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Long-lasting aftereffect of a single prism adaptation: shifts in vision and proprioception are independent

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Abstract After a single adaptation session to prisms with gradually incremented shift magnitude, the prism adaptation aftereffect was measured by open loop mid-sagittal pointing (O) to a visual target without visual feedback. This aftereffect corresponded to the summation of the shift in proprioception, measured by straight ahead pointing without vision (S), and the visual straight ahead judgement (V), measured by verbal stopping of an LED moving from two opposite directions. However, the measurement of the aftereffects made over a period of 7 days revealed significantly different decay curves in V , O and S . Surprisingly the S shift was still present up to 7 days after the training, while V had returned to the original level by 2 h, which was the first measurement after subjects returned to a normal visual environment. O had returned to pre-test level after 1 day. After 3 days Wilkinson's (J Exp Psychol 89:250–257, 1971) additive hypothesis ($O=S-V$) no longer fit the data. Rather " $O=PI-V$ ", where PI (Pr) is the shift in proprioception measured by passive lateral arm movements from left

(right), fitted better during the whole 7 days of aftereffect in our study. Therefore, the aftereffect of our strong prism adaptation revealed, firstly, that classical open loop pointing consisted of aftereffect shifts equal to the summation of the shifts in the two passively measurable aftereffect components, vision (V) and proprioception (PI), rather than with active straight ahead pointing (S). Secondly, the decay of the shift in visual perception and in passively measurable proprioception is independent. The former decays fast, and the latter decays slowly with two separate waves. Thirdly, we suggest that the use of visual perception-dependent spatial codes for visual-manual transformation and the vision-independent internal egocentric reference frame are mutually exclusive. We proposed a model to explain these possible mechanisms.

Keywords Visuo-motor · Visuo-sensory · Sensory-motor · Long-term plasticity · Internal representation

Abbreviations CMI: Neural network coding motor control and effector response for movement from left, · CMr: Neural network coding motor control and effector response for movement from right, · CPI: Neural network coding calibrated perceptual proprioception by movement from left, · CPPr: Neural network coding calibrated perceptual proprioception by movement from right, · CVa: Neural network coding calibrated perceptual visual space, · IEREF: Internal egocentric reference frame, · e-LTP: Early long-term plasticity (including potentiation and depression), · l-LTP: Late long-term plasticity (including potentiation and depression), · O : Open loop pointing test, · PI: Passive proprioceptive straight ahead test from left arm movement, · Pr: Passive proprioceptive straight ahead test from right arm movement, · S : Straight ahead pointing test, · Va : Visual straight ahead test averaged from the two directions of LED movement, · Vl : Visual straight ahead test from left LED movement, · Vr : Visual straight ahead test from right LED movement, · VMT: Visuo-manual transformation.

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Introduction

What are the mechanisms, which integrate the spatial coordinate frames of different modalities in the body? Prism adaptation is a useful tool to dissociate the components used in the coordination of various modalities involved in spatial tasks (Welch 1978, 1986). Adapting to optically shifting prism glasses involves spatial adjustment of eye–arm coordination (Welch 1986; Redding and Wallace 1997a). During adaptation, the subjects' visual information of the world is spatially shifted. Initially, subjects consciously or unconsciously adjust their pointing using visual feedback, a strategic component. Then, through repeated pointing at the correct location with their finger, they unconsciously adapt their eye–hand coordination and the CNS neural network is plastically modified. When the glasses are removed, subjects make opposite pointing errors exposing an adaptation aftereffect.

Additivity

For well-coordinated behaviour, our spatial coding must form a coherent sensory motor closed loop. Therefore, using optically shifting prism glasses to produce a shift of visual sensory inputs can have a knock-on effect that interferes with the complete system, in our periphery and in central neural networks. By modification of the adaptation procedure, the weight of involvement of each component in the prism adaptation process could be changed (Redding and Wallace 1993). For example, during adaptation, the degree of visibility of the hand path of movement modifies the proportions of shifts in visual, proprioceptive, motor and internal egocentric reference frames (Redding and Wallace 1993, 1997a). The speed of pointing movements with the hand also modifies the proportions of shift in the proprioceptive and motor components (Redding and Wallace 2000).

The prism adaptation involves spatial shifts in both vision and felt arm positions (Rock and Harris 1967). Harris (1963) investigated the changes after prism adaptation in visual motor and proprioceptive components, measured by target pointing without visual feedback, i.e. by open loop pointing. He interpreted the shift in straight ahead pointing as proprioceptive shift. Since then, straight ahead pointing without vision has been extensively used as a measure of the magnitude of aftereffect of proprioception (for example, Harris 1963; Wilkinson 1971; Redding and Wallace 1992). Visual straight ahead is usually measured by successive mid-sagittal judgements of laterally moving LEDs travelling from right and left (e.g. Karnath et al. 1991; Redding and Wallace 1992; Farnè et al. 1998; Ferber and Karnath 1999). The summation of the aftereffect shifts in vision and straight ahead pointing was reported to be expressed in open loop pointing. This additivity was first observed by Hay and Pick (1966), and the idea was formalized by Wilkinson (1971) and confirmed by others (Welch et al.

1974; Redding and Wallace 1978; Wallace and Redding 1979). It was therefore thought that all relevant components were expressed in Wilkinson's additivity model ($O = S - V$) (Wilkinson 1971; reviewed in Welch 1986).

Long-term plasticity of prism adaptation aftereffect

Our aim was to measure the adaptation aftereffects systematically in order to dissociate the hidden components by their different time courses of development and decay. Using an adaptation procedure that induced longer duration and larger magnitude of aftereffects could give us more opportunity to dissociate different components (Hatada et al. 2005).

Wallace (1977) confirmed the additivity hypothesis " $O = S - V$ " for up to 40 min during prism exposure in normal subjects but not during the aftereffect. Hay and Pick (1966) studied a 10-day aftereffect after a continuous long prism exposure of 42 days. They studied the magnitude of shift in vision, straight ahead pointing and open loop pointing and first observed the additivity. There were other studies that looked at aftereffects over long duration by up-down reverse and left-right reverse condition, respectively (Shimojo and Nakajima 1981; Sekiyama et al. 2000). However, these studies were carried out after a very long prism exposure of more than 1 month. So it is difficult to see the direct effect of the initial adaptation that could be linked to the cellular plastic mechanisms such as e-LTP and l-LTP expressed in the time ranges of hours or days (Hatada et al. 2000; Kandel 2001; Boyden et al. 2004; Walker 2005). These time ranges of plasticity would result from a single session of relatively short adaptation procedure. Therefore, we used a single session of strong but relatively short prism adaptation in order to have a grip on the onset time of the plastic changes triggered by the prism adaptation.

Methods

This paper reports data collected during a single prism adaptation experiment, in which multiple measures of the aftereffect were taken. Some of the data from that experiment will be published elsewhere (Hatada and Rossetti 2004a, b; Hatada et al. 2005; Y. Hatada et al., submitted).

Apparatus

The same experimental set up was used both during the prism adaptation training and during the aftereffect-measuring sessions (Fig. 1.). The subject was seated at a fixed position relative to the measurement apparatus with head stabilized by a chin rest. The height and position of the chair was adjusted to bring the measurement table just below the chest level for comfort. Pointing direction was measured using a touch tablet that registered the position of the index finger (Rossetti et al. 1998). During all pointing tasks and prism adaptation

training, the subject's left hand rested on his left thigh. At the start of each pointing movement the right index finger rested on the table in front of the subject at lower chest level at an invisible position.

Prism adaptation training

Table 1 shows the prism adaptation training procedure. Seven different wedge, left-shifting, glasses were used for this prism exposure, with shifts of 2, 4, 6, 8, 10, 12 and 15°. The glasses were put on and taken off while the subject's eyes were closed. While wearing the glasses, the subject was asked to point at a comfortable speed, with right index finger, at two fixed targets already marked on the apparatus board which were 10° right and left from the mid-sagittal point, 50 cm in front of the subject. Pointing to the two targets was performed in random order under the instruction of the experimenter. After a total of 20 target pointing movements (10 right and 10 left targets), there was a 5 s pause before the same training procedure was repeated (i.e. 2×20 points with the same glasses). These 40 trials were repeated with progressively increasing prism strengths from 2 to 15°. With the final 15° prism glasses, the 40 trials were repeated twice (i.e. 4×20 points). Finally, the subject walked out from the laboratory in our institute while wearing 15° prism glasses for a session of whole body exposure lasting 45 min during which he could see his own hand and body, and walked and pointed in his normal environment.

Measurement of prism adaptation aftereffects

The first measurement was performed before adaptation training to provide a baseline. Between each level of prism exposures, adaptation was also monitored with straight ahead pointing and open loop pointing (without visual

feedback). Following the prism adaptation procedure, adaptation aftereffects were measured at 0 h (immediately after the whole set of prism adaptation training and a few minutes rest in total darkness, before exposure to any vision at all), and at 2, 4 and 6 h, 1, 2, 3 and 7 days after the final removal of the 15° prism glasses (see Table 1).

Only the data from the pre- and post-test straight ahead pointings, open loop pointing and passive proprioceptive mid-sagittal judgement measurements using the right arm, and visual straight ahead (Table 1, bold) are included in the present report. For measurements of straight ahead pointing (*S*), the subject pointed at a comfortable speed with his index finger at his subjectively felt mid-sagittal plane on the far side of the apparatus board level without visual feedback. Passive proprioceptive straight ahead judgement was measured by two opposite lateral arm movements from right and left sides (*Pr* and *Pl*) as described in Y. Hatada et al. (submitted). The subject's extended right hand was passively moved about 30° right or left from the mid-sagittal plane. First, the hand was moved by the experimenter (at approximately 5°/s) from the right edge until the subject verbally stopped the passive hand movement in the subjective mid-sagittal plain. From that point the subject vertically lowered the hand onto the measuring board. Then the hand was moved from the left edge, by the experimenter whom then stood on the left side of the subject. The two opposite directions were measured 10 times each, giving a total of 20 measurements. Visual straight ahead was measured by judging when a moving LED reached the mid-sagittal plane. The LED moved at a constant speed of 3°/s from left (*Vl*) and right (*Vr*). These measurements were analysed separately for *Vr* and *Vl* as well as the average of the two (*Va*). Open loop pointing (*O*) was measured by sagittal pointing, without visual feedback, to a visual target (the same LED presented at the mid-line). The LED that was used for these measurements was 90 cm away from the starting position of hand and 30 cm above the plane of hand movement. Each measurement included ten trials. Visual and passive arm proprioceptive lateral judgements from right and left were measured ten times each.

Data analysis

Ten measurements of each component were averaged and analysed using repeated-measures ANOVA. Student *t* tests and Dunnett's two-tailed post hoc tests were performed. It is likely that Bonferroni correction of the *t* tests in this situation will be overly conservative, as the eight post-adaptation tests are likely to be correlated and not independent; we therefore used PCA to determine the number of independent factors required to adjust the degrees of freedom.

Subjects

All the seven (three females, four males, 22–45 years) healthy and normal-sighted subjects were right

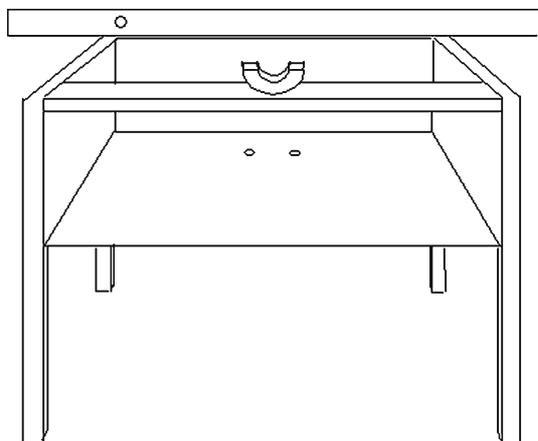


Fig. 1 Picture showing the experimental set up. Targets at 10° left and right of the mid-line were indicated on the touch table. The target LED used for the visual straight ahead measurements moved on a rail at roughly the subjects' eye level. The same LED, presented at the center, was used for open loop pointing target

Table 1 Training procedure and measurement sequence

Event sequence	Stage of training		Measurements			
	Prism state	Pointing at target with visual feedback	Straight ahead pointing (S) Eyes closed	Passive straight ahead test two directions (Pr, Pl) Eyes closed	Visual straight ahead test two directions (Vr, Vl) average of the two (Va) Eyes open in dark	Open loop pointing (O) Eyes open in dark
Pre-test Baseline	Off		10 trials	2x10 trials	2x10 trials	10 trials
Prism adaptation training procedure	Exposure 2°	40 trials				
	Off		10			10
	Exposure 4°	40				
	Off		10			10
	Exposure 6°	40				
	Off		10			10
	Exposure 8°	40				
	Off		10			10
	Exposure 10°	40				
	Off		10			10
	Exposure 12°	40				
	Off		10			10
	Exposure 15°	40				
	Off		10			10
	Exposure 15°	Free walk 45 min				
Post-tests (0hr)	Off		10 trials	2 x 10	2 x 10	10
Post-tests (2hr)	Off		10 trials	2 x 10	2 x 10	10
The same measurements as above were repeated at 4h, 6h and 1, 2, 3, 7 days after returning to normal environment						

Only data from the pre- and post-test straight ahead pointing and open loop pointing measurements using the right arm, and visual straight ahead measurements (bold) are included in the present report. Full measurements were described in previous report (Hatada et al. 2005). Passive proprioceptive mid-sagittal measurement was taken by judgement during passive arm movement at 5°/s from left and right. Visual straight ahead was measured by judgement of an LED moving at constant 3°/s speed from left and right. Open loop pointing was measured by a target sagittal pointing without visual feedback

Dark grey shading Prism adaptation procedure

Light grey shading Period without exposure to the normal visual environment

handed. Although our other studies (Hatada et al. 2005, Y. Hatada et al., submitted) reported eight subjects, one of the eight subjects showed an abnormal relation between vision and straight ahead pointing,

with both shifted in the same direction instead of shifting in opposite directions. This subject was therefore removed from the analysis in this study. In accordance with French law, informed consent was obtained

individually from the subjects before they attended the experiments.

Results

Visual straight ahead judgement measured using lateral LED movement from two opposite positions

Figure 2 shows the deviation of visual straight ahead from pretest for both judgements using LED movements from right to left (Vr) and from left to right (VI) over the time course of 7 days after the prism adaptation procedure, averaged from data of seven subjects. Positive and negative values indicate right and left positions of centre, respectively. A two-way repeated-measures ANOVA with measuring method (Vr and VI) and time (eight time points), as within-subject factors did not show a significant difference between the two measuring methods ($F_{(7,42)}=0.02, P>0.881$) nor a significant interaction effect of the two factors of time and measuring method ($F_{(7,42)}=1.47, P>0.206$). It did, however, reveal that the main effect of time was significant ($F_{(7,42)}=7.77, P<0.001$). Therefore, after adaptation, equivalent visual straight ahead judgements were made in response to LED motion from both directions, justifying our use of the average, *Va*.

The aftereffects of the three measures decay independently

In order to compare the differences in the development of adaptation and the decay of the aftereffect in *O*, *Va* and *S* over time, we compared the magnitudes of deviations of the three. Figure 3 shows the mean (averaged

data from seven subjects) deviations of post-tests from the pre-test of *O*, *Va* and *S*. A two-way repeated-measures ANOVA with type of measuring method (*O*, *Va*, *S*) and time (eight time points) as within-subject factors revealed a significant interaction effect of the two factors of time and measuring method ($F_{(14,84)}=7.76, P<0.001$), the main effect of measuring type was significant ($F_{(2,12)}=7.84, P<0.007$) and the main effect of time was also significant ($F_{(7,42)}=2.90, P<0.015$). Therefore, the three components showed aftereffects that were significantly different from each other and the changes in time course were significantly different from the 7 days of observation. We next analysed the time course of each component.

Very long-lasting aftereffect of O and S, in hours and days, respectively

The *S* aftereffect showed a two-wave pattern with an initial decay to pre-test level at 6 h followed by a return to significance from 1 to 7 days, with peak at 3 days. This aftereffect pattern was previously reported in detail (for eight subjects) in Hatada et al. (2005).

The *O* aftereffect showed a complex, significant pattern of shift with time ($F_{(7,42)}=8.10, P<0.001$). The large immediate rightward shift at 0 h ($P<0.001$ by student *t* tests) to $7.25\pm 1.28^\circ$, rapidly decayed (2 h: $P>0.149$) followed by a return to significance at 4 h (4 h: $P<0.020$) with gradual loss (6 h: $P<0.046$) to non-significance within 1 day ($P>0.062$) to pretest level at 3 and 7 days. It is likely that Bonferroni correction in this situation will be overly conservative as the eight post-adaptation tests are likely to be correlated and not independent; we therefore used PCA to determine the number of independent factors required to adjust the degrees of freedom. Factor analysis revealed 1 factor (principle component analysis,

Fig. 2 Deviation with SEM from pretest by Vr (black), VI (grey) over the time course of 8 days after the prism adaptation procedure, averaged from data of seven subjects. Positive and negative values indicate positions right and left of center, respectively. Asterisk indicates a significant deviation from pretest (tested by student *t* test comparisons with a single value of zero, with Bonferroni correction for number of independent factors as determined by principle component analysis 0.05/2=0.025). * $P<0.05$, ** $P<0.01$, $n=7$

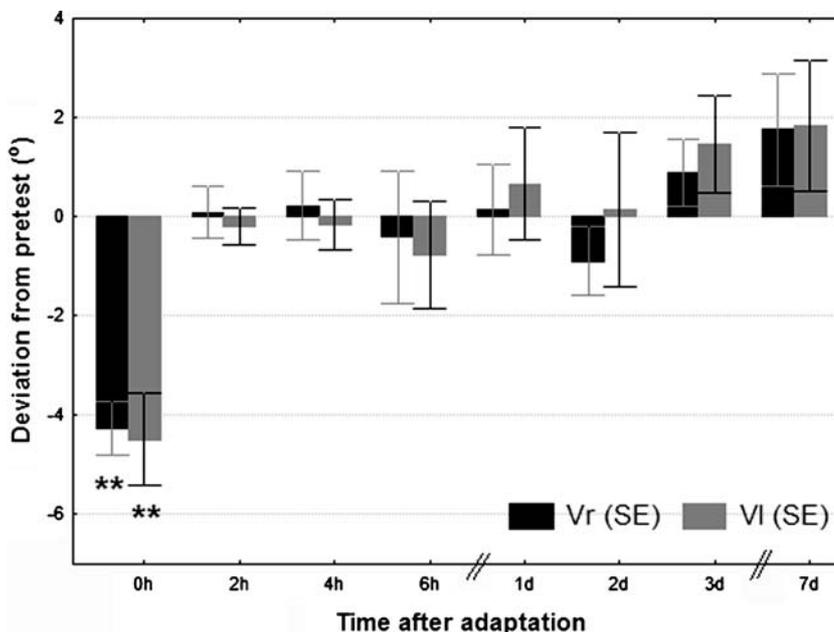
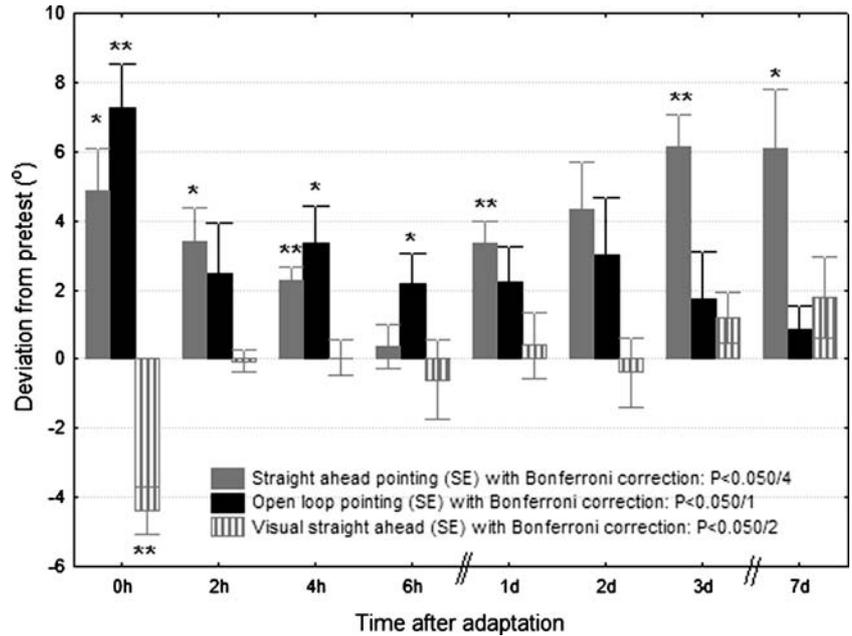


Fig. 3 Deviation with SEM from pretest by O , V and S over the time course of 8 days after the prism adaptation procedure, averaged from the data of seven subjects. Positive and negative values indicate positions right and left of center, respectively. Visual straight ahead judgements (Va) were measured by LED presentation. These data are averaged over movements from right direction and from left direction since the Vr and Vl do not differ significantly. Asterisk indicates a significant deviation from pretest (tested by student t test comparisons with a single value of zero) with Bonferroni corrections (O : $P < 0.050/1$; S : $P < 0.050/4$; Va : $P < 0.050/2$). $n = 7$, * $P < 0.05$, ** $P < 0.01$



77.53% sufficiency by using eigenvalue > 1.000). Therefore, with Bonferroni correction (0.050/1), three out of eight time points (0, 4, 6 h) are significantly shifted.

The aftereffect of Va does not last

The average of the two passive lateral visual straight ahead judgements (Va) showed a significant shift revealed by repeated-measures ANOVA ($F_{(7,42)} = 7.77$, $P < 0.001$). The prism adaptation procedure shifted the Va aftereffect leftward to $-4.37 \pm 0.69^\circ$ (0 h: $P < 0.001$, student t tests with Bonferroni correction 0.050/2), in the opposite direction to the aftereffect of O and S . The aftereffect of Va , however, decayed by the first measurement at 2 h ($P > 0.87$, student t tests) and did not show any significant change afterward.

The aftereffects in Va and S decay independently

The aftereffects measured by vision and straight ahead pointing are thought to be sub-components of the aftereffect measured by O . Therefore, we compared the aftereffects of Va and S .

A two-way repeated-measures ANOVA with measuring method (Va , S) and time (eight time points) as within-subject factors was performed. This revealed a significant interaction effect between the two factors ($F_{(7,42)} = 6.33$, $P < 0.001$) and a significant main effect of measuring type ($F_{(1,6)} = 14.28$, $P < 0.009$). Immediately after the prism adaptation at 0 h, Va and S showed similar magnitudes of shifts from pretest measurements but, as expected, to opposite directions: $-4.37 \pm 0.69^\circ$ ($P < 0.001$ by student t tests) and $4.86 \pm 1.24^\circ$ ($P < 0.008$ by student t tests), respectively. Comparisons between S and Va at each time point showed significant differences at six out of eight time points (0 h: $P < 0.001$; 2 h:

$P < 0.006$; 1 day: $P < 0.022$; 2 days: $P < 0.001$; 3 days: $P < 0.001$; 7 days: $P < 0.001$; by Dunnett's post hoc test). Therefore, the two curves revealed a significant difference in their long-lasting aftereffects. These analyses reveal the time course changes of aftereffect in Va and S are independent of each other.

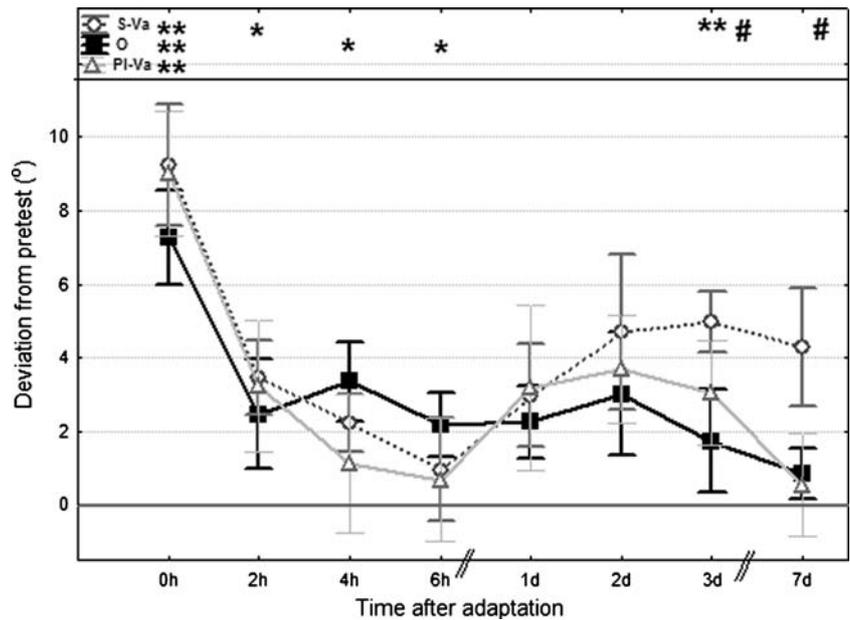
O does not fit the additivity model " $S-Va$ " for the second wave

Figure 4 shows $S-Va$ (additive model) and O together to illustrate the differences between the two. A repeated-measures ANOVA showed a significant interaction effect between the factors $S-Va$ and O ($F_{(7,42)} = 2.75$, $P < 0.019$) and a significant main effect of time ($F_{(7,42)} = 6.433$, $P < 0.001$). The two measuring methods (O and $S-Va$) when compared by Dunnett's two-tailed post hoc tests showed significant differences at 3 days ($P < 0.039$) and 7 days ($P < 0.025$). Repeated-measures one-way ANOVA analysis revealed that $S-Va$ showed a significant main effect of time ($F_{(7,42)} = 6.330$, $P < 0.001$). $S-Va$ showed significant shift at 0 h: $P < 0.001$, 2 h: $P < 0.014$, 4 h: $P < 0.031$, 3 days: $P < 0.001$ and 7 days: $P < 0.038$, student t tests. PCA analysis revealed two factors (77.84% sufficiency by using eigenvalues > 1.000). Therefore, using $0.050/2 = 0.025$ Bonferroni correction, three out of eight time points (0 h, 2 h, 3 days) are significantly shifted. This was different from O , which does not show any significant shift in the second wave. Therefore, this analysis reveals that the aftereffect in the late second wave at 3 and 7 days does not fit into the additivity model of " $S-Va$ ".

O fits " $Pl-Va$ " over 7 days

In our previous study (Y. Hatada et al., submitted), we showed that the shift in S differed from the shift in

Fig. 4 $S-Va$ (additive model) or $Pl-Va$ and O together to illustrate the differences between the two. Deviations of mean were taken individually from eight subjects for $S-Va$, $Pl-Va$ and O . $n=7$. Single asterisk and double asterisk indicate significant shifts from pretest measures within each component tested by student t test with Bonferroni corrections for $S-Va$ and $Pl-Va$ (P): * $P < 0.05/2$, ** $P < 0.005/2$, but not O (only 1 factor by factor analysis, thus no Bonferroni correction). (P): * $P < 0.05$, ** $P < 0.005$. Dunnett's post hoc testes between O and $S-Va$ at each time point revealed a significant difference at 3 days ($P < 0.039$) and 7 days ($P < 0.025$). However, O and $Pl-Va$ did not show any significant difference between the two. Hash indicates significant differences between O and $S-Va$: $P < 0.05$



passively measurable proprioception. We suggested that passively measurable proprioception from the two lateral positions (Pr and Pl) could be purer measurement for proprioception than S . Only Pl was affected by prism adaptation, thus the proprioceptive shift was biased for arm movements in one direction and not for movements in the opposite direction (Pr).

The comparison between “ $Pl-Va$ ” and O , on the contrary, did not show any significant differences between the two (Fig. 4). We analysed the results to test if $Pl-Va$ could represent the aftereffect of O better.

“ $Pl-Va$ ” does not show any significant difference from O over the 7 days of observation

Analysis of O and $Pl-Va$ by a repeated-measures two-way ANOVA showed a significant main effect of time ($F_{(7, 42)}=9.586$, $P < 0.001$); however, it did not show a main effect of the two measuring methods ($F_{(1, 6)}=0.016$, $P > 0.904$) nor showed a significant interaction effect between the two factors ($F_{(7, 42)}=1.32$, $P > 0.266$).

Repeated-measures one-way ANOVA revealed that “ $Pl-Va$ ” showed a significant main effect of time ($F_{(7, 42)}=5.499$, $P < 0.001$). There was only one significant deviation from pre-test at 0 h ($P < 0.002$, student t test with Bonferroni correction $0.05/2=0.025$ with factor analysis using principle component analysis of eigenvalue > 1 , 76.27% sufficiency). Further, the two measuring methods (O and $Pl-Va$) did not show any significant differences by Dunnett's two-tailed post hoc tests over 7 days of observation. The maximum difference was at 4 h ($P > 0.462$). Therefore, these analyses suggest that the magnitude of the shift of $Pl-Va$ did not show significant difference from O over the 7 days of aftereffect.

Discussion

Additivity model does not fit our results

The total shift in hand-eye coordinates in a prism adaptation aftereffect, which is measured by open loop pointing, has been reported to be a linear summation of the shifted aftereffect in vision and proprioception components (Hay and Pick 1966; Wilkinson 1971). Wilkinson's additivity model seems to well describe the total shift of adaptation by its sub-components of vision and proprioception during the adaptation. We confirmed the additivity model for up to 2 days after the adaptation. However, we found that from 3 days after the prism adaptation, Wilkinson's additivity model “ $O=S-Va$ ” did not fit our results. Rather “ $O=Pl-Va$ ” fitted better during the whole 7 days of aftereffect in our study.

Our results showed significant over-additivity of $S-Va$ relative to O at 3 and 7 days. Previously over-additivity was suggested to be attributable to use of more dramatic prismatic distortions such as inversion or right/left reversal conditions (Welch 1986; Choe and Welch 1974) or to motor response learning (Redding and Wallace 1978a). Since we did not use single target pointing nor used such drastic spatial changes during the prism training, such motor-specific response learning was unlikely in our study.

Moreover, our Pl and Pr measurements could not have been affected by motor response learning since they were slow passive arm movements controlled by the experimenter that were verbally halted by the subject. The measurements of O and S were also unlikely to be affected by motor response learning since they were not ballistic movements but were done using subjectively

comfortable speeds of roughly 2 s per pointing action and 5°/s for lateral arm movements during the passive measurements. The movements' speed meant that subjects could correct until they felt that the pointing direction was subjectively satisfactory. In these conditions, the first wave of PI showed a similar magnitude of shift as was measured by the sagittal straight ahead pointing. Therefore, it also does not seem reasonable to think that efferent components contribute a large proportion in our measurements of S .

We also do not believe that adaptation at the peripheral level, i.e. motor efferent, proprioceptive afferent and active/passive modification per se, are relevant to explaining the behavioural aftereffects we found. These issues were previously discussed in Y. Hatada et al. (submitted).

Finally, our powerful training generated prism aftereffects fitting to " $O=S-Va$ " as well as " $O=PI-Va$ " for up to 2 days. Therefore, training artefacts are unlikely explanations for our over-additivity of prism adaptation aftereffect after 3 days of adaptation.

Since " $O=PI-Va$ " fit the data over the complete 7 day period, we suggest this is a superior expression to " $O=S-Va$ " for describing open loop pointing. Why could O be better represented by " $PI-Va$ " than by " $S-Va$ "? We consider the neural network involved in the aftereffect in open loop pointing together with the results of each component of the prism adaptation aftereffect which showed independent decay patterns.

A model based explanation: internal egocentric reference frame (IEREF) is not involved in neural network for the task in open loop pointing

The neural network involved in O , i.e. pointing at a visual target without visual feedback, can be modelled by the circuit shown in [Appendix](#).

When there is an aftereffect shift in O , this may reflect shifts in the calibrations of (1) visual perception component (CVa); (2) visuo-manual transformation (VMT), which is required to transform the visual perceptual spatial input information into a desired arm movement; (3) central controlling signals to peripheral effectors, the signal that drives the execution of the movement and peripheral changes at effector levels, i.e. how the effectors react to the driving signals (CMr and CMI), and also (4) re-afferent signals from the peripheral to the central nervous system (CPr and CPI). Of these, straight ahead pointing does not use (1) CVa and (2) VMT, instead the pointing target relies on the subjective judgement of the mid-sagittal point using an internal egocentric reference frame (IEREF). Straight ahead pointing, however, also uses components 3 and 4 ([Appendix](#)). We calculated the magnitudes of shift in VMT and IEREF from the proposed model as " $VMT=O-(PI-Va)$ ", " $IEREF=S-PI$ ".

We note first that S gradually becomes different from PI, becoming significantly different at 7 days. This suggests that IEREF gradually increased in the second

wave. The remaining large shift of aftereffect in S could be due to a shift in IEREF that is increased with a delayed onset in the second wave. This finding was reported previously and we suggested possible mechanisms involved (Takehara et al. 2003; Y. Hatada et al., submitted). In contrast, the difference between O and $(PI-Va)$ did not become significant over 7 days (Fig. 4). Therefore, the prism adaptation does not produce a significant change of VMT over our 7 days of aftereffect observation. Therefore, the shift in CVa, measured by Va , directly propagates through VMT, to drive the arm movement during open loop pointing. Through the online proprioceptive feedback loop, the arm movement is additionally affected by the shifted CPI.

After prism adaptation, once subjects are exposed in their normal visual environment, normal body coordination (visuo-motor tasks of accurate contact, balance, auditory localization, eyes in head relation) could become the sources of deadadaptation for the visual perceptual shifts. We suggest IEREF does not shift during the initial prism adaptation in the first wave, as discussed above. Redding and Wallace (1996, 1997b) showed that prism adaptation with complete visibility for the path of finger pointing, starting from own hand starting position, did not generate aftereffects. Normal interaction with free visibility of hand after adaptation, therefore, is unlikely to be a source of deadadaptive pressure for the adaptively shifted neural network of internal representation of arm mid-sagittal plane (used for the measurements of S). Further, IEREF seems to develop gradually in the second wave, perhaps through transfer of plasticity from the origin of adaptation. These different early and late aftereffect decay patterns of shift in CVa and IEREF, respectively, suggest that IEREF does not share its neural code of spatial coordinates directly with CVa or with any of the deadadaptation sources explained above.

From these interpretations based on the model, the aftereffect of O shift is affected by the shift of CVa with CPI mostly through unaffected VMT. On the other hand, aftereffect of IEREF developed slowly in the second wave which is independently affected from the shift in CVa. This seems the reason why $O=PI-Va$ fit our results better than $O=S-Va$. These interpretations also suggest that IEREF and VMT are utilized mutually exclusively depending on visual input availability during two active pointings for S and O . The mutual exclusiveness is expressed in the model by the switch that selects between the two inputs ([Appendix](#)).

Conclusion

We showed that different components of prism adaptation aftereffect have independent decay time courses. Also we showed that visual input dependent, egocentric spatial coding and internally represented, visual input independent, egocentric space coding are mutually exclusively employed during different active pointing. We

suggest the aftereffect of prism adaptation could be maintained for a long time if de-adaptive pressure through normal visual space input is avoided, as may be the case for PI and S. Furthermore, internal egocentric reference frame (IEREF) could increase its aftereffect shift after a long delay. This knowledge could be applied generally to rehabilitation through effective training.

Appendix

Model to explain the neural network involved in prism adaptation using right arm

The neural network involved in the tasks of PI, S and O test measurements are shown in Fig. 5a–d. In the pre-test, all the components are in the naïve state. CVa: visual perception, CP: perceptual proprioception, CM: motor command and execution, the three consist of peripheral system and calibrated decoding CNS for Va and P and motor control CNS for M. CPI is the functional neural network whose property can be measured by the task PI. This codes the calibrated perceptual shift of PI. Similarly CP_r and CV_a are the functional neural networks that code the calibrated perceptual shifts of Pr

and Va. V0 indicates a given visual target during open loop pointing at the Cartesian mid-line of the subject. The long-dash double-dotted line indicates the borders between CNS and the peripheral system. Within the entire CNS box, there are direct/indirect connections between all components. The lines here illustrate only the primary direct connections for these tasks. The simple dashed line indicates external signal flow for visual feedback of current arm position during prism adaptation. The short-dash dotted line indicates periphery (arm). IEREF: internal egocentric reference frame. VMT: visuo-arm transformation. Thickness for box lines indicates magnitude of deviation from naïve state. Thick single lined box indicates spatially rightward deviated coding, thick double lined box indicates leftward deviation. Grey lines are not active. The upper switch indicates mutual exclusiveness of IEREF and VMT. The lower switch is switched between the (CM_r-CP_r) circuit and (CMI-CPI) circuit depending on the direction of sagittal pointing of out-/inward arm movements, respectively, during prism adaptation.

Figure 5a depicts conceptual model of the circuit involved in prism adaptation training during late stage. Most adaptation happens during outward arm movement which has visual feedback when the finger reaches the target position, while inward arm movement does

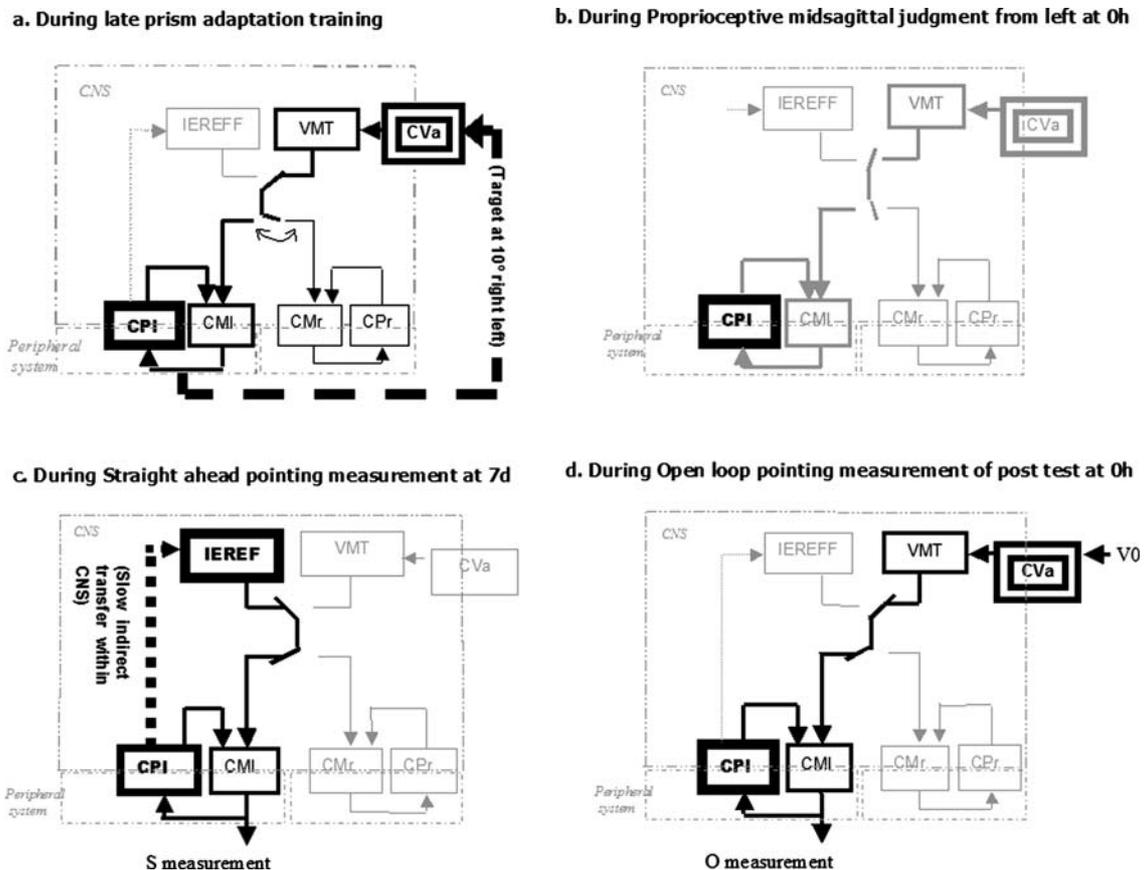


Fig. 5 A model to explain the neural network involved in prism adaptation and its aftereffect using the right arm

not give adaptation input since there is no visual feedback. Therefore, the visual feedback indicated by the dotted line gives an adaptation pressure for mostly the arm movements using the CMI-CPI circuit. Thus adaptation effects are weighted and distributed within this circuit in the system: CVa-VMT-CMI-CPI. Figure 5b depicts the activity during PI test measurement at 0 h. We suggest that this has proprioceptive perceptible signals in CNS as main cause of adaptation and involves a minor contribution from afferent proprioceptive signal from peripheral effectors. Figure 5c depicts the activity during S test measurement on 7th day. We suggest straight ahead pointing uses IEREF instead of VMT since there is no visual input. We suggested that the increase of the magnitude of shift in IEREF could occur through L-LTP transfer via indirect connections within CNS (fine dotted line) from the original coding shifts in components like CPI (see detailed possible mechanisms in Y. Hatada et al., submitted). Fig. 5d depicts the activity during O test measurement at 0 h. Open loop pointing relies on a given visual target (V0) which then is translated through VMT, into motor command (CMI), using afferent proprioceptive feedback and modified calibration in CPI during the pointing arm movement.

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