Journal of Motor Behavior, 2007, Vol. 39, No. 4, 247–258
Copyright © 2007 Heldref Publications

Influence of Feedback Modality on Sensorimotor Adaptation: Contribution of Visual, Kinesthetic, and Verbal Cues

Fabrice R. Sarlegna
UMR Mouvement & Perception
CNRS and Université de la Méditerranée
Marseille, France
Department of Kinesiology
The Pennsylvania State University
University Park

Gabriel M. Gauthier
Jean Blouin
UMR Neurobiologie de la Cognition
CNRS and Université de Provence
Marseille, France

ABSTRACT. In 4 studies, the authors tested the contributions of visual, kinesthetic, and verbal knowledge of results to the adaptive control of reaching movements toward visual targets. The same apparatus was used in all experiments, but the procedures differed in the sensory modality of the feedback that participants (*N*s = 5, 5, 6, and 6, respectively, in Experiments 1, 2, 3, and 4) received about their performances. Using biased visual, proprioceptive, or verbal feedback, the authors introduced a 5° shift in the visuomanual relationship. Results showed no significant difference in the final amount of adaptation to the mismatch: On average, participants adapted to 79% of the perturbation. That finding is consistent with the view that adaptation is a multisensory, highly flexible process whose efficiency does not depend on the sensory channel conveying the error signal.

Keywords: cognition, knowledge of results, motor learning, sensory feedback

Since the early investigations by Helmholtz (1867/1962), researchers have extensively studied the adaptation of goal-directed movements to new environmental conditions to understand how the central nervous system (CNS) maintains the accuracy of human motor behavior. Adaptation is generally measured experimentally as the difference between two control tests carried out just before and immediately after the participant is exposed to a perturbation (Held & Gottlieb, 1958). Investigators have classically used wedge prisms, which displace the visual field by some degrees, to demonstrate humans' ability to adaptively modify their visuomanual relationship on the basis of the visual feedback of reaching performance (for reviews, see Redding, Rossetti, & Wallace, 2005; Welch, 1974). Virtual-reality techniques were used more recently so that those findings could be confirmed and extended (Bock & Girgenrath, 2006; Boy, Palluel-Germain, Orliaguet, & Coello, 2005; Ghez, Krakauer, Sainburg, & Ghilardi, 1999; Roby-Brami & Burnod, 1995; Wang & Sainburg, 2005). It is assumed that the plasticity of the CNS demonstrated through such experiments is responsible for the observed compensatory changes that occur in various sensorimotor systems in response to internal or external alterations (e.g., lesions, growth).

Vision, which provides the CNS with information about target and hand positions, is generally considered to be the main cue leading to sensorimotor adaptation, whereas proprioception is thought to be secondary (Bernier, Chua, & Franks, 2005; Bourdin, Gauthier, Blouin, & Vercher, 2001; Flanagan & Rao, 1995; Proteau, 2005; Robin, Toussaint, Blandin, & Vinter, 2004; Scheidt, Conditt, Secco, & Mussa-Ivaldi, 2005). Harris (1963) originally proposed the long-prevailing hypothesis that proprioception is recalibrated through visual guidance. Harris also suggested that the adaptation of the visuomanual relationship is necessary when there is a discrepancy between visual and proprioceptive information about hand position; that view was later supported by Lackner (1974). Since then, the respective contributions of vision and proprioception in adaptive processes have been extensively studied, whereas the role of cognition in those processes still remains unclear, as pointed out in recent studies (Baraduc & Wolpert, 2002; Clower & Boussaoud, 2000; Malfait & Ostry, 2004). In his pioneer experiment, Harris interviewed participants after they had adapted to wedge prisms. When the prisms were removed for the posttest performed without visual feedback of the hand, most participants reported that they "went back to pointing right at the target," whereas objective measures showed

Correspondence address: Jean Blouin, Laboratoire de Neurobiologie de la Cognition, CNRS et Université de Provence, 3 Place Victor Hugo, Marseille, France. E-mail address: jean.blouin@univ-provence.fr

significant aftereffects. Harris (1963, p. 813) concluded that "clearly, then, the adaptation is not a conscious process."

On the other hand, results obtained by Ingram et al. (2000) indicated that cognition may limit adaptation. The authors tested whether greater adaptation occurs when a discrepancy is consciously detected than when no such conflict is detected. They introduced a discrepancy between visual and proprioceptive (and efferent) information about the final hand position either instantly or gradually while participants performed a series of reaching movements. Participants were aware of the visual perturbation when the mismatch was introduced instantly, yet they never became aware of the gradually introduced perturbation. Ingram et al. observed that adaptation was facilitated when participants were unaware of the visuoproprioceptive mismatch as compared with that when they were aware of the visuoproprioceptive mismatch.

Ingram et al. (2000) also showed with a proprioceptively deafferented patient that proprioception is not an absolute requirement for visuomotor adaptation to occur. That finding has been supported by other observations in human deafferented individuals (Bard, Fleury, Teasdale, Paillard, & Nougier, 1995; Bernier, Chua, Bard, & Franks, 2006; Ghez et al., 1999) and in deafferented monkeys (Taub & Goldberg, 1974). The adaptive capability of deafferented participants facing a visual perturbation appears to contradict Harris's (1963) and Lackner's (1974) proposal that adaptive processes are activated when there is a mismatch between visual and proprioceptive cues. In the absence of proprioception, a mismatch between the visually perceived outcome of the voluntary motor commands and the expected outcome would be sufficient for adaptation to develop. A recalibration of the sensorimotor transformations on the basis of a so-called dominant modality is generally thought to end the discordance, allowing the individuals to regain accuracy in their performance. The results of several studies also have suggested that all modalities involved in the conflict can be modified so that the discordance diminishes (Hay & Pick, 1966; Redding & Wallace, 1992).

In normal conditions, visual and proprioceptive (and efferent) signals provide redundant information with respect to the location of body parts. Verbal knowledge of results, which can be given by an observer, is also a powerful source of information that provides spatial information and increases motor performance (Buekers & Magill, 1995; Schmidt & Lee, 1999). Our goal in the current study was to investigate the effect of sensory feedback modality on visuomotor adaptation. More specifically, we used a perturbation paradigm (i.e., a 5° sensory mismatch) in four very similar experiments to compare how visual, kinesthetic, and verbal signals contribute to the adaptation of the visuomanual relationship.

GENERAL METHOD

A schematic representation of the experimental setup is shown in Figure 1. It consisted of a horizontal, two-layer,

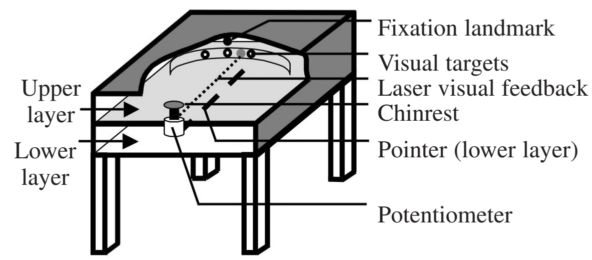


FIGURE 1. Experimental setup used in all feedback conditions. The pointer held by the participant is represented by dashed lines because it was located in the lower layer of the apparatus and participants were unable to see it.

blackened box-like structure (50 cm high, 75 cm wide, and 80 cm deep) placed on a table (90 cm high) and open in the front. Participants sat on an adjustable seat. We standardized head position through use of a chinrest. We asked participants to point to visual targets while they held a pointer with their dominant hand. The pointer was a 57-cm light rod that rotated around a pivot fixed just under the chin, and participants held the rod with their outstretched arm with their index fingertip positioned at the pointer's extremity. We attached a potentiometer, which sampled at 100 Hz, to the rotating axle of the pointer to measure its angular position. The position was instantaneously shown on the monitor and provided us with online feedback about participants' performances. All of the people who participated in this study gave their signed consent to the series of experiments, and the experiments were performed in accordance with the ethical standards of the 1964 Declaration of Helsinki. All participants were naive to our purpose in the experiment and reported that they had normal vision and no known pathology.

Arm movements (essentially adductions and abductions of the outstretched arm in the horizontal plane) were performed under a black board (lower layer of the apparatus), which prevented direct view of the limb, whereas visual targets were located above the black board (upper layer). The targets consisted of three 3-mm-diameter orange light-emitting diodes (LEDs) placed on a circular array (radius = 57 cm) whose center was at the midpoint of participants' interocular segment. The visual targets were placed at 0° (straight ahead), 10° to the left (–10°), and 10° to the right (+10°) of that origin. In conditions with visual feedback of pointing performance, we provided continuous visual feedback through a laser diode fixed on the pointer. The laser diode projected a red dot (3 mm in diameter) on the circular array, 5 mm below the targets.

Before each trial, we asked participants to place their hand approximately 25° to the left or 25° to the right of the apparatus, in a random order. We used the variation of initial hand position, combined with the use of three different target positions, to limit the learning of a stereotyped pattern of response. Participants had to point toward the illuminated target, which remained lit for 800 ms. We instructed participants to produce movements at a comfortable speed to optimize accuracy and to stabilize their hand at the reached position until an auditory signal indicated the end of the trial (3 s after target illumination started). Participants were instructed not to move their eyes and head throughout the experiment. According to previous work, those constraints do not preclude visuomanual adaptation (Kornheiser, 1976; Mather & Lackner, 1981). We placed a fixation landmark above the central target (0°) and instructed participants to maintain gaze direction on that landmark to avoid changes in registered eye direction caused by wearing prisms (for a review, see Kornheiser, 1976). Therefore, participants reached for visual targets seen in perifoveal region while fixating straight ahead, a condition that normally yields small pointing errors (Blouin, Gauthier, Vercher, & Cole, 1996; Prablanc, Echallier, Komilis, & Jeannerod, 1979). We measured movement accuracy when the hand was stabilized. We defined pointing error as the angular difference between the pointing rod and the target vector. We then submitted performance measures to analyses of variance (ANOVAs). We used an alpha value of .05 to test statistical significance and Tukey's method for post hoc analyses.

EXPERIMENT 1

Adaptation to a Prismatic Alteration of the Visuomanual Relationship

As just mentioned, much is known about the adaptive changes that result from the prism-induced alteration of the visuomanual relationship. Still, we assessed adaptation to that classical alteration in the present experimental context as a control experiment. We wanted to compare the results of adaptation with visual feedback to those observed with verbal or kinesthetic feedback of reaching performance.

Method

Five right-handed men aged 20–25 years participated in this experiment. The same participants performed two experimental sessions that involved a prismatic alteration of the visual field 5° either to the left or to the right. We gave them a 30-min break between the sessions; during the break, they returned to normal activities. We counterbalanced the order of sessions across participants. Before each session, participants performed approximately 12 pointing movements without prisms to become familiar with the apparatus and the procedure. Five of those trials were executed with continuous, veridical visual feedback of pointing performance, and about 7 trials were performed without visual feedback. We then conducted a classical prism-adaptation paradigm. Participants performed a 15-trial pretest without prisms and without visual feedback of their pointing performance (5 trials per target); the targets were randomly presented in all conditions. Participants then performed 15 trials with wedge prisms that laterally displaced the visual field by 5° either to the left or to the right, depending on the session, still without visual feedback of their pointing movement. In all prism conditions, we displaced the fixation landmark by 5° in the direction opposite to the prismatic deviation so that participants would look straight ahead. After those pretests, participants produced 60 movements with concurrent visual feedback of pointing performance to adapt to the sensorimotor alteration caused by the prisms (20 trials per target). Immediately after the exposure period, participants executed 15 movements with prisms and without visual feedback of performance (posttest with prisms). Then, the session ended with 15 trials carried out without prisms and without visual feedback of pointing performance (posttest without prisms). We used those five periods to assess (a) how the prisms affected movement performance (*prismatic effect*; the difference between the pretest without prisms and the pretest with prisms), (b) how participants used the visual feedback to adapt to the prismatic perturbation (*exposure effect*; the difference between the pretest with prisms and the end of the exposure period), and (c) how the adaptation was sustained (i.e., the difference between the posttest and the pretest, with prisms [*adaptive effect*] and without prisms [*aftereffect*]). To limit the influence of deadaptation on the results of the present study, we tried to minimize the delay between the experimental periods. We submitted the mean error and the within-participant endpoint variability (i.e., standard deviation of the mean error) to 2 (side: right, left) × 5 (period: pretest without prisms, pretest with prisms, exposure, posttest with prisms, and posttest without prisms) × 3 (target: left, center, right) ANOVAs with repeated measures. For the exposure period, we used the last 15 trials (5 trials per target) to determine mean constant and variable errors.

Results

Figure 2 illustrates the reduction in errors during and after the exposure period with visual feedback, demonstrating that participants adapted to the new visuomanual relationship induced by the prisms. For both sessions, which involved either a leftward or a rightward perturbation, there was a reduction of errors between the pretest with prisms and the end of the exposure period (mean exposure effect = 4.8°, $p < .01$), as revealed by the decomposition of the interaction between side and period, $F(4, 16) = 74.5$, $p < .001$. For example, when participants wore prisms that displaced the visual field to the right, they shifted their pointing responses to the left to reach for the physical target locations. There was also a difference between the pretest with prisms and the posttest with prisms for both sessions ($p < .01$). The adaptive effect was 3.4° on average.

The difference between the pretest without prisms and the posttest without prisms was 1.2° on average for the session with rightward-displacing prisms, and 2.2° on average for the session with leftward-displacing prisms (global mean = 1.7°). However, those aftereffects were not statisti-

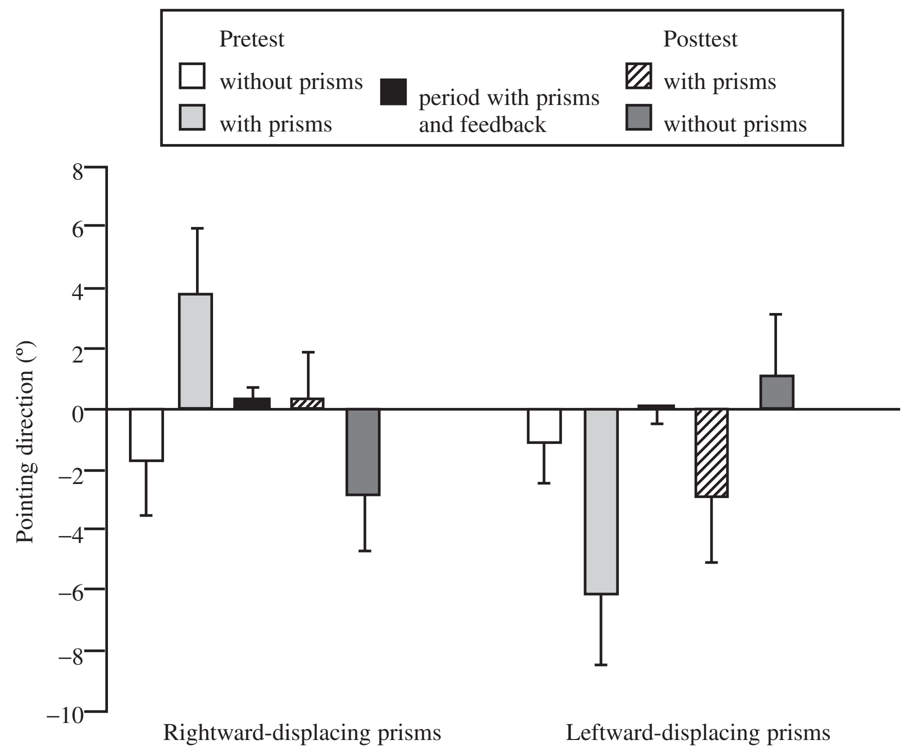


FIGURE 2. Pointing errors of reaching movements as a function of period for leftward- and rightward-displacing prisms. The error bars represent between-participant variability (standard deviation of the individual mean values across participants).

cally significant ($p > .05$). There was no significant effect of target position.

The significant adaptation to the new visuomanual relationship was not associated with an increased variability of the motor performance. Indeed, the endpoint variabilities of the movements performed in pretests and those of the movements performed in posttests were not statistically different ($p > .05$). However, the ANOVA showed that the period had a significant effect on endpoint variability, $F(4, 16) = 7.5$, $p < .01$. The variability at the end of the exposure period ($M = 0.5°$) was significantly smaller than that of any other period ($M = 1.9°$), presumably because participants received visual feedback of their pointing performance during that exposure period.

Discussion

The results of Experiment 1 were consistent with those of previous studies on prism adaptation with visual feedback of pointing performance (Held & Gottlieb, 1958; for reviews, see Redding et al., 2005; Welch, 1974). Participants adapted to the new, prism-induced visuomanual relationship, as indicated by the smaller endpoint errors in the posttest than in the pretest with prisms. On average, adaptive effects reached 3.4°, corresponding to 67% of the 5° prismatic perturbation. The fact that the adaptive change in mean hand direction was not associated with an increase in the endpoint variability during the posttest suggests robust adaptation in this motor task. Prism adaptation is classically interpreted to result from a shift of the proprioceptively derived internal representation of the hand position toward the visually defined hand position (Harris, 1963) or from a change in the transformations between sensory input and motor output (Hardt, Held, & Steinbach, 1971; see also Baraduc & Wolpert, 2002). Adaptive processes are hypothesized to improve the accuracy of subsequent arm movements (Novak, Miller, & Houk, 2003) by optimizing the planning stage of the movement so that the performance relies to a lesser extent on online monitoring mechanisms.

EXPERIMENT 2

Adaptation to a Verbal Alteration of the Visuomanual Relationship

Results from Experiment 1 were consistent with previous findings, highlighting the efficiency of visual information processing in enabling participants to adapt to a systematic visuomanual perturbation. We primarily collected those results to obtain reference data for subsequent experiments. Our goal in Experiment 2 was to determine if participants would show adaptive capabilities when we provided verbal information about their reaching performance.

Method

The same 5 men who took part in Experiment 1 participated in Experiment 2. The latter experiment was performed

2–3 weeks later. The experimental apparatus was the same as the one used in Experiment 1. Participants performed 15 pretest trials without visual feedback of their pointing performance, followed by 60 trials in the adaptive period. Those trials were also performed without visual feedback, but we provided participants with biased verbal feedback about their performance immediately after the reaching movement. We selected the feedback on the basis of the reaching end position with respect to virtual targets located to the left or to the right of the actual targets' positions. The biased feedback was gradually introduced. For example, during the first 30 trials of the session involving a leftward perturbation, we provided feedback on participants' performance with respect to virtual targets located 2.5° to the left of the actual targets' positions (i.e., –12.5°, –2.5°, and 7.5° for the –10°, 0°, and 10° visual targets, respectively). The terminal feedback was based on the following scale: 1 (*largely too much to the left*), 2 (*too much to the left*), 3 (*good*), 4 (*too much to the right*), and 5 (*largely too much to the right*). The participants thus received the feedback "too much to the right" when their movements ended on the visual targets, and they received the feedback "good" when they ended 2.5° to the left of the actual targets. Participants were told "largely too much to the left" or "largely too much to the right" when the error (compared with the virtual target) was greater than 2.5°. For the last 30 trials of the session, we provided the verbal feedback with respect to virtual targets located 5° to the left of the actual targets.

We used the same procedure in the session involving a rightward perturbation. Here, the feedback was given with respect to virtual targets respectively located 2.5° and 5.0° to the right of the actual visual target for the first and last 30 trials of the session. We gradually introduced the shift in the visuomanual relationship to prevent participants from questioning the veracity of the verbal feedback and perceiving a discrepancy between verbal and proprioceptive information, a prerequisite condition for the participants to rely on the feedback given by the experimenter. Following the trials with verbal feedback, participants performed a posttest (15 trials) in which neither verbal nor visual feedback of pointing performance was available. Mean directional error and endpoint variability were submitted to 2 (orientation: right, left) × 3 (period: pretest, exposure, posttest) × 3 (target: left, center, right) ANOVAs with repeated measures. We used three periods in Experiment 2 because, after the pretest, participants received verbal feedback, and the perturbation consisted of the bias of the feedback itself. This protocol, which was also used in Experiments 3 and 4, differed slightly from the one used in the first experiment. We verified whether that perturbation led to adaptaion in the exposure period as well as in the posttest.

Results

None of the participants reported suspicion about the veracity of the verbal feedback of their pointing performance provided by the experimenter. In fact, participants did use the verbal feedback given during the exposure period to modify their movements. That can be seen in Figure 3,

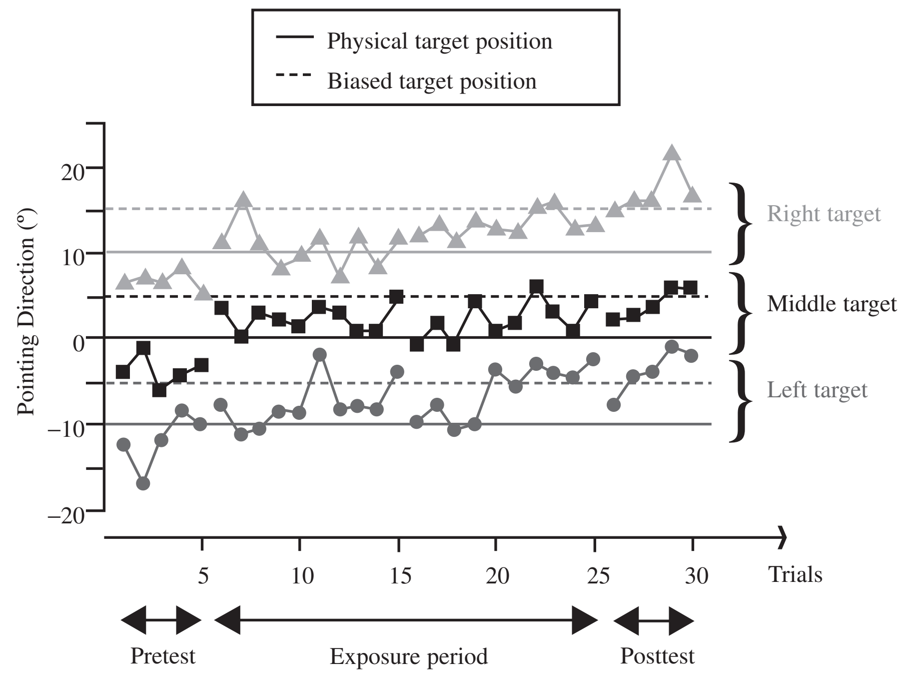


FIGURE 3. Data of a representative participant, showing the evolution of pointing performance (°) as a function of trial number in a session with rightward-biased verbal feedback during the adaptive period.

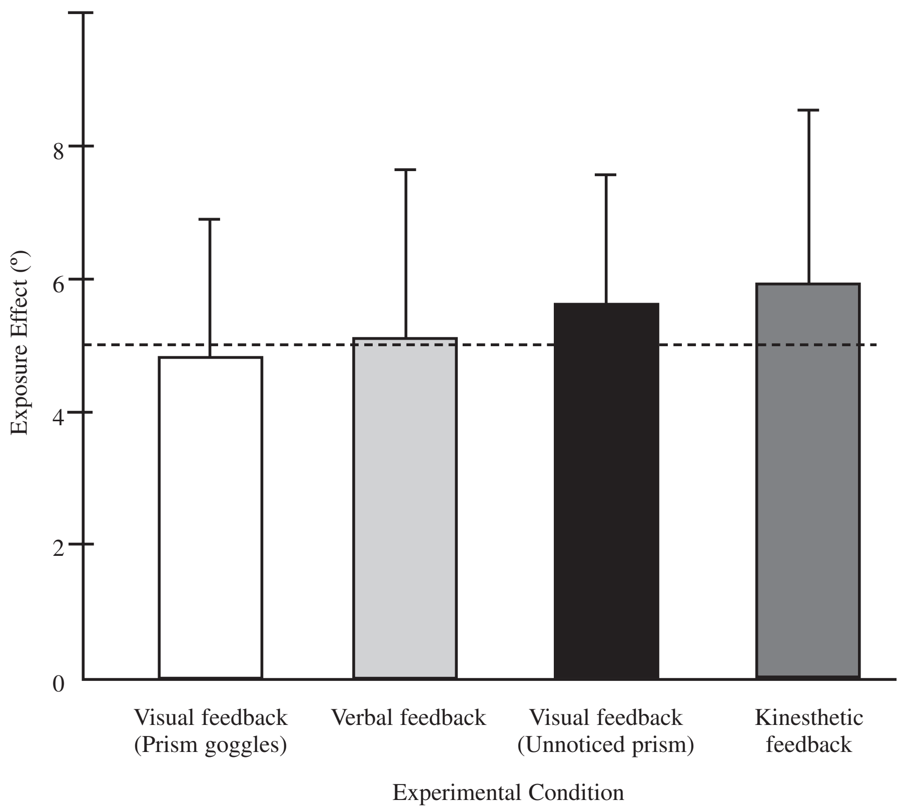


FIGURE 4. Exposure effects (difference between the pretest and the end of the exposure period) in all feedback conditions. The dashed line represents the theoretical value reached if adaptation is complete. The error bars represent between-participant variability (standard deviation of the individual mean values across participants).

which illustrates the time course of pointing performance of a representative participant who received a rightward-biased feedback. Although participants were fairly accurate in the pretest, participants pointed, on average, 4.2° to the left of the targets in the last 15 trials of the exposure period in the leftward-shift session. In the rightward-shift session, participants pointed 5.2° to the right of the targets at the end of the exposure period. The mean exposure and adaptive effects computed from leftward and rightward shifts of the three targets are presented in Figures 4 and 5, respectively (the figures also show the effects found in Experiments 3 and 4, which we will discuss later). The decomposition of the significant interaction between side and period, $F(2, 8) = 31.3$, $p < .001$, showed that in both sessions participants adapted significantly to the new visuomanual relationship between the pretest and the end of the exposure period, $p < .01$. The effect of the exposure period was maintained in the posttest, in the absence of verbal feedback of movement accuracy. Indeed, pointing errors were significantly different between the pretest and posttest for both sessions, $p < .05$. The adaptive effect was 4.7°, on average. There was no significant difference between pointing errors in the posttest and at the end of the exposure period for both sessions, $p > .05$. Despite the significant adaptive modification of the visuomanual relationship, pointing variability was not significantly different between the pretest, the end of the exposure period, and the posttest ($M = 1.9°$).

Discussion

Results of Experiment 2 clearly showed that verbal feedback of movement performance can lead to the adaptation of the arm sensorimotor system. When visual feedback of pointing accuracy was available during the exposure period in Experiment 1, a significant adaptation was evidenced in the posttest. Participants thus processed visual feedback of pointing performance to optimize the accuracy of the subsequent movements. In the second experiment, because we provided the error signal about participants' performance only verbally, they adapted visuomotor transformations on the basis of the verbal knowledge of results, and cognitive processes presumably mediated that adaptation.

Our results do not support Harris's (1963) suggestion that the role of cognition in adaptive changes is negligible. In his study on the role of cognitive processes in visuomotor adaptation, Webster (1969) asked his participants to ignore the errors they could perceive when seeing their reaching movements through wedge prisms. Despite that instruction,

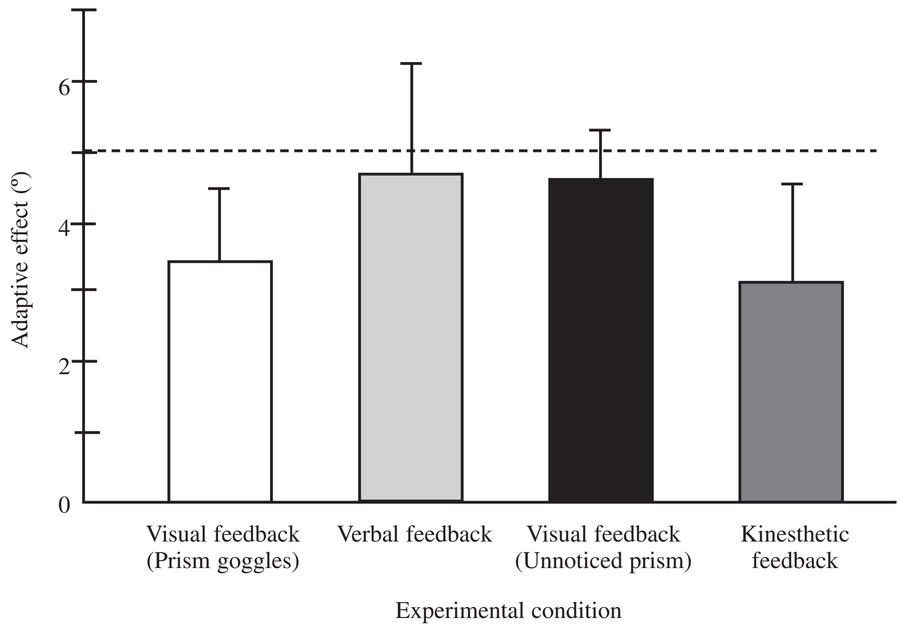


FIGURE 5. Adaptive effects (difference between the pretest and the posttest) in all feedback conditions. The dashed line represents the theoretical value reached if adaptation is complete. The error bars represent between-participant variability (standard deviation of the individual mean values across participants).

participants adapted for about half of the prismatic deviation, suggesting that visuomotor adaptation relied substantially on sensorimotor processes. In contrast, the control group, instructed to compensate for any errors in visual target pointing, exhibited complete adaptation to the prismatic deviation. Webster's results thus indicated a significant contribution of instruction, and therefore cognition, to the adaptive processes. The results of the present study support that notion and are also consistent with findings showing that verbal knowledge of results contributes to the learning of a motor skill (Buekers & Magill, 1995; Schmidt & Lee, 1999; Uhlarik, 1973). The idea that cognition plays a significant role in the adaptive process of reaching movement is furthermore supported by studies showing that concurrent mental tasks (e.g., mental arithmetic) performed during the exposure period largely reduce the amount of visuomotor adaptation as compared with that in conditions without a simultaneous mental task (Eversheim & Bock, 2001; Ingram et al., 2000; Redding, Clark, & Wallace, 1985; Redding & Wallace, 1985).

As stated earlier, Ingram et al. (2000) found that adaptation was significantly greater when the visuomanual alteration was gradually introduced (so that participants were not aware of the perturbation) than when it appeared all at once (see also Robertson & Miall, 1999). Those results could indicate that adaptive mechanisms are enhanced by the sensorimotor processes taking place when participants do not perceive a mismatch between visual and proprioceptive or efferent information of hand position and therefore when participants do not adopt a new cognitive strategy to preserve their motor performance.

Together, the results of those studies suggest that different cognitive factors may affect visuomotor adaptation. Some of those factors would be beneficial to the adaptation (e.g., verbal knowledge of results), whereas others would be detrimental (e.g., conscious detection of a perturbation). Therefore, cognition cannot be considered as a holistic input to the adaptive control loop. Thus, investigators should emphasize the need to carefully identify the actual manipulated cognitive information when they study the role of cognition in sensorimotor adaptive processes.

EXPERIMENT 3

Adaptation to a Visual, Unperceived Bias of the Visuomanual Relationship

As discussed earlier, previous investigations have shown that the conscious detection of errors or of the possible source of errors may perturb the processes leading to sensorimotor adaptation (Buekers & Magill, 1995; Ingram et al., 2000; Jakobson & Goodale, 1989; Kagerer, Contreras-Vidal, & Stelmach, 1997). In Experiment 1, participants may have perceived the prismatic goggles as a potential source of perturbation. We tested the hypothesis that such experimentally induced potential bias could have affected the amount of visually evoked adaptation in Experiment 3. Here, to have the participants unaware of any source of perturbation, we placed the prism along the path of the laser providing the visual feedback of pointing performance. The resulting mismatch between visual and proprioceptive hand information was therefore similar to that in Experiment 1. Considering the previous literature discussed earlier, we hypothesized that the amount of adaptation would be greater with the unperceived perturbation than with the prismatic goggles used in Experiment 1 because the latter setup may lead to the conscious detection of a perturbation in the visuomanual relationship.

Method

Six right-handed participants (4 men and 2 women, aged 20–23 years) took part in Experiment 3. The experimental setup and procedures were similar to those used in Experiments 1 and 2. Because we used a laser fixed on the unseen pointer to provide visual feedback of the pointing movement, we were able to alter the visual feedback by placing a light prism in front of the laser beam without allowing participants to perceive the alteration. The prism shifted pointing visual feedback 5° either to the left or to the right.

Participants performed 15 trials in a pretest without visual feedback of pointing performance and 60 trials in the exposure period with biased visual feedback of performance; the sessions ended with a 15-trial posttest without visual feedback. The order of sessions (i.e., leftward or rightward prismatic deviation) was counterbalanced across participants.

Results

Participants, who never became aware of the 5° visual alteration, adapted to the shifted visual feedback (see Figures 4 and 5). There was a significant adaptive modification of the visuomanual relationship between the pretest and the end of the exposure period ($M = 5.9°$), as revealed by the interaction between side and period, $F(2, 10) = 150.9$, $p < .001$. The modification of the visuomotor transformations during the exposure period was significant in the experimental sessions involving either a leftward perturbation ($M = 4.8°$) or a rightward perturbation ($M = 6.9°$). The difference between the pretest and the posttest ($M = 4.6°$) was also significant for both sessions, $p < .001$. Even though a significant adaptation was observed, there was no significant difference between movement variability in the pretest and posttest ($M = 1.8°$).

Discussion

As was found in several previous studies (e.g., Baraduc & Wolpert, 2002; Bernier et al., 2005; Boy et al., 2005; Flanagan & Rao, 1995; Ghez et al., 1999; Roby-Brami & Burnod, 1995; Wang & Sainburg, 2005), providing participants in our study with altered visual feedback of pointing performance led to a significant adaptation of the sensorimotor–arm system. In the present experiment, participants were interviewed and declared that they were unaware that the visual feedback was experimentally distorted. The resulting amount of adaptation (4.6° on average) was greater, although not significantly, than that observed in Experiment 1 (3.4° on average); in the latter case, participants could perceive an alteration in hand visual feedback by wearing prismatic goggles. In the present experiment, participants presumably interpreted the visually detected pointing errors, which occurred during the exposure period, as stemming from errors in the control of their movements rather than from an experimentally induced artifact.

EXPERIMENT 4

Adaptation to a Proprioceptive Alteration of the Visuomanual Relationship

The first 3 experiments clearly showed that both visual (Experiments 1 and 3) and verbal (Experiment 2) feedback of the arm motor performance can lead to visuomotor adaptation. It has been suggested by several authors that the underlying processes for that adaptation may involve a recalibration of the proprioceptive sensation of limb position (e.g., Bernier et al., 2005; Harris, 1963; for a review, see Redding et al., 2005). According to that suggestion, proprioception would have a secondary role in the adaptive processes because it would be under the influence of other sensory modalities. In fact, the results of the first three experiments of the current study also suggest that the role of proprioception is not critical. For instance, when participants received visual or verbal feedback indicating (erroneously) that they were not on target, they predominantly used exteroceptive feedback over the proprioceptive feedback to modify subsequent movements. That finding suggests that proprioception was largely ignored for certain aspects of movement control in our first three experiments. Our goal in Experiment 4 was to investigate whether the processing of kinesthetic feedback (including proprioceptive and efferent signals) from the upper limb can convey an effective error signal and lead to the adaptive modification of the sensorimotor–arm system. We used a protocol as similar as possible to the three previous experiments to compare the proprioceptive contribution to the adaptive processes with the visual and verbal contributions.

Method

The 6 participants who participated in Experiment 3 also took part in this experiment, which was performed a few weeks later. The apparatus and protocol were similar to those used in the previous experiments. Here, we provided no visual feedback of the pointing movement. Immediately after the end of the pretest (15 trials), we placed three vertical, 1-cm-long metal pins at the ceiling of the lower layer of the apparatus; that layer was out of the participants' view. Participants were told that the pins were aligned with the targets. Depending on the session, however, the pins were placed 5° either to the left or to the right of target locations. During the exposure period, participants had to reach for the visual target and, at the end of their movements they had to lift their index finger to find and touch the metal pin corresponding to the target they were aiming at. Because the arm was at different positions with respect to the visual targets, the perturbation required a realignment

TABLE 1. Summary of Exposure and Adaptive Effects in All Four Feedback Conditions

Side or effect	Experiment 1 Visual feedback (prisms)		Experiment 2 Verbal feedback		Experiment 3 Visual feedback		Experiment 4 Kinesthetic feedback	
Perturbation side	Left	Right	Left	Right	Left	Right	Left	Right
Exposure effect (deg)	3.5	6.2	4.9	5.2	4.8	6.9	5.5	5.7
Mean exposure effect (deg)	4.8		5.1		5.9		5.6	
Adaptive effect (deg)	3.5	3.3	4.2	5.2	4.6	4.6	3.7	2.5
Mean adaptive effect (deg)	3.4		4.7		4.6		3.1	

of the visual and proprioceptive maps through kinesthetic-feedback processing. It should be noted that tactile information did not provide any spatial information other than that the arm reached the pin. We could monitor participants' performance and target position online on the computer screen. For each trial of the exposure period, we verified that participants contacted the appropriate pin and informed them verbally when they reached the wrong pin, something that could happen a few times in the very beginning of the exposure period (i.e., first 10 trials). After the 60 trials of the exposure period, we removed the metal pins, and participants performed a posttest (15 trials) without verbal or visual feedback of their pointing accuracy.

Results

None of the participants reported that the pins were not aligned with the visual targets. Exposure and adaptive effects are represented in Figures 4 and 5, respectively, and also in Table 1, in which we have summarized the results of the four experiments. Participants used the kinesthetic feedback of reaching performance to adaptively shift their visuomotor transformations according to the perturbation, as revealed by the shift in pointing accuracy. The decomposition of the interaction between side and period, $F(2, 10) = 78.9$, $p < .001$, revealed that for both leftward and rightward alterations, the adaptive modification of the visuomanual relationship between the pretest and the end of the exposure period was significant ($M = 5.6°$), $p < .001$. The difference between the errors in the pretest and the posttest was also significant in both sessions ($M = 3.1°$), $p < .01$. The analysis of pointing variability showed that there was no significant difference between the pretest and the posttest ($M = 2.1°$).

Discussion

The main result of Experiment 4 was that when the participants touched a metal pin indicating the erroneous target position at the end of their movements, they used the kinesthetic information of the arm to modify the coordination of the subsequent movements. In the first trials of the exposure period, that kinesthetic information could have been related to the corrective movement or movements performed at the end of the primary movement to touch the pin. Later in the exposure period, the metal pin was reached more directly, and the error signal progressively disappeared. At that point, it is thus likely that participants used kinesthetic information of the upper-limb configuration to consolidate the sensorimotor adaptation.

Our results are consistent with the idea that proprioceptive feedback can lead to the adaptive modification of the visuomanual relationship, as shown in previous studies with inertial loads (Ghez et al., 1999), robot-assisted perturbations (Scheidt et al., 2005), and novel external forces (Coello, Orliaguet, & Prablanc, 1996). Our results are also consistent with those of Lackner (1974, Experiment 2), who installed pins at the physical locations of visual targets seen through wedge prisms. Because the prisms laterally displaced the visual field by 10°, the participants faced a mismatch between visually and proprioceptively defined target positions. Lackner found that participants adapted to 46% of the perturbation, indicating that proprioceptive feedback can contribute to prism adaptation. In the present study, to investigate the role of arm proprioceptive cues in the adaptive processes, we used discordant pin and target positions during the adaptive period without using prism goggles. Participants adapted to 62% of the perturbation, more than the participants in Lackner's study did. Differences in the amount of adaptation found in Lackner's study and ours could result from the use of prism goggles in the experiment of Lackner. Our study thus supports the view that the conscious perception of a perturbation (wearing prisms in Lackner's study) may act as a negative factor on the adaptive processes and may therefore diminish the amount of adaptation (Ingram et al., 2000; Jakobson & Goodale, 1989; Kagerer et al., 1997; Uhlarik, 1973). An additional feature of the present study with respect to previous studies is that we could test whether the amount of adaptation obtained through kinesthetic cues differed from that observed with visual cues. That comparison was possible because we designed the protocols to be as similar as possible.

All four experiments of the present study were performed with 15-trial tests without any external feedback of pointing performance before and after a session in which participants were exposed for 60 trials to a 5°-biased sensory feedback. Depending on the experiment, participants could rely on verbal, visual, or proprioceptive feedback to adaptively modify the sensorimotor transformations. We assigned exposure effects and adaptive effects positive values, and we averaged those values for the side of the perturbation and for the three target positions. Because the same group of participants participated in Experiments 1 and 2 and another group participated in Experiments 3 and 4, we used *t* tests with related samples to compare the shifts in pointing accuracy (exposure effects and adaptive effects) between Experiments 1 and 2 and between Experiments 3 and 4. For all other comparisons, we used *t* tests for unrelated samples.

The comparisons revealed that the exposure effect was greater with the unnoticed visual perturbation (Experiment 3, $M = 5.9°$) than when the participants were aware that prisms were used (Experiment 1, $M = 4.9°$), $t(4) = 2.7$, $p < .05$. The exposure effects resulting from the other experiments were not statistically different, $p > .05$. Moreover, the analyses of the adaptive effects revealed no significant effect of the type of sensory feedback (verbal, proprioceptive, or visual) that participants received about their performance.

GENERAL DISCUSSION

Our goal in the present study was to test whether participants show different amounts of sensorimotor adaptation when knowledge about their motor performance is conveyed by different channels of information. To do so, we used a simple motor skill in which accuracy depended on sensorimotor transformations: manual reaching to a visual target. The feedback the participants received about their performance was visual, verbal, or kinesthetic. The main finding of the study was that when we gave participants the same number of trials to learn to reach to targets in the presence of 5° shifts in the visuomanual relationship, we found no significant differences between the amounts of adaptation driven by visual, kinesthetic, and verbal cues. Therefore, the visuomanual relationship can be adaptively modified when there is a discrepancy between the motor outcome and what participants view, or feel (kinesthetically), or believe (cognitively). That finding is consistent with the idea that adaptation is a multisensory, flexible process in which efficiency does not appear to depend on the sensory channel conveying the error signal. Therefore, the present results not only highlight the plasticity of the sensorimotor system, which allows individuals to preserve movement accuracy despite sustained changes in the visuomanual relationship, but they also emphasize the distributed nature of the CNS. That characteristic organization would be particularly beneficial to purposeful motor behaviors in the context of sensory deprivation (caused either by disease, aging, or the environment).

The role of proprioception in visuomotor adaptation appears particularly interesting. Several studies indicate that proprioception is not mandatory to enable individuals to adapt to various types of perturbations (Bard et al., 1995; Bernier et al., 2006; Ghez et al., 1999; Ingram et al., 2000; Taub & Goldberg, 1974). In the first and third experiments, participants were fairly accurate during the pretests when pointing to the visual target; they brought the hand relatively close to the target. During the exposure period, a visual perturbation was introduced, and in that situation of visuoproprioceptive mismatch, all participants used the visual feedback of hand position rather than the proprioceptive, veridical feedback to control their movements and adapt their sensorimotor transformations. Similarly, in the second experiment with biased verbal feedback, participants were told that their hand was not on target although it actually was. In that situation, there was no visuoproprioceptive mismatch, but there was a discordance between the verbal and proprioceptive feedback of hand position. Our study indicated that the participants systematically used the exteroceptive, verbal feedback rather than their interoceptive, proprioceptive feedback to produce the subsequent arm movements. The observed adaptations show that in our first three experiments, both visual and verbal sources of information dominated the proprioceptive one. When the error signal was given through proprioception in the fourth experiment, however, the processing of proprioceptive feedback of arm position clearly led to a sustained modification of the visuomotor transformations. Therefore, those results suggest that even if proprioception is dominated by other available sources of information, it remains a potential source of information contributing to the processes underlying sensorimotor adaptation.

The principal source of feedback allowing individuals to adapt to sensorimotor perturbations has generally been considered to be vision (Bourdin et al., 2001; Coello et al., 1996; Proteau, 2005; Robin et al., 2004; Scheidt et al., 2005). In a great deal of the research in which the question of multisensory integration in perceptual and motor processes was specifically addressed, however, support for unimodal models of integration was not obtained (Guillaud, Gauthier, Vercher, & Blouin, 2006; Lloyd, Shore, Spence, & Calvert, 2003; Rossetti, Desmurget, & Prablanc, 1995; Sarlegna et al., 2004; Sarlegna & Sainburg, 2007). A great challenge in future investigations will be to determine whether proprioception, vision, and different aspects of cognition jointly contribute to sensorimotor adaptation and, if so, to ascertain the mechanisms that govern the integration.

ACKNOWLEDGMENTS

Centre National de la Recherche Scientifique (CNRS), Centre National d'Etudes Spatiales, Délégation Général pour l'Armement, and the Université de la Méditerranée provided support for this research. The authors are grateful to Sydney Y. Schaefer for helpful comments when reviewing the English in the manuscript and to Guillaume Garreau for his involvement in Experiments 3 and 4. We also thank Alain Donneaud for technical assistance in building the experimental setup and the participants who graciously agreed to take part in the study.

Biographical Notes

Fabrice R. Sarlegna received a doctorate in human movement sciences from the University of the Mediterranean (Marseille, France). He teaches experimental psychology and neuroscience. His research interests include multisensory integration, perception, and motor planning, control, and learning.

Gabriel M. Gauthier received electronics engineering and physiology training from the University of Grenoble (France) and a doctorate in biomedical engineering from the University of Illinois. He then joined the CNRS in Marseille, and he is using cybernetics, behavioural, clinical, and neurophysiological techniques to study the online control of the visuomotor systems, as well as their coordination and adaptive controls. He is currently devoting time and efforts in visiting high schools to promote scientific research.

Jean Blouin received his doctorate in kinesiology at the Université Laval (Québec, Canada) and then joined the French CNRS. He is the head of the Multisensory Control of Movement group in the Laboratory of Neurobiology and Cognition, Marseille. The main goal of this group is to understand the fusion of sensory information during the construction and the updating of the internal representations of the body–environment relationship from the planning of the movement to its execution.

REFERENCES

Baraduc, P., & Wolpert, D. M. (2002). Adaptation to a visuomotor shift depends on the starting posture. *Journal of Neurophysiology, 88,* 973–981.

Bard, C., Fleury, M., Teasdale, N., Paillard, J., & Nougier, V. (1995). Contribution of proprioception for calibrating and updating the motor space. *Canadian Journal of Physiology & Pharmacology, 73,* 246–254.

Bernier, P. M., Chua, R., Bard, C., & Franks, I. M (2006). Updating of an internal model without proprioception: A deafferentation study. *NeuroReport, 17,* 1421–1425.

Bernier, P. M., Chua, R., & Franks, I. M. (2005). Is proprioception calibrated during visually guided movements? *Experimental Brain Research, 167,* 292–296.

Blouin, J., Gauthier, G. M., Vercher, J.-L., & Cole, J. (1996). The relative contribution of retinal and extraretinal signals in determining the accuracy of reaching movements in normal subjects and a deafferented patient. *Experimental Brain Research, 109,* 148–153.

Bock, O., & Girgenrath, M. (2006). Relationship between sensorimotor adaptation and cognitive functions in younger and older subjects. *Experimental Brain Research, 169,* 400–406.

Bourdin, C., Gauthier, G. M., Blouin, J., & Vercher, J.-L. (2001). Visual feedback of the moving arm allows complete adaptation of pointing movements to centrifugal and Coriolis forces. *Neuroscience Letters, 301,* 25–28.

Boy, F., Palluel-Germain, R., Orliaguet, J. P., & Coello, Y. (2005). Dissociation between "where" and "how" judgements of one's own motor performance in a video-controlled reaching task. *Neuroscience Letters*, *386,* 52–57.

Buekers, M. J., & Magill, R.A. (1995) The role of task experience and prior knowledge for detecting invalid augmented feedback while learning a motor skill. *Quarterly Journal of Experimental Psychology, 48A,* 84–97.

Clower, D. M., & Boussaoud, D. (2000). Selective use of perceptual recalibration versus visuomotor skill acquisition. *Journal of Neurophysiology, 84,* 2703–2708.

Coello, Y., Orliaguet, J. P., & Prablanc, C. (1996). Pointing movement in an artificial perturbing inertial field: A prospective paradigm for motor control study. *Neuropsychologia, 34,* 879–892.

Eversheim, U., & Bock O. (2001). Evidence for processing stages in skill acquisition: A dual-task study. *Learning & Memory, 8,* 183–189.

Flanagan, J. R., & Rao, A. K. (1995). Trajectory adaptation to a nonlinear visuomotor transformation: Evidence of motion planning in visually perceived space. *Journal of Neurophysiology, 74,* 2174–2178.

Ghez, C., Krakauer, J., Sainburg, R. L., & Ghilardi, M. F. (1999). Spatial representations and internal models of limb dynamics in motor learning. In M. S. Gazzaniga (Ed.), *The new cognitive neurosciences* (2nd ed., pp. 501–514). Cambridge, MA: The MIT Press.

Guillaud, E., Gauthier, G. M., Vercher, J.-L., & Blouin, J. (2006). Visuoocular and vestibular signal fusion in arm motor control. *Journal of Neurophysiology, 95,* 1134–1146.

Hardt, M. E., Held, R., & Steinbach, M. J. (1971). Adaptation to displaced vision: A change in the central control of sensorimotor coordination. *Journal of Experimental Psychology, 89,* 229–239.

Harris, C. S. (1963). Adaptation to displaced vision: Visual, motor or proprioceptive change? *Science, 140,* 812–813.

Hay, J. C., & Pick, H. L. (1966). Visual and proprioceptive adaptation to optical displacement of the visual stimulus. *Journal of Experimental Psychology, 92,* 319–325.

Held, R., & Gottlieb, N. (1958). Technique for studying adaptation to disarranged hand-eye coordination. *Perceptual & Motor Skills, 8,* 83–86.

Helmholtz, H. von (1962). *Treatise on physiological optics* (Vol. 3 [J. P. C. Southhall, Trans.]). New York: Dover. (Original work published 1867)

Ingram, H. A., Van Donkelaar, P., Cole, J., Vercher, J. L., Gauthier, G. M., & Miall, R.C. (2000). The role of proprioception and attention in a visuomotor adaptation task. *Experimental Brain Research, 132,* 114–126.

Jakobson, L. S., & Goodale, M. A. (1989). Trajectories of reaches to prismatically-displaced targets: Evidence for 'automatic' visuomotor recalibration. *Experimental Brain Research, 78,* 575–587.

Kagerer, F. A., Contreras-Vidal, J. L., & Stelmach, G. E. (1997). Adaptation to gradual as compared with sudden visuomotor distortions. *Experimental Brain Research, 115,* 557–561.

Kornheiser, A. S. (1976). Adaptation to laterally displaced vision: A review. *Psychology Bulletin, 83,* 783–816.

Lackner, J. R. (1974). Adaptation to displaced vision: Role of proprioception. *Perceptual and Motor Skills, 38,* 1251–1256.

Lloyd, D. M., Shore, D. I., Spence, C., & Calvert, G. A. (2003). Multisensory representation of limb position in human premotor cortex. *Nature Neuroscience, 6,* 17–18.

Malfait, N., & Ostry, D. J. (2004). Is interlimb transfer of force–field adaptation a cognitive response to the sudden introduction of load? *Journal of Neuroscience, 24,* 8084–8089.

Mather, J. A., & Lackner, J. R. (1981). The influence of efferent, proprioceptive, and timing factors on the accuracy of eye-hand tracking. *Experimental Brain Research, 43*(3–4), 406–412.

Novak, K. E., Miller, L. E., & Houk J. C. (2003). Features of motor performance that drive adaptation in rapid hand movements. *Experimental Brain Research, 148,* 388–400.

Prablanc, C., Echallier, J. F., Komilis, E., & Jeannerod, M. (1979). Optimal response of eye and hand motor systems in pointing at a visual target. I. Spatio-temporal characteristics of eye and hand movements and their relationships when varying the amount of visual information. *Biological Cybernetics, 35,* 113–124.

Proteau, L. (2005). Visual afferent information dominates other sources of afferent information during mixed practice of a video-aiming task. *Experimental Brain Research, 161,* 441–456.

Redding, G. M., Clark, S. E., & Wallace, B. (1985). Attention and prism adaptation. *Cognition & Psychology, 17,* 1–25.

Redding, G. M., Rossetti, Y., & Wallace, B. (2005). Applications of prism adaptation: A tutorial in theory and method. *Neuroscience & Biobehavioral Review, 29,* 431–444.

Redding, G. M., & Wallace, B. (1985). Cognitive interference in prism adaptation. *Perception & Psychophysics, 37,* 225–230.

Redding, G. M., & Wallace, B. (1992). Effects of pointing rate and availability of visual feedback on visual and proprioceptive components of prism adaptation. *Journal of Motor Behavior, 24,* 226–237.

Robertson, E. M., & Miall, R. C. (1999). Visuomotor adaptation during inactivation of the dentate nucleus. *NeuroReport, 10,* 1029–1034.

Robin, C., Toussaint, L., Blandin, Y., & Vinter, A. (2004). Sensory integration in the learning of aiming toward "self-defined" targets. *Research Quarterly for Exercise and Sport, 75,* 381–387.

Roby-Brami, A., & Burnod, Y. (1995) Learning a new visuomotor transformation: Error correction and generalization. *Cognitive Brain Research, 2,* 229–242.

Rossetti, Y., Desmurget, M., & Prablanc, C. (1995) Vectorial coding of movement: Vision, proprioception, or both? *Journal of Neurophysiology, 74,* 457–463.

Sarlegna, F., Blouin, J., Bresciani, J.-P., Bourdin, C., Vercher, J.-L., & Gauthier, G. M. (2004). Online control of the direction of rapid reaching movements. *Experimental Brain Research, 157,* 468–471.

Sarlegna, F., & Sainburg, R. L. (2007) The effect of target modality on visual and proprioceptive contributions to the control of movement distance. *Experimental Brain Research, 176,* 267–280.

Scheidt, R. A., Conditt, M. A., Secco, E. L., & Mussa-Ivaldi, F. A. (2005). Interaction of visual and proprioceptive feedback during adaptation of human reaching movements. *Journal of Neurophysiology, 93,* 3200–3213.

Schmidt, R. A., & Lee, T. D. (1999). *Motor control and learning: A behavioral emphasis.* Champaign, IL: Human Kinetics.

Taub, E., & Goldberg, I. A. (1974). Use of sensory recombination and somatosensory deafferentation techniques in the investigation of sensory-motor integration. *Perception, 3,* 393–405.

Uhlarik, J. J. (1973). Role of cognitive factors on adaptation to prismatic displacement. *Journal of Experimental Psychology, 98,* 223–232.

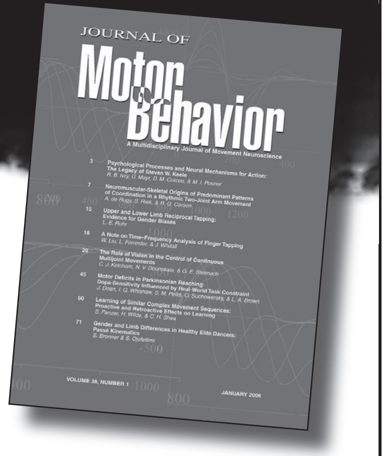
Wang, J., & Sainburg, R. L. (2005). Adaptation to visuomotor rotations remaps movement vectors, not final positions. *Journal of Neuroscience, 25,* 4024–4030.

Webster, R. G. (1969). The relationship between cognitive, motor-kinesthetic, and oculomotor adaptation. *Perception & Psychophysics, 6,* 33–38.

Welch, R. B. (1974). Research on adaptation to rearranged vision: 1966–1974. *Perception, 3,* 367–392.

Submitted February 2, 2006
Revised October 24, 2006

Subscribe Today and Access Content Online!



The *Journal of Motor Behavior* explains the basic processes and mechanisms underlying motor control, learning, and development. The journal publishes articles from such diverse disciplines as biomechanics, kinesiology, movement disorders, neuroscience, psychology, and rehabilitation. A wide variety of articles report empirical findings, mathematical and computational models, and new theories and theoretical perspectives as well as methodological and technological developments. Review essays, rapid communications of exciting new findings, and invited articles by recognized authorities are also featured.

Bimonthly; ISSN 0022-2895
Regular Annual Subscription Rates:
Individual: $100 online only, $105 print and online
Institutional: $235 online only, $235 print only, $282 print and online
Add $29 for postage outside the U.S.

heldref PUBLICATIONS

1319 Eighteenth Street, NW
Washington, DC 20036-1802
P. 800.365.9753 ■ F. 202.293.6130
P. 202.296.6267 ■ www.heldref.org

CALL OR VISIT US ONLINE TO SUBSCRIBE!

Libraries may order through subscription agents.