J Neurophysiol 111: 2554–2559, 2014.
First published March 26, 2014; doi:10.1152/jn.00326.2013.

Simultaneous adaptation of the thumb and index finger of the same hand to opposite prism displacements

Willemijn D. Schot,[1,2] Eli Brenner,[1] and Jeroen B. J. Smeets[1]
[1]*Research Institute MOVE, Faculty of Human Movement Sciences, VU University Amsterdam, Amsterdam, The Netherlands; and* [2]*Center for Motor and Cognitive Disabilities, Utrecht University, Utrecht, The Netherlands*

Submitted 6 May 2013; accepted in final form 24 March 2014

Schot WD, Brenner E, Smeets JB. Simultaneous adaptation of the thumb and index finger of the same hand to opposite prism displacements. *J Neurophysiol* 111: 2554–2559, 2014. First published March 26, 2014; doi:10.1152/jn.00326.2013.—It only takes a few goal-directed hand movements to adapt one's movements to a prism-induced displacement of the visual scene. Adaptation to the displacement leads to errors in the opposite direction from the initial displacement when the prisms are removed. Such aftereffects are thought to arise from some form of spatial realignment of the senses or from motor learning. Here, we show that humans can simultaneously adapt the movements of the thumb and index finger of the same hand to opposing visual displacements. Neither the felt position of the hand nor the visually perceived direction can change in two opposite directions at the same time, ruling out an explanation based on realignment of the senses. It is conceivable that one could learn to adjust the movements differently for the two digits despite the fact that both adjustments would involve the same hand, but such motor learning should not transfer to matching the position of the unseen digit. As transfer was observed when visually matching the position of the unseen digit, motor learning cannot explain all of the results. An explanation involving supplementing proprioception with a memory-based visual estimate of the position of each unseen digit could explain all of the results. Irrespective of the mechanism, we can conclude that it is possible to adapt the perceived locations of the unseen digits without influencing proprioception.

motor control; prism adaptation; motor learning; perceptual realignment

PRISM ADAPTATION HAS PROVIDED a fruitful and powerful paradigm for studying a wide range of phenomena such as procedural memory (Fernandez-Ruiz and Diaz 1999), upper limb control (Galea and Miall 2006), number representation (Hubbard et al. 2005), cerebellar functioning (Martin et al. 1996a; Morton and Bastian 2004), and spatial neglect (Rossetti et al. 1998). In all of these fields, a correct understanding of the process underlying prism adaptation is crucial for further progress.

Within just a few movements, people can adjust to a prism-induced displacement of the visual scene (Harris 1965). Three possible mechanisms have been put forward in the literature to explain this: realignment, motor learning, and relying on memory.

The first mechanism, realignment, is the idea that people realign their vision and proprioception so that the visually perceived position of the hand corresponds to its felt position. It is supported by observed changes in visual and proprioceptive estimates of straight-ahead after adaptation (Hatada et al. 2006; Redding and Wallace 2006) and by the transfer of adaptation aftereffects to the nonexposed hand (Choe and Welch 1974; Hamilton 1964).

The second mechanism, motor learning, is the idea that people adapt the motor commands that are applied for a specific movement. It is supported by the finding that the transfer of prism adaptation is only partial when tested at a different movement speed (Kitazawa et al. 1997), when throwing in a different manner (Martin et al. 1996b), when the hand is visible at movement initiation (Redding and Wallace 1996), or when moving with a different load (Fernandez-Ruiz et al. 2000).

The third mechanism, relying on memory, is supported by the finding that in the absence of visual feedback about the position of the hand, people reliably drift in a certain direction. Smeets et al. (2006) argued that when people move their unseen hand to a visual target, they use not only proprioception to localize their hand, but also a memory-based visual estimate of the hand position. This estimate is updated on the basis of visual information whenever people receive new visual information about the position of their hand. It is updated with efferent information about the displacement each time people move without vision of the hand, so if no new visual information is provided the visual estimate becomes less reliable each time a movement is made. If people optimally combine a proprioceptive estimate with such a memory-based visual estimate of the position of their hand, they will rely increasingly on the proprioceptive estimate when repeatedly pointing at targets without seeing their hand because each movement adds uncertainty to the visual estimate. That is why they reliably drift in a certain direction (the direction of their proprioceptive-visual mismatch). In this scheme, prism adaptation is straightforward: when looking at the hand through prisms, the visual estimate of the hand position is shifted in accordance with the visual displacement of the prism. Later, when vision of the hand is removed, the memory-based estimate still influences the judged position of the hand for some trials. The extent to which this influence transfers to other judgments depends on the extent to which those judgments rely on this memory-based information (i.e., only when vision is involved in the task; Tagliabue and McIntyre 2011).

It has previously been shown that people can simultaneously adapt their arm movements to two opposing visual displacements when each is associated with the movements of a different arm (Galea and Miall 2006; Mikaelian and Malatesta 1974; Prablanc et al. 1975). This observation can be interpreted in terms of any of the three possible mechanisms outlined above. To discriminate between the three possibilities, and to

---

Address for reprint requests and other correspondence: W. D. Schot, Center for Motor and Cognitive Disabilities, Utrecht Univ., Heidelberglaan 1, 3584 CS Utrecht, The Netherlands (e-mail: w.d.schot@uu.nl).

gain further insight into the mechanisms underlying prism adaptation in general, we performed three experiments using opposite displacements for the thumb and index finger of the right hand.

In the main experiment, we investigated whether people can concurrently adapt movements of their right arm to two opposing visual displacements (rotations of the visual image that displace the targets by ~5 cm to the left or the right; see MATERIALS AND METHODS) when the two displacements were associated with tapping opposite sides of a 2.3-cm target cube with either the right thumb or the right index finger. We found that people can indeed simultaneously adapt the movements of the digits to opposing visual displacements. Neither the felt position of the hand nor visual direction can change in two opposite directions simultaneously, so the adaptation could not have taken place at the level of the whole hand. However, the thumb and index finger of one hand could simultaneously adapt in opposite directions if the adaptation is mediated by motor learning or updating one's visual estimate of the position of each (unseen) digit. Moreover, it could have resulted from realigning the senses at the level of the individual digits, although the changes in felt joint angles would have to be quite extreme.

A transfer experiment in which participants felt the position of a cube with the digits of their adapted right hand and indicated the felt position with their unadapted left hand (haptic-haptic matching) did not show any adaptation effects, indicating that proprioceptive realignment of the individual digits does not mediate the adaptation. The lack of transfer to another task that does not require the same movement with the same digits appears to support motor learning as the mechanism of adaptation. However, it could also be regarded as support for relying on visual memory, as we may not observe any consequences of updating memory-based visual estimates in the haptic-haptic matching trials because vision is not considered at all when directly matching two proprioceptive estimates (Tagliabue and McIntyre 2011).

To distinguish further between motor learning and updating the memory-based visual position estimate of each digit, we used a second matching task in which the felt position was matched with a visual marker (visuohaptic matching). If adaptation is based on digit-specific motor learning, we do not expect to see any effect of adaptation because the task does not require the specific movements that were adapted. However, because this second matching task is no longer purely proprioceptive, the displaced visual memory trace of the unseen digit could lead to adaptation effects. There was some transfer to this task, indicating that the adaptation observed in the main experiment was a combination of motor learning and updating the memory-based visual position estimate of each digit.

MATERIALS AND METHODS

Main Experiment

Procedure. The experiment was conducted in accordance with the Declaration of Helsinki and was part of a program that was approved by the Ethics Committee of the Faculty of Human Movement Sciences of the VU University, Amsterdam. Eight participants (ages 24–47 yr, 3 men, 5 women) with no known neurological disorders took part in the experiment after giving their informed, written consent. They were wearing PLATO shutter glasses. Movements of infrared-emitting diodes attached to the fingernails of the thumb and index finger of the right hand were recorded at 250 Hz using an Optotrak 3020 system.

Participants started a trial by grasping the 2.3-cm starting cube (Fig. 1). The shutter glasses were shut. A 2.3-cm target cube was attached to a wooden board at one of three possible target locations (5 cm apart). The board obstructed the participants' vision of the hand until just before contact with the target cube. Before each trial, participants were told either to touch the left side of the target cube with their thumb or to touch the right side of the cube with their index finger. Once the shutter glasses opened, participants moved the appropriate digit to the appropriate side of the target cube.

The pre- and postadaptation phases each consisted of 15 movements with each digit. They were performed with binocular vision. During the adaptation phase, the participant made 45 movements with each digit while viewing the target monocularly through 10 diopter prism glasses that were worn over the shutter glasses. The prism in front of the left eye displaced the image of the target ~5 cm to the right and that in front of the right eye an equal amount to the left.

To cancel any unforeseen biases (left-right in relation to finger-thumb), we performed two sessions. In one session, vision was displaced to the right when tapping with the index finger and to the left when tapping with the thumb (we will use the term "thumb left" to indicate the simultaneous adaptation of the thumb in the leftward direction and the index finger in the rightward direction). In the other session, the displacements were reversed ("thumb right"). The two sessions were performed on separate days with their order counterbalanced across participants. Within each session, trials were presented in pseudorandom order, ensuring that each combi-

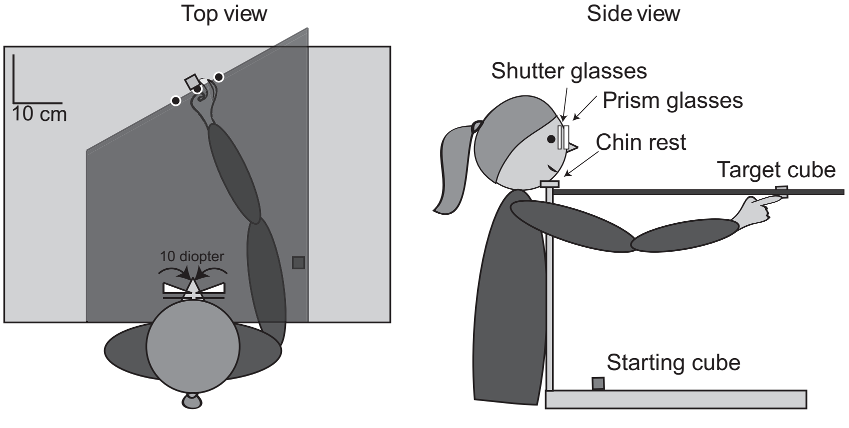

Fig. 1. Top and side views of the experimental setup. Participants made tapping movements from the starting cube to the left side of the target cube with their thumb or to the right side of the target cube with their index finger.

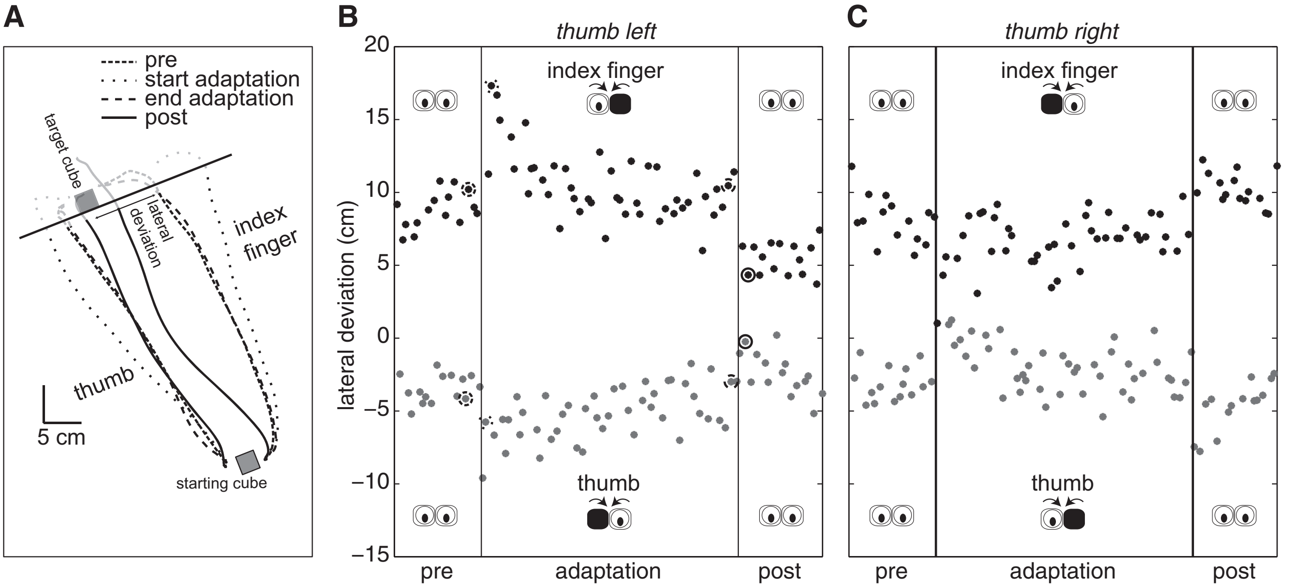

Fig. 2. Single-trial data of a typical participant. *A*: trajectories of the thumb and index finger to the left target position with thumb left adaptation. Paths are shown for the last movement to that target position in the preadaptation phase, the 1st movement to that target position in the adaptation phase, the last movement to that target position in the adaptation phase, and the 1st movement to that target position in the postadaptation phase. Lateral deviation is calculated 1 cm before the infrared-emitting diodes reach the end of the board (ends of black lines). The gray lines show how the movements proceed until the 1st minimum in the velocity profile. In the postadaptation phase, the thumb hits the bottom of the target cube, and the index finger hits the side of the target cube (supposedly earlier than the participant had anticipated), causing the finger to "slide off." *B* and *C*: time course of adaptation of the same participant. Circled trials are the ones drawn in *A*. Opposite patterns of shifts are observed when vision of the index finger was displaced to the right and vision of the thumb to the left (thumb left) and for the opposite combination of displacement and digit (thumb right). Simultaneous adaptation to both displacements is observed for both combinations of displacement and digit.

nation of digit and target location was presented once every six trials.

Data analysis. To make sure that we had a measure of digit position for each trial that is not influenced by movement corrections based on visual or tactile feedback during that trial, we based our analysis on the marker position 1 cm before it crossed the far edge of the board. We determined the lateral position of the active digit at that time relative to the center of the target cube. The distance between the two, along the edge of the board, was determined for each trial (see example trial in Fig. 2*A*). For both the thumb and the index finger, we subtracted the values obtained in the session with the rightward displacement (thumb right and thumb left for the thumb and index finger, respectively) from those obtained in the session with the leftward displacement (thumb left and thumb right for the thumb and index finger, respectively) and divided these values by two (this is the average deviation shown in Fig. 3*A*).

We calculated the adaptation effect by taking the difference between the median lateral deviation over all trials of the preadaptation phase and the median lateral deviation over the first six trials of the postadaptation phase. This adaptation effect itself is not a good indicator of how much subjects are adapted as the effect of an actual 5-cm target displacement on the finger movements is likely to be <5 cm and to differ between subjects (Franz 2003). We therefore determined a corrected adaptation effect by dividing the adaptation effect by the effect that one finds for a real displacement of the same size as the perturbation (either 5 or -5 cm) so that a value of one indicates complete adaptation (this is the corrected adaptation effect shown in Fig. 3*B*). For this division, we determined the lateral deviation that is found with an actual 5-cm target displacement by comparing the

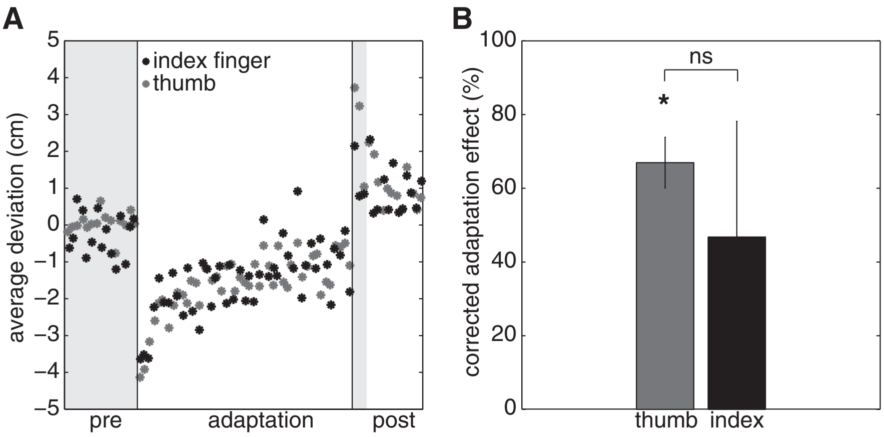

Fig. 3. Average performance of all participants in the main experiment. *A*: time course of adaptation, averaged across the 2 sessions. Negative values are in the direction of the visual displacement. Shaded areas indicate the trials used to calculate the corrected adaptation effect. *B*: corrected adaptation effects (for details about the measures, see MATERIALS AND METHODS). *Statistically significant; ns, not significant.

movements to different target positions for each participant and digit. We tested whether the corrected adaptation effect was significantly larger than zero using one-tailed, one-sample *t*-tests (for each digit separately) and whether there was a difference between the corrected adaptation effects for the two digits using a two-tailed, paired-sample *t*-test.

Transfer Experiments

Procedure. The transfer experiments consisted of two types of trials: touch trials, that were identical to those in the main experiment, and matching trials. For the matching trials, the target cubes were attached underneath the board, 10 cm closer to the participant than the three positions used for the touch trials. This way, participants could match the felt position of the cube below the board with a matching cube above the board without ever seeing the adapted hand. The matching cube had the same width and depth as the target cube and was either hand-held (haptic-haptic matching) or remotely controlled (visuohaptic matching).

Two groups of eight participants took part in the transfer experiments. The first group (haptic-haptic matching group, ages 25–43 yr, 5 women, 3 men) performed 30 touch trials followed by 30 haptic-haptic matching trials in the preadaptation phase. They then performed 60 thumb right adaptation trials (where vision was displaced to the right when viewing the thumb and to the left when viewing the index finger) followed by a postadaptation phase of 30 haptic-haptic matching trials and finally 6 touch trials. During haptic-haptic matching trials, the shutter glasses did not open, so the subject did not receive visual information about the position of either of his or her hands. The experimenter brought either the thumb or the index finger of the participant's right hand to the appropriate side of the target cube. The participant's task was to place the matching cube that he or she held in his or her left hand on the board directly above the target cube that he or she felt with either the index finger or the thumb of his or her right hand. When the participant indicated that he or she was satisfied with the match, the experimenter recorded the positions of both cubes.

The second group (visuohaptic matching group, ages 24–30 yr, 3 women, 5 men) performed 30 touch trials followed by 18 visuohaptic matching trials in the preadaptation phase. They then performed 60 thumb left adaptation trials (where vision was displaced to the left when viewing the thumb and to the right when viewing the index finger) and then a postadaptation phase of 18 visuohaptic matching trials followed by 6 touch trials. During visuohaptic matching trials, the experimenter brought either the thumb or the index finger of the participant's right hand to the appropriate side of the target cube underneath the board. The matching cube was now attached to a string that was strung around the board in such a manner that the cube could be moved by pulling on the string with the left hand close to the body (pulling the left part of the loop downward moved the cube to the left, and pulling the right part of the loop downward moved the cube to the right). When the digit was touching the target cube, the shutter glasses opened (both eyes), and the participant's task was to align the visible matching cube attached to the string with the target cube that he or she felt with his or her right hand underneath the board. When the participant indicated that he or she was satisfied with the match, the experimenter recorded the positions of both cubes.

Data analysis. To make sure that people could in fact simultaneously adapt the movements of the thumb and index finger of the same hand to opposing visual displacements, we took the touch data (analyzed in the same way as for the main experiment) of all 16 participants and tested whether the corrected adaptation effects of the thumb and the index finger were significantly larger than 0 using 2 1-tailed, 1-sample *t*-tests. We also tested whether the amount of adaptation was different for the 2 digits using a 2-tailed, paired-sample *t*-test. Because each participant only did either the thumb right or thumb left adaptation, instead of subtracting the leftward from the rightward displacements for each digit, we just calculated the percentage of the corrected adaptation effect for each digit.

The corrected adaptation effect during haptic-haptic and visuohaptic matching trials was calculated in an analogous manner to the effect in the touch trials. Adaptation effects in the haptic-haptic matching trials were corrected for matching errors in depth by extrapolating all positions along a line from the estimated position between the two eyes until they intersect with the edge of the board. These intersection points were used in further calculations. Such a correction was not necessary for the visuohaptic matching trials as the matching cube was constrained in depth by the string.

We tested whether adaptation effects were significantly larger than zero with one-tailed, one-sample *t*-tests and whether there were systematic differences between the adaptation effects between the touch and the matching tasks with two-tailed, paired-sample *t*-tests.

RESULTS

Providing monocular vision through a differently oriented prism for each digit initially made participants make the expected errors (Figs. 2 and 3), but they quickly adapted to the opposing visual displacements so that performance shifted toward their baseline performance during the preadaptation phase, although it never quite reached such performance. When the prisms were removed, the movements of both digits diverted in the opposite directions from the initial errors even though participants knew that the prisms had been removed, an aftereffect indicating that the improved performance was based on adaptation rather than on a strategic process (Welch et al. 1993).

The amount of adaptation of the thumb and the index finger was not significantly different [$t(7) = 0.698$, $P = 0.508$; Fig. 3*B*], but although the corrected adaptation effect was clearly significantly larger than zero for the thumb [67 ± 7%, $t(7) = 9.78$, $P < 0.001$], there was only a trend for it to be larger than zero for the index finger [47 ± 31%, $t(7) = 1.49$, $P = 0.09$].

Transfer Experiments

In the main experiment, we investigated whether people could adapt the movements of the thumb and index finger of the same hand to opposing visual displacements. It seems that they can: the amount of adaptation did not differ between the digits, although the adaptation of the index finger only showed a trend in the expected direction. We proceeded with two more experiments with two aims: first, to replicate our finding that people could simultaneously adapt the movements of the thumb and index finger of the same hand to opposing visual displacements; and second, to investigate the transfer of the adaptation to two other tasks. To achieve these goals, we replicated the main experiment, introducing a second task before and after the adaptation phase of the touch task to measure the transfer to other tasks (matching).

Replication. The results of the combined touch trials in both transfer experiments (irrespective of the matching task) confirmed that both the movements of the thumb [35 ± 9%, $t(15) = 3.805$, $P = 0.001$] and the index finger [39 ± 8%, $t(15) = 4.656$, $P < 0.001$] adapted to the visual displacement (Fig. 4*A*). Again, there was no significant difference between the amount of adaptation of the thumb and the index finger [$t(15) = 0.311$, $P = 0.760$]. That the nonsignificant difference

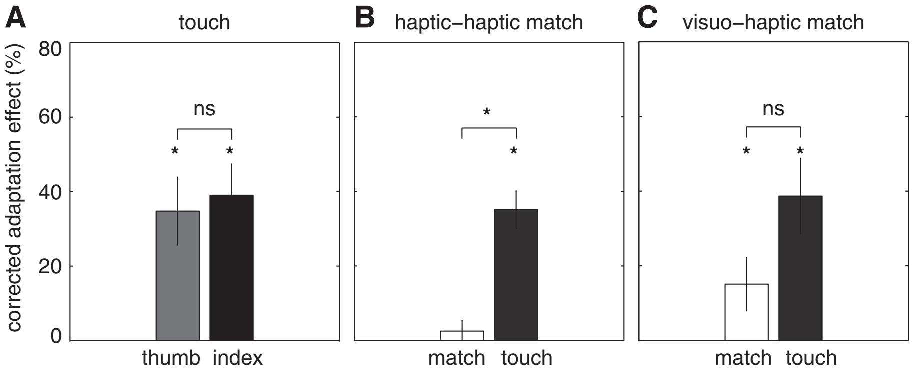

Fig. 4. Corrected adaptation effects in the 2 transfer experiments. *A*: results of the touch trials of both experiments for each digit. *B* and *C*: results of the haptic-haptic and visuohaptic matching experiments. *Statistically significant.

was in the opposite direction from the nonsignificant difference in the main experiment (slightly less rather than more adaptation for the thumb) is evidence that the digits adapt about equally. Therefore, for further analysis of the transfer experiments, we averaged the adaptation effects of the thumb and index finger.

Haptic-haptic matching. The adaptation during touch trials did not systematically influence haptic-haptic matching [3 ± 3%, $t(7) = 0.857$, $P = 0.21$; Fig. 4*B*]. This is not due to a lack of adaptation since the aftereffect was clearly present in the touch trials performed after the haptic matching trials [35 ± 5%, $t(7) = 7.031$, $P < 0.001$]. The amount of adaptation in the touch trials is significantly higher than in the match trials [$t(7) = 8.128$, $P < 0.001$].

Visuohaptic matching. The adaptation during touch trials did influence visuohaptic matching significantly [15 ± 7%, $t(7) = 2.110$, $P = 0.037$; Fig. 4*C*]. The aftereffect was also present in the touch trials performed after the haptic matching trials [39 ± 10%, $t(7) = 3.824$, $P = 0.004$]. The amount of adaptation in the touch trials is not significantly different from the amount of adaptation in the matching trials [$t(7) = 1.577$, $P = 0.159$] despite the apparent difference between the mean values. This suggests that although adaptation during touch trials influenced visuohaptic matching systematically, the extent to which it did so differed strongly between participants. Perhaps subtle differences between the tasks, and between how individuals performed the tasks, reduced the transfer to different extents in different participants. This interpretation is supported by the fact that we did not find a positive correlation between participants' aftereffects in the matching trials and in the touch trials [$r(6) = -0.49$, $P = 0.22$].

DISCUSSION

We showed that participants could adapt movements of the digits of the same hand to prisms with different orientations. Prism adaptation is frequently explained by realignment of people's visually perceived directions with the felt position of their hand to ensure that the visually perceived position of the hand corresponds to its felt position. The design of the current study rules out such an explanation for the data presented here. Although the adaptation was performed while viewing with a single eye, participants saw the target cube with both eyes during the postadaptation phase, so the simultaneous adaptation in opposite directions for the two digits cannot be mediated by eye-dependent changes in the judged visual direction of the target cube. Also, since the same hand made similar movements when tapping with the index finger as when tapping with the thumb, the adaptation cannot be mediated by changes in the felt position of the hand. In principle, realignment could have taken place in the joints of the individual digits, but the absence of transfer to the haptic-haptic matching task shows that this is not the case.

The results of the visuohaptic matching experiment show that there is at least some transfer from touch trials to the visuohaptic matching trials. As these matching trials did not involve any active movement of the right hand of the participants, such transfer cannot be explained by motor learning. Therefore, we conclude that adaptation is at least partly mediated by memory-based visual position estimates of the right hand having been updated. The observation that the average adaptation effect in the matching trials is considerably lower than in the touch trials yet the difference between the adaptation effects in the touch trials and matching trials is not significant shows that there is considerable between-subject variability in the amount of transfer. There are several possible reasons for such variability. Some participants may have mainly updated memory-based visual position estimates of the unseen digits to cope with the visual displacements, whereas others may have mainly relied on motor learning. Alternatively, for some subjects, the adaptation might have been more constrained to a specific area of the workspace than for others (Ghahramani et al. 1996; Krakauer et al. 2000). Whatever the reason, the results demonstrate that the idea that when vision of the hand is removed, people combine proprioceptive estimates of the position of their hand with memory-based visual information does not only explain the drift that is observed when moving to visual targets with an unseen hand, as demonstrated in the Smeets et al. (2006) paper, but also is applicable to prism adaptation, as suggested in the discussion of that paper.

GRANTS

This research was funded by Netherlands Organisation for Scientific Research Maatschappij- en Gedragswetenschappen (NWO/MaGW) under Grants 400-03-021 and 453-08-004.

DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the author(s).

AUTHOR CONTRIBUTIONS

W.D.S., E.B., and J.B.J.S. conception and design of research; W.D.S. performed experiments; W.D.S. analyzed data; W.D.S., E.B., and J.B.J.S.

interpreted results of experiments; W.D.S. prepared figures; W.D.S. drafted manuscript; W.D.S., E.B., and J.B.J.S. edited and revised manuscript; W.D.S., E.B., and J.B.J.S. approved final version of manuscript.

REFERENCES

Choe CS, Welch RB. Variables affecting the intermanual transfer and decay of prism adaptation. *J Exp Psychol* 102: 1076–1084, 1974.

Fernandez-Ruiz J, Diaz R. Prism adaptation and aftereffect: specifying the properties of a procedural memory system. *Learn Mem* 6: 47–53, 1999.

Fernandez-Ruiz J, Hall-Haro C, Diaz R, Mischner J, Vergara P, Lopez-Garcia JC. Learning motor synergies makes use of information on muscular load. *Learn Mem* 7: 193–198, 2000.

Franz VH. Planning versus online control: dynamic illusion effects in grasping? *Spat Vis* 16: 211–223, 2003.

Galea JM, Miall RC. Concurrent adaptation to opposing visual displacements during an alternating movement. *Exp Brain Res* 175: 676–688, 2006.

Ghahramani Z, Wolpert DM, Jordan MI. Generalization to local remappings of the visuomotor coordinate transformation. *J Neurosci* 16: 7085–7096, 1996.

Hamilton CR. Intermanual transfer of adaptation to prisms. *Am J Psychol* 77: 457–462, 1964.

Harris CS. Perceptual adaptation to inverted, reversed, and displaced vision. *Psychol Rev* 72: 419–444, 1965.

Hatada Y, Rossetti Y, Miall RC. Long-lasting aftereffect of a single prism adaptation: shifts in vision and proprioception are independent. *Exp Brain Res* 173: 415–424, 2006.

Hubbard EM, Piazza M, Pinel P, Dehaene S. Interactions between number and space in parietal cortex. *Nat Rev Neurosci* 6: 435–448, 2005.

Kitazawa S, Kimura T, Uka T. Prism adaptation of reaching movements: specificity for the velocity of reaching. *J Neurosci* 17: 1481–1492, 1997.

Krakauer JW, Pine ZM, Ghilardi MF, 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, Thach WT. Throwing while looking through prisms. I. Focal olivocerebellar lesions impair adaptation. *Brain* 119: 1183–1198, 1996a.

Martin TA, Keating JG, Goodkin HP, Bastian AJ, Thach WT. Throwing while looking through prisms. II. Specificity and storage of multiple gaze-throw calibrations. *Brain* 119: 1199–1211, 1996b.

Mikaelian HH, Malatesta V. Specialized adaptation to displaced vision. *Perception* 3: 135–139, 1974.

Morton SM, Bastian AJ. Prism adaptation during walking generalizes to reaching and requires the cerebellum. *J Neurophysiol* 92: 2497–2509, 2004.

Prablanc C, Tzavaras A, Jeannerod M. Adaptation of the two arms to opposite prism displacements. *Q J Exp Psychol* 27: 667–671, 1975.

Redding GM, Wallace B. Adaptive spatial alignment and strategic perceptual-motor control. *J Exp Psychol Hum Percept Perform* 22: 379–394, 1996.

Redding GM, Wallace B. Generalization of prism adaptation. *J Exp Psychol Hum Percept Perform* 32: 1006–1022, 2006.

Rossetti Y, Rode G, Pisella L, Farne A, Li L, Boisson D, Perenin MT. Prism adaptation to a rightward optical deviation rehabilitates left hemispatial neglect. *Nature* 395: 166–169, 1998.

Smeets JB, van den Dobbelsteen JJ, de Grave DD, van Beers RJ, Brenner E. Sensory integration does not lead to sensory calibration. *Proc Natl Acad Sci USA* 103: 18781–18786, 2006.

Tagliabue M, McIntyre J. Necessity is the mother of invention: reconstructing missing sensory information in multiple, concurrent reference frames for eye-hand coordination. *J Neurosci* 31: 1397–1409, 2011.

Welch RB, Bridgeman B, Anand S, Browman KE. Alternating prism exposure causes dual adaptation and generalization to a novel displacement. *Percept Psychophys* 54: 195–204, 1993.