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

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Keywords: Motor control, prism adaptation, motor learning, perceptual realignment

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Abstract

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 than 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 matching the unseen digit’s position visually, motor learning cannot explain all the results. An explanation involving supplementing proprioception with a memory-based visual estimate of the position of each unseen digit could explain all 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.
Introduction

Prism adaptation has provided a fruitful and powerful paradigm for studying a wide range of phenomena such as procedural memory (Fernandez-Ruiz & Diaz, 1999), upper limb control (Galea & Miall, 2006), number representation (Hubbard, Piazza, Pinel, & Dehaene, 2005), cerebellar functioning (Martin, Keating, Goodkin, Bastian, & Thach, 1996a; Morton & Bastian, 2004) and spatial neglect (Rossetti et al., 1998). In all 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, Rossetti, & Miall, 2006; Redding & Wallace, 2006) and by the transfer of adaptation aftereffects to the non-exposed hand (Choe & 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, Kimura, & Uka, 1997), when throwing in a different manner (Martin, Keating, Goodkin, Bastian, & Thach, 1996b), when the hand is visible at movement
initiation (Redding & 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 do not only use proprioception to localize their hand, but also a memory-based visual estimate of the hand’s 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’s position is shifted in accordance with the prism’s visual displacement. 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 & 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 & Miall, 2006; Mikaelian & Malatesta, 1974; Prablanc, Tzavaras, & Jeannerod, 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 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 about 5 cm to the left or the right; see 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 digits’ movements 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 un-adapted 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 (Tagliaube & McIntyre, 2011).

To further distinguish 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 (visuo-haptic 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

Eight participants (age 24-47, 3 males, 5 females) with no known neurological disorders took part in the experiment after giving their informed 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 (Figure 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 post-adaptation 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 about 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 pseudo-random order, ensuring that each combination 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 active digit’s lateral position 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 Figure 2a). 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 figure 3a).

We calculated the adaptation effect by taking the difference between the median lateral deviation over all trials of the pre-adaptation phase and the median lateral deviation over the first six trials of the post-adaptation 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 less than 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 1 indicates complete adaptation (this is the corrected adaptation effect shown in figure 3b). For this division, we determined the lateral deviation that is found with an actual 5 cm target displacement by comparing the movements to different target positions for each participant and digit.

We tested whether the corrected adaptation effect was significantly larger than 0 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 (visuo-haptic matching).

Two groups of eight participants took part in the transfer experiments. The first group (haptic-haptic matching group, age 25-43, 5 females, 3 males) performed 30 touch trials, followed by 30 haptic-haptic matching trials in the pre-adaptation 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 post-adaptation 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 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 they held in their left hand on the board directly above the target cube that they felt with either the index finger or the thumb of their 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 (visuo-haptic matching group, age 24-30, 3 females, 5 males) performed 30 touch trials, followed by 18 visuo-haptic matching trials in the pre-adaptation 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 post-adaptation phase of 18 visuo-haptic matching trials followed by 6 touch trials. During visuo-haptic 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 they felt with their 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 two one-tailed one-sample t-tests. We also tested whether the amount of adaptation was different for the two digits using a two-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 visuo-haptic 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 visuo-haptic matching trials as the matching cube was constrained in depth by the string.

We tested whether adaptation effects were significantly larger than 0 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 (Figure 2 and Figure 3), but they quickly adapted to the opposing visual displacements so that performance shifted towards their baseline performance during the pre-adaptation phase, although it never quite reached such performance. When the prisms were removed, the movements of both digits
diverted in the opposite directions than 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, Bridgeman, Anand, & Browman, 1993).

**Figure 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 pre-adaptation phase, the first movement to that target position in the adaptation phase, the last movement to that target position in the adaptation phase, and the first movement to that target position in the post-adaptation phase. Lateral deviation is calculated 1 cm before the IREDs reach the end of the board (ends of black lines). The grey lines show how the movements proceed until the first minimum in the velocity profile. In the post adaptation-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.

The amount of adaptation of the thumb and the index finger was not significantly different ($t(7)=0.698$, $p=.508$, Figure 3b), but although the corrected adaptation effect was clearly significantly larger than 0 for the thumb ($67\pm7\%$, $t(7)=9.78$, $p<.001$), there was only a trend for it to be larger than 0 for the index finger ($47\pm31\%$, $t(7)=1.49$, $p=.09$).
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 aimed at two things: 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%, $t(15)=3.805$, $p=.001$) and the index finger (39±8%, $t(15)=4.656$, $p<.001$) adapted to the visual displacement (Figure 4a). Again, there was no significant difference between the amount of adaptation of the thumb and the index finger ($t(15)=0.311$, $p=.760$). That the non-significant difference was in the opposite direction than the non-significant 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.

**Figure 4** Corrected adaptation effects in the two transfer experiments. **a.** Results of the touch trials of both experiments for each digit. **b-c.** Results of the haptic-haptic and visuo-haptic matching experiments.

**Haptic-haptic matching**

The adaptation during touch trials did not systematically influence haptic-haptic matching (3±3%, $t(7)=0.857$, $p=.21$, Figure 4b). 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%, $t(7)=7.031$, $p<.001$). The amount of adaptation in the touch trials is significantly higher than in the match trials ($t(7)=8.128$, $p<.001$).
Visuo-haptic matching

The adaptation during touch trials did influence visuo-haptic matching significantly (15±7%, t(7)=2.110, p=.037, Figure 4c). The aftereffect was also present in the touch trials performed after the haptic matching trials (39±10%, t(7)=3.824, p=.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=.159), despite the apparent difference between the mean values. This suggests that although adaptation during touch trials influenced visuo-haptic 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) = -.49, p = .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 post-adaptation 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 visuo-haptic matching experiment show that there is at least some transfer from touch trials to the visuo-haptic 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, Wolpert, & Jordan, 1996; Krakauer, Pine, Ghilardi, & Ghez, 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. paper (2006), but is also applicable to prism adaptation, as suggested

 in the discussion of that paper.


Acknowledgments

This research was funded by NWO/MaGW under grant number 400-03-021 and 453-08-

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References


Figure Captions

Figure 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.

Figure 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 pre-adaptation phase, the first movement to that target position in the adaptation phase, the last movement to that target position in the adaptation phase, and the first movement to that target position in the post-adaptation phase. Lateral deviation is calculated 1 cm before the IREDs reach the end of the board (ends of black lines). The grey lines show how the movements proceed until the first minimum in the velocity profile. In the post adaptation-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.

Figure 3 Average performance of all participants in the main experiment. A. Time course of adaptation, averaged across the two 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 the methods section).
Figure 4 Corrected adaptation effects in the two transfer experiments. a. Results of the touch trials of both experiments for each digit. b-c. Results of the haptic-haptic and visuo-haptic matching experiments.
(a) Diagram showing pre and post adaptation stages with lines indicating lateral deviation. (b) Graph showing lateral deviation (cm) for thumb left and index finger in pre, adaptation, and post phases. (c) Similar graph for thumb right.
a touch

b haptic–haptic match

c visuo–haptic match

corrected adaptation effect (%)

- thumb
- index

match touch

* * ***

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