

Task-Specific Sensorimotor Adaptation to Reversing Prisms

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Task-specific sensorimotor adaptation to reversing prisms. *J Neurophysiol* 93: 1104–1110, 2005. First published September 22, 2004; doi:10.1152/jn.00859.2004. We tested between three levels of visuospatial adaptation (global map, parallel feature modules, and parallel sensorimotor transformations) by training subjects to reach and grasp virtual objects viewed through a left-right reversing prism, with either visual location or orientation feedback. Even though spatial information about the global left-right reversal was present in every training session, subjects trained with location feedback reached to the correct location but with the wrong (reversed) grasp orientation. Subjects trained with orientation feedback showed the opposite pattern. These errors were task-specific and not feature-specific; subjects trained to correctly grasp visually reversed-oriented bars failed to show knowledge of the reversal when asked to point to the end locations of these bars. These results show that adaptation to visuospatial distortion—even global reversals—is implemented through learning rules that operate on parallel sensorimotor transformations (e.g., reach vs. grasp).

INTRODUCTION

In daily life, the transformations required for human visual-motor behaviors are continually modified and adjusted, sometimes radically, to acquire completely new behaviors (Wolpert and Kawato 1998). It is not always clear what roles global versus modular internal representations play in implementing and maintaining such behaviors (Clower and Boussaoud 2000; Shadmehr and Moussavi 2000; Sperry 1952). In particular, it is still not clear whether the brain represents global aspects of external visual space through a global internal representation (or “map”), an array of parallel feature modules, or a parallel compendium of “task-specific” sensorimotor transformations (Bedford 1989; Welch 1986).

One way to test between these models is to adapt the eye-hand coordination system to distortions in visual feedback. For example, adaptation to optical “displacing prisms,” which produce a lateral shift between the visual stimulus and the normally required movement, is thought to reflect a recalibration of the sensorimotor map (Jeannerod and Biguer 1987). Adaptation to displacing prisms is thought to tap into the normal processes that maintain accurate visuomotor performance (Proteau 1992) and is thought to involve only local recalibrations of input–output relations (Harris 1963; Held and Hein 1958).

In contrast, adaptation to optical “reversing prisms,” which produce a dramatic, global reversal of all the normal spatial

contingency rules between visual input and motor output, is generally assumed to involve a global recalibration process (Bedford 1989; Harris 1965; Stratton 1897; Welch 1986). Some subjective reports in the classical literature, however, have suggested that even after some aspects of the reversed visual world, such as object location, were “seen” correctly, other aspects, such as object orientation, could remain reversed (Kohler 1951). If verified objectively, this would be consistent with a modular view of spatial adaptation. Further experiments would be required to determine whether these modules are organized along feature-based (perceptual) or task-specific (sensorimotor) lines.

In this study, we quantitatively tested between three models of visuospatial calibration (global map, modular perception, modular sensorimotor) by measuring the three-dimensional orientation and location of the wrist, before, during, and after adaptation to left-right reversing prisms, while subjects reached toward virtual oriented bars at various horizontally displaced positions. The key point of our experiment was that clear visuospatial information about the left-right reversal was always present in the training set, but the *task* was varied to discern the underlying mechanism, i.e., whether this information was incorporated into a global learning rule, a feature-based learning rule, or task-specific “sensorimotor” learning rules.

METHODS

The reaching and grasping movements of 20 right-handed subjects were recorded with two OPTOTRAK 3-D motion tracking systems. Subjects were required to grasp a virtual target rectangle (4×1.2 cm), which was presented at one of five different locations (11, 13, 15, 17, and 19 cm from the left edge of an LCD screen and 11 cm above the bottom edge) in one of three different orientations (-45 , 0 , or 45° relative to the horizontal). Virtual objects were used in these experiments because real three-dimensional objects would provide proprioceptive/tactile feedback, which would immediately inform the subject that they had missed the target—thereby making a “baseline” condition impossible. One calibration trial was collected for every position \times orientation combination, and these trials were later used in the analysis to determine reference positions and orientations to which all other reaches during the experiment were compared.

Following the calibration trials, a bite-bar/prism assembly was put into position. A right-left reversing Dove prism ($12.5 \times 3 \times 3$ cm) was mounted in a black Plexiglas frame 37.5 cm from the LCD screen. PLATO spectacles (Translucent Technologies, Toronto, Canada) were mounted to the far side of the prism assembly and were used to control presentation time. Subjects wore an eye-patch over their left eye, and the bite bar was used to align the subject’s right eye

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with the prism assembly. All of the stimuli were restricted to a 14×11.5 -cm window so that the middle target position (15 cm from the left edge of the LCD screen) fell at the center of the prisms view. [A mirror or rotation transformation on the symmetric stimuli would be ambiguous in a purely perceptual judgment (e.g., left-right versus up-down reversal), but this was not relevant to our task since subjects were allowed to view the asymmetric hand during training.]

The subjects performed a baseline task in which they were required to reach out and grasp the rectangle under open-loop conditions (4 repetitions of each position \times orientation combination). At the start of the experimental trial, the PLATO spectacles would clear, allowing the subject a view of the target through the prism. The target would remain on the LCD screen while the subject's hand was depressing the start paddle. When the subject lifted their hand off the start paddle toward the target, a diamond patterned mask briefly appeared (250 ms), the spectacles went opaque, and subjects had to reach toward the rectangle without visual feedback.

The subjects then underwent one of four training sessions. Subjects were considered "trained" once they could successfully perform five accurate grasps consecutively. In the Pure Location training session, subjects were only provided with location information in the form of target disks (1.2 cm diam) presented at random positions along the same horizontal plane that the targets appeared during the baseline task. Once contact was made with the LCD screen, a laser dot was positioned between the subjects' fingers, and they were given a 500-ms feedback glimpse of the laser and the target disk after they lowered their hand. In the Hand Location training session, subjects were presented with the same stimuli as the Pure Location training but were allowed a feedback glimpse of their hand and the target. In the Orientation training session, a rectangle was presented at the middle target position at random orientations from -60 to 60° relative to the horizontal, with subjects receiving a glimpse of their hand and the target. Finally, during the Full Cue training session, subjects were presented with rectangles at varying orientations and locations along the horizontal plane and were allowed a glimpse of their hand and the target. Following training, the subjects were re-run on the baseline task.

We tested the modular perception theory by training subjects on the Orientation task and having them perform a baseline and test pointing task to a red rectangle with a blue square region on one end of the rectangle. This rectangle was presented at one of eight orientations in the middle screen position, and subjects were asked to point to the blue square region on the rectangle. After learning to correctly grasp the optically reversed bars during the Orientation training condition, we retested them on the blue square pointing task. In addition, to further determine if any "location" training took place, we also had subjects perform a pointing task to blue circles, which were presented alone on the screen in the same locations that the blue square regions had occupied.

Dependent measures

Custom software was used to compute rotation vectors that represented any instantaneous arm position as the result of a virtual rotation from a fixed reference position to the current position. In the space-fixed right-handed coordinate system, the rotation vector is defined by

$$r = \tan(\theta/2) \cdot \bar{n} \quad (1)$$

where \bar{n} represents the direction of the rotation axis, and $\tan(\theta/2)$ denotes the amount of rotation by an angle θ about that axis. The x component of the rotation vector describes the torsional orientation (clockwise/counterclockwise) of the arm. The calibration reaches were used as reference positions to determine "reach errors" to the right or left of the calibration position and "orientation errors" that were clockwise or counterclockwise to the calibration orientation.

RESULTS

Prior to adaptation, subjects who viewed the targets through the reversing prism reached to both the wrong location and orientation—i.e., toward the reversed visual image of the target (Fig. 1A). As an initial control, we tested five subjects to see if they could correct these errors if trained on a task where they received a visual feedback glimpse of the target stimulus together with the hand's final location and orientation (Full Cue). We retested the subjects' responses without visual feedback. Adaptation was quantified by considering the postadaptation errors in reach location (Fig. 1B) and grasp orientation (Fig. 1C) as a function of the preadaptation errors. Here a slope of one signifies *no* adaptation and a slope of zero signifies *complete* adaptation. Subjects trained in the full-cue condition consistently showed near-perfect adaptation of their grasps to both the reversed location [$F(4,16) = 64.75, P < 0.001$] and orientation [$F(2,8) = 160.13, P < 0.001$] of the targets.

Global versus modular adaptation

Was the underlying mechanism for this adaptation a global (if perhaps context-dependent) left-right sensorimotor reversal or some more modular learning rule? To determine this, we repeated the above process on additional subjects, while limiting their visual feedback in a feature- or task-related manner. During training, subjects either reached toward oriented bars located at a fixed central position (Fig. 2, A and D) or toward circles located at different horizontal positions (Fig. 2, B and E). In each case, the stimuli and feedback provided evidence that the visual world had been reversed (left to right). The use of a global strategy would predict that the subjects would gain this general knowledge and apply it to the different tasks. When subjects were tested on the full stimulus array, however, they only showed adaptation to the component on which they were trained: either reach location {Fig. 2, A ($P > 0.05$) and B [$F(4,16) = 95.72, P < 0.001$] } or grasp orientation {Fig. 2, D [$F(2,8) = 5.78, P < 0.05$] and E [$F(2,8) = 6.52, P < 0.05$] }.

Subjects did show a slight, but significant, orientation correction after training on target location [$F(2,8) = 6.52, P < 0.05$; Fig. 2E]. This correction could be attributed to the visual feedback the subjects received from seeing the orientation of their hand. When another group of subjects received pure location feedback about their hands, as provided by a laser dot (Fig. 2, C and F), the orientation correction of the grasping movements was completely absent ($P > 0.05$; Fig. 2F). These results show that, despite the information present in the scene about the reversal of the visual stimuli, subjects did not apply a global cognitive strategy, relying instead on recalibration of either the "reach location" or "grasp orientation" systems.

Feature- versus task-specific

In the preceding experiment, stimulus features (i.e., location and orientation) and aspects of the sensorimotor task (i.e., reach and grasp) were linked. Therefore, up to this point, we cannot distinguish whether subjects were learning to apply a modular perceptual rule to stimulus features (which could then be applied to multiple tasks) or whether they were relearning modular sensorimotor transformations. To test between these two models, we trained a new set of subjects on the Orientation

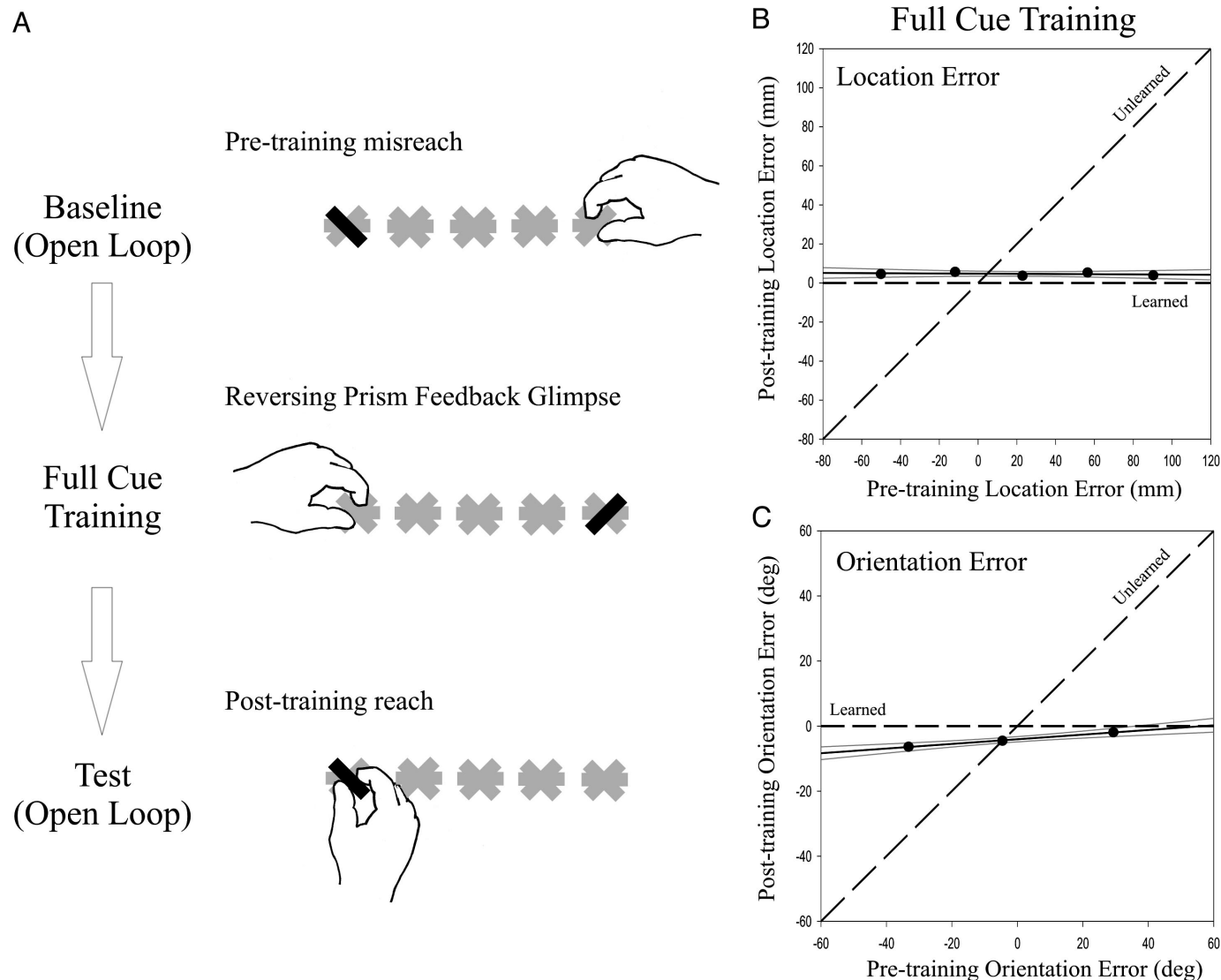


FIG. 1. A: schematic of the experimental design. Post-training location and orientation errors are plotted as a function of pretraining location (B) and orientation (C) errors for target locations and target orientations. Each point in the figures is an average of 5 subjects. After Full Cue training, subjects showed a correction from baseline for the prism reversal effect in the orientation and position of their reach and grasp. Dashed line labeled Unlearned represents where the data would fall if there was no adaptation; dashed line labeled Learned represents complete adaptation. Top and bottom boundaries of the 95% CIs for the post-training error are presented as gray lines.

task (where the target bar was presented at different orientations at the central position) and varied the test task.

After training, subjects were asked to indicate the top or bottom of the oriented bars by pointing to a blue region at one end of the rectangle. If the subjects had gained perceptual knowledge that the orientated bars were reversed left-from-right, they would know that the horizontal position of the bars' ends were reversed and thus point toward the correct locations. Orientation-trained subjects pointed to the correct vertical location of the blue region, but failed to account for its left-right reversal ($P > 0.05$; Fig. 3A). Their behavior in this task was no better than the performance in another test in which the subjects were asked to point toward circles that were positioned in the same locations that the blue end-bar regions had occupied ($P > 0.05$; Figs. 3C). One might argue that the subjects performed poorly on the "point to the square" task because their orientation training used a uniform bar rather than the bar (with blue end regions) that was used in this test. However, control tests on subjects with full-cue adaptation,

using the uniform bar, showed that completely adapted subjects could perform both tasks with a high degree of consistency [$F(14, 56) = 12.48, P < 0.001$; Fig. 3, B and D]. Thus even though our subjects later reported that they were consciously aware of some kind of reversal during training, their adaptation was not driven by general spatial knowledge or by knowledge of spatial orientation. Rather, it seems that a sensorimotor recalibration of the grasp-orientation system was carried out.

DISCUSSION

Our results provide a dramatic demonstration of the parallel organization of sensorimotor transformations and their role in representing visual space. Despite the left-right reversal information present in the scene in all of our training sessions, which provided strong cues for a simple global visuospatial learning rule, our subjects relied on recalibrations of either the

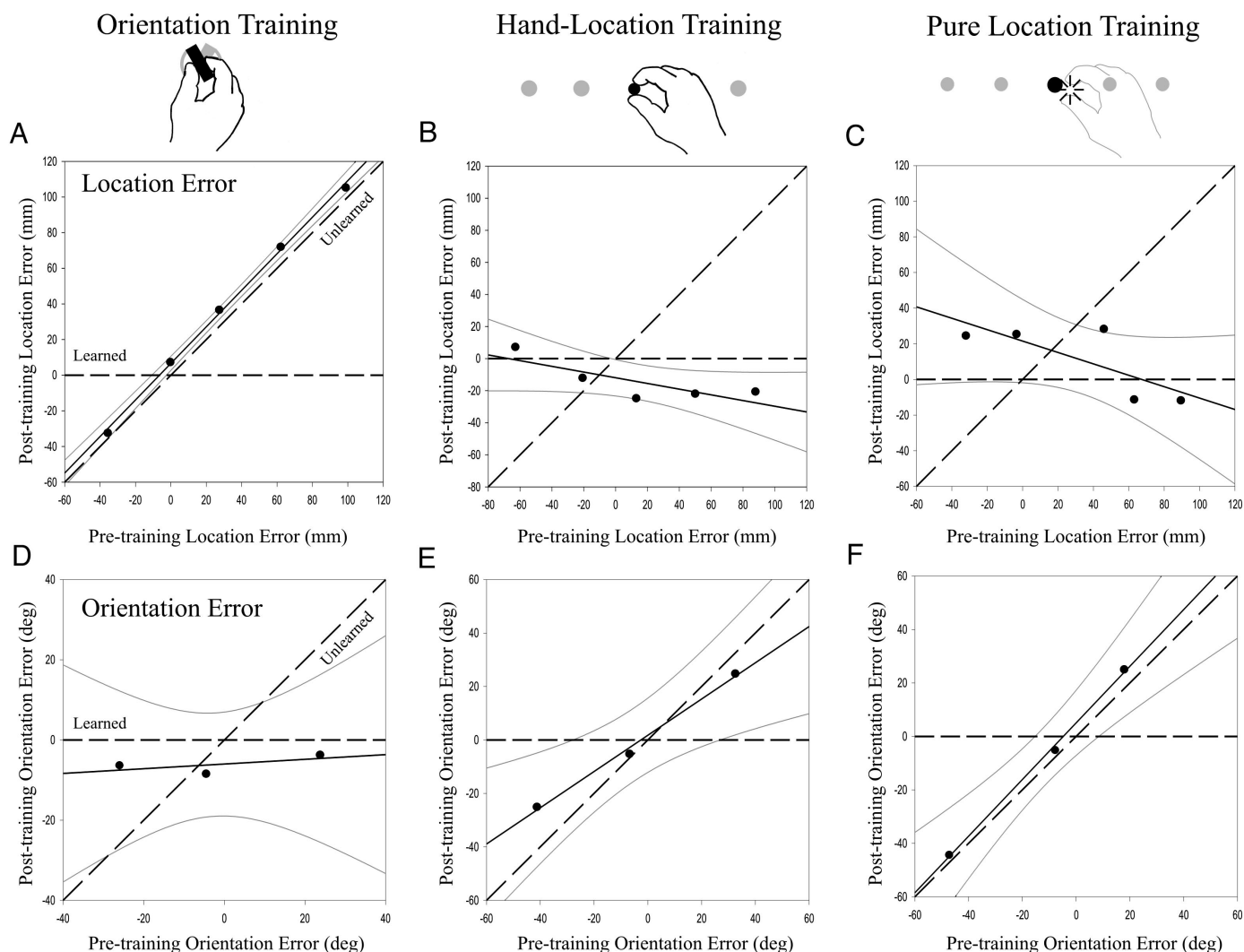


FIG. 2. Post-training location and orientation errors are plotted as a function of pretraining location and orientation errors. Orientation trained subjects corrected their orientation from baseline (*D*) but continued to reach to the wrong location (*A*). When subjects were allowed to view the orientation of their hand during the location training session (Hand Location), they not only corrected their location from baseline (*B*) but also showed a significant correction in their orientation (*E*). It appears that even a glimpse of the hand provides enough orientation feedback to allow for a correction by the grasp (orientation) system. A Pure Location training session was devised that removed orientation information by presenting a laser dot at the hand's former location. When the orientation information was removed from the scene, subjects reached with the correct location [$F(4,16) = 21.35, P < 0.001$; *C*] but wrong grasp orientation ($P > 0.05$; *F*). Therefore there was no transfer of learned information from the reach (location) system to the grasp (orientation) system or visa versa. Dashed lines labeled Unlearned represents where the data would fall if there was no adaptation; dashed lines labeled Learned represents complete adaptation. Top and bottom boundaries of the 95% CIs for the post-training error are presented as gray lines.

“reach location” or “grasp orientation” systems, depending on the training task.

These results might seem surprising if one begins from the assumption that the subjects would consciously notice the sensorimotor reversal in our task (this reversal is indeed quite obvious) and use this knowledge to affect a global sensorimotor reversal strategy that they could use while looking through the prism goggles. Based on postexperimental reports, our subjects did, in fact, notice the left-right reversal, and yet they all showed a *task-dependent* adaptation. It seems that there was also a strong dissociation between visual cognition and actual performance in these tasks.

Similar dissociations between visual cognition and motor control have been shown previously when motor systems failed to respond significantly to subtle visual illusions (Aglioti et al. 1995; but see Smeets and Brenner 1999 for an alternative

view¹), or when subjects compensated for changes in visual stimuli that were too subtle for perceptual recognition (Goodale et al. 1986). In such situations, individual sensorimotor systems may show adaptation without any conscious awareness of the adapting stimulus.¹

However, in the case of such subtle manipulations, it is perhaps not quite so surprising that the cognitive and motor systems might show some dissociation (Goodale et al. 1986). In our study, there was a dramatic dissociation, not only between visual cognition and motor control (apparently) but

¹Our results seem to be inconsistent with the Smeets and Brenner model, which proposes that grasping movements are planned in terms of the target positions of the index finger and thumb rather than in terms of grasp location and orientation. In this experiment, if subjects were planning grasping movements in terms of finger locations, one would not have expected to see a dissociation between orientation and location.

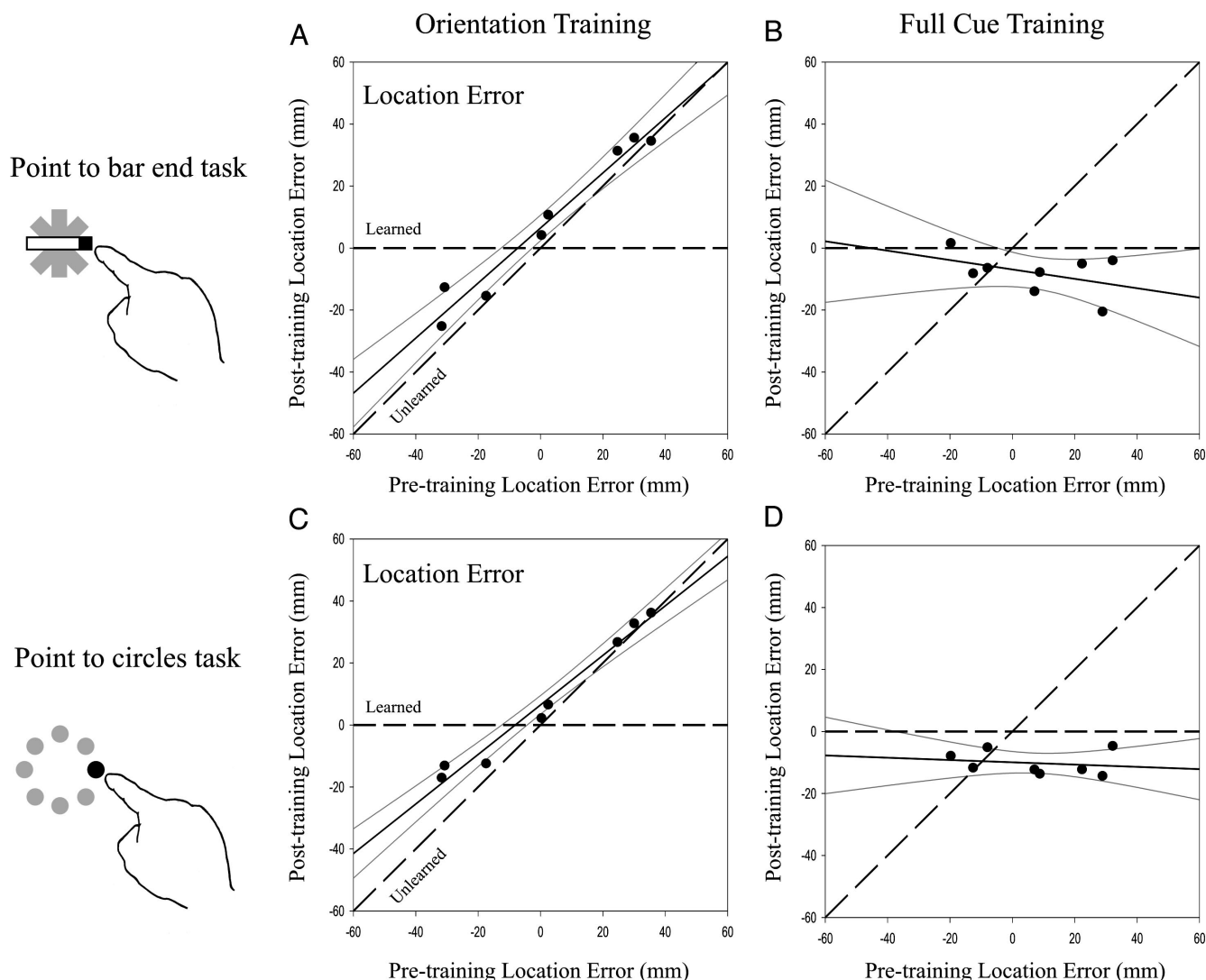


FIG. 3. To test for the possibility of modular perceptual learning, subjects were required to point to a blue region at the end of a rectangle oriented about the middle target location (A and B), and in another task, were required to point to blue circles that were positioned in the same locations as the blue regions at the end of the rectangle (C and D). Post-training location errors are plotted as a function of pretraining location errors for both tasks. When subjects underwent Orientation training, their reaching movements were not corrected on both tasks (A and C). When a separate group of subjects underwent Full Cue training, they were able to successfully indicate the correct position of the top or bottom of the rectangle (B) and accurately point to the target circles (D). Dashed lines labeled Unlearned represents where the data would fall if there was no adaptation; dashed lines labeled Learned represents complete adaptation. Top and bottom boundaries of the 95% CIs for the post-training error are presented as gray lines.

also between different aspects of the motor learning task (which is what we measured directly in our experiment). Thus our study is the first, to our knowledge, to show modular sensorimotor adaptation during such a dramatic, clearly noticeable dissociation between retinal and motor coordinates.

At first glance, “anti-pointing” experiments would also seem to produce a dramatic left-right reversal in visual-motor coordinates; in anti-pointing, subjects are instructed to reach in a direction opposite to the perceived location of the stimulus (Connolly et al. 2000; DeSouza et al. 2003; Hallett 1978). However, anti-pointing and reversing-prism adaptations are fundamentally different. Reversing prisms result in a motor command that produces an inappropriate spatial output (incongruent corollary discharge). In anti-pointing tasks, the motor command produces a congruent corollary discharge. Furthermore, anti-pointing is not believed to alter subjects’ perceptions of the visual stimulus (Fisher and Weber 1992). In

contrast, reversing prism adaptation dissociates vision from proprioceptive feedback provides direct visual feedback of errors in grasp orientation and reach location and does not require any specialized instruction. Perhaps it is for these reasons that reversing prism adaptation does affect perception. This may thus have deeper implications for spatial vision and the nature of perceptual knowledge.

Also surprising, from the viewpoint of vision based on the perception and cognition traditions, is our finding of a clear dissociation between learning in the reach and grasp systems. However, this use of local task-specific learning resonates with several findings from the motor learning literature. For example, although subjects learn to generalize a novel load in terms of both amplitude and rate (Goodbody and Wolpert 1998), this shows a rapid decay for changes in movement direction (Gandolfo et al. 1996). Similarly, learned responses to a visual rotation show a local decay in generalization (Krakauer et al.

2000; Tong and Flanagan 2003; Tong et al. 2002). In the prism goggle literature, Martin et al. (1996) found that adaptation to wedge (displacing) prisms was specific both to the body part trained and the type of motor task.

Furthermore, these results are consistent with the known cortical physiology of the visuomotor transformations for reach and grasp, in particular, the observations from primate neurophysiology that there are separate visuomotor reach and grasp systems in anterior intraparietal area (AIP) and medial intraparietal area (MIP), respectively, of the posterior parietal cortex (Andersen et al. 1998; Gallese et al. 1994; Mountcastle et al. 1975; Murata et al. 1996; Sakata et al. 1997; Snyder et al. 2000; Taira et al. 1990). Lesions to these parietal areas often result in deficits attributable to inaccuracies in transforming between visual and motor coordinate systems (Andersen 1987). These two parallel streams appear to provide a possible neural substrate for the independent adaptations that we observed.

Presumably, task-specific learning is a safer, more parsimonious strategy for the brain than applying global learning rules to early visual transformations every time we make a mistake in ordinary life. Interestingly, in our experiment, even a slight glimpse of the hand during location training provided enough orientation feedback to allow for a mild, but significant, correction by the grasp (orientation) system. Such an effect did not occur after orientation information, even though there was location information present—again, from the glimpse of the hand. The reason for this asymmetry may be that the “costs” associated with an orientation error are much smaller than the costs of a location error. In other words, if one reaches the right way with the wrong grasp orientation, the required correction is much less dramatic than if one were to reach to the wrong location with the right grasp.

Does such a modular system preclude global learning? Not necessarily: adaptation would be enhanced when enough different error signals agree, as we observed in the better overall performance in both reach and grasp in our Full Cue condition compared with our other learning conditions. Under the right conditions (i.e., with the right sensorimotor contingencies and sufficient training sets), such error signals could promote adjustments that look feature-based or even global, but these different strategies are only possible given a modularity in the underlying neural mechanisms.

Once properly adapted, such parallel systems have the capacity to simulate a complete internal spatial representation of the external world, even when this representation only exists as a concatenated series of transformations within parallel streams (Colby and Goldberg 1999; Henriques et al. 1998; Klier et al. 2001; Morgan 2003; Smith and Crawford 2001). What remains to be seen is whether there are any other aspects of what we call “perceptual knowledge: that cannot be explained in these terms. If not, knowledge of the world would simply equate to a complete set of correctly calibrated relationships between sensory input and motor output.

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REFERENCES

- Aglioti S, DeSouza JF, and Goodale MA.** Size-contrast illusions deceive the eye but not the hand. *Curr Biol* 5: 679–685, 1995.
- Andersen RA.** Inferior parietal lobule function in spatial perception and visuomotor integration. In: *Handbook of Physiology: The Nervous System. Higher Functions of the Brain*, edited by Plum F and Mountcastle VB. Rockville, MD: American Physiological Society, 1987, p. 483–518.
- Andersen RA, Snyder LH, Batista AP, Buneo CA, and Cohen YE.** Posterior parietal areas specialized for eye movements (LIP) and reach (PRR) using a common coordinate frame. In: *Novartis Foundation Symposium*, edited by Bock GR and Goode JA. New York: Wiley, 1998, p. 109–122.
- Bedford FL.** Constraints on learning new mappings between perceptual dimensions. *J Exp Psychol Hum Percept Perform* 15: 232–248, 1989.
- Clower DM and Boussaoud D.** Selective use of perceptual recalibration versus visuomotor skill acquisition. *J Neurophysiol* 84: 2703–2708, 2000.
- Colby CL and Goldberg ME.** Space and attention in parietal cortex. *Ann Rev Neurosci* 22: 319–349, 1999.
- Connolly JD, Goodale MA, Desouza JFX, Menon RS, and Vilis T.** A comparison of frontoparietal fMRI activation during anti-saccades and anti-pointing. *J Neurophysiol* 84: 1645–1655, 2000.
- DeSouza JF, Menon RS, and Everling S.** Preparatory set associated with pro-saccades and anti-saccades in humans investigated with event-related fMRI. *J Neurophysiol* 89: 1016–1023, 2003.
- Fisher B and Weber H.** Characteristics of “anti” saccades in man. *Exp Brain Res* 89: 415–424, 1992.
- Gallese V, Murata A, Kaseda M, Niki N, and Sakata H.** Deficit of hand preshaping after muscimol injection in monkey parietal cortex. *Neuroreport* 5: 1525–1529, 1994.
- Gandolfo F, Mussa-Ivaldi FA, and Bizzi E.** Motor learning by field approximation. *Proc Natl Acad Sci USA* 93: 3843–3846, 1996.
- Goodale MA, Pelisson D, and Prablanc C.** Large adjustments in visually guided reaching do not depend on vision of the hand or perception of target displacement. *Nature* 320: 748–750, 1986.
- Goodbody SJ and Wolpert DM.** Temporal and amplitude generalization in motor learning. *J Neurophysiol* 79: 1825–1838, 1998.
- Hallett P.** Primary and secondary saccades to goals defined by instructions. *Vision Res* 18: 1279–1296, 1978.
- Harris C.** Adaptation to displaced vision: visual, motor, or proprioceptive change? *Science* 140: 812–813, 1963.
- Harris CS.** Perceptual adaptation to inverted, reversed, and displaced vision. *Psychol Rev* 72: 419–444, 1965.
- Held R and Hein AV.** Adaptation of disarranged hand-eye coordination contingent upon re-afferent stimulation. *Percept Motor Skills* 8: 87–90, 1958.
- Henriques DYP, Klier EM, Smith MA, Lowy D, and Crawford JD.** Gaze centered remapping of remembered visual space in an open-loop pointing task. *J Neurosci* 18: 1583–1594, 1998.
- Jeannerod M and Biguer B.** The directional coding of reaching movements: a visuomotor conception of spatial neglect. In: *Neurophysiological and Neuropsychological Aspects of Spatial Neglect*, edited by Jeannerod M. New York: North Holland, 1987, p. 87–113.
- Klier EM, Wang H, and Crawford JD.** The superior colliculus encodes gaze commands in retinal coordinates. *Nat Neurosci* 4: 627–632, 2001.
- Kohler I.** Über Aufbau und Wandlungen der Wahrnehmungswelt. *Österreichische Akademie Wissenschaften Sitzungsberichte Philosophisch-Historische Klasse* 227: 1–118, 1951.
- Krakauer JW, Pine ZM, Ghilardi MF, and Ghez C.** Learning of visuomotor transformations for vectorial planning of reaching trajectories. *J Neurosci* 20: 8916–8924, 2000.
- Martin TA, Keating JG, Goodkin HP, Bastian AJ, and Thach WT.** Throwing while looking through prisms. II. Specificity and storage of multiple gaze-throw calibrations. *Brain* 119: 1183–1198, 1996.
- Morgan MJ.** *The Space Between Our Ears: How the Brain Represents Visual Space*. London: Weidenfeld and Nicholson, 2003.
- Mountcastle VB, Lynch JC, Georgopoulos A, Sakata H, and Acuna C.** Posterior parietal association cortex of the monkey: command functions for operations within extrapersonal space. *J Neurophysiol* 38: 871–908, 1975.
- Murata A, Gallese V, Kaseda M, and Sakata H.** Parietal neurons related to memory-guided hand manipulation. *J Neurophysiol* 75: 2180–2186, 1996.
- Proteau L.** On the specificity of learning and the role of visual information for movement control. In: *Vision and Motor Control*, edited by Proteau L and Elliott D. Amsterdam: North-Holland, 1992, p. 67–103.

- Sakata H, Taira M, Murata A, Gallese V, Tanaka Y, Shirikata E, and Kusunoki M.** Parietal visual neurons coding three-dimensional characteristics of objects and their relation to hand action. *Exp Brain Res* 25: 237–254, 1997.
- Shadmehr R and Moussavi ZMK.** Spatial generalization from learning dynamics of reaching movements. *J Neurosci* 20: 7807–7815, 2000.
- Smeets JB and Brenner E.** A new view on grasping. *Motor Control* 3: 237–271, 1999.
- Smith M and Crawford JD.** Self-organizing task modules and explicit coordinate systems in a neural network model for 3-D saccades. *J Comput Neurosci* 10: 127–150, 2001.
- Snyder LH, Batista AP, and Andersen RA.** Intention-related activity in the posterior parietal cortex: a review. *Vision Res* 40: 1433–1441, 2000.
- Sperry RW.** Neurology and the mind-brain problem. *Am Scientist* 40: 291–311, 1952.
- Stratton GM.** Vision without inversion of the retinal image. *Psychol Rev* 4: 463–481, 1897.
- Taira M, Mine S, Georgopoulos AP, Murata A, and Sakata H.** Parietal cortex neurons of the monkey related to the visual guidance of hand movement. *Exp Brain Res* 83: 29–36, 1990.
- Tong C and Flanagan JR.** Task-specific internal models for kinematic transformations. *J Neurophysiol* 90: 578–585, 2003.
- Tong C, Wolpert DM, and Flanagan JR.** Kinematics and dynamics are not represented independently in motor working memory: evidence from an interference study. *J Neurosci* 22: 1108–1113, 2002.
- Welch RB.** Adaptation of space perception. In: *Handbook of Perception and Human Performance, Sensory Processes and Perception*, edited by Bogg KR, Kaufman L, and Thoman JP. New York: Wiley, 1986, p. 24.21–24.25.
- Wolpert DM and Kawato M.** Multiple paired forward and inverse models for motor control. *Neural Networks* 11: 1317–1329, 1998.