Concurrent adaptation of left and right arm to opposite visual distortions

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Summary

Previous research has shown that subjects can adapt with either arm to an opposite visual distortion, and the two adaptive states can then be used in sequence to control the respective arm. To extend this finding, we exposed the left and right arm of our subjects alternately for 20 s each to opposite-directed rotations of the visual field, and determined the time-course of adaptation, as well as the aftereffects without visual feedback under uni- and bimanual conditions. Our data confirm that two adaptive states can co-exist in the sensorimotor system, one for each arm. We further found that the time-course of adaptive improvement was similar for both arms, that the improvement was present as early as the first movement after a change of arm and discordance, and that the magnitude of adaptation was similar to control data yielded by a single arm and discordance. Taken together, these findings suggest that the two adaptive states were formed concurrently, and without mutual interference. We also observed significant aftereffects. They were smaller but still appreciable under bimanual conditions, i.e., the two arms moved at the same time in different directions even though they were aimed at a common visual target. This outcome indicates that the two adaptive states were not merely of a strategic nature, but rather changed the rules by which sensory information was transformed into motor outputs; it also suggests that the two states not only co-exist, but also can concurrently be engaged in movement control. The reduction of the aftereffect under bimanual conditions was attributed to the well-known phenomenon of bimanual coupling, which is unrelated to adaptation.

Key words: psychomotor performance; human information processing; physiological adaptation; transfer; inhibition

Introduction

Several studies have documented that subjects who adapt to a visual distortion using *one* arm subsequently show signs of adaptation even when using the *other*, unpractised arm (Hamilton 1964; Cohen 1967; Freedman 1968; Choe et al. 1974; Imamizu et al. 1995; Sainburg et al. 2002). This intermanual transfer of adaptation has been interpreted as evidence that that the underlying neural mechanism is located in the sensorimotor pathways *upstream* from the branching point for left versus right arm control (Imamizu et al. 1995). However, such a view seems too simplistic when the available findings are considered in detail. Thus, intermanual transfer of adaptation was often incomplete, i.e., initial performance with the second arm was distinctly inferior to final performance of the first (Choe et al. 1974) (Sainburg et al. 2002); furthermore, intermanual transfer was completely absent under some experimental constraints, such as stabilized versus free head (Hamilton 1964), continuous versus terminal arm vision (Cohen 1967), or over- versus undertraining of the first arm (Freedman 1968). Clearly, such observations of partial and/or conditional transfer are not compatible with a single, hard-wired location of an obligatory adaptive mechanism within a unidirectional processing stream.

Recent work has provided a more elaborate concept of intermanual transfer (Sainburg et al. 2002) (Wang et al. 2003). Subjects first adapted to a visual rotation using one arm, and were then tested under the same *or the reversed* rotation using the other arm. The authors found that the very first movement of the other arm was indistinguishable from a naïve arm, whether visual rotation was reversed or not. Subsequent movements of the other arm showed a small but significant benefit with respect to a naïve arm if visual rotation remained the same, but neither a benefit nor a penalty if visual rotation was reversed. In contrast to the latter findings, other authors reported a distinct penalty when the *same arm* remained in use after reversal of visual rotation (Krakauer et al. 1999; Wigmore et al. 2002; Bock et al. 2003), probably because of the need to gradually de-adapt before starting to adapt in the opposite direction (Bock et al. 2003). The pattern of these findings suggests that training of the first arm establishes an adaptive state linked to the pathways controlling that arm. If the first, probing movement of the other arm determines that this state is still adequate, it can be linked to the control pathways for the other arm as well, thus yielding intermanual transfer. If, however, the adaptive state is not useful to the other arm, it is not linked to its control pathways.

The results of the above work leave open the question whether bimanual adaptation is achieved by a single (Taylor et al. 1980), or rather by two distinct neural mechanisms (Parlow et al. 1989). In the former case, the evolving adaptive state would be accessible by both arms to yield intermanual transfer if the visual rotation remains the same; if not, the adaptive state would be relinquished and a new one would gradually form. Indeed, previous work suggests that an adapted state can be quickly abandoned, at least under some experimental conditions (Welch et al. 1993; Cunningham et al. 1994; Martin et al. 1996; Ghahramani et al. 1997; Osu et al. 2004). In the latter case, the adaptive state would be firmly linked to one arm, but it could be copied into a second neural mechanism and linked to the other arm if the distortion remains unchanged; if not, a new adaptive state would gradually emerge in the second neural mechanism.

To distinguish between the above alternatives, one could test whether the first arm remains adapted in the original direction even after the second arm has adapted in the reversed direction: A positive answer would strongly support the existence of two mechanisms, and a negative one would clearly agree with the single-mechanism view. This test was not done in the above work (Wang et al. 2003), but it was carried out in earlier, not well-cited studies (Mikaelian et al. 1974; Prablanc et al. 1975; Martin et al. 1980). In the latter studies, subjects were exposed to a lateral visual shift in one direction while using one arm, and in the opposite direction while using the other arm. Manual performance during exposure was not assessed, but the magnitude of adaptation was determined by asking subjects before, and again after exposure, to point first with one and then with the other arm at visual targets without seeing their arms. All studies accordingly observed that after exposure, pointing responses of both arms were adaptively displaced, to the left for one arm, and to the right for the other. This finding was interpreted as evidence for the existence of arm-specific adaptation[1], in accordance with the two-mechanism view.

The present study further explores arm-specific adaptation. Besides confirming its existence, we wanted to determine whether arm-specific adaptation

- is observable with other visual distortions besides lateral shifts: it is possible that opposing lateral shifts are easily compensated by adding an opposite-directed bias to the proprioceptive feedback of either arm, while other distortions may require adaptive solutions which are not that easily converted between left- and right-arm use;
- is established concurrently for both arms, or rather sequentially (first one arm and then the other): previous studies were not designed to address this issue;
- invokes mutual interference between the two evolving, opposite-directed adaptive states, as known from previous work on unimanual adaptation (see above);

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[1] It should be noted that two of the above studies (Mikaelian et al., 1974; Prablanc et al., 1975) suffer from a design flaw, such that arm-specific adaptation could be confounded with eye-specific, or even hemispace-specific adaptation. Firm evidence for arm-specific adaptation therefore rests with a single study (Martin et al., 1980).

- is maintained even if both arms jointly move towards a common visual target, which would imply that both adaptive states can be concurrently and independently engaged in motor control.

Methods

Eight healthy volunteers were tested, aged 21 to 24 years. Five were male and three female, all were right-handed, and none of them had previous experience in similar research. All subjects signed an informed consent statement before participating. This study was pre-approved by the Ethics committee of the German Sport University, and has therefore been performed in accordance with the ethical standards laid down in the 1964 Declaration of Helsinki.

The experimental apparatus is outline by the scheme in Fig. 1. Computer-generated visual targets were presented on a vertical screen viewed by subjects through a tilted mirror, such that they appeared in a horizontal plane. Subjects left and right hand were supported on two horizontal surfaces, one 7.5 cm above and the other 7.5 cm below the apparent targets. This setup quickly produced visual capture, in that subjects felt both arms in the perceived target plane. The 3D-position of both index fingertips was registered by the Fastrak® motion analysis system at 60 Hz.

Subjects were asked to point quickly and accurately with their index finger from a central starting dot towards visual targets, which appeared in a quasi-random sequence at one of 16 equidistant locations along an imagined circle of 7 cm radius about the starting dot. Each target was presented for 750 ms, and was then replaced by the starting dot, which remained on until the finger returned to the centre. The next target was then displayed, etc. Due to the mirror, subjects were unable to directly see their responses, but the registered position of their index fingertip could be displayed to them as a cursor along with the targets. This visual feedback could be veridical, rotated by 60 deg about the starting dot, or absent (see below).

The experiment was subdivided into episodes of 20 s, which allowed the execution of up to 15 movements, depending on the experimental phase. Episodes were separated by breaks of 5 sec. The experiment started with 12 *baseline* episodes where visual feedback was either veridical or absent, and subjects either used their left, right, or both arms to point at each target; the sequence of feedback and arm conditions is illustrated in Fig. 2. Next came 40 *adaptation* episodes alternating between left and right arm use; in episodes with the left arm, we distorted visual feedback by a rotation of 60 deg clockwise, and in episodes with the right arm, of 60 deg counterclockwise. The experiment closed with 12 *post-adaptation* episodes where visual feedback was absent, and subjects used their left, right, or both arms according to the sequence in Fig. 2.

In unimanual episodes, the arm not being used was held off to the side of the testing area. Half of the subjects performed these episodes in the order left-right-left-right…, and the other half in the order right-left-right-left… In bimanual episodes, both arms moved concurrently towards the same visual target, with a +/- 7.5 cm vertical offset due to the distance between the horizontal surfaces. Half of the subjects started the persistence phase with unimanual, and half with bimanual responses.

Results

Fig. 1 shows recordings of feedback cursor paths for uni- and bimanual pointing responses before, during, and after adaptation to the visual rotation. The responses were actually aimed at targets in eight different directions, but are normalized with respect to a target above the starting dot. Baseline responses (Fig. 1 b&c) appear reasonably accurate. Early during the adaptation phase (Fig. 1 d), the cursor deviates clockwise at movement onset for responses with the left, and counterclockwise for responses with the right arm, thus reflecting the imposed distortion; later during the course of movement, the cursor typically curves back towards the target, thus reflecting response corrections. Near the end of the adaptation phase (Fig. 1 e), cursor paths are again aimed at the targets with reasonable accuracy, as a sign of adaptive improvement. During the post-adaptation phase (Fig. 1 f&g) responses miss the target in a direction opposite to that observed during the adaptation phase, in the sense of a negative aftereffect; this time, no evidence for response corrections can be discerned (cf. Fig. 1 f&g with Fig. 1 d.) The magnitude of aftereffect is larger for uni- than for bimanual responses.

For further analyses, we calculated the initial error of each response as the angle between required and actual response direction at the time of peak velocity[2]. The across-subject means and standard deviations of these values are plotted in Fig. 2. It can be seen that the initial error was small during the baseline phase, irrespective of feedback and arm condition. At the onset of the adaptation phase, the error abruptly increased in the positive or negative sense, depending on the arm, and then gradually declined in parallel for both arms, without reaching 0 deg. This adaptive improvement

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[2] The pattern of findings was the same when errors were calculated 150 ms after response onset, rather than at peak velocity.

was confirmed by an analysis of variance (ANOVA) of *absolute error* during the adaptation phase, using the within-factors Episode and Arm: only the effect of Episode was significant (F(19,133) = 41.42; $p<0.001$), which indicates that arm-specific adaptation took place, and that it was established in parallel for both arms.

Even if adaptation is established in both arms concurrently, it is still conceivable that the two evolving adaptive states mutually interfere, thus reducing the magnitude of adaptation achieved by the end of the adaptation phase. If so, one should expect that adaptation is more profound if only a single arm and rotation sense is used. Such data are indeed available from a study with the same apparatus and pointing task, where subjects simply rested for various lengths of time rather than adapting their second arm (Bock and Thomas, in preparation)[3]. Since the two studies used different episode lengths, we cannot quantitatively compare the time-course of adaptation, but we can compare the magnitude of adaptation after a given time. Thus in the present study, the two arms reached a mean absolute error of 16.59 +/- 12.30 deg after each adapted for 19 episodes, or 380 s. In the other work, the right arm reached an absolute error of 14.68 +/- 9.94 deg after 385 s. These two data sets are not significantly different (t(9) = 0.38; $p > 0.05$), i.e., we can not confirm the existence of mutual interference during bimanual testing.

It is still conceivable that interference does exist, but is limited to the first movement(s) after a switch of hands and distortions. We scrutinized this possibility by analysing *only the first movements of each episode*: Fig. 3 illustrates that the absolute error of those movements was near 60 deg for the first two episodes, and then gradually and

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[3] Pause length in that work varied between 1 and 40 s. There was no effect of pause duration on adaptive improvement for pauses of 5 s or more, and we therefore feel confident in using data from 5 to 40 s groups (n=35) as a control for the present study.

consistently decreased throughout the adaptation phase. The error of the first and second episode (i.e., the initial episode of each arm) was not significantly different from 60 deg ($t(7) = 0.74$; $p > 0.05$ and $t(7) = 1.07$; $p>0.05$, respectively). Thereafter, the error always averaged less than 60 deg, and decayed with a slope of –0.65 deg/episode, which is significantly different from zero ($t(302) = -8.77$; $p < 0.001$).

Clearly, the data in Fig. 3 are not compatible with the existence of interference, which should manifest as a gradual *increase* rather than decrease of errors. Nor are the data compatible with the notion of probing movements (see Introduction), which should manifest as a consistent error magnitude of about 60 deg. (As an exception, the first movement of the second adaptation episode is, arguably, compatible both with interference and probing.) Instead, our data are in accordance with the view that each episode starts in the adaptive state which was achieved by the end of the last episode with the *same* hand.

The post-adaptation phase in Fig. 2 is characterized by a marked negative aftereffect for both hands, which is more apparent for uni- than for bimanual responses. An ANOVA of the *absolute error*, using the within-factors Arm (L, R), Block (episode 53 - 58, episode 59 – 64), Response Type (uni-, bimanual), and Repetition (1,2) yielded significant effects of Block ($F(1,7) = 30.55$; $p<0.001$), Response Type ($F(1,7) = 28.94$; $p<0.01$) and their interaction ($F(1,7) = 7.50$; $p<0.05$), confirming that the aftereffect was stronger under uni- than under bimanual conditions, and that it decayed with time, particularly for unimanual responses. Although the aftereffect was generally smaller for bimanual responses, it was still reliable: the signed error of bimanual pointing differed significantly between right and left arm during the first and second block of the post-adaptation phase, but it didn't differ during the corresponding baseline episodes 11 &

12 (Scheffe's test: $p<0.01$, $p<0.01$, $p>0.05$, respectively). Thus, the two arms moved concurrently in the same direction before, but in different directions after adaptation.

Discussion

Our study evaluated sensorimotor adaptation in a pointing task by exposing subjects' two arms in an interleaved fashion to opposite visual rotations. Pointing errors were small during baseline conditions, increased substantially - in opposite directions for the two arms - at the onset of exposure, and then gradually decreased again; the time-course of this adaptive improvement being similar for both arms. These findings confirm that two opposing adaptive states can co-exist in the sensorimotor system, one for each arm (Mikaelian et al. 1974; Prablanc et al. 1975; Martin et al. 1980; Wang et al. 2003), and thus supports the existence of two separable neural mechanisms for adaptation (see Introduction). Furthermore, our study extends previous data to visual distortions other than lateral shifts, and establishes that the two opposing adaptive states can evolve concurrently, i.e., second arm adaptation needs not be delayed until the first arm is largely adapted.

The fact that both adaptive states are established in parallel doesn't exclude the possibility that each interferes with the formation of the other. However, our data provide no evidence for such a view: the first movements of each episode didn't become less, but rather *more* accurate with time, and the magnitude of adaptation was not smaller than in control subjects exposed to just a single visual distortion with a single arm. The evident lack of interference when adapting two arms to conflicting visual distortions stands in remarkable contrast to the strong interference yielded when adapting a *single* arm to such distortions (Krakauer et al. 1999; Bock et al. 2001;

Wigmore et al. 2002; Bock et al. 2003). It therefore appears that two distinct adaptive states can evolve without penalty if each is linked to a different, but not if both are linked to the same limb. The available data leave open whether this linkage is hard-wired, with two adaptive states implemented within arm-specific segments of the sensory-to-motor pathways, or whether it rather is functional, with usage of a given arm serving as a cue to switch between two available states. The latter alternative would correspond with the observations that cues, such as colour (Cunningham et al. 1994; Osu et al. 2004) starting location (Ghahramani et al. 1997), and serial order (Welch et al. 1993; Martin et al. 1996) can be successfully utilized for switching between adaptive states. However, further work will be needed to better understand the conditions for the formation and maintenance of separate adaptive states in their sensorimotor system, and for their assignment to different experimental conditions.

It is widely accepted that adaptive improvement can be achieved by two types of processes. One is the *recalibration* of sensory-to-motor transformation rules, and the other is *strategic adjustment* through cognitive schemes, anticipation, and/or feedback-based response corrections (Redding 1996; McNay et al. 1998). It is thought that improvements during exposure to a visual distortion reflect both processes, while negative aftereffects are mainly related to recalibration. Following these arguments, the significant aftereffects observed during the present post-adaptation phase indicate that at least part of the adaptive improvement was achieved by means of recalibration. Thus, the two concurrent adaptive states were not merely of a strategic nature, but rather changed the rules by which sensory information was transformed into motor outputs. Furthermore, the distortions employed in the present study don’t lend themselves easily to cognitive strategies. For example, targets in some locations had to be reached by convergent, but other targets by divergent movements of the two limbs. A simple rule, such as reversing movement direction, would be adequate under lateral displacements of vision, but not under visual rotations.

We found negative aftereffects not only when each arm pointed separately in alternate episodes, as in the preceding adaptation phase, but also when both arms moved jointly towards a common visual target. This indicates that the two adaptive states did not just co-exist in the sensorimotor system; rather, they could even be actively and simultaneously engaged in movement control. Interestingly, the observed aftereffects were quantitatively smaller under bi- then under unimanual testing; this reduction was only temporal since aftereffects largely recovered when unimanual testing resumed, and it therefore probably doesn't reflect mutual interference between adaptive states. More likely, the reduction is not related to adaptive processing but rather reflects a temporary functional coupling in the control of both arms. A large number of earlier studies revealed that bimanual movements towards one single or two separate targets tend to assimilate in the spatial and temporal domain, both with respect to average performance and on a trial-to-trial basis (e.g., (Schmidt et al. 1979; Kelso 1984; Heuer 1986; Franz 1997; Tresilian et al. 1997; Heuer et al. 2001). Since clear signs of bimanual independence were also documented (e.g., Schmidt et al. 1979; Heuer 1986; Boessenkool et al. 1999), it was concluded that some aspects of bimanual performance are controlled jointly and others separately, or, that bimanual performance is controlled through separate channels with some degree of cross-talk. In any case, bimanual assimilation could well explain why in our post-adaptation phase, left and right arm responses were more similar under bi- than under unimanual conditions.

In conclusion, our study confirms that two conflicting adaptive states can co-exist in the sensorimotor system, one for each arm, and provides evidence that both states can evolve concurrently, can be activated at the same time, and don’t mutually interfere.

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Figure legends

Fig. 1. a. Schematic view of the setup, with screen (S), mirror (M), and the two horizontal support surfaces (H). **b.**- **g.** Sample response paths of one subject for the left (open circles) and right (filled circles) hand towards the eight possible targets, normalized with respect to a target above the starting dot. Individual plots show **b.** unimanual and **c.** bimanual responses during the baseline phase without visual feedback, **d.** unimanual responses at the beginning and **e.** near the end of the adaptation phase, as well as **f.** unimanual and **g.** bimanual responses during the post-adaptation phase. Note the negative aftereffect in the post-adaptation phase, which is also present – though smaller – under bimanual conditions, i.e., the two arms move at the same time in different directions, even though both respond to a common visual target.

Fig. 2. Initial error across all subjects in the different experimental episodes. Symbols represent means and bars the corresponding standard deviations, plotted separately for the left (open circles) and right (filled circles) arm. FB denotes the presence of visual feedback, while uni and bi refer to uni- and bimanual responses. Since the order of left- versus right-hand testing, and uni- versus bimanual testing, was counterbalanced across subjects (see Methods), the plotted temporal sequence of data points is strictly valid for only ¼ of our subjects. Note the the existence of aftereffects both under unimanual and (smaller) under bimanual conditions.

Fig. 3. Absolute initial error across all subjects for the first movement of each adaptation episode. Symbols represent means, bars standard deviations, and the sloping line the linear fit. Since the sign of the errors has been discarded, both left- and right-arm data appear above the abscissa.

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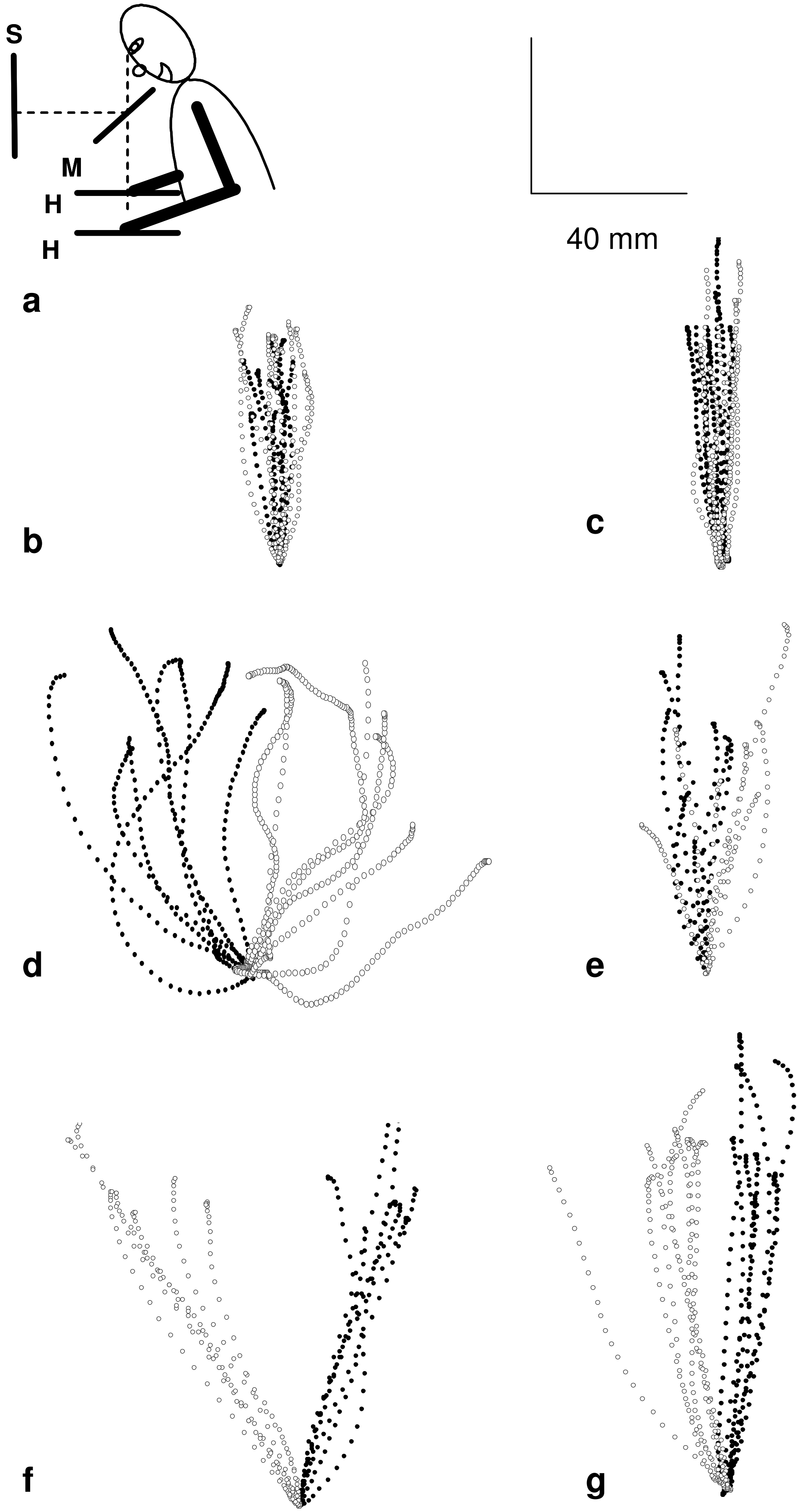
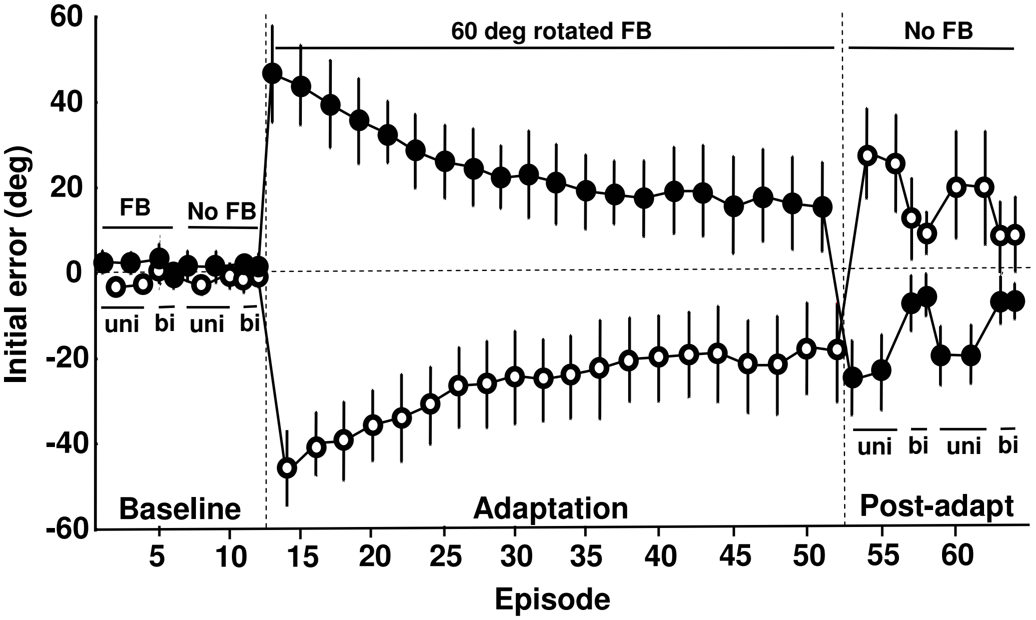
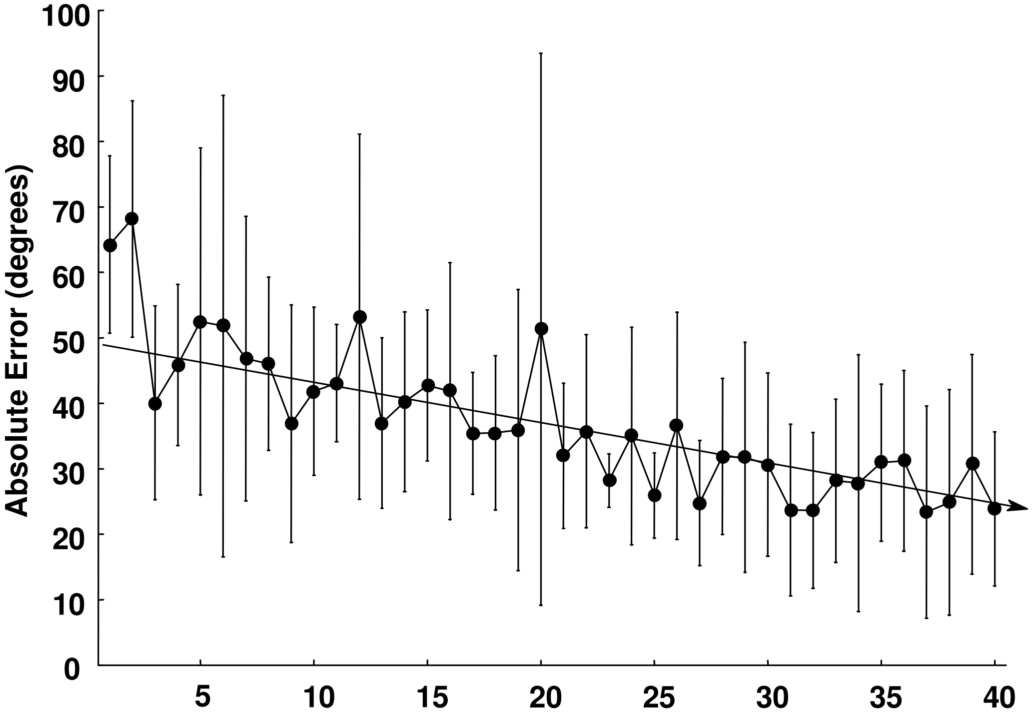


Fig. 1



60 deg rotated FB
No FB
FB
No FB
uni
bi
uni
bi
uni
bi
uni
bi
Baseline
Adaptation
Post-adapt
Initial error (deg)
60
40
20
0
-20
-40
-60
5
10
15
20
25
30
35
40
45
50
55
60
Episode

Fig. 2



Absolute Error (degrees)
100
90
80
70
60
50
40
30
20
10
0
5
10
15
20
25
30
35
40

Fig. 3