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2 **Adaptation of egocentric distance perception under**  
3 **telestereoscopic viewing within reaching space**

4 **Anne-Emmanuelle Priot · Rafael Laboissière ·**  
5 **Olivier Sillan · Corinne Roumes · Claude Prablanc**

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8 **Abstract** Telestereoscopic viewing provides a method to  
9 distort egocentric distance perception by artificially  
10 increasing the interpupillary distance. Adaptation to such a  
11 visual rearrangement is little understood. Two experiments  
12 were performed in order to dissociate the effects of a  
13 sustained increased vergence demand, from those of  
14 an active calibration of the vergence/distance mapping.  
15 Egocentric distances were assessed within reaching space  
16 through open-loop pointing to small targets in the dark.  
17 During the exposure condition of the first experiment,  
18 subjects were instructed to point to the targets without  
19 feedback, whereas in the second experiment, hand visual  
20 feedback was available, resulting in a modified relationship  
21 between vergence-specified distance and reach distance.  
22 The visual component of adaptation in the second experi-  
23 ment was assessed on the unexposed hand. In the post-tests  
24 of both experiments, subjects exhibited a constant distance  
25 overestimation across all targets, with a more than twice  
26 larger aftereffect in the second one. These findings suggest

two different processes: (1) an alteration in the vergence 27  
effort following sustained increased vergence; (2) a cali- 28  
bration of the vergence/distance mapping uncovering the 29  
visual component of adaptation. 30  
31

**Keywords** Adaptation · Vergence · Binocular · 32  
Reaching space · Egocentric distance perception 33

**Introduction** 34

Reaching forward to grasp an object or to point to a target 35  
requires one to correctly evaluate its distance and direction. 36  
Egocentric distance is estimated from retinal and extra- 37  
retinal cues (Gogel and Tietz 1979; Cutting and Vishton 38  
1995; Cutting 1997; Genovesio and Ferraina 2004; Blohm 39  
et al. 2008). In order to get insight into the way the central 40  
nervous system (CNS) builds a body-centered representa- 41  
tion of objects within near space, random sensory altera- 42  
tions can be introduced (Goodale et al. 1986; Prablanc and 43  
Martin 1992; Desmurget et al. 1999; Prablanc et al. 2003) 44  
as well as a continuous and systematic exposure to sensory 45  
alterations (Held and Freedman 1963; Prablanc et al. 1975; 46  
Kornheiser 1976; Kitazawa et al. 1997; Morton and Bastian 47  
2004; Mon-Williams and Bingham 2007). In the latter case, 48  
the CNS can adapt to the new inter-sensory coupling 49  
in order to build up a coherent and unified representation. 50

The present study aimed at understanding how the 51  
estimation of egocentric distance is affected by exposure to 52  
systematic visual alteration, namely the wearing of a 53  
telestereoscope. A telestereoscope is a simple device 54  
composed of two pairs of lateral, parallel mirrors placed in 55  
front of the eyes of the subject, artificially increasing the 56  
interpupillary distance (IPD). As early as the seventeenth 57  
century, Kepler and Descartes proposed that the radial 58

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59 distance to the point of fixation could be inferred from a  
60 triangulation process by using the convergence angle of the  
61 two lines of sight and the known IPD (Wade 1998). In this  
62 case, manipulation of the IPD would result in predicted  
63 modifications of egocentric distance estimation as vergence  
64 demand is modified. Artificially increasing the IPD by a  
65 given multiplicative factor of  $N$  increases the tangent of  
66 required convergence angle for all viewing distances by the  
67 same factor. Following this geometrical interpretation,  
68 Helmholtz proposed that “subjects viewed an exact  
69 reduced scale model of the world” through the telestereo-  
70 scope. Increasing the IPD by a factor of  $N$  would scale  
71 down the apparent distances by the same factor (Helmholtz  
72 1910; Valyus 1966).

73 Fisher and Ciuffreda (1990) conducted the first experi-  
74 ment on adaptation of egocentric distance perception under  
75 telestereoscopic viewing. Subjects assessed the distance  
76 and depth of a pyramidal target located within reaching  
77 space (33 cm) before and after a 30-min period of  
78 telestereoscopic exposure involving locomotion and visu-  
79 motor activities. A perceptual aftereffect consisting of  
80 increased apparent target distance and depth was observed,  
81 concomitant with an increase in tonic vergence state.

82 The wearing of opposite-base prisms is an alternative  
83 way to modify the relationship between vergence and  
84 perceived distance. Prolonged exposure to prisms is known  
85 to induce adaptation with corresponding distance estima-  
86 tion aftereffects when viewing is restored to normal  
87 (Wallach and Frey 1972; Wallach et al. 1972; Wallach and  
88 Smith 1972; Craske and Crawshaw 1974; von Hofsten  
89 1979; Owens and Leibowitz 1980; Ebenholtz 1981).  
90 Two main factors have been proposed to explain these  
91 aftereffects. The first one is a calibration of the mapping  
92 between vergence signal and perceived distance (referred  
93 hereafter as the *calibration of the vergence/distance map-*  
94 *ping*) arising from the conflict between altered vergence  
95 signal and unaltered monocular cues such as linear per-  
96 spective, motion parallax or familiar size (Wallach and Frey  
97 1972). The second one is a tonic change in the eyes muscles  
98 or eye muscle potentiation (EMP) (Ebenholtz 1974; Ebe-  
99 nholtz and Wolfson 1975; Paap and Ebenholtz 1977; Ebe-  
100 nholtz 1981; Ebenholtz and Fisher 1982). Both factors  
101 could be responsible for aftereffects, depending on expo-  
102 sure conditions (Welch 1986; Howard and Rogers 2002).

103 Vergence demands differ with regard to the optical  
104 device used. Prisms introduce a constant bias in the  
105 required convergence angles over all distances, whereas  
106 increasing the IPD by a given multiplicative factor with a  
107 telestereoscope increases the tangent of required conver-  
108 gence angle for all viewing distances by the same factor. In  
109 the present study, the adaptation of egocentric distance  
110 perception to telestereoscopic viewing within reaching  
111 space was investigated. Such an adaptive process may arise

112 primarily from two components: an induction component  
113 induced by sustained fixation through the telestereoscope,  
114 and a calibration component based on distorted hand visual  
115 feedback. In order to disentangle these components, we  
116 designed two experiments differing only by the feedback  
117 given to the subject during exposure. In the pre- and post-  
118 tests of both experiments, egocentric distance was esti-  
119 mated by open-loop pointing (i.e. without visual feedback  
120 of the hand) to the perceived location of the targets.

121 In Exp. 1, perceived distance under telestereoscopic  
122 viewing exposure was assessed by open-loop pointing.  
123 Throughout this paper, the distance given by the pointing  
124 gesture is referred as *reach distance*. Care was taken to  
125 limit the available cues for distance to the altered vergence  
126 during telestereoscopic viewing exposure. In that case, the  
127 expected aftereffect in Exp. 1 should originate mainly from  
128 the EMP mechanism. In order to ensure this, we designed  
129 the experiment such that the farthest target would appear at  
130 a distance of 195 mm from the eyes, which is below the  
131 point of balance between the actions of the medial and  
132 lateral recti muscles, called the physiological point of rest  
133 (PPR) (Ebenholtz and Wolfson 1975). The empirical value  
134 of the PPR is close to 300 mm (Paap and Ebenholtz 1977).  
135 Consistent with previous studies, we expected an EMP-  
136 related increase in perceived distance over the whole range  
137 of targets after removal of the telestereoscope.

138 The goal of Exp. 2 was to study the adaptive processes  
139 arising from active visuomotor exposure to the telestereo-  
140 scope. Held (1965) has shown that active experience is a  
141 key factor for perceptual adaptation to laterally displacing  
142 prisms. Active interaction with the environment also  
143 resulted in greater adaptation to prism-induced alteration of  
144 apparent distances (Owens and Leibowitz 1980; Ebenholtz  
145 1981). In the exposure phase of Exp. 2, subjects underwent  
146 a discrepancy between vergence-specified distance and  
147 reach distance. Such a conflict may elicit visuomotor  
148 adaptation, whatever the specific contributions (motor,  
149 proprioceptive and visual) of the different adaptive com-  
150 ponents might be (Kornheiser 1976; Welch 1986; Redding  
151 and Wallace 1990). The present study focused on the visual  
152 component of adaptation only and investigated the poten-  
153 tial calibration of the vergence/distance mapping as mea-  
154 sured from the unexposed hand. Indeed, visuomotor  
155 adaptation is restricted to the exposed hand, whereas only  
156 the visual component of adaptation is available to the  
157 unexposed hand (Harris 1965). Comparable amounts of  
158 EMP are likely to be induced in both experiments, since  
159 these experiments differed only by the presence of a visual  
160 feedback. Calibration of the vergence/distance mapping  
161 requires the presence of this kind of feedback, whereas  
162 EMP does not. Any difference in the aftereffects of Exp.1  
163 and 2 should thus be attributed to a calibration process.  
164 After removal of the telestereoscope, any theoretical

165 rescaling should result in an increase in the gain of the  
166 vergence/distance mapping, and thus a distance overesti-  
167 mation aftereffect. Hence, the aftereffect of Exp. 2 is  
168 expected to be larger than the aftereffect of Exp. 1, as it  
169 involves both the EMP-related aftereffect and the calibra-  
170 tion-related aftereffect.

## 171 Materials and methods

### 172 Subjects

173 All 24 recruited subjects gave informed consent. The  
174 experiments were conducted in accordance with the Decla-  
175 ration of Helsinki and under the terms of local legislation.  
176 All subjects were screened for good stereoscopic vision and  
177 none had past history of binocular disorder. All subjects  
178 had normal or corrected-to-normal vision. Prescribed  
179 correction, if any, was worn during the experiments.  
180 All subjects had to maintain single and clear vision over the  
181 whole range of targets by the end of the training phase.  
182 Twelve subjects were retained in Exp. 1 (six women and  
183 six men, mean age 38, ranging from 21 to 64) and twelve  
184 subjects were retained in Exp. 2 (six women and six men,  
185 mean age 34, ranging from 21 to 64). Five subjects par-  
186 ticipated in both experiments, with at least a 2-week delay  
187 between experiments.

### 188 Apparatus and procedure

189 Figure 1a presents the telestereoscope and the optical path  
190 through telestereoscopic viewing. The telestereoscope  
191 consisted of two pairs of mirrors positioned parallel to each  
192 other, angled at 45°. The telestereoscope used in our  
193 experiments displaced the line of sight of each eye laterally  
194 by 70 mm. The tangent of required convergence angle was  
195 thus increased by approximately  $N = 3.2$  times for a sub-  
196 ject with a 64-mm IPD while fixating an object within near  
197 space. It can be noted that the telestereoscope also  
198 increases the path length of the light rays, shifting the  
199 virtual image (optical eye-to-target distance) by 70 mm  
200 further away. This decreases the accommodation level. The  
201 ratio of convergence to accommodation is therefore  
202 increased. The relationship between  $y_v$  (vergence-specified  
203 distance through telestereoscope) and  $y_a$  (optical eye-to-  
204 target distance, i.e. accommodation-specified distance) is  
205 given by:  $y_a/y_v = \text{IPD}'/\text{IPD} = N$ .

206 We used as visual stimuli nine red light-emitting diodes  
207 (LED, 635 nm wavelength) located vertically above the  
208 subject's head (see Fig. 1b). As the subject observed the  
209 targets through a central half-silvered mirror tilted 45° with  
210 respect to the vertical fronto-parallel plane, the ramp of  
211 LEDs appeared horizontal. Direct vision through the mirror

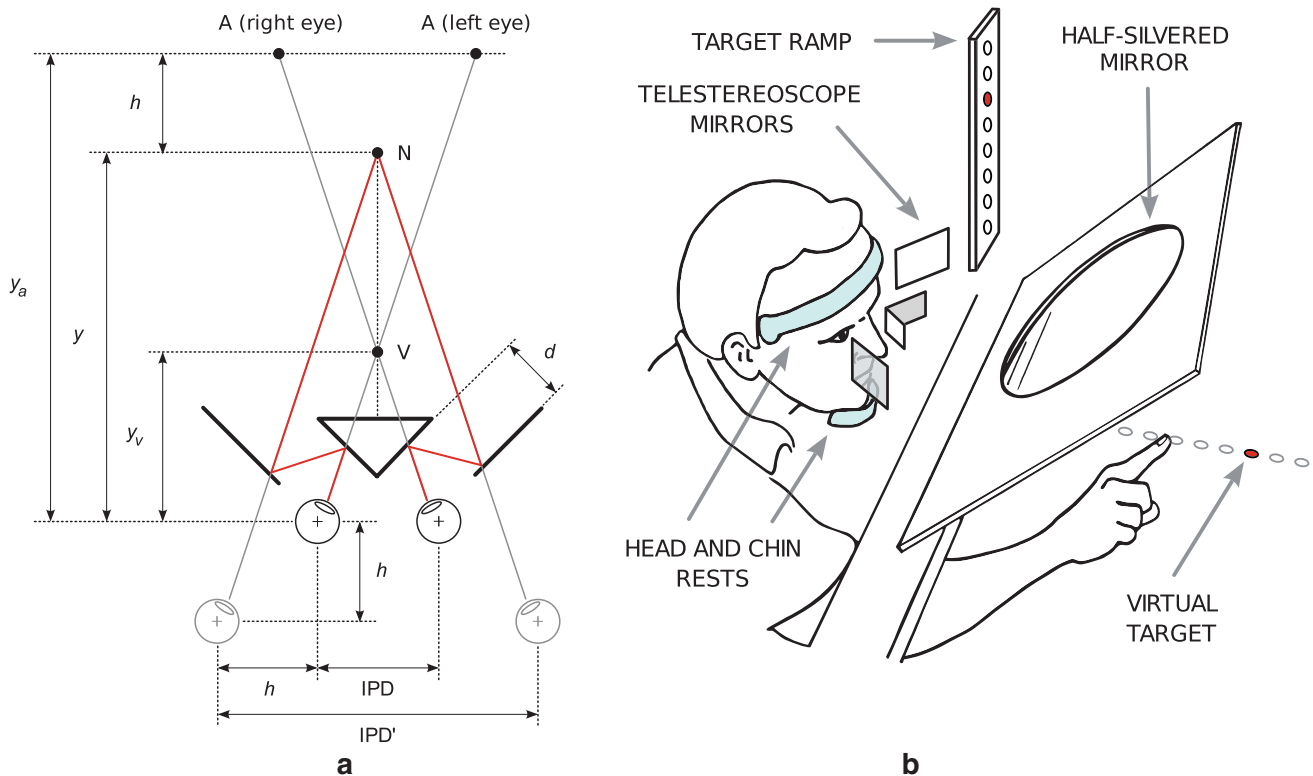
could be prevented by an occluding screen placed behind  
the mirror. The targets were aligned 350 to 510 mm from  
the cornea along a horizontal axis in the sagittal plane,  
20 mm below the ocular plane. Head movements were  
restrained using a forehead and a chin rest.

In all experiments, distance estimates were assessed by  
open-loop pointing (i.e. without visual feedback of the  
hand) with the right hand. Indeed, visual egocentric dis-  
tance estimated by pointing response has been found to be  
half as variable than verbal estimation (Foley 1977;  
Bingham and Pagano 1998) and more accurate. While the  
assessment of target distances by verbal responses involves  
mainly the occipito-temporal connection (i.e. the ventral  
pathway), a direct hand pointing response, under full spa-  
tial compatibility between the stimulus and the effector,  
and free of physical constraints, involves essentially the  
dorsal occipito-parietal connection (i.e. the dorsal path-  
way), as proposed by Goodale and Milner (1992). Hand  
pointing distance estimation is rather robust and weakly  
sensitive to cognitive judgments. A 2-mm infrared-emitting  
diode (900 nm wavelength) was attached to the fingertip,  
whose position was recorded at 250 Hz with an Optotrak  
3020, Northern Digital Inc., a system for recording  
3D movement. During the experiments, all pointing  
movements were performed in a totally free open space  
preventing any tactile feedback.

In preliminary tests, distance estimation of familiar  
objects under telestereoscopic viewing in a natural  
environment was assessed through verbal judgment.  
We noticed that objects with familiar size led to some  
ambiguity in judging egocentric distances. Some subjects  
perceived the objects to be near, likely relying on increased  
convergence. Other subjects perceived them further, likely  
relying on the decreased apparent size of the object.  
In order to reduce such an effect, we used small (3-mm  
diameter) LED targets. Virtual targets were used to prevent  
tactile feedback. The apparatus was calibrated using the  
Optotrak. A LED marker was mechanically displaced until  
two experimenters on both right and left sides of the half-  
silvered mirror judged it coincident with the target image  
seen through the mirror. We estimate the accuracy of this  
procedure to be smaller than 1 mm.

### Experiment 1

A classical paradigm including three blocked conditions,  
pre-test, exposure to telestereoscopic viewing and post-test  
(Helmholtz 1910; Held and Freedman 1963), was carried  
out in an otherwise dark room. In all pre-tests, post-tests  
and exposure phase, the estimated distance was assessed by  
open-loop pointing toward the targets seen through the  
tilted central mirror. Cues for target distance during the  
exposure condition were restricted to altered oculomotor



**Fig. 1** **a** Telestereoscope geometry. Inner and outer vertical mirrors are parallel and slanted at  $45^\circ$  from the sagittal plane. They are separated by an orthogonal distance  $d$ . The interpupillary distance is IPD and the apparent interpupillary distance IPD'. Virtual eyes are shown in gray and are displaced backwards and outwards by a distance  $h = d\sqrt{2}$ . The fixation point is represented by the dot labeled N (for “natural” viewing condition), placed at distance  $y$  from the subject’s eyes. Gray lines represent the direct lines of sight from the real and virtual eyes. The red line is the reflected light-path from the target to the eyes. Fixation at the dot labeled N requires the convergence of the two lines of sight onto the dot labeled V, at

distance  $y_v$  from the subject’s eyes. The optical eye-to-target distance is  $y_a$ . The dots labeled A (right eye) and A (left eye) represent, respectively the virtual target images seen by right and left eyes.  $y$ ,  $y_v$  and  $y_a$  correspond, respectively to the physical distance to the target, the distance as specified by vergence and the distance as specified by accommodation. **b** Experimental setup. The subject is looking through the telestereoscope mirrors while resting his head and chin. The pronated right hand points to the estimated position of the target behind the half-silvered mirror. The virtual position of the target is shown in red, as well as the lit LED in the target ramp

263 cues (i.e. vergence and accommodation). This is an  
 264 induction rather than an adaptation paradigm as no feed-  
 265 back was available during exposure (Ebenholtz 1981). We  
 266 chose to use the same (right) hand for exposure and test  
 267 conditions in Exp. 1 in order to compare pointing responses  
 268 with and without the telestereoscope (i.e. to reveal the  
 269 distortion of perceived distance).

270 Each of the nine targets was presented ten times in a  
 271 random order. A single target only was lit at a time. There  
 272 was a 3-s dark interval between offset of the previous target  
 273 and onset of the next one, in order to reduce any existing  
 274 inter-target disparity between two successive stimuli. Each  
 275 condition lasted about 10 min. Subjects underwent training  
 276 trials without telestereoscope and without any feedback for  
 277 a few minutes just before the pre-test, in order to become  
 278 familiar with the pointing task. Before the exposure con-  
 279 dition, subjects were trained under telestereoscopic view-  
 280 ing until they were able to fuse the targets at all distances.

No pointing response was required during this training  
 281 phase. Although most of the included subjects reported  
 282 diplopia and/or blurring through the telestereoscope at the  
 283 beginning of the training phase, they all reported single and  
 284 clear vision over the whole range of targets by the end of  
 285 the training phase.  
 286

In all conditions, subjects were instructed to point as  
 287 accurately as possible with their unseen right index fin-  
 288 gertip (moving in a free open space), at the perceived  
 289 location of the target. Then, they validated the pointing  
 290 response by pushing a button with the hanging stationary  
 291 left hand, and returned the right hand to a rest position  
 292 close to the chest. In the exposure condition, subjects were  
 293 instructed to wait until they totally fused onto the target,  
 294 before initiating their pointing response. In the rare  
 295 instances when fusion was not possible (mostly for the  
 296 nearest targets), the trial was aborted and the next random  
 297 trial was presented. The aborted trials were presented after  
 298



299 the end of the full trial sequence, intermixed with new  
300 random trials until ten repetitions of each target were  
301 collected. The post-test condition followed the exposure  
302 condition by a few minutes.

### 303 *Experiment 2*

304 The experimental setup was the same as in Exp. 1. The pre-  
305 and post-tests were carried out exactly in the same way as  
306 in Exp. 1, by open-loop pointing to the target with the right  
307 hand. In contrast to Exp. 1, the left hand was used for  
308 pointing during telestereoscopic viewing exposure, and  
309 hand visual feedback was allowed by removing the  
310 occluding screen behind the half-silvered mirror. Instead of  
311 directly seeing their left hand, subjects saw a red LED  
312 attached to the left index fingertip in an otherwise dark  
313 room in order to prevent hand or finger familiar size cue.

314 As in Exp. 1, subjects had to totally fuse onto the target  
315 before initiating the pointing response. They were  
316 instructed to point their left index finger as accurately as  
317 possible at the perceived location of the virtual target.  
318 Adjustment movements were allowed until the fingertip  
319 LED coincided with the virtual target. Then, the subject  
320 validated his or her response by pushing a button with the  
321 hanging and stationary right hand. Failure in binocular  
322 fusion resulted in trial abortion.

323 The left hand was used for pointing in the exposure  
324 condition of Exp. 2, whereas the right unexposed hand was  
325 used in the pre- and post-test conditions in order to isolate  
326 the visual component of aftereffect adaptation. In any type  
327 of visuomotor adaptation, the total aftereffect is a combi-  
328 nation of visual, proprioceptive and hand motor compo-  
329 nents (Welch 1986). The two latter ones are restricted to  
330 the exposed limb. Indeed, previous studies on short-term  
331 visuomotor pointing adaptation to prism lateral displace-  
332 ment showed that these components are not transferred  
333 from the exposed limb to any other limb (Harris 1963,  
334 1965; Hamilton 1964; Prablanc et al. 1975; Elliott and  
335 Roy 1981; Martin et al. 1996; Kitazawa et al. 1997).  
336 Conversely, when a visual component has developed, it is  
337 available for all effectors and an interlimb transfer is  
338 observed (Kornheiser 1976; Wallace and Redding 1979).  
339 Thus, using the unexposed right hand for distance assess-  
340 ment underscored the visual component of adaptation only,  
341 uncontaminated by the short-term visuomotor adaptation of  
342 the exposed left hand. Consequently, care was taken to  
343 avoid any contact between right and left hands throughout  
344 the experiment, which could have introduced some inter-  
345 limb proprioceptive and/or motor transfer. It was necessary  
346 to run Exp. 2 after Exp. 1 for the five subjects enrolled in  
347 both experiments, in order to prevent any knowledge of  
348 result that would have been obtained during the Exp. 2  
349 exposure.

### Data analysis

The fingertip position in 3D was measured as the average  
over the 40 ms following the onset of the push button. For  
the data analysis, the measured variable was the pointing  
distance along a horizontal axis in the sagittal plane located  
20 mm below the ocular plane. The origin of this axis lays  
at the coronal plane passing at the subject's cornea, making  
it appropriate for the assessment of egocentric distance  
estimation.

Inside a condition, the measured pointing distance  
depended on the target distance. To check for possible  
temporal drifts in the pointing behavior over the course of  
the open-loop conditions, we used a linear model that is  
described in the Appendix. Linear models are classically  
used to describe the functional relationship between target  
distance and distance estimation assessed by manual set-  
ting (Ebenholtz 1981; Mon-Williams and Tresilian 1999).  
The relationship between target distance and pointing dis-  
tance is referred hereafter as the *target-to-pointing*  
*mapping*.

For each subject, an ANCOVA was performed to assess  
the aftereffect, using the pointing distance as dependent  
variable, the condition as a 2-level factor (pre- vs. post-test  
in both Exp. 1 and Exp. 2, and pre-test vs. exposure in Exp.  
1), and the target distance as a continuous factor. The  
aftereffect is defined as the signed difference between  
post- and pre-test mean pointing distances (see Appendix).  
Repeated-measures ANCOVAs were performed on each  
group of subjects for Exp. 1 and Exp. 2. *T*-tests were  
performed to compare aftereffects in Exp. 1 and Exp. 2.  
To better understand the changes between the pre-test and  
the exposure conditions in Exp. 1, a MANOVA was per-  
formed using the mean pointing distance and the regression  
slope as dependent variables and pre-test vs. exposure  
condition as a 2-level factor.

## Results

### Preliminary analysis

For each experiment, we checked for the presence of out-  
liers in the group of subjects, based on the global afteref-  
fect. For each subject and for each experiment, the *z*-score  
was computed. Subjects whose *z*-score laid outside  
the  $\pm 2.0$  interval were considered outliers and removed  
from the analysis. This happened only in Exp. 1 for one  
subject.

Check for possible temporal drifts in the pointing  
behavior over the course of the open-loop conditions was  
performed before averaging the data (see Appendix). Some  
subjects exhibited an increase in the mean pointing

398 distance and/or the slope of the target-to-pointing mapping  
 399 over the course of a condition block, while others exhibited  
 400 a decrease. We ran two-sided  $t$ -tests on the set of values of  
 401 time-coefficients for each experiment and for each condi-  
 402 tion, which showed that the group means were not signif-  
 403 icantly different from zero. The  $t$ -tests for the mean  
 404 pointing distance time-coefficient had a minimum  
 405  $P > 0.14$  and the  $t$ -tests for the slope time-coefficient had a  
 406 minimum  $P > 0.27$ . We concluded that no systematic  
 407 temporal trend was found in the group. For the remaining  
 408 analysis in this paper, we will consider the subjects'  
 409 responses to be stationary inside each condition block.

#### 410 Individual analyses

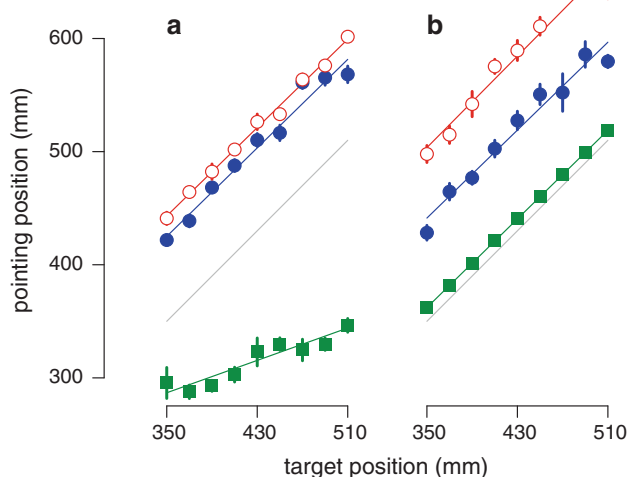
411 In Fig. 2, pointing distance is plotted as a function of target  
 412 distance for two different subjects, one in Exp. 1 (left  
 413 panel) and the other in Exp. 2 (right panel). ANCOVAs  
 414 between pre- and post-tests showed that the condition  
 415 factor was significant for all subjects ( $P < 0.05$ ), except for  
 416 two subjects in Exp. 1 who presented aftereffects close to  
 417 zero. The linear dependency on the target distance was, as  
 418 one would expect, reliable for all subjects ( $P < 0.001$ ) in  
 419 both experiments. In Exp. 1, the fitted slope ranged from  
 420 0.45 to 1.15, with mean value 0.81 (SD = 0.20) in the pre-  
 421 test condition, and from 0.30 to 1.19, with mean value 0.77  
 422 (SD = 0.27) in the post-test condition. Values for Exp. 2  
 423 were similar, with the slope varying from 0.56 to 1.10,

424 mean value 0.85 (SD = 0.18) in the pre-test, and from 0.55  
 425 to 1.19, mean value 0.82 (SD = 0.20) in the post-test.

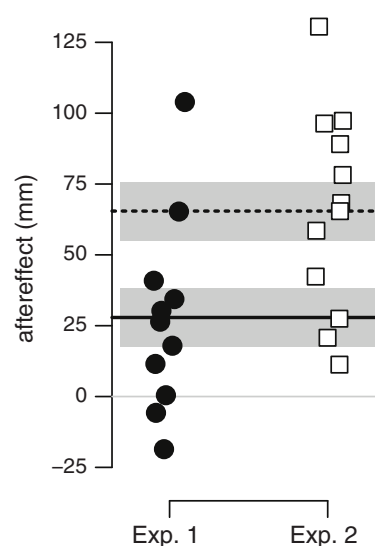
426 In Exp. 1, the interaction between condition and target  
 427 distance was significant for three subjects, while in Exp. 2 it  
 428 was significant for four subjects (maximum  $P < 0.05$ ). The  
 429 individual aftereffect values for Exp. 1 and Exp. 2 are  
 430 presented in Fig. 3. Each subject is represented by a point  
 431 and the horizontal lines indicate the mean value for each  
 432 experiment. The colored horizontal strips represent the  
 433 standard errors on the estimation of the mean. In Exp. 1, the  
 434 mean value of the aftereffect was 28 mm (SD = 34 mm).  
 435 The values ranged from -18 mm to 104 mm. In Exp. 2, the  
 436 aftereffect averaged to 65 mm (SD = 36 mm), with mini-  
 437 mum and maximum values equal to 11 mm and 130 mm,  
 438 respectively. The aftereffect values computed for each  
 439 subject will be used below in the  $t$ -tests.

#### 440 Group analysis

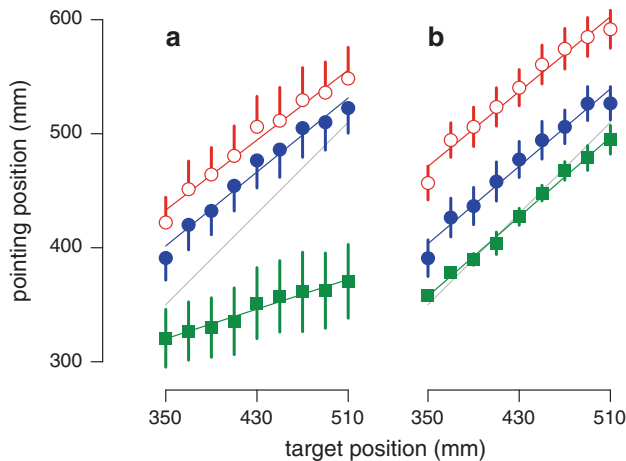
441 The global behavior of the group of subjects in both  
 442 experiments is shown in Fig. 4. This figure is similar to  
 443 Fig. 2, but the points represent now the mean results for the  
 444 group. Repeated-measures ANCOVA between pre- and  
 445 post-test conditions showed significant results for the target  
 446 distance factor ( $F[1,10] = 129$ ,  $P < 0.001$ , in Exp. 1, and  
 447  $F[1,11] = 247$ ,  $P < 0.001$ , in Exp. 2). The condition factor  
 448 was significant in both experiments ( $F[1,10] = 7.21$ ,  
 449  $P < 0.03$ , in Exp. 1, and  $F[1,11] = 40.4$ ,  $P < 0.001$ , in



**Fig. 2** Individual examples of distance estimation for Exp. 1 (panel a) and Exp. 2 (panel b) for two different subjects. In both panels, each point represents the average value of the pointing distance (vertical axis) for each target (horizontal axis), in each condition (blue-filled circles: pre-test, green-filled squares: exposure, red open circles: post-test). Standard errors are indicated by vertical bars. Regression lines for each condition are shown in the respective colors. The gray line indicates the ideal response under normal viewing



**Fig. 3** Aftereffects in Exp. 1 and 2. The vertical axis represents the aftereffect, computed as the difference in the mean pointing distance from the pre- to post-test conditions. Each subject in each experiment is represented by a point (filled circles for Exp. 1 and open squares for Exp. 2). Horizontal lines show the mean value of the aftereffect in each experiment (solid line for Exp. 1 and dotted line for Exp. 2). Gray horizontal strips represent the  $\pm 1$  SE interval of the estimation of the means



**Fig. 4** Distance estimation mean across subjects, in Exp. 1 (panel **a**) and Exp. 2 (panel **b**). Conventions are the same as in Fig. 2 (blue-filled circles: pre-test, green-filled squares: exposure, red open circles: post-test). Standard errors are indicated by vertical bars. In the left panel, the error bars are plotted on one side only, for sake of clarity. Regression lines for each condition are shown with the corresponding color. The gray line indicates the ideal response under normal viewing

450 Exp. 2). The interaction between condition and target distance  
451 was not significant ( $F[1,10] = 0.72$ ,  $P > 0.41$ , in  
452 Exp. 1, and  $F[1,11] = 1.19$ ,  $P > 0.3$ , in Exp. 2). As it was  
453 shown in the previous section, the assumption of parallelism  
454 in the target-to-pointing regression lines between pre-  
455 and post-test failed for seven subjects out of 23. However,  
456 the lack of interaction between the condition and target  
457 distance factors as revealed by the group ANOVAs indicated  
458 that it is reasonable to assume such a parallelism at the  
459 group level.

460 One-sided paired  $t$ -tests were run on the aftereffect sizes  
461 for each experiment. The mean value of aftereffect in Exp.  
462 1 was 28 mm (SE = 10 mm) and significantly greater than  
463 zero ( $t[10] = 2.69$ ,  $P < 0.02$ ). This was also the case for  
464 the mean value 65 mm (SE = 10 mm) in Exp. 2  
465 ( $t[11] = 6.38$ ,  $P < 0.001$ ). The difference in the aftereffect  
466 size across both experiments was assessed through an  
467 unpaired one-sided  $t$ -test. Exp. 2 has a significantly higher  
468 aftereffect than Exp. 1 ( $t[21] = 2.57$ ,  $P < 0.01$ ).

469 Exposure condition in Exp. 1

470 To better understand the changes between the pre-test and  
471 the exposure conditions in Exp. 1, we conducted a multi-  
472 variate analysis (MANOVA) on the mean pointing distance  
473 and slope. The data for the 11 subjects in Exp. 1 are shown  
474 in Fig. 5b. The theoretical curves for the natural viewing  
475 condition (N), as well as the vergence-specified (V) and  
476 accommodation-specified distance (A) are illustrated in  
477 Fig. 5a. The linear-regression coefficients of these

478 theoretical curves are represented in Fig. 5b. They were  
479 computed assuming a mean IPD of 64 mm and a frontal  
480 separation between mirrors of 70 mm (see Material and  
481 methods). The MANOVA revealed a significant difference  
482 across conditions ( $F[2,19] = 10.7$ ,  $P < 0.001$ ), indicating  
483 a difference in both mean pointing distance and slope  
484 between Exp. 1 and Exp. 2.

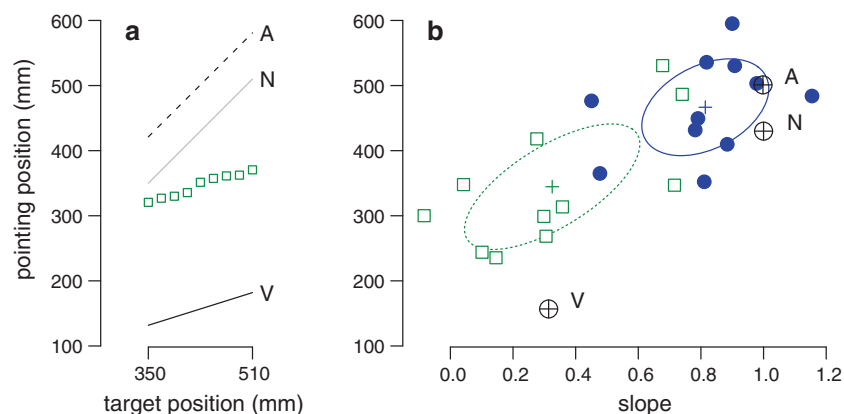
485 In the exposure condition of Exp. 1, the mean slope  
486 across subjects was 0.32, with standard error equal to 0.07.  
487 One-sided  $t$ -tests indicated that this value was significantly  
488 greater than zero ( $t[10] = 4.57$ ,  $P < 0.001$ ) and lower than  
489 1 ( $t[10] = 9.75$ ,  $P < 0.001$ ). We compared this mean slope  
490 with the slope predicted by using the vergence information,  
491 which is 0.31, through a two-sided  $t$ -test and no significant  
492 difference was found ( $t[10] = 0.13$ ,  $P > 0.89$ ). The use of  
493 the vergence information also predicts that the mean  
494 pointing distance should be 157 mm. The mean pointing  
495 distance for the group during the exposure condition of  
496 Exp. 1 was 314 mm, with a 31-mm standard error. This  
497 value was significantly greater than the value predicted  
498 ( $t[10] = 5.05$ ,  $P < 0.001$ ). For all subjects, the mean  
499 pointing distance was greater than 157 mm, with a 236-mm  
500 minimal value.

## 501 Discussion

### 502 Temporal evolution of target-to-pointing mapping

503 As in all adaptation or induction processes, there is both a  
504 rising acquisition function during the exposure phase and a  
505 corresponding post-exposure decline. This decline may be  
506 the result of a return to normal visual or visuomotor  
507 experience (i.e. de-adaptation), or the result of some  
508 spontaneous decay (Welch 1986). The spontaneous decay  
509 is much longer than the de-adaptation decay (Hamilton and  
510 Bossom 1964). The EMP-related aftereffect decay was  
511 expected to occur in both Exp. 1 and Exp. 2 post-tests,  
512 whereas the lack of visuomotor feedback in Exp. 2 post-test  
513 did not allow de-adaptation of the calibration of the ver-  
514 gence/distance mapping. In both experiments, these time  
515 constants should exist and be large enough in comparison  
516 with the duration of the condition blocks, otherwise we  
517 should have measured no aftereffect. However, the tempo-  
518 ral analysis did not show a significant variation over time  
519 for the group of subjects, but a large inter-subject vari-  
520 ability was found both in the amount and in the direction  
521 of the drift. Brown et al. (2003) and Wann and Ibrahim (1992)  
522 have already shown substantial amounts of proprioceptive  
523 drifts for reach movements. The expected adaptation- or  
524 induction-related temporal evolution may have been  
525 masked by the noise in open-loop hand pointing. Signifi-  
526 cant and significantly different aftereffects were obtained





**Fig. 5** **a** Theoretical responses using the different signals used for distance estimation under telestereoscopic viewing. The pointing distance (*vertical axis*) is plotted against the target distance (*horizontal axis*). The *solid line* represents the distance as specified by vergence (*V*) and the *dashed line* shows the distance as specified by accommodation (*A*) for a telestereoscope with a 70-mm frontal separation between mirrors. The *gray line* represents the physical distance to the target under natural viewing (*N*). The mean group response for each target is shown with *green open squares*. **b** Change in the linear-regression coefficients between pre-test and exposure

conditions in Exp. 1. The *slope* is represented in the *horizontal axis* and the mean pointing distance in the *vertical axis*. Each point corresponds to the values fitted for one subject in one of the two conditions, *blue-filled circles* for the pre-test phase and *green open squares* for the exposure phase. The 1-SD ellipses are shown (*solid blue line* for the pre-test and *green dotted line* for the exposure condition), as well as the mean value for each phase (*crosses*). *Circles with crosses* represent the theoretical values for the coefficients in each case (*V*, *A* and *N*, as above)

527 in Exp. 1 and 2 despite all drifts and noise in open-loop  
528 pointing.

529 Exp. 1: the induction paradigm

530 The first aim of the present study was to investigate ego-  
531 centric distance estimation under telestereoscopic viewing  
532 in a reduced visual cue environment without any feedback,  
533 and distance estimate alteration following sustained  
534 increased convergence.

535 The distance estimate aftereffect following the induction  
536 paradigm may be accounted for by changes in oculomotor  
537 adjustments, namely the increase in tonic vergence and/or  
538 increase in accommodative vergence gain. Vergence-  
539 specified distances ranged from 134 mm to 195 mm during  
540 exposure, which is below the value of 300 mm found for  
541 the PPR (Ebenholtz and Wolfson 1975). Sustained fixation  
542 to a target closer than this distance should elicit EMP  
543 inducing an increased tonic vergence (Ebenholtz 1974;  
544 Ebenholtz and Wolfson 1975; Paap and Ebenholtz 1977).  
545 Such a change in tonic vergence results in increased esti-  
546 mated distance. Binocular distance estimation is believed  
547 to rely on the departure from rest convergence rather than  
548 on absolute convergence (von Hofsten 1976). Any  
549 manipulation that changes rest convergence alters the effort  
550 required to fuse for all distances (Foley 1991). A shift of  
551 the rest convergence toward a shorter distance (i.e. an  
552 increase in tonic vergence) results in a reduced conver-  
553 gence effort, which leads to distance overestimation  
554 (Owens and Leibowitz 1980; Ebenholtz 1981; Ebenholtz

and Fisher 1982; Shebilske et al. 1983; Fisher and Ciuffreda 1990). The second candidate for oculomotor adaptation is a change in accommodative vergence gain. The natural cross-coupling between accommodation and convergence is altered during telestereoscopic viewing and such a conflict has been found to be solved through an increased accommodative vergence gain (Miles et al. 1987; Bobier and McRae 1996). However, the use of a small light target in the present experiment reduced the accommodative stimulus, thus decreasing the accommodative drive to convergence as well as the accommodation and vergence mismatch. Some residual visual cues (such as accommodation, LED-size and LED-luminance) were present during the telestereoscopic exposure phase in Exp. 1. A calibration of the vergence/distance mapping may have been induced by a discrepancy between vergence-specified distance and residual cues signals for distance, leading to an increased slope of the target-to-pointing mapping. However, these weak residual visual cues are unlikely to have provided an efficient signal for distance.

575 According to Helmholtz's scaling theory, perception  
576 through a telestereoscope is such that "it will seem as if the  
577 observers were looking not at the natural landscape itself,  
578 but at a very exquisite and exact model of it", reduced in  
579 scale in the ratio  $IPD'$  to  $IPD$  (Helmholtz 1910). We did  
580 not obtain such a reduction of visual space during exposure  
581 phase in Exp. 1. The difference between observed and  
582 predicted estimated distances under telestereoscopic  
583 viewing may be explained by both the above consider-  
584 ations on oculomotor adjustments and a down-weighting of

585 the contribution of vergence information. In the exposure  
586 condition, the estimated distances were greater than the  
587 vergence-specified distances, for all subjects. The training  
588 phase of binocular fusion took several minutes. It is likely  
589 that some EMP had already risen up during that period.  
590 Indeed, tonic vergence adaptation to prisms is known to  
591 start changing within the first minute of exposure (Schor  
592 1979a; Hung 1992). Furthermore, a temporal analysis at  
593 the group level did not show any consistent effect of time  
594 on pointing response during the 10-min exposure condi-  
595 tion. As described above, EMP might partially explain why  
596 the actual estimated distances were greater than those  
597 specified by vergence.

598 Pointing responses during exposure were actually located  
599 between vergence and accommodation-specified dis-  
600 tances. This raises the possibility that different cues were  
601 combined with vergence for target distance estimate.  
602 Tresilian and Mon-Williams (1999) found that the presence  
603 of additional distance cues lowered the effects of the prism  
604 on perceived distance. In Judge and Bradford's experiment  
605 (1988), no confirmation of Helmholtz's scaling theory was  
606 found. These authors suggested that other cues may com-  
607 pete with binocular cues to modify the telestereoscope  
608 scaling factor. The influencing cues proposed in these two  
609 studies were monocular or binocular and were provided by  
610 the background scene or the changing size of the target.  
611 In the present study, even though most of the natural dis-  
612 tance cues were eliminated, accommodation, LED-size and  
613 LED-luminance cues may have down-weighted vergence  
614 cues. The reliability of vergence information is indeed  
615 known to decrease with the amount of the discrepancy  
616 between vergence and other cues (Landy et al. 1995;  
617 Tresilian et al. 1999). Mon-Williams and Tresilian (2000)  
618 suggested that accommodation provides distance informa-  
619 tion through the accommodative vergence signal rather  
620 than through accommodation per se. Sustained exposure to  
621 an accommodative demand beyond the fixation distance  
622 may lead to increased tonic vergence (Schor 1979b) and  
623 thus greater estimated distances than as specified by ver-  
624 gence. However, the LED targets represented a poor  
625 stimulus to accommodation.

626 Interestingly, the mean slope (across subjects) of the  
627 target-to-pointing mapping under telestereoscopic viewing  
628 was not significantly different from the one predicted by  
629 using the vergence information according to Helmholtz's  
630 scaling theory. Further scrutiny of the individual data  
631 revealed a very large variability of the individual slopes.

## 632 Effect of visuomotor exposure in Exp. 2

633 The second and main goal of the present study was  
634 to examine the effect of visuomotor exposure on the  
635 plasticity of the vergence/distance mapping. A much larger

(2.3 times) aftereffect in distance estimation was found in  
Exp. 2 as compared to Exp. 1. In the same vein, Ebenholtz  
(1981) found a three-time greater aftereffect following a  
prism adaptation paradigm than following an induction  
exposure paradigm. Feedback was provided by both motor  
and visual monocular cues in Ebenholtz' adaptation  
paradigm.

The use of the hand contralateral to the exposed hand for  
distance estimation during pre- and post-test, without inter-  
hand contact in Exp. 2, prevented any potential hand pro-  
prioceptive or motor transfer. Thus, the hand pointing  
aftereffect of Exp. 2 can be considered as a reliable esti-  
mate of the visual distance aftereffect, uncontaminated by  
the short-term visuomotor adaptation of the exposed hand.

This visual aftereffect, in Exp. 2, involves two potential  
components: oculomotor adaptation and calibration of  
vergence/distance mapping. The former is assumed to be  
the same as in Exp. 1. Indeed, target sequence, visual and  
oculomotor tasks were exactly the same in both experi-  
ments. The two experiments differed only by the visual  
feedback from the fingertip available during hand pointing  
in Exp. 2 but not in Exp. 1. Ebenholtz (1981) proposed that  
the amount of fusional stimuli present in the scene influ-  
ences the aftereffect, EMP aftereffect increasing with  
greater stimulated retinal areas, as more disparity detectors  
are triggered. The vision of the LED on the left fingertip in  
Exp. 2 cannot be considered as an additional fusible  
stimulus as subjects were instructed to keep fixation onto  
the target during pointing. Moreover, it is unlikely that this  
additional LED point light provided a significantly differ-  
ent stimulus for accommodation. As Owens and Leibowitz  
(1980) and Owens (1986) found that interaction with a  
natural environment enhances the aftereffect due to EMP,  
care was taken in the current study to perform the pointing  
task in an otherwise dark room, the only visual stimuli  
being the fixated LED targets and the fingertip LED.

Since the contribution of oculomotor adaptation to the  
aftereffect is likely the same in both experiments, the  
increase in the aftereffect size from Exp. 1 to Exp. 2 may  
be explained by a calibration process. Calibration origi-  
nates in the discrepancy between altered and veridical cues,  
the latter being either visual or coming from interaction  
with the environment (Wallach and Frey 1972; Wallach  
et al. 1972; Wallach and Smith 1972). Similarly, Mon-  
Williams and Bingham (2007) have documented that reach  
distance is altered in response to distorted feedback (visual  
or haptic). Here, calibration of the vergence/distance  
mapping may arise from the discrepancy between altered  
vergence-specified distance and actual reach distance. As  
in Exp. 1, the residual visual cues present during the Exp. 2  
exposure are unlikely to have provided an efficient signal  
for calibration of the vergence/distance mapping. During  
the Exp. 2 exposure, the target was seen closer than its

689 physical position. In the first trials in Exp. 2, subjects  
690 strongly undershot the target and had to make a secondary  
691 correcting movement to bring the fingertip LED in spatial  
692 coincidence with the target. As the target was a virtual  
693 image seen through the central half-silvered mirror, there  
694 was neither finger-to-target masking nor any tactile feed-  
695 back. Finger size cues were also precluded as subjects only  
696 saw a point light on their fingertip.

697 As telestereoscopic viewing increases disparity, it mod-  
698 ifies the perceived egocentric and target-to-fingertip relative  
699 distances, as well as the perception of motion in depth of the  
700 fingertip LED. There are different sources of error during  
701 the exposure condition: (1) an inconsistency between vision  
702 and proprioception of the fingertip, irrespective of the  
703 presence of a target (Craske and Crawshaw 1974), (2) an  
704 inconsistency between the expected fingertip LED visual  
705 feedback (derived from the efferent copy) and its actual  
706 visual feedback, irrespective of the presence of a target  
707 (Held and Hein 1958), (3) a terminal in-depth reaching error  
708 (Kitazawa et al. 1995; Magescas and Prablanc 2006) given  
709 by the increased disparity of the fingertip LED and (4) a  
710 discrepancy between the kinesthetic sensed hand motion  
711 and the resulting change in disparity of the fingertip LED.  
712 Increased disparity of the fingertip LED may have played a  
713 role during the end part of the movement only when the  
714 fingertip LED came into the narrow field of view through  
715 the telestereoscope (around 20°). Moreover, calibration of  
716 the vergence/distance mapping likely resulted from spatial  
717 inconsistency (items 1, 2 and 4 above) rather than from  
718 performance error (item 3) (Redding and Wallace 1997).

719 One potential issue is the extent to which the subjects  
720 were actually fusing the targets. Indeed, if the targets fell  
721 within Panum's area, subjects might have perceived the  
722 targets as single but without their eyes in alignment. If they  
723 were unable to accurately verge upon the targets this might  
724 have influenced the pattern of results. The tolerance range is  
725 Panum's fusion area, which is 15–30 arcmin (Ogle 1932;  
726 Schor et al. 1984). We calculated for the target range during  
727 exposure the maximum error in egocentric distance, which  
728 corresponds to a vergence error of 15–30 arcmin. This  
729 distance error increased with target distance, which means  
730 that there was a larger tolerance to fusion error for the  
731 greater distances. However, the maximum error was only  
732 1.2–2.5 mm for the nearest target and 2.6–5 mm for the  
733 farthest target. Such errors can be considered as negligible.

734 A bias rather than a gain change for the calibration of  
735 the vergence/distance mapping in Exp. 2

736 The present telestereoscope paradigm involved exposure to  
737 an increased IPD. Calibration of the vergence/distance  
738 mapping induced by conflicting vergence-specified dis-  
739 tance and actual reach distance was expected to lead to an

740 increased slope (i.e. an increased gain) of the target-to-  
741 pointing mapping in Exp. 2. As a matter of fact, the post-  
742 test slope was not significantly different from that of the  
743 pre-test and a nearly constant bias was observed.

744 A possible interpretation is that change in gain of the  
745 vergence/distance mapping is not an inherent consequence  
746 of exposure to increased IPD. The nature of the aftereffect  
747 may depend on the exposure conditions. The lack of a  
748 distance-dependent effect may have been due to limitations  
749 on the exposure environment. First, we avoided rich  
750 uncontrolled environments in order to isolate the specific  
751 role of vergence in adaptation within reaching space. The  
752 poor visual environment limited the number of sources of  
753 error. Second, the assessment of distance perception was  
754 limited to reaching space in order to get an accurate mea-  
755 sure of absolute distance with the most accurate method (i.e.  
756 by hand pointing). In addition, reaching space represents the  
757 locus of maximum interaction between perception and the  
758 oculomotor system. However, this restricted exposure range  
759 limited the strength of the distance-dependent error signals.  
760 Finally, the exposure duration was limited.

761 We found that a bias represented the adaptive response to  
762 such an optical distortion of vision under our experimental  
763 conditions. The obtained bias may be an economic way for  
764 the CNS to solve the conflict in the short term. Although a  
765 bias in the post-test might reflect a reduction of the conflict,  
766 the amount of adaptation was limited. Such a limited per-  
767 ceptual adaptation is comparable to that observed with short  
768 duration exposures to lateral prisms (Welch 1986).

769 A similar phenomenon was also observed by many  
770 authors (Fisher and Ciuffreda 1990; Bobier and McRae  
771 1996) in the adaptation of the cross-couplings between  
772 vergence and accommodation. Exposure to an increased  
773 IPD calls for a change in cross-couplings gain (Miles et al.  
774 1987). However, Fisher and Ciuffreda (1990) and Bobier  
775 and McRae (1996) obtained a bias in tonic vergence rather  
776 than a change in the accommodative vergence gain when  
777 the range of fixation distances was restricted. It indicates  
778 that both the nature and amount of the observed oculo-  
779 motor adjustments depend on exposure conditions. Restriction  
780 of fixation distances during exposure seems to favor tonic  
781 adaptation (Miles et al. 1987; Bobier and McRae 1996).  
782 At the opposite, exposure to a constantly changing stimulus  
783 has been reported to reduce or prevent  
784 tonus adaptation (Paap and Ebenholtz 1977).

## 785 Conclusion

786 In the present study, exposure to telestereoscopic viewing  
787 was shown to produce a distance estimation aftereffect  
788 consisting of two components: a response to a sustained  
789 convergence demand onto the oculomotor system, and a



790 response to an inter-sensory conflict or to a conflict between  
791 expected and actual visual feedback. These two components  
792 were disentangled using different exposure paradigms. The  
793 calibration of the vergence/distance mapping resulting from  
794 distorted visual feedback consisted in a constant bias rather  
795 than the expected change in gain. Further studies are needed  
796 to determine whether the observed failure in a complete  
797 calibration is caused by limited distance exploration, too  
798 short exposure duration, or the nature and the intensity of  
799 the oculomotor/visuomotor conflict.

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## 806 Appendix

807 The distance estimated by pointing was assumed to be  
808 linearly correlated with both target distance and time. The  
809 coefficients were computed for the five open-loop condi-  
810 tions (pre- and post-tests in Exp. 1 and 2, and exposure in  
811 Exp. 1), according to the following model:

$$y = a(t) + b(t) \times (x - x_0)$$

813 where  $t$  is the time elapsed since the beginning of the pre-  
814 test, post-test or exposure conditions,  $x$  is the target  
815 distance,  $y$  is the pointing distance and  $x_0$  is the mean value  
816 of the target distances (430 mm). Since the target distance  
817 mean value is subtracted from  $x$ , the term  $a(t)$  corresponds  
818 to the mean pointing distance at a given instant  $t$ . The  
819 coefficient  $b(t)$  is the instantaneous slope of the target-to-  
820 pointing mapping. A simple linear model is assumed for  
821 describing the temporal evolution of  $a$  and  $b$ :

$$a(t) = a_0 + a_1(t - t_0)$$

$$823 \quad b(t) = b_0 + b_1(t - t_0)$$

825 where  $t_0$  is the reference instant at the middle of each  
826 condition. The coefficients  $a_0$  and  $b_0$  correspond to the  
827 global mean values for the pointing distance and slope  
828 during the same condition. The time-variation coefficients  
829  $a_1$  and  $b_1$  are related to the temporal evolution of the linear  
830 coefficients of target-to-pointing mapping.  
831

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