Abstract

Theory and data from normal prism adaptation are applied toward understanding the ameliorating effects of prism adaptation for left unilateral neglect patients. Neglect is proposed to be, at least in part, a dysfunction in selection of the region of space appropriate for the task at hand. Normally, a task-work space is strategically sized and positioned (calibrated) around the task-relevant objects. Patients show deficits in both strategic abilities: the task-work space is pathologically reduced in size and patients cannot strategically shift its position. Prism adaptation (spatial realignment) ameliorates dysfunctional positioning, but not sizing of the task-work space. Realignment shifts the egocentric coordinates of a sensory–motor reference frame, thereby bringing at least part of the neglected hemispace into the dysfunctional task-work space: prism adaptation substitutes for dysfunctional positioning, but not sizing of a task-work space. However, such amelioration of dysfunctional positioning may enable relearning of strategic processes (calibration), perhaps, even partially restoring the ability to appropriately size the task-space. Investigation of therapeutic prism adaptation requires methods that permit identification of both the calibration dysfunction and ameliorating realignment.

Keywords: Realignment; Recalibration; Aftereffects; Muscle-potentiation; Motor control

Contents

1. Introduction ................................................................. 2
2. Basic concepts of motor control ......................................................... 2
3. Prism adaptation .......................................................... 4
  3.1. Calibration and alignment ..................................................... 4
  3.2. Localized realignment and spatial mapping .......................... 5
  3.3. The prism adaptation paradigm ........................................... 6
  3.4. Muscle-potentiation ......................................................... 8
  3.5. Methodological implications .............................................. 8
4. Unilateral neglect ............................................................... 9
  4.1. Clinical tests ............................................................. 9
  4.2. Amelioration by prism adaptation ......................................... 9
  4.3. Summary ............................................................... 11
5. A theoretical proposal .......................................................... 12
  5.1. Neglect as dysfunctional calibration .................................... 12
  5.2. Therapeutic effect of prism adaptation ............................... 13
  5.3. Persistence of amelioration .............................................. 15

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1. Introduction

A short period of adaptive pointing toward targets optically displaced rightward by prisms ameliorates many clinical symptoms of right-hemisphere stroke patients who neglect their left-hemispace (Rossetti et al., 1998). The therapeutic effect of prism adaptation on unilateral neglect is becoming an increasingly important research area in neuropsychology (for reviews, see Mattingley, 2002; Rode, Psella, Rossetti, Farnè, & Boisson, 2003; Rossetti & Rode, 2002). In the present paper, we seek to further this research effort by interpreting the therapeutic effect in terms of the most current data and theory of normal prism adaptation (Redding & Wallace, 1993, 1997a, 2002, 2003a). We believe it incumbent upon researchers who apply prism adaptation for therapeutic purposes that they be conversant with normal prism-adaptation theory and method (see also, Redding, Rossetti, & Wallace, 2005).

In the 100 years since its discovery, prism adaptation has been interpreted first in terms of perceptual theory (Held & Hein, 1958; Kohler, 1951/1964; von Helmholtz, 1909/1962) and later in terms of learning theory (Bedford, 1989; Welch, 1978). These early explanations of prism adaptation have now been incorporated into a motor control interpretation (Redding & Wallace, 1993, 1997a). Understanding normal prism adaptation necessarily requires some understanding of motor control; prism adaptation is a particular example of adaptive perceptual–motor control. Therefore, we must begin with a review of the basic concepts from motor control relevant to prism adaptation.

With necessary motor control concepts in hand, we review the current state of data and theory in prism adaptation and draw out the methodological implications for application of the procedure. We then survey the research showing therapeutic effects of prism adaptation on unilateral neglect. Next, we apply current prism adaptation theory to explain therapeutic effects. Finally, we conclude with recommendations that may increase our understanding of prism-adaptation therapeutic effect. Note carefully that our purpose is not to explain all of the various facets of unilateral neglect. Rather, our modest goal is to understand how prism adaptation ameliorates at least some kinds of neglect.

2. Basic concepts of motor control

This review of perceptual–motor control is selective. It is neither meant to be exhaustive of this large area of data and theory nor even to necessarily represent all of the most central problems that concern motor-control theorists. We present only the concepts relevant to prism adaptation (see also Redding & Wallace, 1997a). For more detailed treatments, we refer the interested reader to books by Rosenbaum (1991) and Schmidt (1999) and reviews by Kawato (1996a,b).

When one undertakes a routine, perceptual–motor, goal-directed task a number of strategic processes are activated at different levels of a hierarchical representation of the goal–behavior. For example, the intention to grasp a coffee cup retrieves a previously learned coordinative structure (synergy) linking sensory–motor systems from eye to hand (a different coordination of sensory–motor systems would be retrieved, for example, by the intention to walk to the restroom). Retrieval of an eye–hand coordinative linkage constitutes a super-ordinate or generalized movement plan (schemas), a plan to use the hand on some seen object, a plan for control (guidance) of the limb by visual input. If the task were to look at one’s wristwatch, for example, the reverse direction of guidance of the eye by limb proprioception and a different generalized movement plan would be retrieved. The generalized movement plan includes input–output details at subordinate levels to achieve a task-specific movement plan.

On the input (visual–motor) side a regional work space is identified to include the goal object among surrounding objects that might constitute obstacles to movement: inclusion of the entirety of, for example, visual space and its contents would produce an unduly heavy computational load and consequential performance errors. A regional task-work space might be thought of as the focus of spatial attention, but whenever possible we adopt a description in terms of task parameters, with minimal invocation of endogenous processes. We call such strategic positioning of the task-work space and its contents within a larger reference frame “calibration”, the process of setting the spatial parameters for a specific task. Information from the visual task-work space is used to select a more specific movement plan, ultimately specifying the movement path required to negotiate obstacles to reach the goal object (coffee cup). Of course, the specific movement plan includes specification of a grasping (rather than, for example, a touching) hand posture. This visually prescribed movement plan is sent as a feedforward movement command structure to the limb.

A feedforward movement plan involves a predicted movement sequence such that deviations can be anticipated and quickly corrected before they can occur or at least before they can become large. For example, inertial differences be-
tween limb segments can be predicted and accounted for in the movement plan; slippage of the grip on the cup handle can be similarly anticipated. Thus, feedforward control is not limited by the relatively slow response time of feedback control (for a review, see Desmurget & Grafton, 2003).

On the output (propiroceptive–motor) side, the processes that control the limb interpret the feedforward command structure, calibrate a limb task-work space accordingly, and execute the command. If the hand-starting position is visible, its position is specified in the visually derived command structure (visual calibration), but otherwise, limb control depends upon local proprioceptive information (propiroceptive calibration) to interpret the feedforward command. If the moving limb becomes visible, visual feedback can be used to send corrective commands coded in terms of relative distance and direction to the goal object (i.e., feedback movement vector commands rather than feedforward position commands). Novel tasks must be learned slowly by trial-and-error associative pairing of appropriate input-output conditions identified by trial by trial (knowledge of results), but highly practiced tasks (skills) may be largely automatic. Ideally, if the input-output relationships are perfectly predictable (closed skills; Poulton, 1957), a feedforward model of the controlled system might be learned perfectly, showing error-free performance without online feedback correction. Indeed, a highly automated behavior may even be elicited unintentionally by appropriate situational conditions, for example, the presence of a telephone in the hand may result in calling home, rather than the intended call to a friend.

However, most skilled goal-behaviors require at least the intention to act and many require more conscious processes like deliberately searching for the coffee cup or telephone with orienting movements. Moreover, although calibration of a task-work space is strategically flexible in response to sudden changes in the environment or changes in intention, once a task-work space has been specified, conscious awareness is largely restricted to the contents of the task-work space, for example, one is much less aware of a computer screen, keyboard, etc. when concentrating on retrieving a coffee cup (indeed, an attempt to include both computer and coffee cup in the task-work space can result in spilled coffee on the keyboard).

Hierarchical goal-behavior movement plans accommodate both generalization and specificity of learning. The more super-ordinate levels of a movement plan will generalize to similar tasks, for example, any task requiring use of the hand on seen objects. Branching subordinate levels of a movement plan specify more task-specific movement plans, for example, pointing toward rather than grasping an object. Movement plan selection consists of in-parallel examination of all levels of the hierarchy until a complete plan is found or until a more specific branch must be learned to accommodate the task at hand. For the adult, intact organism, it is uncommon that any novel task must be learned “from scratch”.

We call the selection/creation and execution of task-appropriate movement plans “strategic control”. Error in execution (performance feedback) produces strategic refinement of a movement plan, especially at lower levels of the hierarchy, and adjustment in execution of the plan. For example, if the coffee cup tilts when lifted, the grasp component is almost immediately recalibrated to be more appropriate to the shape of the cup. If it looks like the cup handle will be missed, the terminus of the reach may be adjusted to meet with the handle (online visual feedback recalibration), and/or the terminus of the programmed reach may be adjusted the next time, we reach for the cup (offline recalibration by knowledge of results). If the elbow disturbs the arrangement of papers on the desktop, a different limb posture may be used the next time, we reach for coffee. A variety of strategies are available to the skilled actor for correcting performance error, including online feedback recalibration and offline knowledge of results recalibration.

A final and central problem for adaptive perceptual–motor performance is that coordinated systems have different reference frames or spatial coordinate axes. For example, spatial positions for the visual–motor (retinas-eye muscles) system are coded along coordinate axes centered on the head, while spatial positions for the proprioceptive–motor system are likely coded along coordinate axes centered on the shoulder: an origin difference between coordinate axes. The visual–motor reference frame is also mostly oriented frontally, while the proprioceptive–motor system is mostly oriented laterally: an orientation difference between coordinate axes. Of course, origin and orientation differences between reference frames vary with different postures (e.g., head and limb), but once variability due to range of movement (e.g., head and shoulder movement) is taken into account, constant differences remain (e.g., between visual and limb reference frames) for the adult intact organism.

Consequently, movement commands formulated in one sensory–motor coordinate system must be transformed for successful use by another receiving sensory–motor coordinate system. For example, the lateral difference between head and shoulder must be added to spatial position commands from the visual system to the limb system. We call the process of adjusting for these constant differences in spatial coordinates between sensory–motor systems “alignment”: transforming spatially coded positions from one coordinate system into another. Misalignment occurs when the constants change, for example, when ordinary neural cell death causes slow drift of coordinate axes in the adult intact organism. Misalignment in the developing organism occurs more quickly, but still slowly in everyday terms, when, for example, limb length increases in a matter of weeks and hand position no longer has the same coded position in visual–motor and proprioceptive–motor coordinate systems. Realignment is necessary to re-establish veridical spatial mapping among sensory–motor systems: adjustment in transformational constants.

Prism adaptation affords an almost unique opportunity to experimentally study misalignment and realignment. Alignment might be served by calibration, but in the next section,
we present evidence from prism adaptation that calibration and alignment are dissociated processes (see also, Clower & Boussaoud, 2000; Weiner, Hallett, & Funkenstein, 1983; Welch & Sampanes, 2004). Calibration is the ordinary spatial remapping required by relative changes in coordinate systems arising from, for example, head and shoulder movement. Alignment is the extraordinary spatial remapping required by changes in the constants relating coordinate systems arising from, for example, prismatic displacement of the visual field.

3. Prism adaptation

In this section, we review the evidence for the several different kinds of adaptive processes evoked by prism exposure, with particular attention to recalibration and realignment, detailing the localized nature of realignment and illustrating the prism-adaptation procedure in terms of these two primary adaptive processes. We conclude with consideration of the methodological procedures necessary to identify the source of prism adaptation in a particular research enterprise.

3.1. Calibration and alignment

Perhaps, the most direct empirical evidence for the calibration–alignment distinction comes from the differential effects of visual and proprioceptive calibration on error in target pointing during exposure to prismatic displacement (Redding & Wallace, 2001, 2002). As has long been known (Bowditch & Southard, 1880; Desmurget, Rossetti, Prablanc, Stelmach, & Jeannerod, 1995), visual calibration by sight of the limb in the starting position reduced response variability (variable error) compared to proprioceptive calibration when the limb was not seen in the starting position. However, response accuracy (constant error) was greater with visual calibration than proprioceptive calibration. The prismatic misalignment produced greater constant error, while the greater precision of visual calibration decreased variable error.

This finding not only suggests that calibration and alignment are dissociable, but also that alignment is “transparent” to calibration, that calibration does not “see” or “know” the present state of alignment, that alignment does not have to be computed by calibration. Performance errors arising from misalignment are treated as errors of calibration to be corrected by recalibration.

Additional evidence comes from comparison of direct effects of prismatic displacement during exposure with aftereffects obtained after prism exposure (e.g., Redding & Wallace, 1993). With repeated exposure trials exposure performance errors (direct effects) quickly disappeared, but aftereffects increased more slowly and did not achieve complete compensation for the prismatic displacement. Moreover, in later trials direct effects tended to show overcompensation, error opposite the initial direction produced 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.

Traditionally, rapid error correction in prism adaptation (recalibration) has been recognized as “conscious correction” (Welch, 1978), but this term depreciates the complexity and pre-conscious partially automatic nature of motor control (Redding & Wallace, 1993, 1997). When a movement plan fails to achieve its goal, as happens during prism exposure, online feedback corrects performance error (recalibration) or knowledge of results from earlier trials can recalibrate the target position for the movement plan, improving performance on following trials.

Further evidence of the calibration–alignment dissociation is that prism aftereffects of realignment can occur in the absence of detectable performance error that would activate recalibration (Dewar, 1971; Howard, 1968; Howard, Antis, & Lucia, 1974; Jakobson & Goodale, 1989; Templeton, Howard, & Wilkinson, 1974; Uhlarik, 1973). For example, Howard (1968) reported aftereffects using a prismatic shaping procedure for a target pointing exposure task. On the first trial, the prismatic displacement was set to zero and between each successive pointing movement the displacement was increased in quarter-degree steps until a maximum of 15° of displacement was achieved on the last trial. Because the pointing error produced by each increment was within the subjects’ mean pointing error, subjects experienced no performance error and were completely unaware that any prismatic displacement had occurred. These findings suggest not only that realignment is a non-conscious process, but also that performance error per se is not the stimulus for realignment; realignment is motivated by spatial discordance between expected (feedforward predicted) position and the position actually achieved by performance (see below). However, performance error is (sometimes consciously) the stimulus for recalibration.

Another line of evidence for the calibration–alignment distinction is the different stimulus conditions for realignment aftereffects and reduction of exposure direct effects. Redding and Wallace (1996, 1997b) demonstrated that if the entire movement path from starting limb position to target was visible during target pointing under prismatic displacement, direct effects (pointing error during exposure) and aftereffects did not occur, i.e., recalibration by visual feedback occurred, but realignment did not occur. Under such conditions, the relative distance and direction from starting position to target is not affected by the prismatic displacement and movement can be entirely controlled by visual feedback employing vector direction–distance movement codes. In contrast, if the movement path is occluded with only starting limb position and target visible, both direct effects and aftereffects appeared (Redding & Wallace, 2001).

The difference between these two conditions is that movement in the latter condition was initiated by feed-
forward position commands and, even though logically possible, vector commands were only employed for online visual feedback correction. These results suggest that the stimulus for realignment is the spatial discordance between the feedforward expected position and the position achieved by online visual feedback or offline knowledge of results. Of course, expected and achieved positions differ because of the prismatic displacement (see also Redding & Wallace, 1997a).

Calibration and alignment also make different demands on central processing capacity. For example, Redding, Radi, and Lurito (1992) measured the effect of cognitive load on error in target pointing (direct effects) and realignment after-effects. Cognitive load was manipulated by requiring mental arithmetic simultaneously with target pointing during prism exposure compared to a control condition without mental arithmetic. Aftereffects were not substantially different whether or not mental arithmetic was required, but pointing error during exposure (direct effects) was reliably greater throughout the exposure period when mental arithmetic was required. These results suggest that recalibration requires central processing capacity, but realignment is automatic so long as the exposure task can be performed well enough to enable detection of spatial discordance. Calibration is a high-level process in the sense that some attention is required, but alignment is low-level, removed from demand on central processing capacity (see also Redding, Clark, & Wallace, 1985; Redding & Wallace, 1985).

The calibration–alignment processing distinction may also correspond to localization of function in cerebrum and cerebellum, respectively (Jeannerod & Rossetti, 1993). The ability to adapt to prismatic displacement remains with intact cerebellum but damaged posterior parietal cortex (Baizer, Kralj-Hans, & Glickstein, 1999; Martin, Keating, Goodkin, Bastian, & Thach, 1996; Weiner et al., 1983).

A final line of evidence is the difference in generalization of calibration and alignment. For example, Kitazawa, Kimura, and Uka (1997) varied the speed of target pointing movements during training (prism exposure) relative to that in the test condition (post-exposure). Prism adaptation with slow movements did not generalize to fast movements and vice-versa. The typical inverted U-shape associative generalization gradient appeared around the training value; prism adaptation was largest when movement speed at test was the same as movement speed during training and decreased as movement speed at test was increasingly different from movement speed during training. These findings are consistent with an associative learning component (calibration) for prism adaptation, where generalization depends upon the similarity between exposure and post-exposure conditions (see also Redding & Wallace, 2003a; Welch, 1978; Welch, Bridgeman, Abbott, & Brownman, 1993).

In contrast, Bedford (1989, 1993a,b) found that training with a single visual–proprioceptive stimulus pair during prism exposure generalized globally in post-exposure to untrained pairings of visual and proprioceptive positions. These findings suggest a non-associative, dimensional learning component (alignment) for prism adaptation that maps entire dimensions (see also Guigon & Baraduc, 2002; Redding & Wallace, 1997a, 2004b). Spatial realignment shows “complete” generalization within the changed spatial maps, but it does not transfer to other reference frames not involved in the realignment.

3.2. Localized realignment and spatial mapping

The evidence for realignment of local reference frames is substantial. For example, Redding and Wallace (1990) varied the time (early to late) at which the moving limb was visible during target pointing with prismatic displacement. When the limb was visible early, about halfway to the target, realignment aftereffects were largely localized in the proprioceptive hand–head sensory–motor system, as measured by pre-post-exposure change in pointing straight-ahead of the nose without vision. The locus of realignment aftereffects gradually changed as visual feedback of the moving limb was delayed until sight of the limb occurred only at the terminus of movement when aftereffects were largely localized in the visual eye–head sensory–motor system, as measured by pre-post-exposure change in non-manual (verbal) adjustment of a target to appear straight-ahead of the nose. Moreover, the algebraic sum of proprioceptive and visual realignment was equal to the total realignment in the eye–hand coordination loop, as measured by pointing at a straight-ahead target without visual feedback or knowledge of results. Similar results are obtained (e.g., Redding & Wallace, 1992, 1993, 1994; Uhlirik & Canon, 1971) when the limb is continuously visible during the later half of the pointing movement (concurrent exposure) or only at the terminus of the pointing movement (terminal exposure) and with mental imagery (Finke, 1979).

These results suggest that alignment is localized in the transformations that map spatial coordinates between independent sensory–motor systems. Each sensory–motor system seems to have a unique transform that links it to all other sensory–motor systems. For purposes of alignment, sensory–motor systems may be linked through a noetic nexus (possibly in the cerebellum), a switching-point that routes spatial information from the various sensory–motor systems through a common reference frame. Strategic control sets

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2 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. Note, however, that because of the prism-bearing goggles, concurrent exposure usually allows sight of the limb only over the terminal half of the pointing movement.

3 Neurophysiological investigations (for reviews, see Andersen, Snyder, Bradley, & Xing, 1997; Colby & Goldberg, 1999; Stein, 1992) have

Fig. 1. Normal alignment and normal calibration are illustrated for eye–hand coordination in pointing toward an egocentrically straight-ahead target (filled dot) with concurrent visual and proprioceptive feedback. The eye-hand sensory–motor system involves coordination of component visual–motor eye–head and proprioceptive–motor hand–head sensory–motor systems. The task-work space (small ellipse) for each component system is calibrated in size and position to match the demands of the particular task and calibration of component systems is reflected in coordination. Spatial mapping (arrows) of each task-work space shows alignment with the noetic reference frame (large ellipse) common to all sensory–motor systems. The noetic reference frame is assumed to be veridical, a good approximation to (objective) extrinsic space.

These conclusions suggest that alignment and calibration cooperate in producing adaptive perceptual–motor performance: alignment provides that basic underlying common reference frame for coordinated systems, while calibration provides the strategic setting of spatial parameters for a particular task.

In summary, calibration is a higher-level, sometimes attentional process that is blind to lower-level, largely automatic alignment. Calibration operates to reduce ordinary performance error, while alignment reduces spatial discordance between reference frames by responding to expected–achieved differences in performance. Calibration shows associative learning, while alignment shows dimensional learning.

3.3. The prism adaptation paradigm

Fig. 1 is a schematic summary of the adaptive state prior to prism exposure in terms of the central concepts of calibration and alignment mapping of task-work space. Spatial mapping in Fig. 1 represents both short-term calibration (selection of a task-work space within the noetic reference frame) and long-term alignment (positioning of the task-work space in coordinates common to all sensory–motor systems). The task is coordination of the eye-hand sensory–motor system in pointing toward an egocentrically straight-ahead target and involves component task-work spaces for visual–motor eye–head and proprioceptive–motor hand–head sensory–motor systems. Fig. 1 illustrates normal alignment of sensory–motor systems within the noetic reference frame and normal calibration of task-work spaces on egocentric straight-ahead. Note that if the target were, for example, to the right of egocentric straight-ahead, task-work spaces would be calibrated to center on the rightward target. Of course, prismatic displacement has no initial effect on the proprioceptive–motor hand–head task-work space, but the coordinated eye-hand task-work space is shifted rightward, i.e., pointing toward an objectively straight-ahead target will be shifted rightward, where the displaced visual target appears. Fig. 2 illustrates the initial consequences of rightward prismatic displacement. The visual–motor eye-head task-work space is shifted rightward, i.e., straight-ahead in the visual–motor eye-head system is displaced rightward and the visual task-work space is recalibrated to the right of egocentric straight-ahead specified by the noetic reference frame. Of course, prismatic displacement has no initial effect on the proprioceptive–motor hand–head task-work space, but the coordinated eye-hand task-work space is shifted rightward, i.e., pointing toward an objectively straight-ahead target will be shifted rightward, where the displaced visual target appears. Fig. 2 illustrates the state prior to any realignment, but where adaptive recalibration shifts the task-work space to center on the (prismatically displaced) rightward position of the target.

Fig. 3 illustrates the common case, where some realignment occurs in both of the component systems. Realignment shifts the visual eye-head task-work space leftward and the proprioceptive head–hand task-work space rightward, i.e., the straight-ahead position of the eyes comes to correspond to the position necessary to fixate the prismatically displaced hand in the straight-ahead position while the straight-ahead hand comes to feel in the position necessary to point toward a straight-ahead, but prismatically displaced visual target.
Additive realignment restores centering of the coordinated eye–hand task-work space on the noetic reference frame, i.e., opposite directions of realignment for component systems combine to produce vertical performance when the eyes and hand are coordinated during prism exposure. Illustrated shifts in task-work space arise solely from realignment, although recalibration response to remaining performance error may also contribute to positioning of task-work spaces.

Fig. 4 illustrates the additive aftereffects of realignment when the prismatic displacement has been removed. The visual eye–head task-work space is shifted rightward, i.e., an objectively straight-ahead visual target appears to the left and must be positioned toward the right to appear straight-ahead. The proprioceptive hand–head task-work space is shifted leftward, i.e., the hand, which has acquired a rightward coded position when straight-ahead, must be positioned toward the left to feel straight-ahead. Coordination produces a leftward shifted eye–hand task-work space, i.e., when eye and hand are coordinated, pointing toward a straight-ahead visual target, which looks to the right, requires a hand position to the left of its felt straight-ahead position. Again, the illustrated shifts in task-work spaces arise solely from realignment, although calibration may also operate.

Fig. 5 illustrates recovery of normal alignment after the prismatic displacement is removed. Restoration of normal realignment and calibration proceeds in the same fashion as previously illustrated for adaptation to prismatic displacement. Initial consequences of re-exposure to the normal environment are like those illustrated in Fig. 2, but with leftward rather than rightward “displacement”. Normal exposure corresponds to the concurrent visual and proprioceptive feedback illustrated in Fig. 3, producing realignment in both the visual–motor eye–head and proprioceptive–motor hand–head sensory–motor systems, but now in opposite directions from the realignment illustrated in Fig. 3. Like Fig. 1, Fig. 5 illustrates normal alignment of sensory–motor systems within the noetic reference frame and normal calibration of task-work spaces on egocentric straight-ahead.
3.4. Muscle-potentiation

Recalibration and realignment are not the only consequences of prism exposure. Sensory–motor asymmetry introduced by prismatic displacement can produce change in the actual posture of body parts. Asymmetric motor exercise during prism exposure can modify the reference set point of an effector (e.g., eye or limb muscles) and thereby its posture (Ebenholtz, 1974, 1976; Ebenholtz & Fisher, 1982). Such muscle-potentiation produces aftereffects that match the direction of realignment aftereffects (Paap & Ebenholtz, 1976).

For example, the asymmetric eye posture required to fixate a straight-ahead target that appears to the side during prism exposure biases the straight-ahead eye position in the direction of the prismatic displacement. Similarly, if the visual target is objectively positioned opposite the prismatic displacement and appears visually straight-ahead asymmetric exercise of the eyes is avoided, but 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 & Wallace, 1978, 1988b). However, muscle-potentiation cannot be the sole source of aftereffects because they occur in the absence of asymmetric exercise (Craske & Crawshaw, 1975, 1978; Crawshaw & Craske, 1974; Redding & Wallace, 1987, 1988c).

3.5. Methodological implications

Prism exposure evokes all the mechanisms of adaptive perceptual–motor performance in all their complexity (Redding & Wallace, 1997a). At least three classes of adaptive processes are elicited by prism exposure: postural adjustment (muscle-potentiation), strategic control (including recalibration), and spatial realignment. Any or all of these might be the source(s) of neglect amelioration. All of these 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). The complexity of prism adaptation requires methods to distinguish among these various contributions, especially in therapeutic application. Redding
Unilateral neglect is a complex deficit in patients with unilateral (usually right-hemisphere) brain lesions to explore adaptation to explain therapeutic effects. Then we offer a theoretical proposal based in normal prism adaptation, where a horizontal line is (usually) centered on the body’s mid-sagittal plane, the patient shows an ipsilesional bias. The same bias appears in allocentric line bisection (e.g., the landmark task), where the patient selects (non-manually) from among pre-marked lines. In target cancellation, where a page of mixed symbols is presented and the patient is asked to draw a mark through a subset of the symbols, cancellation is largely restricted to the ipsilesional side of the page. When asked to copy a drawing the patient typically reproduces only the ipsilesional side. Similar omission occurs when the patient is asked to draw an object from memory, to copy a drawing, or to name locations from a mental image. When asked to read a page of text or single words, patients may only recite text on the ipsilesional side.

4. Clinical tests

Traditional clinical tests include line bisection, target cancellation, copying, drawing, and reading. In manual line bisection, where a horizontal line is (usually) centered on the body’s mid-sagittal plane, the patient shows an ipsilesional bias. The same bias appears in allocentric line bisection (e.g., the landmark task), where the patient selects (non-manually) from among pre-marked lines. In target cancellation, where a page of mixed symbols is presented and the patient is asked to draw a mark through a subset of the symbols, cancellation is largely restricted to the ipsilesional side of the page. When asked to copy a drawing the patient typically reproduces only the ipsilesional side. Similar omission occurs when the patient is asked to draw an object from memory, to copy a drawing, or to name locations from a mental image. When asked to read a page of text or single words, patients may only recite text on the ipsilesional side.

4.2. Amelioration by prism adaptation

Clinical and everyday symptoms of left unilateral neglect are ameliorated for unusually prolonged periods following a short time of adaptation to rightward prismatic displacement (for reviews, see Bisiach & Vallar, 2000; Heilman, Watson, & Valenstein, 2003; 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 modality specific, 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.

4.1. Clinical tests

Prior to prism exposure patients pointed, on average, about 9 or 70% compensation for the 10 optical displacement, which is much larger than the 30% shown by normal control participants. This aftereffect and accompanying clinical amelioration of neglect appeared only for rightward prismatic displacement, not for leftward displacement. Another relevant feature of the procedure is that participants only saw their
Employing the same prism exposure procedure in a case study, Rode, Rossetti, Li, and Boisson (1998/1999) demonstrated amelioration of symptoms as measured by manual pointing toward egocentric straight-ahead without vision, drawing a daisy from memory, and naming towns from a mental map of France. The patient (JCG) showed a large 9° leftward aftereffect in pointing straight-ahead, symmetrical drawing of a daisy from memory compared to asymmetrical drawing before prism exposure, and named far more towns from the left side of the mental map after prism exposure. Symptom amelioration partially persisted for 24 h for drawing from memory, but not for naming from a mental map.

An important feature of Rode et al.’s (1998/1999) results is that the horizontal range of named towns after prism exposure was larger than before and towns to the right of the mental map were “neglected” after prism exposure even though they had been named before. Another important feature is that, in contrast with Rossetti et al. (1998), prior to prism exposure, the patient showed a 5° contralesional bias in pointing straight-ahead without vision (see also Farnè, Ponti, & Lădăvăs, 1998). Also, like Rossetti et al. (1998), the after-effect was unusually large: 9.0° or 90% of the 10° optical displacement.

Pisella, Rode, Farnè, Boisson, and Rossetti (2002) repeatedly measured performance on line bisection and pointing straight-ahead without vision in two patients before and after a period of 4 days following a single prism exposure using the Rossetti et al. (1998) procedure. Prior to prism exposure, both patients showed a rightward, ipsilesional bias in pointing straight-ahead (9.4°) and line bisection. Immediately after prism exposure, both patients showed a 9° leftward shift in straight-ahead pointing, but this aftereffect decreased over the course of the first post-exposure day and then stabilized for the following 3 days. One patient (PE) showed a persistent post-exposure absence of bias in straight-ahead pointing while the other (SA) returned to the pre-exposure bias. In contrast, patient PE showed no amelioration of line bisection bias while patient SA showed immediate reduction in line bisection bias that persisted for the four-day post-exposure testing period.

An important result from Pisella et al.’s (2002) study was the absence of a correlation between performance on the straight-ahead pointing and line bisection tasks. Also, like Rossetti et al. (1998) and Rode et al. (1998/1999), the after-effect was unusually large: 9.0° or 90% of the 10° optical displacement. Pisella et al. also reported that one of their patients (SA) seemed to have developed conscious awareness of her condition following prism adaptation, with consequential deep anxiety and depression.

Farnè, Rossetti, Tonio, and Lădăvăs (2002) assessed target pointing without visual feedback and performance on a battery of tests that included clinical measures (e.g., cancellation, bisection, and drawing) and behavioral measures (e.g., telephone dialing, menu and article reading, telling and setting time, and coin and card sorting), including tests for far space (room description), near space (object reaching) and personal space (removing “fluff” from the body). 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 2 weeks (10 times/week); target pointing without visual feedback was measured before and after each prism exposure. The test battery was administered before and then 2 days, 1 and 5 weeks after the 2-week treatment period.

Before prism exposure, patients, on average, showed no bias in target pointing (0.0°). Patients evidenced a leftward after-effect in target pointing immediately after prism exposure (2.7°) that decreased, but persisted for 6–12 h (1.4 and 1.3°, respectively). Clinical and behavioral measures revealed increasing amelioration of neglect in average percentage of correct responses: pre-treatment (64), after 2 days (80), after 1 week (88), and after 5 weeks (90). Amelioration of neglect for far and near space tests revealed a similar pattern in a decrease in percentage of omission errors from pre-treatment (18) to 1 day (5) with no significant change in following test periods. Amelioration of neglect for personal space did not reach statistical significance, but revealed a similar pattern in percentage of omissions across the four test periods (14, 5, 0, and 0, respectively). Frassinetti et al. also noted that preliminary data from four of the six patients suggests that amelioration may have lasted as long as 17 weeks after the end of treatment.

An important finding of Frassinetti et al. (2002) was the persistence of amelioration for as long as 5 weeks for clinical tests and everyday behaviors, visual-only as well as manual–visual tasks (like Farnè et al., 2002), and for
far-to-personal space with repeated administration the prism adaptation procedure. Also like Farné et al. (2002) and in contrast with previous studies, the immediate aftereffect of 2.7° or 27% of the 10° prismatic displacement was comparable to that usually obtained with normal participants. Finally, Frassinetti et al. reported another patient that did not show an aftereffect of prism exposure and no amelioration of neglect. Berberovic, Pisella, Morris, and Mattingley (2004) assessed pointing straight-ahead without vision and performance on judgments of the temporal order of stimuli presented successively (SOA = 0–1296 ms) in opposite visual fields before and after adaptation for four left unilateral neglect patients. The prism exposure procedure was presumably similar to that employed by Rossetti et al. (1998). Patients pointed repeatedly at targets left and right of objective straight-ahead, but prismatically displaced 15° in the rightward direction, for 5–10 min with the limb visible during the terminal half of the movement. Before prism adaptation patients showed a slight ipsilesional bias (0.9°) in straight-ahead pointing and after prism adaptation, an aftereffect appeared in the contralesional direction (3.5°). Before prism adaptation patients showed the usual ipsilesional bias in temporal-order judgments, requiring that the left stimulus precede the right stimulus by 427 ms, before it was judged to appear first. After prism adaptation, ipsilesional bias was reduced to 98 ms.

Berberovic et al.’s (2004) important finding is that prism adaptation ameliorated the ipsilesional attentional bias common in unilateral neglect, such that “prism adaptation helps to re-balance the distribution of spatial attention” (p. 1199). Note, also that the magnitude of the prism exposure aftereffect of 3.5° or 23% of the 15° prismatic displacement was comparable to that usually found in normal prism adaptation. Berberovic et al. report another, fifth patient who showed an aftereffect in the anti-adaptive rightward direction.

In a single case study Ferber, Dunkerdt, Joannis, Goltz, and Goodale (2003) assessed pointing straight-ahead without vision, “happier” judgments of pairs of chimeric faces (posing halves smiling or not), and fixation eye movements during 10 s of exploring single chimeric faces before and after adaptation to 10° rightward prismatic displacement. An ipsilesional bias in straight-ahead before prism adaptation (16.7°) was reduced after adaptation (2.4°), but still in the ipsilesional direction. The ipsilesional bias in selecting happier (smiling) faces on the right before prism adaptation (91.7%) was unchanged after prism adaptation, even though the bias in fixation eye movements to the right half of a face (74.1%) was reduced (20.3%) after prism adaptation. In a following prism-adaptation session, the patient showed improvement on clinical cancellation tests of neglect.

The important conclusion of Ferber et al. (2003) was that prism adaptation does not ameliorate the deficit in awareness of contralesional stimuli even though the bias in eye movements is reduced. However, it is important to note that this patient showed extreme bias in straight-ahead pointing before prism adaptation and even the unusually large and overcompensating aftereffect of 14.3° or 143% of the 10° displacement was not enough to shift subjective straight-ahead into the contralesional space. Moreover, the modal shift in eye movements from ipsilesional to contralesional sides was only about 5°. Arguably, prism adaptation was not sufficiently great enough to ameliorate the extreme neglect for this patient. The amelioration of bias in cancellation tests may reflect the added benefit of a second prism-adaptation session.

In a single case study of a chronic neglect patient, McIntosh, Rossetti, and Milner (2002) assessed manual cancellation, copying drawings, manual line bisection and finding the center of a haptically explored circle before and after prism adaptation at 40, 41, and 42 weeks post-stroke. The prism adaptation treatment followed the procedure of Rossetti et al. (1998). Explicit measures of aftereffects were not obtained, but informal observation confirmed that aftereffects did occur (R. McIntosh, personal communication, March 2005). Amelioration occurred for visual-manual ipsilesional bias (cancellation, copying, and line bisection) and for the non-visual manual bias (haptic centering). Cancellation omissions on the left side decreased pre-to-post adaptation by about 21% in week 40 and about 80% in week 42. A similar pattern of left side omissions occurred in drawings. Ipsilesional bias in line bisection decreased pre-to-post adaptation by about 24% in the first week and about 42% in the last week. Lateral ipsilesional bias in haptic circle bisection decreased pre-to-post adaptation by about 39% in the first week and about 25% in the last week. The important finding of McIntosh et al. (2002) is that prism exposure ameliorates non-visual haptic, as well as visual components of neglect.

4.3. Summary

The following conclusions about the ameliorating effects of prism exposure on unilateral neglect may be drawn from this sample of research. Amelioration seems to require adaptation to the prismatic displacement as evidenced by the presence of aftereffects, simply exposing patients to prismatic displacement is not sufficient. Amelioration may occur even when neglect symptoms do not appear for a pre-exposure test that shows a post-exposure aftereffect. Aftereffects with patients can be markedly larger than is usually found with normal participants, but need not be so for amelioration to occur; indeed, unusually large aftereffects can appear in the absence of amelioration.

Amelioration extends to sensory–motor and cognitive tasks (including the distribution of spatial attention) beyond the specific sensory–motor task employed in prism exposure, amelioration extends to non-visual components of neglect, amelioration persists long after the aftereffects of prism exposure have disappeared, and patients may even show continued improvement. Available data are unclear as to whether prism adaptation ameliorates deficits in conscious awareness. Amelioration may extend to all regions of egocentric space: personal, near, and far space. Finally, left-neglect patients
Fig. 6. Normal alignment and dysfunctional calibration are contrasted with normal alignment and calibration illustrated in Fig. 1. Unilateral neglect is conceptualized as dysfunctional spatial mapping (arrows) of the task-work space (small ellipse) only on the ipsilesional side and reduced ability to adaptively recalculate size and position of the task-work space, but normal alignment remains intact. Consequently, an egocentrically straight-ahead target (dot) remains centered in the common noetic reference frame (large ellipse) and the patient only responds to the right-hemispace. The case illustrated includes dysfunctional calibration in both the visual-motor eye-head and proprioceptive-motor hand-head sensory-motor systems and consequential dysfunction in eye-hand coordination.

appear to adapt only to rightward, not leftward prismatic displacement, while normal participants adapt equally well to either direction of displacement.

5. A theoretical proposal

Calibration, rather than alignment, seems to be a more likely process involved in unilateral neglect. Calibration involves spatial attention and allocentric as well as egocentric representation, processes known to be dysfunctional in neglect patients (Colby & Goldberg, 1999; Mapstone et al., 2003; Milner & Goodale, 1995). And different task-work space calibrations are required for different sensory-motor reference frames (e.g., visual, proprioceptive, auditory, and tactile). Therefore, dysfunctional calibration (neglect) may have different, and perhaps, multiple loci in different patients (Farné et al., 1998; Pavani, Ladavas, & Driver, 2003).

5.1. Neglect as dysfunctional calibration

Pathological right-hemispace bias in selection of a task-work space, as illustrated in Fig. 6 (cf. Fig. 1), would produce many (but not all) unilateral neglect symptoms in right brain damaged patients. In this view, neglect is produced by a narrowing of the normal task-work space toward the right-hemispace and decreased ability to adaptively position the task-work space, but is not otherwise different in kind from the normal restriction of behavior (and awareness) to the confines of a task-work space. For example, if visual-motor (eye-head) calibration is dysfunctional, then picture drawing, line cancellation, and line bisection will be biased rightward toward the available egocentric task-work space. Bisection judgments of premarked lines would also be biased rightward toward the center of the available allocentric task-work space. An allocentric task-work space (not shown in Fig. 6) is a “projection” of an egocentric task-work space into extra-personal space, but still aligned with the noetic reference frame (Milner & Goodale, 1995). Similarly, if proprioceptive-motor (hand-head) calibration is dysfunctional, patients will tend to produce responses only in the right-hemispace with behavioral consequences like those for visual-motor calibration dysfunction. Dysfunctional calibration may itself arise from dysfunction in higher cognitive processes (e.g., attention and spatial memory), but our purpose here is to understand how low-level realignment ameliorates higher-level calibration dysfunction.

Note that calibration of a task-work space can be dysfunctional while noetic reference remains functional. An egocentric frame may still be referenced to noetic straight-ahead (i.e., aligned with other sensory-motor systems), but only the right-hemispace selected in the task-work space, see Fig. 6. Therefore, vertical egocentric straight-ahead (and other egocentric positions) may still be available for patients and pointing or grasping movements may be unaffected, at least in the available hemispace (Chieffi, Gentilucci, Allport, Sasso, & Rizzolatti, 1993; Farné et al., 1998; Mattingley, Husain, Rorden, Kennard, & Driver, 1998). The bias of egocentric straight-ahead that is sometimes observed may arise from the strategic tendency to identify straight-ahead with the center of the task-work space. Individual differences among patients in this tendency may, then, account for the variable nature of egocentric straight-ahead in patients before prism exposure (cf. Rode et al., 1998/1999; Rossetti et al., 1998; Pisella et al., 2002). We would expect that patients for whom egocentric straight-ahead is not preserved should not show therapeutic effects of prism adaptation as conceived in the following section.

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Perseveration in patients with unilateral neglect (Mastly, Woldt, Watson, & Warburton, 2002) may reflect normal intrusion of stimuli outside the task-work space. Prism adaptation also seems to ameliorate such graphic perseveration (Zilli, Bottini, & Vallar, 2003).
Fig. 7. Rightward prismatic displacement with dysfunctional recalibration is contrasted with normal recalibration illustrated in Fig. 2. Prismatic displacement substitutes for dysfunctional calibration by mapping (arrows) the egocentric straight-ahead target (dot) into the center of the dysfunctional visual–motor eye–head task-work space (small ellipse), coding a rightward position in the common noetic reference frame (large ellipse). The proprioceptive–motor hand–head system is (initially) unaffected by the prismatic displacement, but because the proprioceptive–motor hand–head retains noetic straight-ahead (albeit to the extreme left of the task-work space), eye–hand coordination shows the usual erroneous response rightward of the target and patients are, therefore, able to perform the prism exposure task.

Fig. 8. Additive realignment with calibration dysfunction is contrasted with additive realignment in component sensory–motor systems illustrated in Fig. 3. Developing realignment in both visual–motor eye–head and proprioceptive–motor hand–head sensory–motor systems substitutes for dysfunctional calibration by mapping (arrows) the egocentric straight-head target (dot) into the center of the component task-work spaces (small ellipses), coding left and right noetic positions (large ellipse), respectively, and additive realignment enables adaptive eye–hand coordination in patients.

5.2. Therapeutic effect of prism adaptation

Therapeutic effects of realignment on left-hemispace calibration dysfunction (neglect) may occur by means of a transparent shift in origin for the underlying coordinate systems (realignment). Fig. 7 (cf. Fig. 2) illustrates how visual straight-ahead is shifted by prismatic displacement into the pathologically narrowed task-work space because dysfunctional calibration does not reposition the task-work space. Of course, proprioceptive straight-ahead is not initially affected by the displacement, but eye–hand coordination responds to the apparent rightward position of a straight-ahead visual target.

Fig. 8 (cf. Fig. 3) illustrates the common case of additive realignment for both visual–motor eye–head and proprioceptive–motor hand–head sensory–motor systems, for example, with concurrently available visual and proprioceptive feedback. Note carefully that because realignment is dimensional, affecting all points in visual and proprioceptive reference frames, the position of the dysfunctional task-work spaces are also shifted. Realignment substitutes for dysfunctional calibration by repositioning task-work spaces, but does not ameliorate the dysfunctional extent of task-work spaces. As illustrated in Fig. 8, additive realignment enables adaptive eye–hand coordination in patients during prism exposure.

Fig. 9 (cf. Fig. 4) illustrates the additive aftereffects of realignment in patients. Note that realignment has centered the narrowed task-work spaces on egocentric straight-ahead, thereby ameliorating task-work space bias (neglect) at least for the duration of aftereffects. Patients will report and respond to stimuli on either side of egocentric straight-ahead, albeit still for a limited range, and even though objective straight-ahead is not perceived as such. Again, the aspect of dysfunctional calibration responsible for reduced ability to strategically adjust the extent of the task-work space is not ameliorated by spatial realignment.

Fig. 10 (cf. Fig. 5) illustrates the consequence of re-exposure to undistorted visual input. Readaptation removal

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5 Fig. 7 may also illustrate the reduction in disproportionate ipsilesional bias produced by lateral stimulation (e.g., vestibular) that reduces neglect (Valle et al., 1997). The difference may be that the shift produced by prismatic displacement can be made more persistent by realignment.
Fig. 9. Additive realignment aftereffects with calibration dysfunction are contrasted with the additive aftereffects of realignment illustrated in Fig. 4. Relative to the common noetic reference frame (large ellipse), spatial mapping (arrows) of the task-work space (small ellipse) that substituted for dysfunction calibration during exposure are reversed when prismatic displacement no longer present; for realignment aftereffects, the task-work space is spatially mapped rightward for the visual–motor eye–head system and leftward for the proprioceptive–motor hand–head system. Additive aftereffects of component realignment produce leftward pointing toward the egocentrically straight-ahead target (dot) in the coordination of the eye–hand system. Therefore, patients show aftereffects of prism adaptation.

Fig. 10. Normal realignment with calibration dysfunction is contrasted with normal readaptation to the normal environment illustrated in Fig. 5. With return to the undistorted environment, realignment of task-work spaces (small ellipses) consists in spatial remapping (arrows) onto the common noetic reference frame (large ellipse) in the same manner as illustrated in Figs. 7–9 and corresponding Figs. 3–4. Because calibration is dysfunctional realignment to normal visual input results in maintenance of task-work space centering on egocentric straight-ahead (dot) and persistent amelioration of neglect.

Beneficial effects of prism adaptation would depend both upon the nature of the calibration dysfunction and the realignment. In general, realignment may correct for dysfunctional positioning of the task-work space, but not for the pathological narrowing of the task-work space, which may arise from higher cognitive dysfunctions. Transparent realignment of the spatial map for a sensory–motor system in which calibration is dysfunctional shifts the center of the sensory–motor reference frame into the dysfunctional task-work space, thereby ameliorating neglect. If prism exposure conditions are such that realignment does not occur for the dysfunctional sensory–motor system, amelioration will not occur.

For example, if the calibration dysfunction (neglect) is biased task-work space selection of the right, ipsilesional hemispace in the visual–motor (eye–head) sensory–motor system and exposure conditions produce visual realignment by terminal or near terminal visual feedback in target pointing, then adaptation to rightward prismatic displacement would transparently shift the origin of the visual–motor reference frame to the right. Such a visual shift would bring the neglected left-hemispace into the narrowed task-work space, thereby ameliorating neglect.

6 This straightforward prediction may need to be qualified by the possibility that the pattern of behavior for a coordinative structure in which realignment occurs in a functional sensory–motor system may be such as to affect the dysfunctional calibration in another component sensory–motor system. However, the present state of knowledge does not support further development of this possibility.
For the same calibration dysfunction in the visual–motor system if prism exposure conditions are such as to produce only realignment of the proprioceptive–motor (head–hand) sensory–motor system (e.g., very early visual feedback availability in target pointing), the visual–motor calibration dysfunction would not be corrected and neglect would not be ameliorated. If, however, calibration dysfunction is localized in the realigned proprioceptive–motor system, then amelioration effects would appear with these exposure conditions; the transparent leftward shift in origin of proprioceptive reference frame would produce more responses in the neglected hemispace.

Because common prism exposure conditions are such as to produce some realignment in both visual–motor and proprioceptive–motor systems, some neglect amelioration is likely to appear regardless of the locus of the calibration dysfunction, even if both systems suffer from calibration dysfunction (neglect), as illustrated in Fig. 6. Total benefit from prism adaptation would be a function of the sum of local realignment in visual–motor and proprioceptive–motor systems.

Note carefully that because only the position, not the size, of the dysfunctional task-work space is changed by realignment, some neglect may remain for the eccentric left-hemispace. For the dysfunctional system, alone signs of neglect should be restricted to the contralesional hemispace. For the coordinative structure, clinical signs of neglect should be less and limited to the eccentric right-hemispace; stimuli outside the selected task-work space may sometimes be “neglected” (see Rode et al., 1998/1999).

In any case, neglect would be ameliorated around the center of the relevant reference frame. The operative term here is “amelioration”: realignment does not restore the dysfunctional size of the task-work space, only dysfunctional positioning.

Conceptualization of neglect as dysfunctional task-work space calibration for particular sensory–motor systems suggests an interesting prediction about the clinical signs of neglect. When calibration dysfunction is present for only one of two coordinated sensory–motor systems (e.g., eye–head and hand–head), the task-work spaces for the two systems will be different in size. If we assume that in such cases the size of the task-work space for the coordinative structure (e.g., eye–hand coordination) is the average of noetic coordinates for the component spaces, then, the signs of neglect will be different for the coordinative structure than for the dysfunctional system tested alone. For the coordinative structure, clinical signs of neglect should be less and limited to the eccentric left-hemispace, but may also appear in the eccentric right-hemispace. For the dysfunctional system, alone signs of neglect should be restricted to the contralesional hemispace. In so far as we are aware, these predictions have not been tested.

Other assumptions are possible. For example, the size of the guided system task-work space might be set by the guiding sensory–motor system. In this case, the outcomes would be much like those discussed above for averaging except when the guiding system has normal calibration and the guided system has dysfunctional calibration. Here, exercise of the coordinative structure might produce no signs of neglect. Thus far, research has not clearly identified the locus (loci) of neglect and has not manipulated direction of guidance. So, although this seems an unlikely outcome, it remains a possibility yet to be tested.

5.3 Persistence of amelioration

Importantly, the repositioning of the task-work space mediated by realignment would persist after the prisms have been removed and the patient readapted to normal mappings of perceptual–motor space, see Fig. 10. Normal realignment transparently changes the underlying noetic coordinates of the task-work space in the same way the prism-induced realignment does and the latter, therefore, carries over to the former even though (and because) calibration remains dysfunctional.

Thus, prismatic displacement ameliorates neglect during prism exposure, immediately after realignment to prismatic displacement, and after prism exposure when normal realignment has occurred. Centering an egocentric reference frame in the available task-work space may provide the opportunity for the patient to relearn task-specific recalibrations. Calibrations are remembered for frequently recurring tasks and recalibration may occur rapidly whenever task conditions recur (Redding & Wallace, 1997a, 2002, 2003a; see also Martin, Norris, Greger, & Thach, 2002). Perhaps, such calibration relearning might even enlarge the dysfunctional task-work space so that the extent of neglect may be decreased after the prism adaptation treatment (cf. Rode et al., 1998/1999). Amelioration by realignment might, therefore, provide the basis for restoring calibration functionality, another possibility to be tested.

5.4 Extraordinary aftereffects

Patients may show prism exposure aftereffects at levels far greater than is usually found for normal subjects. For example, Rossetti et al. (1998) found the aftereffect in the hand–head proprioceptive–motor system to be about 70% of the 10° prismatic displacement for patients, while normal control subjects showed the more usual aftereffect of about 30% (see also Ferber et al., 2003; Pisella et al., 2002; Rode et al., 1998/1999). Such extraordinarily large aftereffects may be explained by dysfunctional calibration that removes a limit on spatial realignment.

Realignment can be limited by strategic recalibration that prevents detection of the misalignment (Redding, 1981; Redding & Wallace, 1993, 1997a). For example, a virtual target position to the left of the visible, prismatically displaced target can be selected for feedforward initiation of limb movement. With such a side pointing strategy, performance error will be reduced without visual feedback correction, the limb will achieve the commanded (expected) position, no discordance will be detected, and no realignment will occur. To the extent that such limiting recalibration is disabled by calibra-
tion dysfunction in neglect patients, they will show greater realignment aftereffects than normal subjects.\(^1\)

5.5. Directional asymmetry in prism adaptation

Rossetti et al. (1998) reported that patients with right posterior parietal damage and left neglect were unable to adapt to leftward prismatic displacement, whereas normal subjects adapt to either direction of displacement (Redding & Wallace, 1987, 1998c; Welch, 1978). More completely, patients were slow to reduce pointing error during prism exposure and while the proprioceptive–motor aftereffect was in the adaptive direction, it was not statistically reliable (personal communication, Yves Rossetti, September, 2003). Such results for left neglect patients and leftward prismatic displacement are not surprising if neglect arises from dysfunctional calibration of the task-space.

Leftward prismatic displacement would shift the origin of the visual–motor reference frame to the left and outside a narrowed task-work space. Patients with calibration dysfunction in their visual–motor system would, therefore, have difficulty in specifying targets in their task-work space to initiate a pointing response. Similarly, patients with calibration dysfunction in their proprioceptive–motor system would tend to make responses only in the right-hemispace and experience difficulty in initiating pointing responses toward targets outside of their pathologically narrowed task-work space. Therefore, patients would be slow to initiate and correct target pointing responses during exposure and the infrequent opportunities to compare expected and achieved positions would reduce discordance detection and realignment (Redding & Wallace, 1993, 1997a, 2002).

More might be said about directional asymmetry in prism adaptation. Several studies (Berberovic & Mattingley, 2003; Colet, Pisella, Bernieri, Rode, & Rossetti, 2000; Michel et al., 2003) have found a small neglect-like rightward bias on line bisection and Landmark tasks in normal subjects following exposure to leftward, but not rightward optical displacement. Discussion of such results, however, would be, perhaps, premature and beyond the present scope and would require more space that presently available. We reluctantly postpone such discussion to another time.

6. Conclusions and recommendations

We have suggested that unilateral neglect is, at least in part, a dysfunction in selection of the region of space appropriate for the task at hand. Normally, people strategically size and position (calibrate) their task-work space around the task-relevant objects. However, patients seem to show deficits in both strategic abilities; the task-work space is pathologically reduced in size and patients cannot strategically shift its position. We propose that prism adaptation ameliorates dysfunctional positioning, but not sizing of the task-work space. Prism adaptation (realignment) shifts the egocentric coordinates of a sensory–motor reference frame, thereby bringing at least part of the neglected hemispace into the dysfunctional task-work space. In this manner, prism adaptation substitutes for dysfunctional positioning, but not sizing of a task-work space. However, such amelioration of dysfunctional positioning may enable relerning of strategic processes (calibration), perhaps, even partially restoring the ability to appropriately size the task-space.

Identification of the exact nature of the therapeutic effect of prism adaptation requires knowing both the sensory–motor system(s) for which calibration is dysfunctional and the sensory–motor system(s) in which realignment occurs. These requirements mean that investigations of therapeutic prism adaptation need to acquire pre- and post-test measures of the component sensory–motor systems exercised by the prism exposure task to identify both the loci of calibration dysfunction and ameliorating realignment aftereffects. It will also be necessary to manipulate the locus of realignment to determine the most beneficial kind of prism exposure treatment for patients with different kinds of neglect. Because postural adjustments and strategic control can also produce prism exposure aftereffects it will further be necessary to control for these confounding processes by, respectively, manipulating the locus of asymmetrical sensory–motor exercise in the prism exposure task and employing aftereffect tests that measure realignment in the component sensory–motor systems implicated in prism exposure.

Investigations of neglect amelioration by prism adaptation have tended to obtain only one aftereffect measure of realignment or none at all. Berberovic et al. (2004), Ferber et al. (2003), Pisella et al. (2002), Rode et al. (1998/1999), and Rossetti et al. (1998) obtained only a proprioceptive shift measure. Farnè et al. (2002) and Frassinetti et al. (2002) obtained only a combined visual–proprioceptive measure and the similarity with the exposure task (target pointing) raises the possibility that ordinary skill learning might have transferred to the aftereffect test. Therefore, we cannot know the locus of ameliorating realignment or be confident that the aftereffects were uncontaminated. Frassinetti et al. (2002) also reported amelioration of neglect dyslexia and change in eye movements during reading toward that of normal readers (see also Angeli, Benassi, & Ládavas, 2004). These results are consistent with predictions for visual realignment amelioration of visual neglect, but without a behavioral test of change in visual straight-ahead and a concurrent exposure comparison, we cannot have confidence in this analysis. McIntosh et al. (2002) did not obtain explicit aftereffect measures and we cannot determine the relationship between amelioration and prism adaptation per se.

Investigations of neglect amelioration by prism adaptation have also tended to use only one level of visual feedback de-
lay and consequently have obtained predominately only one kind of realignment. Berberovic et al. (2004), Farne et al. (2002), Ferber et al. (2003), McIntosh et al. (2002), Poisella et al. (2002), Rode et al. (1998/1999), and Rossetti et al. (1998), all employed concurrent exposure (early visual feedback), while only Frassinetti et al. (2002) employed terminal exposure (late visual feedback). It may be that a match between visual neglect and visual realignment was responsible for the persistence of neglect amelioration in Frassinetti et al. (2002), but without a concurrent exposure comparison, we cannot confirm this hypothesis. It may also be that the variable amount of amelioration observed across different studies and patients may be due to match/mismatch between locus of neglect and realignment. Manipulation of feedback delay can test this hypothesis.

All of the cited investigations of neglect amelioration by prism adaptation employed, on average, objectively centered visual targets for pointing during exposure. Consequently, muscle-potentiation aftereffects in the visual system may have contributed to amelioration. It may also be the case that amelioration of postural imbalance in left-hemiparetic patients (Tilikete et al., 2001) by prism exposure arose from muscle-potentiation aftereffects. These hypotheses cannot be evaluated without manipulation of exercise symmetry.

Among the various theoretical accounts of neglect, the present proposal is most compatible with attentional accounts (e.g., Kinsbourne, 1993). Calibration is an attention-like process that, when dysfunctional, produces a biased task-work space selection which increases the salience of the right-hemisphere, but (as in normal motor control) does not preclude influence from the left-hemisphere (cf. Bartolomeo et al., 2003). Some representational accounts (e.g., Bisiach, 1993), in contrast, seem to preclude left-hemisphere intrusions because the left half of the task-work space is “amputated” (Bisiach, Bulgarrelli, Sterzi, & Vallar, 1983). However, for representational accounts, where the left-hemisphere is linearly “compressed” rightward (Chokron, Bernard, & Imbert, 1997; Halligan & Marshall, 1991) intrusions seem possible (but see Bartolomeo et al., 2003). The previously discussed linear nature of spatial remapping in alignment (e.g., Bedford, 1989) suggests that prism adaptation should be able to ameliorate linear compression of space or biased attention, but not amputation. Failure to find prism adaptation amelioration might, therefore, indicate an amputation basis for neglect. Prism adaptation may provide a method for distinguishing different kinds of neglect that arise from processing or structural dysfunctions.

This analysis and critique does not depreciate the importance of extant investigations of the ameliorating effects of prism adaptation on unilateral neglect. Discovery of such amelioration surely ranks among the most important in neuropathology. Nevertheless, these investigations, however, ground breaking, should be considered preliminary (see also Beverdorff & Heilman, 2003; Mattingley, 2002). More controlled studies are needed to inform both the nature of neglect and prism adaptation. Dysfunctional calibration itself may arise from high cognitive processes (e.g., attention and spatial memory) and the question remains how (or if) ameliorating recalibration by realignment extends to such higher-level dysfunctions.

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