Visuomotor Adaptation: Dependency on Motion Trajectory

Christian Kaernbach[1], Lutz Munka[1], and Douglas Cunningham[2]

[1] Institut für Allgemeine Psychologie, Universität Leipzig
[2] Max-Planck Institut für Biologische Kybernetik, Tübingen
Christian@Kaernbach.de

Abstract. The present contribution studies the rapid adaptation process of the visuomotor system to optical transformations (here: shifting the image horizontally via prism goggles). It is generally believed that this adaptation consists primarily of recalibrating the transformation between visual and proprioceptive perception. According to such a purely perceptual account of adaptation, the exact path used to reach the object should not be important. If, however, it is the transformation from perception to action that is being altered, then the adaptation should depend on the motion trajectory. In experiments with a variety of different motion trajectories we show that visuomotor adaptation is not merely a perceptual recalibration. The structure of the motion (starting position, trajectory, end position) plays a central role, and even the weight load seems to be important. These results have strong implications for all models of visuomotor adaptation.

1 Introduction

In order to pick up an object, its visual location must be converted into the appropriate motor commands. Introducing an optical transformation (e.g., shifting the image horizontally via prism goggles) initially impairs this ability. The visuomotor system rapidly adapts to the discrepancy, however, returning performance to near normal.

von Helmholtz (1867), who was among the first to describe prism adaptation, reported that if one hand was active during adaptation, the other hand would also show an adaptation effect. It has by now often been demonstrated that intermanual transfer of adaptation is either very small or non-existent[1]. It is really quite striking that both hands have to adapt independently from each other. Consequently, prism adaptation can not be fully explained by "recalibrating" only visual perception so as to represent the seen location of an object correctly in spite of the prism goggles. However, this does not rule out a purely perceptual account of adaptation: the recalibration could

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[1] Some studies (e.g. Choe and Welch, 1974) report intermanual transfer of adaptation. It is not clear, however, in how far this might be due to cognitive strategies. If participants are either ignorant of the effect of the goggles or repeatedly instructed to base their actions on their actual perception and not on cognitive strategies, intermanual transfer of adaptation is generally absent.

affect the proprioceptive perception of spatial location, i.e. the felt position of the arm. The proprioception of the active limb would have adapted while the proprioception of the passive limb would show no adaptation effects.

This notion of “perceptual learning” (e.g. Bedford, 1999) is seductive. As long as it is only the perceptual input that is recalibrated it is conceivable that spatial knowledge is represented centrally, in a kind of master data base, with all sensory systems providing calibrated spatial information. This data base would then in turn serve to provide the motor scripts with coordinate information of the objects that are to be dealt with. The performance difference for the active and the passive limb would be due to the different calibration status of the proprioceptive input to the central spatial representation from these limbs.

A central representation of spatial knowledge agrees well with the introspectively felt unity of phenomenal experience. However, it has been shown that phenomenal experience is not prerequisite for correct visuomotor behavior. Stratton (1897) has shown that wearing inverting goggles (turning the image 180°) perfect visuomotor coordination could be obtained within a few days. Phenomenally, however, the world was still upside down. It is still a matter of debate whether after a week or two phenomenal experience would also adapt; the important point here is that there is evidence for a dissociation between visuomotor and phenomenal adaptation. Comparable results were reported by Kohler (1951). On a similar line of thought evidence from blindsight cases (Pöppel et al., 1973) put into question the relevance of phenomenal experience for visuomotor functioning.

If visuomotor adaptation depends not only on the (active versus passive) limb but also on the exact motor trajectory, then a central representation of spatial knowledge would be less tenable. Instead, spatial knowledge would then be more easily and parsimoniously explained as distributed knowledge, closely related to a variety of possible motor scripts. Some initial evidence for such a dependency comes from Martin et al. (1996) who demonstrated that there was no transfer of adaptation from underhand to overhand throwing. Here, we examine this effect with the well-studied pointing task, as well as with types of movements that are more closely related than underhand and overhand throwing.

2 Experiment 1: Reaching Below/Above a Bar

Instead of measuring the adaptation effect directly, it has become common practice to measure the Negative Aftereffect (NAE), comparing motor performance before and after adaptation to prism goggles. It represents an excellent measure of adaptation as it compares two absolutely identical situations (unaltered vision) so that all observable changes in motor performance can only be due to the adaptation to the prism goggles that occurred in the meantime.

In Experiment 1 we measured the NAE for two different types of trajectories: Participants (N=72) had to touch a cross presented at eye level on a touch screen 30 cm in front of them. Two different trajectories were possible: reaching to the cross from below or (swinging the arm backwards) from above the horizontally extending bar that served as chin rest (Fig. 1). Location performance without feedback was determined for both trajectories of both hands before and after adaptation of a single trajectory of one hand to prism goggles (17° horizontal displacement). Testing was done on centrally located targets, while adaptation took place at horizontally displaced targets.

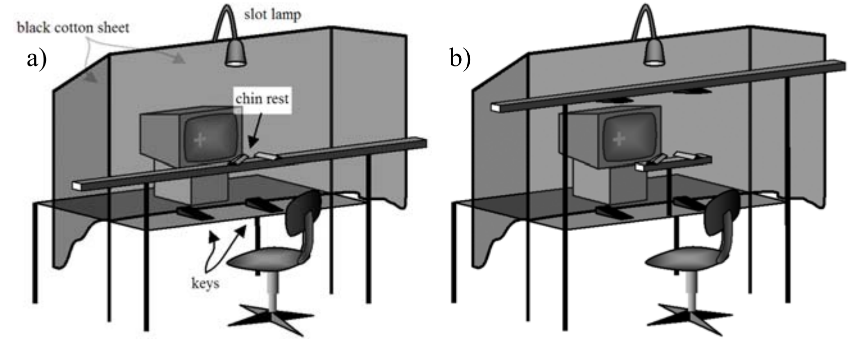

Fig. 1. a) Setup for Experiment 1. A thin black cotton sheet was hung in front of the touch screen, and the room light was shut off, with a dim slot lamp illuminating the hand while touching the screen. This procedure prevented additional visual cues whilst not hampering touching the screen or seeing the bright cross. b) The horizontally extending bar that served as chin rest was reduced in size for Experiments 2 to 6 so as to support the chin without hampering the more sweeping motions of those experiments. The top bar was used in Experiment 2.

The NAE was compatible with zero for both trajectories of the unadapted hand. This confirms the well-known finding that there is no intermanual transfer. More importantly, the NAE was significantly different for the adapted trajectory (46mm, 8.7°) as compared to the other trajectory of the same hand (26mm, $p<0.01$). That is, despite the fact that the starting positions were identical and end positions very similar, there was only partial *intramanual* transfer. The fact that there was partial transfer, rather than the complete absence of transfer found with overhand versus underhand throwing, reflects the greater similarity of the motions used here.

3 Experiment 2: Pointing from Different Starting Positions

While in Experiment 1 the starting position was identical for both types of trajectories, the end positions were slightly different. In order to exclude the possibility that this caused the weak intramanual transfer, Experiment 2 was run using different starting positions and identical end positions. The setup differed from that of Experiment 1 in that the chin rest did not extend horizontally, and there was a horizontal bar mounted 90 cm above the table, with two additional keys mounted beneath that bar. Participants (N=21) performed a total of 45 sessions, starting the pointing movement either at a low (desktop key) or a high position (key mounted beneath top bar). Location performance without feedback was determined for both starting positions before and after adaptation to a single starting position while wearing prism goggles. – The NAE was again significantly different for the adapted starting position (80 mm) as compared to the other starting position (51 mm, $p<0.01$).

4 Experiment 3: Interposing Inward/Outward Circles

In Experiments 1 and 2, either the starting positions or the end positions differed. In Experiment 3, participants (N=14, performing a total of 32 sessions) started the pointing movement at the same position (at the key on the desk top), and ended it with the same end position. Instead of moving their hand directly from the key to the cross, they had to interpose an inward or outward circular movement. They were instructed to circumscribe a region “the size of a head”, like writing a kind of “O” in the air, after releasing the key, and before touching the screen. Location performance without feedback was determined for both trajectories before and after adaptation to a single trajectory while wearing prism goggles. – Even with identical starting and end positions, the NAE was significantly different for the adapted trajectory (59 mm) as compared to the other trajectory (49 mm, $p<0.01$). The difference is, however, smaller than in Experiments 1 and 2: The NAE for the two trajectories differed by 17%, whereas the difference was around 40% in the other two experiments.

5 Experiment 4: Pointing with/without a Weighted Wristband

In Experiments 1 to 3, trajectories differed. In Experiment 4, transfer of adaptation was studied for *exactly the same trajectory*, varying this time the load of the moving arm by applying a weighted wrist band (440 g) in some of the trials. Participants (N=11) performed a total of 36 sessions. Again, location performance without feedback was determined for both conditions before and after adaptation to a single condition while wearing prism goggles. – Varying only the load of the moving arm, the NAE was again significantly different for the adapted condition (55 mm) as compared to the other condition (44 mm, $p<0.05$). The NAEs differed by about 22%.

6 Experiment 5: Generalization to Vertically Distributed Targets

In Experiments 1 to 4, we made use of the fact that adaptation generalizes horizontally: Participants adapted to targets that were to the side of the centrally located targets used in the pre- and post-tests (see methods of Experiment 1). Generalization of adaptation horizontally to other targets has been demonstrated before (Bedford, 1993). As prism goggles displace the image horizontally, this is not too surprising. By the same token, it is not necessarily clear that adaptation will generalization vertically. In Experiment 5, participants (N=14, performing 20 sessions) adapted to a high target position, or to a low position, or alternately to both these positions. Their location performance before and after adaptation was tested at a high, a medium and a low target position. In order to obtain a good separation (30 cm, corresponding to 53° visual angle) between high and low target positions, the monitor was rotated 90°.

Figure 2 shows the results. When adapting to the high target position, this condition showed the largest NAE, with a gradual decrease of the NAE as the tested position departs from the adapted one. The differences between testing the high target position and the other two target positions is significant ($p<0.05$). The same trend is present when adapting to the lower target position, although this trend did not reach significance. When adapting alternately to both high and low target positions, no significant differences are to be found.

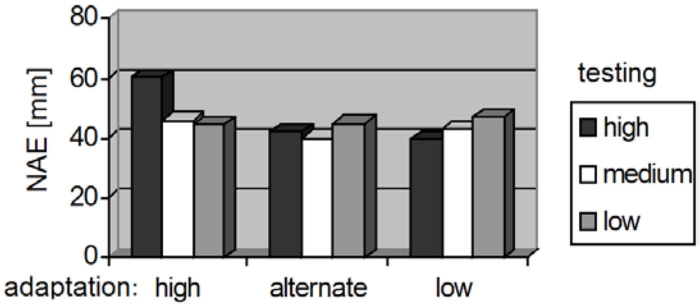

Fig. 2. Results of Experiment 5. NAE as a function of adapted and tested target position.

As can be seen in Fig. 2, generalization for vertically distributed targets is not perfect. The effect is, however, too small to be evaluated well within the distances that can be realized on a rotated touch screen. Future experiments will include target positions outside the touch screen area.

7 Experiment 6: Effect of Terminal/Full Feedback

In a final experiment we assessed the effect of feedback and the speed of adaptation. In the previous experiments, adaptation took place under “full feedback”, i.e. the participants could watch their hand as it moved towards the target. Under full feedback, participants usually produce only small location errors, correcting errors of the ballistic part of the motion while approaching the screen. These data do not allow analysis of the dynamics of the adaptation process. In Experiment 6, participants (N=19, performing 28 sessions) adapted either alternately under full feedback and under no feedback (with the no-feedback trials yielding information on the state of the adaptation), or under “terminal feedback”: In this condition, the lamp went off when the participant released the key, and went on again when the screen was touched. We reasoned that under terminal feedback the participant would realize the true mistake of the ballistic movement which would be obscured under full feedback due to the possibility to correct the movement “on the fly”. We expected that terminal feedback would induce a stronger adaptation effect. – Figure 3 reveals that indeed terminal feedback induces a stronger NAE than full feedback ($p<0.01$). The initial adaptation speed seems not to be affected, but the final adaptation level is greater after terminal feedback.

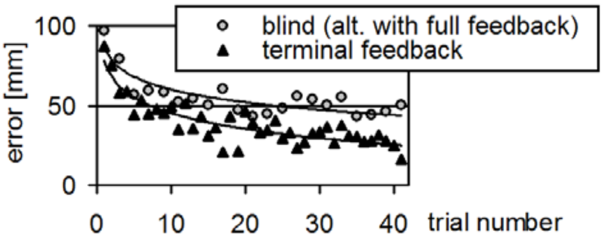

Fig. 3. Results of Experiment 6. Location error during adaptation session as a function of trial number and feedback condition.

Conclusion

Our data demonstrate that, in a variety of cases, spatial adaptation is motor specific: *Knowing where is knowing how to* (see also the reinterpretation of the *what* and *where* systems by Milner and Goodale, 1995). While spatial knowledge seems to be distributed, we nonetheless phenomenally experience it as a unitary entity. Even if “left arm knowledge” differs from “right arm knowledge” (due, e.g., to adaptation of one arm), we do not perceive any ambiguity when seeing an object. The cause of this dissociation might be elucidated by considering the purpose served by the experienced unity of spatial knowledge. Phenomenal experience is a late product of evolution, enabling the individual to plan coherent sequences of actions (and anticipate their consequences), as has e.g. been demonstrated with rats (Tolman, 1948). For such a purpose it would probably be cumbersome to be aware of the fragmentation of spatial knowledge, including possible inconsistencies. Simple aim-directed reactions to visual input (as in pointing or grasping) have developed earlier and are apparently implemented independently at a level closely related to motor performance.

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