with Kitazawa et al.'s conclusions, we find little reason to believe that realignment (visual or proprioceptive shift) occurred in their study. The aftereffects observed were almost certainly due to transfer of recalibration and it is not surprising that such associative learning was contingent upon movement speed. And strategic recalibration (side-pointing) likely precluded detection of misalignment and consequential realignment. Some confounding of muscle potentiation aftereffects in the limb may have occurred, but such effects are likely to have been small relative to the large effect of strategic recalibration. Muscle potentiation would have also reduced the likelihood of realignment. Still, Kitazawa et al.'s unqualified use of the term 'aftereffect' is confusing. Only a careful reading reveals the authors' acknowledgment that aftereffects can appear for different reasons.

Martin et al. (1996a) employed the prism adaptation procedure to study the specificity of calibration in visual-motor control for different tasks. Their subjects performed ball-throwing movements toward an objectively straight-ahead target during pre-exposure, prism exposure, and post-exposure, with visual feedback for throwing accuracy in all phases. Ten subjects used the right hand during exposure and the left hand followed by the right hand in post-exposure. Another ten subjects made overhand throwing during exposure and underhand throwing following by overhand throwing in post-exposure. Aftereffects[10] appeared for the trained hand, but not for the untrained hand. Half of the subjects showed aftereffects for the trained overhand throwing, but not for the untrained underhand throwing. Results for the other five subjects were mixed: three showed smaller aftereffects for untrained than trained throwing and two showed equal aftereffects for both untrained and trained throwing. From these results Martin et al. concluded that recalibration is largely specific to the conditions of training[11].

Two aspects of Martin et al.'s method are important in the present context. First, the fact that exposure and post-exposure tasks were identical except for the manipulated similarities in throwing limb and type of throwing makes this study another example of transfer of training. Moreover, the interval between throws allowed for strategic recalibration (side throwing) and differential transfer was aided by the obvious change in conditions when the prism goggles were removed and change made in throwing limb or type of throwing. Second, the type of throwing condition used where the limb is briefly visible at the end of the throwing movement has been shown to produce largely realignment in the hand–head proprioceptive system (Redding and Wallace, 1998), which is known to produce little or no transfer between limbs (e.g. Redding and Wallace, 1988a).

Martin et al.'s identification of automatic 'motor adaptation' as the locus of task-specific adaptation matches the requirements for strategic calibration. Strategic recalibration is specific to exposure conditions, but realignment is not. To the extent that recalibration occurred, realignment was limited and the exposure conditions used likely limited any realignment to the hand–head proprioceptive system: muscle potentiation produced by asymmetric exercise of the visual system would also have limited visual realignment. Proprioceptive realignment does not transfer between limbs[12] and the mixed results for type of throwing likely arose from individual differences in recognizing the transfer of training task demand: subjects who accepted the task as transfer of training overrode proprioceptive realignment, but the other subjects demonstrated realignment aftereffects. Of course, without explicit tests for realignment we cannot be confident of this interpretation. It is likely that if tests for visual and proprioceptive realignment had been included, only proprioceptive realignment would have appeared and only for those subjects showing non-specificity for type of throwing.

These examples of application of the prism adaptation procedure to the study of ordinary motor control illustrate the need to methodologically distinguish among the possible sources of aftereffects: muscle potentiation,

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[9] Interestingly, most studies of prism adaptation do not involve surface contact and may have different dynamics (Redding and Wallace, 1990). Surface contact may evoke force modulation and different results might appear without surface contact.

[10] For statistical analysis (Martin et al., 1996a) apparently used the first three post-exposure throws, whereas measurement of aftereffects should have been restricted to first throw before visual feedback or knowledge of results could reduce their magnitude. Nevertheless, the data Martin et al. display show proper aftereffects for the first post-exposure throw.

[11] Martin et al. (1996a) also showed long-term specificity of prism vs. non-prism conditions for two additional subjects. Such dual adaptation has been discussed elsewhere (Redding and Wallace, 2003a) and we do not repeat that discussion here.

[12] There is a long history of interest in intermanual transfer of prism adaptation (for a review, see the work of Welch (1978)). The consensus seems to be that realignment is limb-specific, but that any transfer can be attributed only in part to realignment in other sites like eye–head and head–trunk relationships (Redding and Wallace, 1988a).

strategic recalibration, and spatial realignment. Both studies can be taken as investigations of strategic calibration, but the conclusions would have been more strongly supported if adequate controls for muscle potentiation and spatial realignment had been included. Similar examples of the application of prism adaptation as a transfer of training procedure to study strategic recalibration include Fernández-Ruiz et al. (2000), Kitazawa et al. (1995), Martin et al. (2002) and Roller et al. (2001).

We now turn to a consideration of the application of prism adaptation in treatment for unilateral neglect. Unilateral neglect is a deficit in patients with unilateral (usually right hemisphere) brain lesions to explore and respond to stimuli occurring in the contralesional side of space (for reviews, see the works of Bisiach and Vallar (1988), Heilman et al. (1993) and Vallar (1998)). The majority of patients show lesions in the posterior parietal area, especially at the parietal-temporal interface. The deficit is largely restricted to the contralesional side, is dissociated from primary sensory and motor deficits, may be localized by sensory modality, may appear as an ipsilesional bias in egocentric reference frames, may appear for personal as well as extra-personal space, and conscious awareness may be more or less completely lost for the contralesional side of space. Clinical and everyday symptoms of left unilateral neglect are ameliorated for prolonged periods following a short time of adaptation to rightward prismatic displacement (for reviews, see the works of Rode et al. (2003) and Rossetti and Rode (2002)).

Rossetti et al. (1998) discovered that a short period of pointing toward targets centered around objective straight ahead but viewed through prisms that displaced the visual field 10° in the rightward direction (50 pointing movements for an exposure period of 2–5 min) ameliorated left unilateral neglect symptoms in 6 patients for as long as two hours. Aftereffects were measured by pre-post exposure pointing toward the body midline ahead without vision. Amelioration of neglect by prism adaptation was found to be contingent upon the presence of aftereffects, although amelioration persisted longer than did the aftereffects.

For present purposes the following aspects of Rossetti et al.'s method are important. The dissimilarity between exposure and post-exposure tasks makes it unlikely that the aftereffects were simply measures of strategic recalibration: the aftereffects provided measures of hand-trunk proprioceptive realignment. The concurrent exposure used likely produced predominantly proprioceptive realignment that represented an average contribution of more than 60 percent of the prismatic displacement. Asymmetric exercise of the visual system during exposure might have produced muscle potentiation aftereffects, but change in the visual system was not measured.

It seems clear that spatial realignment is likely to be the necessary pre-condition for neglect amelioration, but the relationship between kinds of realignment and neglect amelioration is not known. Pre-post measures of aftereffects in both the visual and proprioceptive systems and prior knowledge of the locus of neglect are needed. Manipulation of the locus of asymmetric exercise is also needed to control for the contribution of muscle potentiation aftereffects.

Frassinetti et al. (2002) assessed target pointing without visual feedback and performance on a battery of tests for neglect that included clinical and behavioral measures, including tests for far space, near space, and personal space. Six patients experienced prism exposure (pointing toward targets while wearing 10° rightward displacing prisms with only the finger tip visible at the terminus of the movement) twice daily over a period of two weeks (10 times per week): target pointing without visual feedback was measured before and after each prism exposure. The test battery was administered before, two days, one week and five weeks after the two-week treatment period. Patients evidenced a leftward aftereffect in target pointing immediately after prism exposure that decreased, but persisted for six to 12 h. Clinical and behavioral measures revealed apparent improvement for the treatment period[13].

In the present context, the following are important aspects of Frassinetti et al.'s methodology. The use of the same task (target pointing) during exposure and post-exposure raises the possibility that patients accepted a transfer of training interpretation and that the aftereffects arose from transfer of strategic recalibration. On the other hand, the terminal exposure condition is known to produce realignment largely or entirely in the visual eye–head sensory-motor system (Redding and Wallace, 1993, 1990, 1992, 1994, 2004a) and, therefore, the aftereffects may reflect visual system realignment. Asymmetric exercise of the visual system during exposure could also have produced muscle potentiation contributions to aftereffects.

Frassinetti et al.'s methodology does not permit identification of the source of the observed aftereffects. It seems likely that aftereffects arose, at least partially, from spatial realignment, but as with Rossetti et al. (1998), pre-post measures of aftereffects in both the visual and proprioceptive systems and prior knowledge of the locus of neglect are needed to identify the relationship between kinds of realignment and neglect. Measurement of visual and proprioceptive aftereffects would also enable assessment of the contribution of strategic recalibration to the obtained aftereffects. Manipulation of the locus of asymmetric exercise is also needed to control for the contribution of muscle potentiation aftereffects. In general, patient studies should include a control group that receives all treatments except the prismatic displacement (i.e. placebo).

These examples illustrate the need for further investigation in the application of prism adaptation to neuropathology. The methodology employed does not yet permit

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[13] However, it should be noted that Frassinetti et al., (2002) no-treatment control group did not control for possible benefit from repeated experience at pointing.

unequivocal identification of the source of aftereffects upon which neglect amelioration seems contingent. Pre-post measures of aftereffects in both the visual and proprioceptive systems, prior knowledge of the locus of neglect, manipulation of realignment locus by varying delay of visual feedback during exposure (the point in the movement path where feedback becomes available), and manipulation of the locus of asymmetrical exercise would go far toward resolving the ambiguity regarding the nature of both neglect and the ameliorating effects of prism adaptation. Similar applications of prism adaptation to unilateral neglect that have replicated and extended the basic findings include Berberovic et al. (2004), Farnè et al. (2002), Ferber et al. (2003), Maravita et al. (2003), Pisella et al. (2002), Rode et al. (1998/1999) and Tilikete et al. (2001).

5. Conclusions and recommendations

Prism adaptation is not a simple process. Exposure to prismatic displacement evokes all of the processes of adaptive perceptual-motor performance, including postural adjustments (esp. muscle-potentiation), strategic control (esp. recalibration), and differential spatial realignment of various sensory-motor reference frames. Prism adaptation can be used for many different applications, but minimal methodological standards should be met before the procedure is developed for a specific application. Indeed, the versatility of the paradigm makes it all the more important that standards be established for distinguishing among the several kinds of adaptation, all of which are evoked in some amount by prism exposure.

Applications of prism adaptation should recognize the different nature of direct effects and aftereffects of prism exposure. Direct effects of prismatic displacement during prism exposure are sensitive to all three kinds of adaptive processes: postural adjustment, strategic control (esp. recalibration), and spatial realignment. Error reduction during prism exposure is a composite of contributions and such adaptation is ambiguous with respect to its source. Proper aftereffect measures (described below) can identify realignment contributions and the difference between direct effects and aftereffects can be used to estimate the contribution of other adaptive processes during exposure (Redding and wallace, 1993). Measurement of perceived posture during prism exposure can further isolate postural adjustment contributions (Redding and Wallace, 2003b, 2004a).

Traditionally, aftereffects without feedback have been assumed to measure ‘true’ adaptation, but research has shown that aftereffects also can reflect contributions from postural adjustment, strategic recalibration, and spatial alignment (Redding and Wallace, 1993, 2003a,b, 2004a, 1978, 2001, 1987, 1988b, 2004b). Identifying the kind(s) of adaptation measured by aftereffects requires more complex methodology.

Muscle potentiation is the most likely source of postural adjustment aftereffects and can be assessed by manipulating asymmetric exercise during exposure. However, because asymmetric exercise in some systems is unavoidable, assessment of muscle potentiation requires comparison of aftereffects following symmetric and asymmetric exercise of each component motor system implicated in prism exposure. The locus of asymmetric exercise can be manipulated by varying the average position of targets for pointing during prism exposure (Redding and Wallace, 1978, 1988a; Craske and Crawshaw, 1975, 1978; Crawshaw and Craske, 1974; see also the works of Redding and Wallace (1987) and (1988b)). When targets are centered around the objective straight ahead the visual system is asymmetrically exercised, but exercise of the proprioceptive system is largely symmetrical and any aftereffects due to postural adjustment should appear in the visual system. On the other hand, if targets are objectively centered on a position opposite the direction and equal to the amount of prismatic displacement, the converse is true in locus of exercise symmetry and postural adjustment aftereffects.

Manipulating the similarity of the exposure and post-exposure task can assess strategic recalibration aftereffects because they are associative in nature (Redding and Wallace, 2003a, 2004b). However, this procedure only provides a relative measure of recalibration aftereffect. The difference between aftereffects for post-exposure tests similar and dissimilar to exposure measures associative recalibration, but the remainder of the aftereffect may arise from other sources. (Accounting for the complete aftereffect requires further measurement of muscle potentiation and spatial realignment). Of course, like all proper aftereffect measures, post-exposure tests should not provide feedback to prevent contamination by retraining. Further, there should be minimal discontinuity between exposure and post-exposure to maximize measurement of associative transfer.

Assessment of spatial realignment aftereffects requires different exposure and post-exposure tasks. Because realignment is localized, assessment requires separate aftereffect measurement of each of the sensory-motor systems implicated in exposure. An aftereffect from the exposure task repeated in post-exposure can be assumed to measure total realignment only if it equals the sum of component tests (i.e. the additivity test (e.g. Redding and Wallace, 1978; Wallace and Redding, 1979; Welch et al., 1974)). Manipulation of visual feedback delay from early to late in movement can be used to produce predominate realignment in a particular sensory-motor system (i.e. concurrent to terminal exposure; (Uhlarik and Canon, 1971; Redding and Wallace, 1990, 1992, 1994, 1988a, 2000). Varying the locus of realignment in this manner can help to identify the locus of realignment relevant to the particular application. Aftereffects should be obtained without feedback and exposure should be clearly discontinuous with post-exposure to minimize contributions of strategic control.

More specifically with regard to realignment aftereffect assessment, pre-post exposure tests of straight ahead should be obtained for the visual (eye–head), proprioceptive (hand–head), and visual-proprioceptive (eye–hand) sensory-motor systems (or corresponding measures when, for example, the auditory ear–head sensory-motor system is involved). Examples of the three kinds of tests can be found in Redding and Wallace (1993), (2001) and (2000). Note carefully that all tests of this kind have both sensory and motor components. Traditional appellations and abbreviations are misleading. The visual shift (VS) test involves coordination of both retinal and oculomotor components. The proprioceptive shift (PS) test involves coordination of both proprioception and limb muscle commands. The visual-proprioceptive test is sometimes called the negative aftereffect (NA) or total shift (TS) test and involves sensory-motor coordination of visual-motor and proprioceptive-motor systems.

The visual test requires non-manual (e.g. verbal) adjustment of a target to look straight ahead. The proprioceptive test requires manual pointing to felt straight ahead without vision. The visual-proprioceptive test requires manual pointing toward a straight-ahead visual target without sight of the limb. Realignment for rightward prismatic displacement produces a rightward shift (pre-post difference) in visual straight-ahead and leftward shift in proprioceptive straight-ahead and visual-proprioceptive straight ahead. The logical basis for these empirically confirmed aftereffect directions is as follows.

During exposure, a straight-ahead limb position is required to achieve the straight-ahead target, but the target is visually coded positioned to the right by the amount of the displacement (or some portion of the displacement if visual capture occurs; (Redding and Wallace, 2003b, 2004a)). This spatial discordance can be resolved by a shift in proprioceptive limb position such that the straight-ahead limb is felt positioned to the right. Now, in the aftereffect test, for the limb to feel straight ahead it must be positioned to the left, opposite the direction of the exposure displacement. Alternatively, spatial discordance can be resolved by changing the visually coded position of the target to agree with the proprioceptively coded position of the limb. In this case, a rightward visual position comes to signify straight ahead. And in the aftereffect test, a visual stimulus must be positioned to the right, in the direction of displacement, to appear straight ahead (Redding and Wallace, 1998). Leftward visual-proprioceptive shift measures the sum of (total) realignment in both the visual system (where an objective straight-ahead target looks to the left) and the proprioceptive system (where the objectively straight-ahead limb now feels to the right): the limb is positioned to the left of the apparently leftward target.

A final caution is urged in the use of virtual reality simulations of prism adaptation (e.g. Baraduc and Wolpert, 2002; Bock, 1992; Ingram et al., 2000; Norris et al., 2001; Wolpert et al., 1994, 1995). Clower and Boussaoud (2000) have shown that aftereffects appeared when the prism exposure period provided actual visual feedback about limb position, but not when feedback was computer generated, even though performance during prism exposure was identical for the two conditions. Discordance detection depends upon the object unity assumption (Welch and Warren, 1980; Welch, 1994): the assumption that coordinates in different intrinsic spatial representations come from the same object in extrinsic space. Several justifications of this assumption have been proposed (Bedford, 1993b, 1994, 2001; Radeau, 1994; Redding, 2001) and Redding and Wallace (1997a) discuss this correspondence problem at some length.

The caution here is that virtual reality simulations may not produce spatial realignment because conditions for the object unity assumption are not present (or at least not without extensive training in the virtual environment). Moreover, when aftereffects do occur in such simulations (Baraduc and Wolpert, 2002; Bock, 1992; Norris et al., 2001) they may reflect transfer of training in strategic recalibration rather than realignment. Also, simulations may deploy different coordination strategies that affect discordance detection and spatial realignment (cf. Ingram et al. (2000) and Redding et al, (1992)). The above methodology may be adapted to simulations of prism adaptation to identify the source of aftereffects.

This analysis and critique does not depreciate the importance of applications of prism adaptation. Prism adaptation is uniquely suited for investigation of spatial alignment, including the behavior of misaligned systems in early stages of exposure and later developing realignment, but the procedure also evokes other kinds of adaptive processes, processes that must be controlled if the full benefit of application is to be achieved. With proper controls, the prism exposure procedure can also be employed to study strategic control (sensory-motor coordination) and postural adjustment. Our understanding of prism adaptation can be improved by brain imaging experiments in conjunction with behavioral controls that target a particular type of response to prism exposure. The application of prism adaptation to neuropathology promises to reveal the interface between sensory-motor coordination and high level cognition, opening new perspectives for the rehabilitation of cognitive disorders (Rossetti et al., 2004).

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