

Adaptation of eye and hand movements to target displacements of different size

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Abstract Previous work has documented that the direction of eye and hand movements can be adaptively modified using the double-step paradigm. Here we report that both motor systems adapt not only to small direction steps (5° gaze angle) but also to large ones (28° gaze angle). However, the magnitude of adaptation did not increase with step size, and the *relative* magnitude of adaptation therefore decreased from 67% with small steps to 15% with large steps. This decreasing efficiency of adaptation may reflect the participation of directionally selective neural circuits in double-step adaptation.

Keywords Saccades · Arm movements · Motor learning · Adaptation · Double step

Introduction

The double-step paradigm is an established method for evaluating the adaptive plasticity of the sensorimotor system: visual targets are presented in one location first, and are displaced in a consistent fashion shortly thereafter. Subjects initially aim their responses toward the first target

location and correct them thereafter; with ongoing practice, however, responses are adaptively modified and the need for corrections decreases. Adaptive changes have been documented with the double-step paradigm both for the amplitude (McLaughlin 1967; Deubel 1987; Alahyane et al. 2004) and the direction of ocular saccades (Deubel 1987; Chen et al. 2006; Bock et al. 2008), as well as for the amplitude (Magescas and Prablanc 2006) and the direction of aimed hand movements (Bock et al. 2008).

Several studies have evaluated the transfer of double-step adaptation between the oculomotor and the arm motor system. A substantial transfer was observed from the direction of reactive saccades to that of hand movements and vice versa (Bock et al. 2008), from the amplitude of volitional saccades to that of hand movements (Cotti et al. 2007), but not from the amplitude of reactive saccades to that of hand movements (Krölller et al. 1999; Cotti et al. 2007), nor from the amplitude of reactive saccades to that of volitional saccades or vice versa (Deubel 1995). It has therefore been concluded that the two motor systems can access a common adaptive mechanism under some but not under all experimental conditions.

The present study was designed to provide more insight into the mechanism for double-step adaptation of eye and arm *directions*. In previous work, steps of target direction did not exceed 8° of visual angle, and thus required only a small adaptive change. One purpose of the present study was to find out if adaptation remains equally efficient for larger target displacements. The second purpose was to determine whether adaptation is cumulative, in that subjects exposed to a given step size benefit from a previous adaptation to smaller steps. This was shown to be the case for adaptation to distorted visual feedback (Abeele and Bock 2001; Bock et al. 2003), and we now expand that work to double-step adaptation.

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Methods

Forty-four females and twenty males participated. They were 20–46 years old, right-handed, and exhibited no overt sensory or motor deficits except for vision corrected by contact lenses. All subjects were inexperienced with sensorimotor research, and all signed their informed consent to this study, which was pre-approved by the authors' institutional Ethics Committees.

Experimental procedures were generally the same as in our previous study (Bock et al. 2008). A visual target was presented in the center of a computer screen for 760–1500 ms, and then jumped onto an imagined circle of 11 cm radius around the center. There it appeared in one of eight randomly selected directions (0, 45, 90, ..., 315°, where 0° denotes rightwards and 90° upwards on the screen). In single-step trials, the target remained steady on the circle for 760 ms. In double-step trials, the target jumped 200 ms later¹ along the circle by -10 , -30 , or -60 °, depending on subject group, and then remained steady for 640 ms. Each experimental session consisted of episodes with 20 trials each, separated by rest breaks of several seconds to avoid fatigue.

Subjects sat at a distance of 40 cm from the screen, and were instructed to follow the target quickly and accurately, either with their eyes while keeping their hands still, or with their right hand while fixating straight ahead. In the latter case, subjects saw a cursor on the screen which moved congruently with their hand. The experiment started with a *baseline phase* of two single-step episodes, continued with an *adaptation phase* of 30 double-step episodes, and concluded with an *aftereffect phase* of two single-step episodes. Subjects were subdivided into eight groups of eight. Groups E-10, E-30, and E-60 responded with their eyes, and experienced during the adaptation phase target jumps of -10 °, -30 °, or -60 °, respectively. For group E-10-30-60, target jumps were -10 ° during the first ten adaptation episodes, -30 ° during the next, and -60 ° during the last ten adaptation episodes. Groups H-10, H-30, H-60, and H-10-30-60 underwent the corresponding regimes while responding with their hand.

Data were collected in two laboratories. In one, eye movements were registered by DC-electrooculography (EOG), calibrating the signal after each five episodes; the signal was digitized with 100 Hz for storage and later analysis. Hand movements were recorded with a computer mouse, bypassing commercial mouse drivers because of their delays, averaging, and dynamic distortions. In the

¹ We decided for a constant rather than a saccade-triggered interstep interval in order to keep the paradigm similar for eyes and hand. We have recently shown that saccadic direction adapts equally well and shows comparable aftereffects with both types of interval (Grigорова et al. 2010).

other laboratory, eye movements were registered by an infrared-light sensitive oculometer (ISCAN Inc. with RK-426PC pupil corneal reflection tracking system) with a resolution of 1°, and hand movements by a digitizing tablet (CalComp Drawing Board III) with a resolution of 0.25 mm; both signals were sampled at the rate of 50 Hz, and were smoothed twice by three-point central averaging.

The collected data were analyzed by an interactive computer program which determined *saccade direction* as the difference between non-displaced target direction and the direction of the primary saccade, *initial hand direction* as the difference between non-displaced target direction and hand direction 100 ms after movement onset, as well as *hand and arm reaction time* as the interval between appearance of the non-displaced target and movement onset.

Movements were disregarded when hand or eye reaction times exceeded 400 or 270 ms, respectively, since previous work documented that initial hand direction (van Sonderen et al. 1988) and primary saccade direction (Becker and Jürgens 1979) would begin to show an influence of the second step with longer reaction times. For subsequent statistical testing, we calculated the median response direction and the median reaction time for each subject and episode.

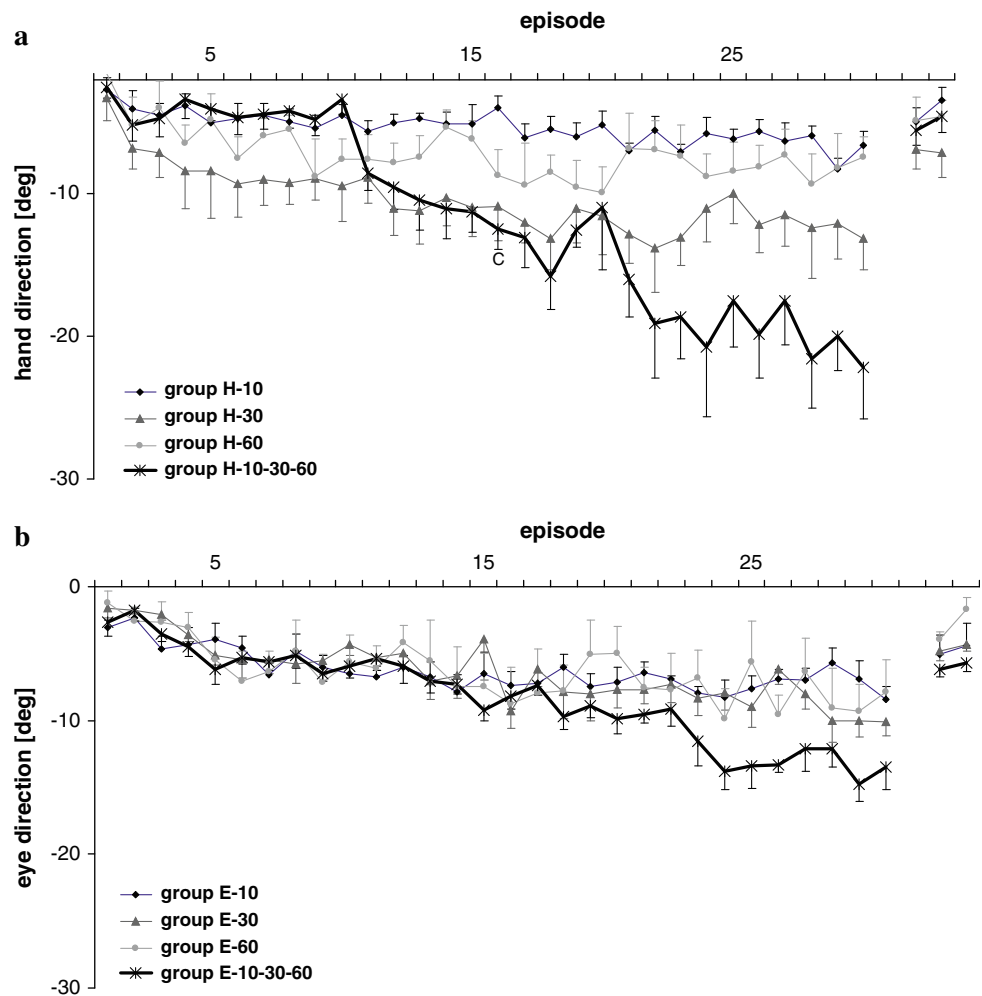
Subjects from a given group that were tested in different laboratories yielded similar results, and statistical comparisons of key episodes confirmed this similarity; we therefore combined the data from both laboratories for statistical testing. The baseline-corrected values were submitted to two-way analyses of variances (ANOVAs) with the between-factor Group and the within-factor Episode. Post hoc comparisons were made with Fisher's LSD-tests.

Data collected in groups E-10, E-30 and E-60 have also been analyzed as part of another study, which compares saccadic adaptation with fixed and with saccade-triggered interstep intervals (Grigорова et al. 2010).

Results

Figure 1 depicts the across-subject means of movement direction for groups responding with their hand (left part) or eyes (right part). All groups gradually changed their response direction during the adaptation phase, and a part of this change was preserved during the aftereffect phase. Conspicuous differences between groups emerged toward the end of the adaptation phase but did not persist afterward. In accordance with these observations, ANOVA of the adaptation phase yielded a significant effect of Episode ($F_{(29,203)} = 33.28$, $P < 0.001$), Group ($F_{(7,56)} = 3.00$, $P < 0.01$), and their interaction ($F_{(29,1624)} = 3.48$, $P < 0.001$).

Fig. 1 Response direction of subject groups adapting their hand (a) or eyes (b) to double-step targets. Symbols indicate across subjects' means, and bars standard errors of each episode. The last two episodes represent the aftereffect phase with single-step targets



Post hoc analysis of the last two adaptation episodes confirmed that response direction was larger in H-10-30-60 than in H-60 (both $P < 0.01$), larger in E-10-30-60 than in E-60 (both $P < 0.001$), and larger in H-30 than in H-10 and H-60 (second last episodes $P < 0.05$, last episodes $P < 0.001$), but it did not differ between H-60 and H-10 (both $P > 0.05$), nor between E-60, E-30, and E-10 (all $P > 0.05$). Thus, we found no consistent effect of step size, but an effect of abrupt versus incremental step regimes. Post hoc analysis further revealed that response direction in the first adaptation episode with -30° steps differed between groups with abrupt and incremental step regime (H-30 versus H-10-30-60: $P < 0.01$, E-30 versus E-10-30-60: $P < 0.05$), as did response direction in the first adaptation episode with -60° steps (H-60 versus H-10-30-60: $P < 0.001$, E-60 versus E-10-30-60: $P < 0.001$). Thus, pre-adaptation to a smaller step had a beneficial effect on the subsequent adaptation to a larger step.

The relative magnitude of adaptation, defined from the mean response direction of the last two adaptation episodes as

$$\frac{\text{response direction}}{\text{step size}} \times 100 \tag{1}$$

decreased for hand movements from 68% in H-10, to 42% in H-30, to 13% in H-60 and 35% in H-10-30-60. It decreased in a similar fashion for eye movements, from 67% in E-10, to 37% in E-30, to 17.5% in E-60 and 23.5% in E-10-30-60.

Eye registrations from the groups adapting with hand movements revealed that subjects produced on the average 1.07 inadvertent eye movements (IEM) per adaptation episode. Adding each subject's number of IEM as a covariate to the hand adaptation analysis yielded no significance for that covariate ($F_{(1,27)} = 1.79$, $P > 0.05$), suggesting that IEM had little effect on hand adaptation.

ANOVA of the aftereffect phase was significant for Episode only ($F_{(1,56)} = 5.71$, $P < 0.05$), i.e., aftereffects were comparable in all groups, with a tendency to decrease from the first to the second aftereffect episode. The relative magnitude of aftereffects was calculated in accordance with Eq. (1), and again decreased from 10° steps to 60°

steps, as illustrated in Fig. 2. Again IEM was not a significant covariate for the hand adaptation groups ($F_{(1,27)} = 4.05$, $P > 0.05$).

The reaction time during the baseline phase was 205.20 ± 16.90 ms for saccades and 283.94 ± 25.02 ms for hand movements. It decreased in all groups at the onset of adaptation by 11.38 ± 19.11 ms, and then increased again toward the baseline level. Accordingly, ANOVA led to a significant effect of Episode only ($F_{(29,1595)} = 4.58$, $P < 0.001$). The reaction time increased in all groups during the aftereffect phase by 5.01 ± 15.60 ms, yielding again a significant effect of Episode only ($F_{(1,56)} = 6.47$, $P < 0.05$).

Discussion

In accordance with previous work (Deubel 1987; Chen et al. 2006; Bock et al. 2008), we found that the direction of eye and of hand movements can be adaptively modified in a double-step paradigm. Two observations indicate that this result is not an artifact of subjects waiting for the second target step before planning a response: First, the reaction time did not increase during the adaptation phase but even slightly decreased, and second, the interval between second step and response onset was shorter than the minimum time required for the reprogramming of saccades (Becker and

Jürgens 1979) and hand movements (van Sonderen et al. 1988, 1989).

We further found that eye and hand directions adapted not only to small target steps, as used in previous work, but also to much larger target steps. When expressed as gaze angle rather than as angle on the screen, our smallest step was about 5° and thus was comparable to earlier studies, while our largest step was as big as 28° . However, eye and hand adaptations to large steps was much less efficient than that to smaller ones, since the relative magnitude of adaptation decreased from about 67% with 10° steps to as little as 15% with 60° steps. Accordingly, the relative magnitude of aftereffects decreased from about 37% with 10° steps to about 6% with 60° steps.

The adaptive improvement with 60° steps was substantially larger under an incremental regime (H-10-30-60 and E-10-30-60) than under an abrupt regime (H-60 and E-60). However, the difference between regimes vanished during the aftereffect phase. Since adaptive improvement is thought to reflect sensorimotor recalibration as well as workaround strategies, while aftereffects are thought to reflect recalibration alone (Redding and Wallace 1996; McNay and Willingham 1998; Clower and Boussaoud 2000; Pisella et al. 2004; Bock 2005), it would appear that the incremental regime facilitated strategies but not recalibration. This is in contrast to earlier work on adaptation to distorted visual and to force fields, where incremental regimes were found to reduce rather than encourage strategies (Kagerer et al. 1997; Malfait and Ostry 2004; Michel et al. 2007; Kluzik et al. 2008). It is therefore conceivable that strategies play a different role in double-step adaptation and in other adaptation types.

It has been observed in the past that saccadic adaptation is directionally tuned: it shows transfer to untrained saccade directions, but the magnitude of this transfer decreases as the difference between trained and untrained saccade directions increases (Frens and van Opstal 1994; Noto et al. 1999). This phenomenon has been attributed to the directional tuning of deep-layer collicular neurons (Ottes et al. 1986; Lee et al. 1988). Those neurons discharge most vigorously before saccades of a given direction, and the magnitude of their discharge decreases as the difference between actual and preferred saccade direction increases. It has therefore been argued that an adaptive recalibration of those neurons should transfer only within the range of their directional tuning curve. Our present data could be interpreted in an analogous way, i.e., adaptive recalibration could be limited by the size of collicular tuning curves, and the relative magnitude of adaptation should therefore decrease when target steps exceed that limit. Indeed, when the previous data on adaptation transfer and collicular activity are replotted in the same format as our own data in Fig. 2, the emerging

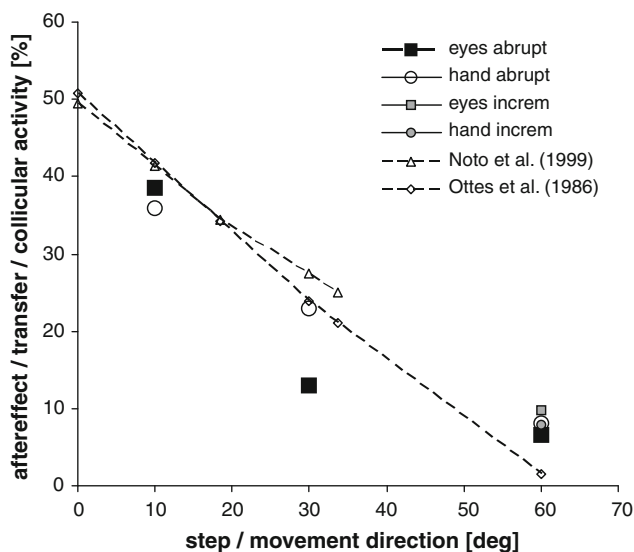


Fig. 2 Relative magnitude of aftereffects in subject groups adapting their hand (filled circles) or eyes (filled squares) to target steps which were introduced abruptly (black) or incrementally (gray). Also plotted is the magnitude of adaptation transfer to untrained directions (solid line: adopted from Noto et al. 1999), and the tuning of deeper collicular activity by saccade direction (dashed line: adopted from Ottes et al. 1986). The latter data were scaled such that the firing rate 10° off the neuron's optimal direction became numerically equivalent to the mean of relative eye and arm aftereffects with 10° target steps

similarity is consistent with the notion of a common neural substrate for all three data sets.

The above considerations suggest that double-step adaptation may reside in neural circuits which include directionally selective collicular cells. The similar circuits may be involved in the double-step adaptation of eyes and arm, since the directional tuning of both motor systems is comparable in Fig. 2. Indeed, arm movement related activity has been registered in the superior colliculi (Werner et al. 1997, Stuphorn et al. 2000, Lunenburger et al. 2001). However, this is not to say that the colliculi play a predominant role, let alone the exclusive role in double-step adaptation. Rather, other brain areas are likely to contribute as well, notably the cerebellum, whose involvement in adaptation has been documented by a number of neuroimaging and lesion studies (Desmurget et al. 1998, 2000; Straube et al. 2001; Thach et al. 1992; Alahyane et al. 2008; Werner et al. 2009; Xu-Wilson et al. 2009).

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