BEHAVIOURAL BRAIN RESEARCH

Research report

Retinal and extra-retinal contribution to position coding

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Abstract

Though considerable effort has been expended on demonstrating the importance of extraretinal cues in distance perception (e.g. state of vergence), recent studies have shown that enriching the visual image brings about a decrease of perceptual underestimation of distance as observed otherwise, providing that contextual information is situated in the proximal space with regard to target position. The fact that a similar effect was observed when viewing monocularly was suggesting a prevalence of retinal input in distance coding. The present study, investigating reaching movements performed monocularly or binocularly in three successive visual scenes (dark–structured–dark), gave evidence for this assumption. Whatever the vision condition, a dark environment gave rise to an underestimation of target distance, which disappeared instantaneously when a structured background was unexpectedly provided. The sudden return to the dark condition resulted in a progressive drift towards underestimation. These findings strongly suggest that structured retinal information influences widely the perception of target distance. They show in addition that retinal signals may contribute to the calibration of non-retinal sources of information. The putative implication of the posterior parietal cortex in this dual influence is discussed.
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1. Introduction

Since the pioneering work carried out by Woodworth [43], a recurrent issue in the studies relating to visuo-motor control concerns the way that visual inputs are used to determine the location (in terms of distance and direction) of a visual target that the hand will reach towards. In the light of a large body of psychophysical studies that have addressed this issue, it is quite well acknowledged that two types of signals derived from the visual system may be involved in distance perception, namely retinal and extraretinal signals [3,4,32]. By extraretinal signals is meant the position of the eyes obtained from non-retinal sources, including oculomotor command to displace the fovea towards a visual target (copy of motor efference), and proprioceptive cues transmitted from anatomical structures in the eye muscles (mainly vergence information). Contrasting

with this, retinal signals are independent of eye position and refer mainly to physical aspects of the image that stem from the optical projection of the external world (for a review see [9]).

How retinal and extraretinal signals are integrated to give rise to a coherent and accurate perception of distance is still largely unknown, in particular in the context of action [3,8,13]. Despite the lack of a dominant theory concerning the integration of sensory signals, studies questioning visuomotor interactions have, in general, acknowledged extraretinal signals as a prevailing source of information in the determination of target position [15,20]. In particular, the reminiscent idea that the vergence signal is prevalent in position coding or distance perception is still widely vivid [37,38]. The main arguments were that shifts in the perceptual estimate of target position were observed when people with weakened eye muscles attempted to look at visual targets [27], or when a deviation in the orientation of one eye, whether through a mechanical perturbation [6] or using wedge-prism spectacles [37], was introduced in

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healthy subjects. The interpretation of such perceptual effects induced by abnormality in ocular control has differed according to either the inflow [35] or outflow [19] theory of position coding.

However, several data argued against this radical view. For instance, mislocation resulting from weakened eye muscles, or mechanical perturbation of eye position have been found to substantially vanish in the presence of a structured visual scene, suggesting the existence of strong interactions between retinal and extra-retinal signals in position coding [5,27]. Furthermore a more accurate representation of gaze direction was observed when extraretinal signals are combined with retinal input, even when the latter was a simple laser spot on the retina [2]. This outcome was interpreted as suggesting that retinal inputs can be thought of as having a gating function that enables the extraretinal signals to be further processed [2]. However, what is observed for direction coding does not seem to hold for distance coding. Indeed, recent studies have shown that the accurate determination of target position in a reaching task requires a wide and textured visual scene, and not a single spot on the fovea, particularly when targets at different distances have to be discriminated [11]. In particular a substantial underestimation of target distance (with virtually no effect on the perception of its orientation) was reported when the retinal signals were impoverished due to a reduction in the size of the visual scene [10], or when the target was presented in a dark environment [17]. However, spatial inaccuracy was found to decrease providing that the visual scene was structured, even by the addition of few contextual elements [40]. The location of contextual information in relation to the self and target also plays a part in determining reaching accuracy, with elements placed in the space through which the reach occurs conferring the most benefit [12]. In agreement with the strong involvement of retinal signals in distance perception, recent psychophysical studies have pinpointed that egocentric signals such as vergence are not accurate enough to provide in themselves an accurate estimation of the spatial gap separating the observer from a visual target [37].

From these findings, it appears obvious that retinal signals represent a prevalent source of information in distance coding, as generally the gain associated with structured retinal signals does not deteriorate when vision turns monocular [12], except in impoverished visual environments [32,33]. However, this does not exclude a calibration of extra-retinal signals from retinal input as an alternative explanation. Indeed, following the introduction of a dark visual scene, drifts in eye position [26] or segmental proprioceptive input [42] have been well documented. These drifts never occur when structured retinal information is provided.

Thus, it is not clear yet whether a structured retinal input allows per se better distance perception, or whether it contributes calibrating extra-retinal information. The present study was designed to address this issue. Spatio-temporal accuracy of open-loop pointing movements towards targets perceived (monocularly or binocularly) in three successive visual scenes (dark–structured–dark) was analysed. Because being suddenly provided with a structured environment was not expected by participants, an instantaneous improvement of spatial performance would establish retinal signals as a prevailing source of information in distance coding. Conversely, a progressive improvement of spatial performance through movement rehearsal would be rather in favour of a calibration process. Indeed, studies about sensory-motor realignment (using either wedge-prism spectacles [31], telestereoscope [39] or video-controlled [28] situations) have shown that elimination of motor errors takes several trials (generally more than ten) and is achieved mainly through proprioceptive recalibration (e.g. [29]). Whatever the way participants adapt to the introduction of a structured visual scene, similar but opposite effects were expected when suddenly coming back to the initial dark condition.

2. Materials and methods

2.1. Subjects

One group composed of eight self-declared volunteers and right-handed subjects (five males and three females), participated in the experiment. All the participants, ranging in age from 24 to 32 years, had normal vision and were naive as to the purpose of the study.

2.2. Apparatus and procedure

The experimental device consisted of a rectangular box (60 cm high, 100 cm wide and 70 cm deep) with one side left open. The inside of the box was divided horizontally by an upward-facing reflecting mirror. With the head resting on the upper part of the box in front of the open side, only the top half of the box was visible to the participant, but he or she was able to move his or her arm into the bottom half. A computer monitor (20 in. Trinitron by Philips) was placed upside-down on the top surface of the apparatus, so that the image generated by the computer was reflected in the mirror. Due to optical geometry, participants could see a virtual target (8 mm red dot) on the bottom surface of the box when they looked at the mirror. Three targets positioned along the frontal axis (0 or ± 5 cm from the sagittal axis) at 27.5 cm from the starting point were used as stimuli. Targets were displayed either in darkness or together with a background (a 24×18 cm

textured surface) composed of aligned yellow dots (9 lines of 7 elements of 5 mm).

Participants were positioned in front of the apparatus with the forehead on the top of the box, and were instructed to perform standard two-dimensional reaching movements (with special emphasis being placed on accuracy) towards the visible target. No visible information from the external environment was available and direct visual control of the hand was precluded by the mirror except when the hand was located at the starting position. No knowledge of results concerning terminal accuracy was given to the participant during the whole experiment. Reaching movements were performed with or without the presence of a visual background, but presented always in the same order: dark pre-exposure/exposure to background/dark post-exposure. The visual stimulus (respectively, target with background or target alone) was switched on when the stylus held by the participant's right hand reached the starting position. To prevent motor anticipation, visual information was presented following a random period of 0.5–1.5 s. Participants completed a total of 360 trials, with three successive sessions of 120 trials (60 trials towards the central target and 30 trials towards each of the two sideways targets, presented in a random order). No rest period was provided between sessions and the participants could not anticipate when the change from one visual scene to the other would occur. Furthermore, participants were requested to perform successive reaching movements at a natural but regular pace, so that the period of time taken for each movement could be roughly estimated afterwards. Binocular and monocular vision conditions were also performed in blocked sessions counterbalanced across subjects.

2.3. Data recording and processing

Coordinates (x, y) of the trajectory were registered from a digitiser tablet (Wacom UD-1825, sample rate: 100 Hz), with a spatial resolution of 0.5 mm. Endpoint positions of individual movements were used to compute constant and variable terminal errors. In relation to our working hypothesis, constant errors were decomposed into radial (performance in amplitude) and angular (performance in direction) values. Radial error was evaluated from the distance between movement vector length and target vector length (a negative sign ($-$) was used for undershoot, and a positive one ($+$) otherwise). Angular error corresponded to the angle between the starting position-to-target vector and the starting position-to-end movement position vector (a negative sign ($-$) was used for deviations to the right of the target, and a positive one ($+$) otherwise). Variable error was assessed by confidence ellipses (95%) of the scatter of trajectory end positions, but computed for the centre target only. Several variables of the confidence

ellipses were computed for each combination of vision condition and background exposure. The ellipse surface (in millimetres squared) provided an estimate of the global pointing variability (over 60 scores) in each experimental condition. The length of the smaller and the greater axis of the pointing distribution was, respectively, given by the variables minor axis length and major axis length (in millimeters). The ratio of the lengths of the two ellipse axes (major-minor axes lengths ratio) provided an estimate of the ellipse morphology, i.e. elongation. The greater this ratio the more the ellipse was elongated. The ellipse major axis orientation (in degrees) was computed relative to mean movement direction. Generally, major axis of confidence ellipse is collinear to hand path [31], and evaluates the directional accuracy of the motor response, whereas the elongation of the ellipse informs about the amplitude accuracy. Kinematic (peak velocity) and temporal (movement time, percentage taken by the acceleration period) parameters were also examined from hand path.

For the sake of clarity and to prevent significant effect due to non-relevant local variations, statistical analyses were carried out on average scores computed every ten trials. Thus, the initial 360 values were gathered into 12 blocks of ten trials in each of the three successive visual scenes (labelled hereafter pre-exposure, exposure, and post-exposure to background information), giving together 36 average values for each visual condition (monocular or binocular). Statistical analyses were carried out through a three-way analysis of variance (ANOVA: 'Block number $(1–12)$' $\times$ 'Vision condition (binocular-monocular)' $\times$ 'Background exposure' (pre-exposure/exposure/post-exposure) with repeated measures to test for principal effects. Data relating to the various target positions have been pooled for statistical investigations. All significant main effects were further delineated using paired t-tests (with Bonferroni adjustments of probability of comparison-wise type 1 error α from the desired family-wise type 1 error (at the 5% level) to account for multiple comparison procedure) and interactions were broken down into simple effects for local comparisons.

3. Results

3.1. Constant error

Concerning the performance in amplitude (radial error, see Fig. 1a), although radial error tended to be slightly but consistently broader in monocular viewing (respectively, -29 and -25 mm), this difference did not reach significance ($F(1,7) = 0.27$; $P > 0.05$). The greater effect was obtained when comparing the effect of exposure to background ($F(2,14) = 37.81$; $P < 0.01$). For the pre- and post-exposure conditions, performance
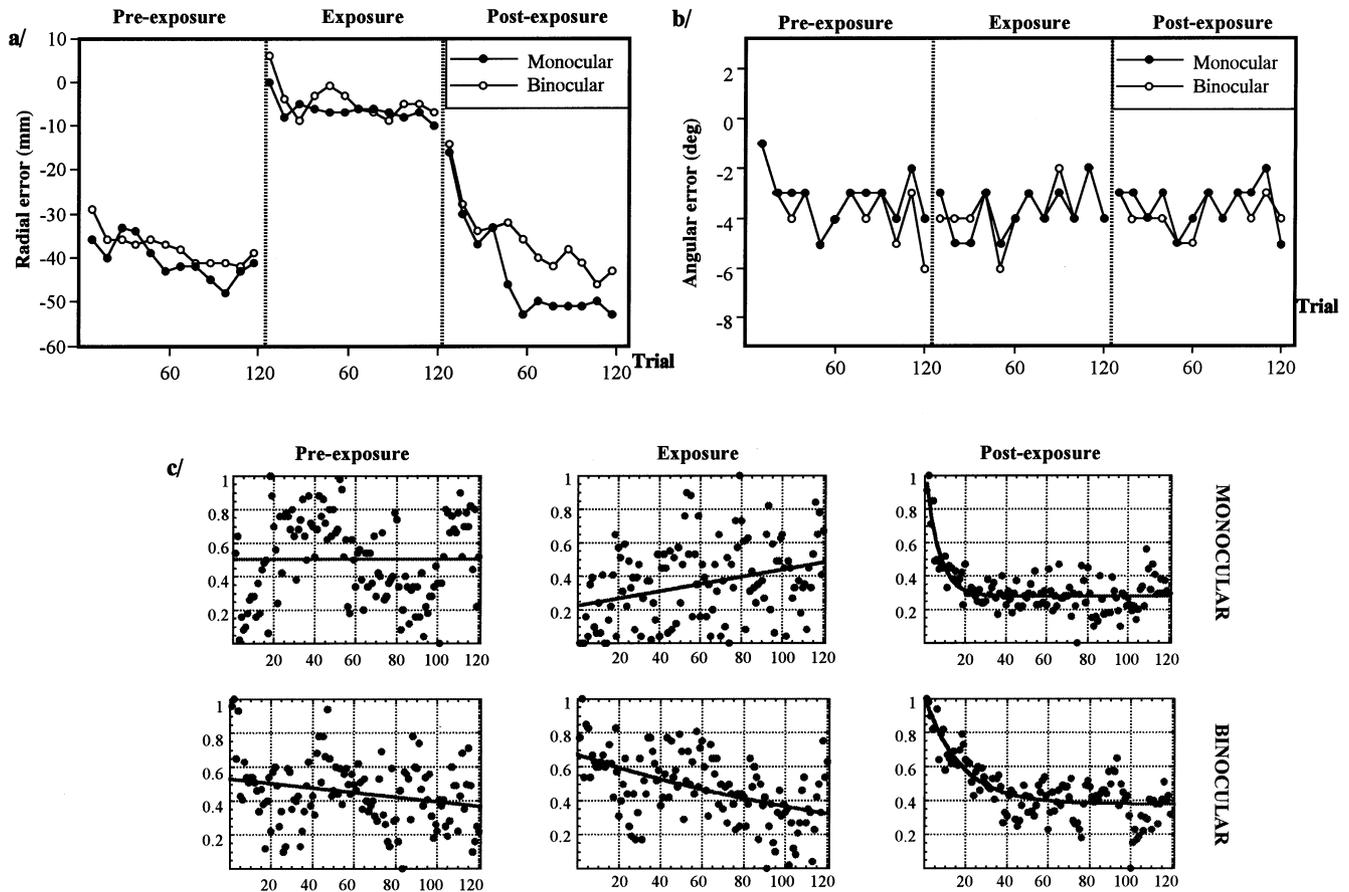
Fig. 1. (a) Radial and (b) angular error over the successive blocks of 12 trials as a function of the vision condition (monocular or binocular) for the pre-exposure, exposure and post-exposure conditions. (c) Time course of normalised radial error and best fitted function for a representative participant.

was characterised by a large undershoot (-39 and -39 mm, respectively), whatever the vision condition ($F(2,14) = 1.13$; $P > 0.05$). Conversely, when exposed to background, distance error decreased substantially (-5 mm) indicating that the performance was very accurate. Strikingly, the increase of accuracy was very sudden (from the first trial in the exposure condition) and of great magnitude (the increase of movement amplitude being 3.5 cm).

A tendency for the undershoot to increase during the first few trials was also observed (on average B1: -14 mm, B6: -29 mm, B12: -32 mm, $F(11,77) = 12,45$; $P < 0.01$). However, this effect was present when performing in darkness only ($F(22,154) = 3.39$, $P < 0.01$), as shown by the simple effects associated with the interaction ($F(11,77) = 2.11$ and $F(11,77) = 11.42$; $P < 0.01$ for the pre- and post-exposure condition, respectively, $F(11,77) = 1.25$; $P > 0.05$ for the exposure condition). But pairwise comparisons using a Bonferroni correction of type I error (the corrected significance level α was 0.001 for the family-wise comparisons) showed that radial error varied in the post-exposure

session only, and regularly increased during the first four blocks of trials ($t(154) = 9.59$, $t(154) = 5.56$, $t(154) = 3.56$, $t(154) = 4.39$; all $P < 0.001$ when compared with the last one). The progressive increase of undershoot was of great magnitude (3.5 cm) and constitutes one of the striking finding in the present study.

The peculiarity of the post-exposure condition is well illustrated by the time course data for individual subjects which was fitted better by an exponential function in this condition only, the scatter of terminal positions being stable in the pre-exposure and exposure conditions as shown by the horizontal main axis of linear approximation (see Fig. 1c). This denoted a progressive drift towards underestimation in the post-exposure condition only, which lasted for about the first 40 trials (i.e. for about 240 s, see below).

Concerning the performance in direction (angular error, see Fig. 1b), statistical analysis showed that though participants pointed consistently to the right of the target ($-3.5°$) orientation of the trajectory was affected by neither the vision condition ($F(1,7) = 0.02$;

$P > 0.05$), nor the structure of the visual scene ($F(2,14) = 0.51$; $P > 0.05$). However, there was a block effect ($F(11,77) = 19.64$; $P < 0.01$), which interacted with the structure of the visual scene ($F(22,154) = 2.85$; $P < 0.01$). This was simply due to the fact that pointing movements finished their course slightly more to the left during the first few blocks when compared with the last one, but only in the pre-exposure and post-exposure conditions (respectively, $F(11,77) = 9.41$ and $F(11,77) = 6.45$, both $P < 0.01$ for the simple effects associated with the interaction).

3.2. Variable error

Though terminal positions of pointing movements tended to be more scattered in the monocular (2315 mm^2) than in the binocular vision condition (1990 mm^2) when comparing the ellipse surface, this difference did not reach significance ($F(1,7) = 1.48$; $P > 0.05$, see Table 1). However, ellipse surface was broader in the pre- (2278 mm^2) and post-exposure (2570 mm^2) conditions than in the exposure condition (1610 mm^2, $F(2,14) = 6.56$; $P < 0.01$; see Fig. 2). This effect was not different in the monocular and binocular vision condition ($F(2,14) = 2.56$; $P < 0.05$).

Concerning the ellipse major axis orientation, the value 180° means an orientation of the major axis of the ellipse collinear to movement main direction. The average ellipse major axis orientation was 181° on average and was influenced by neither the vision condition (monocular: 181°, binocular: 181°, $F(1,7) = 0.02$; $P > 0.05$), nor the exposure condition (pre-exposure: 176°, exposure: 187°, post-exposure: 180°, $F(2,14) = 3.45$; $P > 0.05$). There was also no interaction between the two main factors ($F(2,14) = 0.27$; $P > 0.05$).

The ratio of the lengths of the two ellipse axes (major-minor axes lengths ratio) provided an estimate of the ellipse elongation. This ratio was 2.07 on average which indicate a tendency for the variable error to be more pronounced along the axis expressing the amplitude of the movement than along the orthogonal axis. It was not influenced by the vision condition (monocular: 1.94 and binocular: 2.20, $F(1,7) = 0.59$; $P > 0.05$). It was, however, smaller in the exposure (1.63) than the pre- (2.01) or post-exposure (2.56) condition ($F(2,14) = 6.20$; $P <$

0.01). This observation indicated that the reduction of ellipse surface in the exposure condition (see above) was mainly due to a reduction of end-point dispersion along the major axis parallel to movement direction. No interaction between the vision and exposure factors was noted ($F(2,14) = 0.05$; $P > 0.05$).

3.3. Movement time and duration of acceleration period

Movement time was 469 ms on average and was not influenced by the vision condition ($F(1,7) = 0.42$; $P > 0.05$), but by the visual environment ($F(2,14) = 9.98$, $P < 0.01$, see Table 2). It was longer for the exposure condition (495 ms) than for the pre- (452 ms) and post-exposure (459 ms) conditions (respectively, $t(14) = 4.16$ and $t(14) = 3.49$, both $P < 0.01$), whatever the vision condition ($F(2,14) = 0.60$; $P > 0.05$). Finally, movement time was greater in the first block of trials (486 ms) than in the remaining blocks of trials (mean value: 467 ms, $F(11,77) = 4.02$, $P < 0.01$), but this factor interacted with the background exposure factor ($F(22,154) = 2.65$, $P < 0.01$). This was due to the fact that movement time remained virtually stable in the pre-exposure condition, was longer at blocks 1 and 2 in the exposure condition, and was longer at blocks 1–4 in the post-exposure condition when compared with the last block ($F(11,77) = 1.53$, $F(11,77) = 2.65$, and $F(11,77) = 6.28$, with $P > 0.05$, $P < 0.01$ and $P < 0.01$, respectively, as simple effects associated with the interaction).

The proportion of time taken by the acceleration phase (extending from movement onset to peak velocity) was not influenced by whether the vision condition was monocular (57%) or binocular (56%, ($F(1,7) = 1.07$; $P > 0.05$), nor by the background exposure factor (pre-exposure: 57%, exposure: 56%, post-exposure: 57%, $F(2,14) = 3.13$; $P > 0.05$). It was, however, smaller in the first block (56%) than in the last block (57%; $F(11,77) = 2.64$, $P < 0.01$), but independently of the exposure condition ($F(22,154 = 0.97$, $P > 0.05$).

Interestingly, the time taken to perform each set of 120 trials was not dependent upon the background exposure factor ($F(2,12) = 2.30$; $P > 0.05$), or the vision condition ($F(1,6) = 1.71$; $P > 0.05$). By dividing this total time by the amount of trials performed in each experimental condition, we roughly estimated the time

Table 1

Mean value and standard deviation (in brackets) for ellipse surface, ellipse major axis orientation and major-minor axes lengths ratio as a function of the vision condition (monocular vs. binocular), and the exposure condition (pre-exposure, exposure, post-exposure)

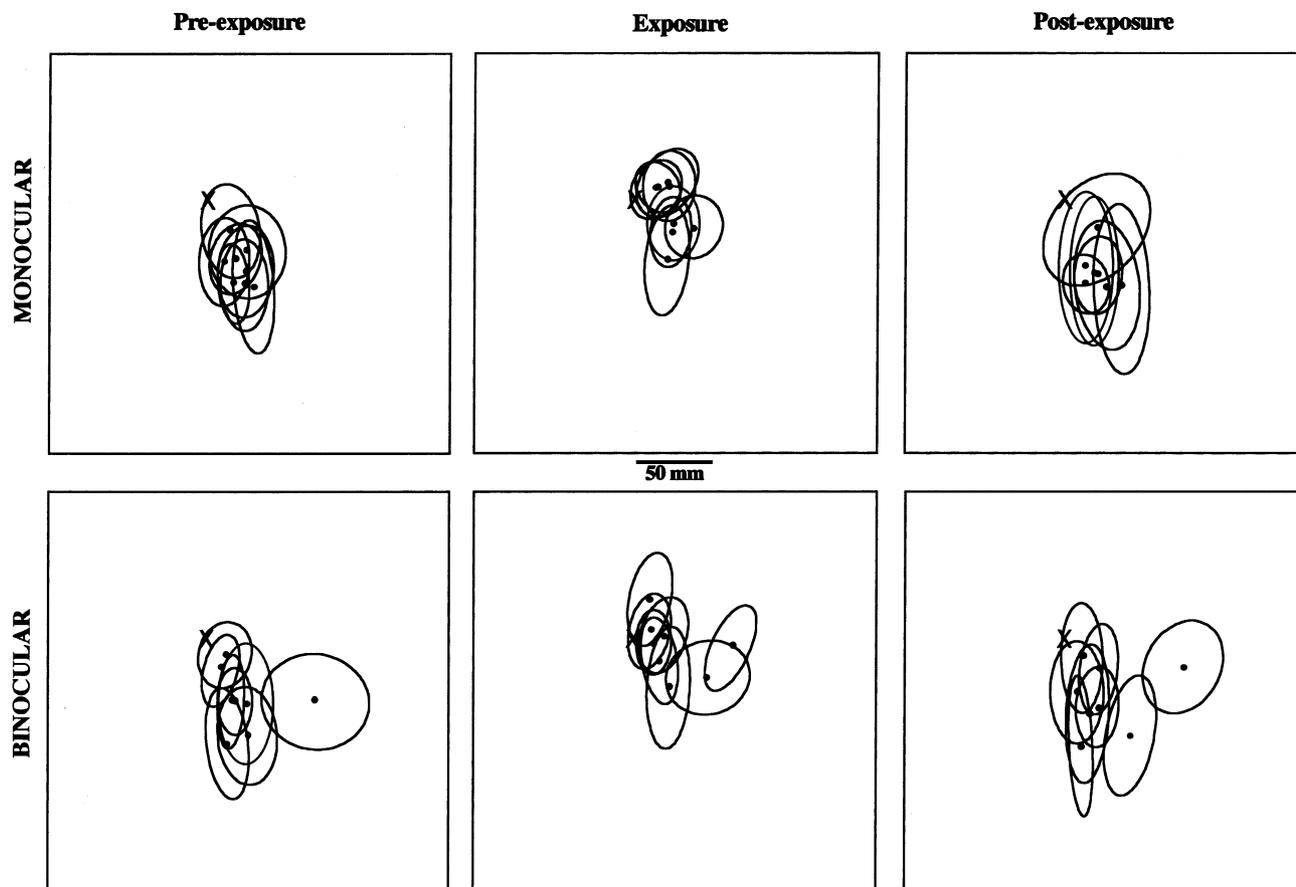|	Monocular			Binocular		
	Pre-exposure	Exposure	Post-exposure	Pre-exposure	Exposure	Post-exposure
Ellipse surface (mm^2)	2247 (590)	1554 (386)	3145 (1336)	2308 (1820)	1667 (556)	1996 (705)
Ellipse orientation (°)	176 (8)	188 (18)	178 (12)	176 (10)	186 (12)	181 (6)
Axes ratio	1.90 (0.40)	1.49 (0.30)	2.44 (0.93)	2.12 (0.97)	1.81 (0.26)	2.68 (1.21)

Fig. 2. Mean end-point and confidence ellipse (95%) for the eight participants in the pre-exposure, exposure and post-exposure conditions for the monocular and binocular vision conditions. The cross indicates target position.

taken to perform a single trial, which on average was: 6.2, 5.9, and 5.8 s in the monocular condition; 6.2, 6.5, and 6.1 s in the binocular condition for the pre-exposure, exposure and post-exposure conditions, respectively.

3.4. Peak velocity

Peak velocity was 845 mm s^{-1} on average and was not influenced by the vision condition ($F(1,7) = 0.07$; $P > 0.05$), but by the background exposure ($F(2,14) = 5.85$, $P < 0.05$). It was broader in the exposure condition (892 mm s^{-1}) than in the pre- (838 mm s^{-1}) and post-exposure (802 mm s^{-1}) conditions (respectively, $t(14) = 2.40$ and $t(14) = 3.40$; $P < 0.016$ when using a Bonferroni correction), whatever the vision condition ($F(2,14) = 0.45$; $P > 0.05$). Finally, peak velocity was greater in the first three blocks of trials (871, 877 and 869 mm s^{-1}) than in the remaining blocks (mean value: 835 mm s^{-1}, $F(11,77) = 3.48$, $P < 0.01$), but this factor interacted with the background exposure factor ($F(22,154) = 1.79$, $P < 0.05$). This was due to the fact that peak velocity was higher during the first few blocks in the pre- and post-exposure conditions ($F(11,77) =$

2.54 and 2.86; $P < 0.01$), but remained nearly stable in the exposure condition ($F(11,77) = 0.64$; $P > 0.05$ as shown by the simple effects associated with the interaction).

The fact that the changes in spatial performance were mainly caused by an adjustment of the motor parameters at the motor programming level was further evaluated by analysing the correlation between peak velocity and movement extent and between movement time and movement extent. This analysis was carried out including the experimental condition variations, i.e. including on the one hand the last 20 trials of the pre-exposure condition and the first ten trials of the exposure condition, and on the other hand the last 20 trials of the exposure condition and the first ten trials of the post-exposure condition. The underlying assumption was that if the change in performance when modifying the background structure was mainly due to perceptually induced motor parameters adjustment, then a high correlation between kinematic parameters and movement extent should be observed for these trials.

Regression coefficient (r) which measures the degree of linearity between peak velocity and movement extent was significant for the pre-exposure/exposure trials ($r =$

Table 2
Mean value and standard deviation (in brackets) for movement time (MT), peak velocity (PV), percentage of time taken by acceleration period (%AP) as a function of the vision condition (monocular vs. binocular), the exposure condition (pre-exposure, exposure, post-exposure) and the block of trials (only blocks 1, 6 and 12 are shown)

	Monocular									Binocular								
	Pre-exposure			Exposure			Post-exposure			Pre-exposure			Exposure			Post-exposure		
	B1	B6	B12	B1	B6	B12	B1	B6	B12	B1	B6	B12	B1	B6	B12	B1	B6	B12
MT (ms)	437 (45)	436 (47)	456 (54)	516 (76)	481 (64)	473 (63)	474 (55)	440 (48)	430 (47)	476 (35)	454 (40)	466 (43)	527 (49)	504 (63)	499 (65)	495 (54)	470 (70)	472 (63)
PV (mm s^{-1})	884 (216)	851 (258)	804 (201)	913 (236)	916 (247)	911 (234)	878 (185)	792 (202)	820 (215)	858 (107)	839 (110)	802 (114)	864 (57)	888 (69)	882 (107)	835 (107)	794 (106)	760 (114)
%AP (ms)	58 (3)	59 (4)	59 (3)	55 (2)	57 (3)	57 (4)	57 (2)	58 (3)	57 (3)	57 (7)	56 (4)	53 (3)	54 (4)	55 (4)	57 (3)	58 (5)	57 (5)	57 (5)

0.62, $t(28) = 4.18$; $P < 0.01$) and for the exposure/post-exposure trials ($r = 0.70$, $t(28) = 5.19$; $P < 0.01$). Statistical analysis (performed on Z-transform scores) showed that these values did not differ significantly ($F(1,7) = 1.27$; $P > 0.05$), and were not influenced by whether the vision was monocular or binocular ($F(1,7) = 3.77$, $P > 0.05$). Data for a representative participant are plotted in Fig. 3. One observes a concomitant increase or decrease of peak velocity and movement extent, the latter being dependent on background condition. Note also that peak velocity increased suddenly and remained virtually stable when appending background information, whereas it decreased progressively when removing background information (trials one, five and ten are flagged in Fig. 3). Regression coefficient (r) measuring the degree of linearity between movement time and movement extent was significant for the pre-exposure/exposure trials ($r = 0.74$, $t(28) = 5.82$; $P < 0.01$) and for the exposure/post-exposure trials ($r = 0.54$, $t(28) = 3.39$; $P < 0.01$). These values did not differ significantly ($F(1,7) = 3.01$; $P > 0.05$), and were not influenced by whether the vision was monocular or binocular ($F(1,7) = 0.29$, $P > 0.05$). Considering individual trials, the pattern of results was similar than that obtained with

peak velocity, i.e. a concomitant increase or decrease of movement time and extent which depended on background condition. Movement time increased suddenly and remained virtually stable when appending background information, whereas it decreased progressively when removing background information.

4. Discussion

The general behaviour in the absence of a structured visual scene was an undershooting of the target, with virtually no effect on directional performance, suggesting a large underestimation of target distance. The lack of structured retinal signals appears thus as an unpropitious situation for accurate distance appraisal. The tendency in darkness for the spatial performance to be worst in the monocular than in the binocular condition (in terms of underestimation and variability) replicates previous findings [12], and suggests furthermore that vergence signal is used predominantly in impoverished visual condition and improves distance coding. Strikingly, underestimation of target distance was instantaneously eliminated as soon as a structured visual scene
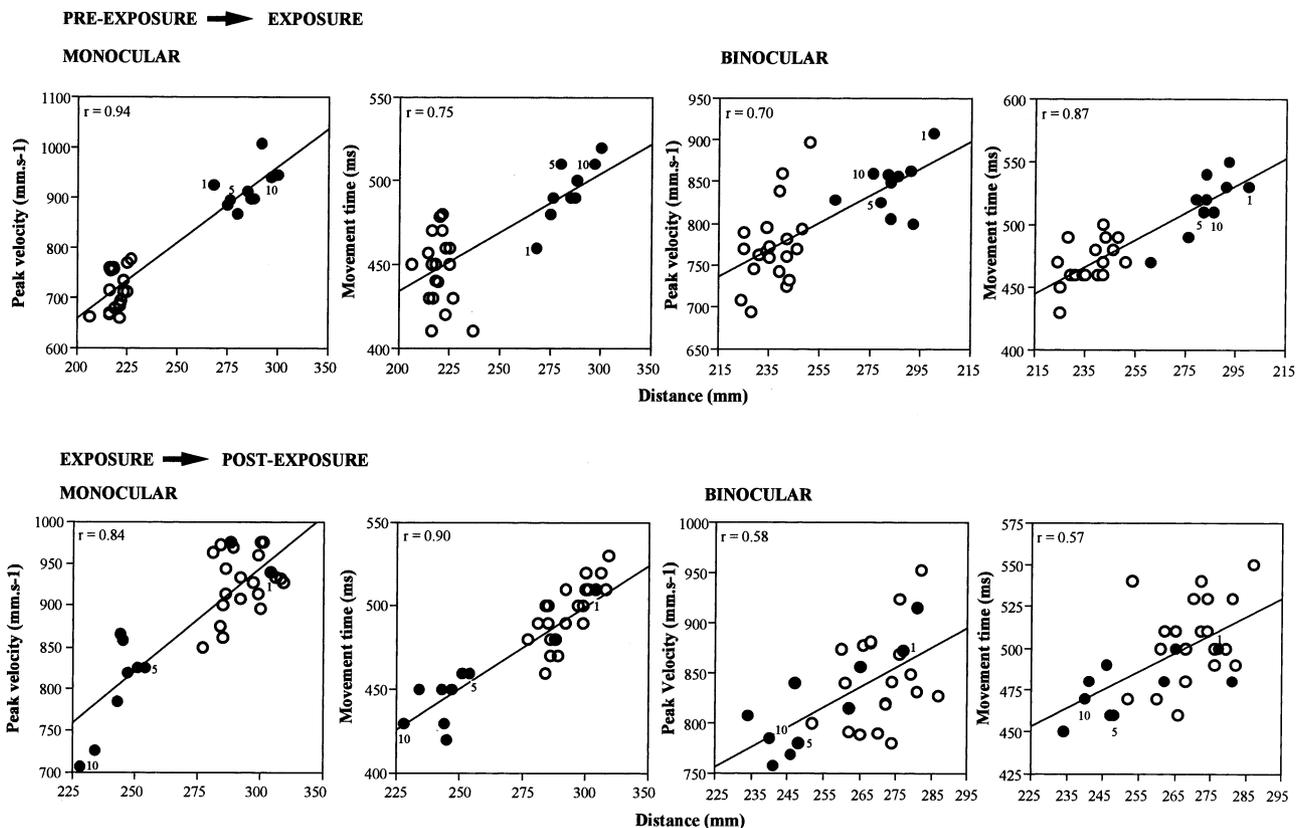

Fig. 3. Correlation between peak velocity and movement extent and between movement time and movement extent for a representative participant. The trials under consideration were on the one hand the last 20 trials (open circle) of the pre-exposure condition and the first ten trials (solid circle) of the exposure condition, and on the other hand the last 20 trials (open circle) of the exposure condition and the ten first trials (solid circle) of the post-exposure condition. Trials one, five and ten following the change of background condition are shown.

was provided (the increase of movement amplitude was 3.3 cm, i.e. 10% of the actual distance). Because the same effect was observed in both monocular and binocular vision conditions, this establishes retinal signals as a prevailing source of information in distance coding [11,17]. It is noteworthy that a concurrent interpretation could be that enriching retinal signals had the effect of improving the accuracy of extra-retinal signals and was not involved as such in distance coding. According to this assumption, distance coding would rely preferentially on vergence signal (with a possible influence of accommodation signal) in both the dark and structured visual environments [37]. However, two observations argue against this interpretation. First, in the present study the monocular and binocular performances were strictly identical in the presence of a structured visual scene, but not in the dark condition. Second, a recent study performed by Erkelens [16] demonstrated that perceived position of a visible target during monocular viewing is based on signals of the viewing eye only when the other eye is occluded by closing it (instead for instance of putting an occluder in front of an open eye) and when background information is provided. Both of these requirements were respected in the present study, at least with regard to the exposure condition.

Furthermore, the increase of trajectory length was accompanied by a concomitant increase of movement time and peak velocity. However, because the proportion of time taken by the acceleration phase was not influenced by the presence or absence of background information, one concludes that the benefit gained from structured retinal signals is accounted for by improvement in distance perception, rather than enhanced on-line control of hand trajectory. This interpretation is supported by the significant linear trend between peak velocity and movement extent, and by the variations of peak velocity and movement time which mimicked variations of movement extent.

However, though confirming previous conclusions about the contribution of retinal signals to distance perception [11,12,17], the striking result in the present study was the non-equivalence between appending or removing background information. Whereas instantaneous improvement in distance performance was observed in the former case, a long lasting and regular drift towards underestimation was observed in the latter case despite the constant availability of the visual target. This contrasting influence of adding or removing background information seems to indicate that in addition to supplying distance cues, retinal signals contribute to the calibration of extra-retinal signals. Indeed, the fact that the drift was present for four blocks of ten trials on average (which corresponds to about 240 s of practice) is reminiscent of the proprioceptive drift reported for the sensation of arm position following visual occlusion

[42]. In the quoted study, subjects were required to estimate, by pointing with their right finger, the position of the unseen controlateral index finger position. The main observation was that spatial accuracy became progressively inaccurate following visual occlusion, as confirmed by a 'steady linear drift' observed during the first 120 s of proprioceptive assessment.

It is noteworthy that the drift in the perception of target distance cannot be assigned to a bias in the perceived location of one's hand due to a lack of visibility of hand trajectory during the whole experimental session [41]. The hand was perceived visually before movement onset, which has been shown to eliminate spatial error due to a lack of calibration of arm proprioception [15]. It seems also not being the consequence of a progressive impairment of stored information in short-term visuo-spatial memory. Several studies dealing with motor performance towards memorised illusory figure (like the Müller–Lyer illusion, [18]) have indeed shown that the sensorimotor system can hold veridical egocentric information about location, but for about 2 s [7,31], with the consequence that large deviations are observed for greater duration of visual suppression. This limit of action relevant visuo-spatial memory is obviously too short to account for the drift reported in the present study (impairment of spatial accuracy was indeed maximum after about 240 s of practice on average). Pointing in the dark towards a memorised target in the absence of visual illusion has moreover been shown to influence mainly the variable error, with almost no effect on the constant error [30]. Finally, in the absence of contextual information no contraction of the working space has been reported when performing towards a target that remains visible during the whole action, even when vision of hand trajectory and knowledge of results are not provided [23]. Because the target was always visible in the present study, the increase of radial error could hardly be the result of a deficit of the visuo-spatial memory, but was obviously the consequence of an inaccurate position coding due to progressive drift of extra-ocular signals when darkness was reintroduced.

Altogether these data fit quite well with the modified weak fusion model of distance coding [24]. According to this model, an object's apparent physical distance stems from a weighted linear combination of the individual distance cues that the visual system can use. Because different distance cues provide qualitatively different kinds of information (which is confirmed in the present study), the weight assigned to a specific cue might depend on the estimated reliabilities of each cue and the relationship of the distance specified by each cue. For the purpose of consistency, those cues which do not provide accurate distance information have to be promoted using information and parameters supplied by the more reliable cues. Here, we showed that in visuo-

manual task a more heavy weight is ascribed to retinal signals for distance perception and that they are additionally used to promote extra-retinal signals.

It is worth noting that the opposite influence has been reported in previous studies, supporting a task dependent use of various spatial cues. For instance, individuals with visual form agnosia, who are unable to perceive many of an object's characteristics, are much more disadvantaged in the control of their grasp when binocular information is removed than are normal observers [25]. The fact that these individuals scaled their grasp much less accurately under the monocular viewing condition, despite showing normal binocular grasping, suggests that the visuomotor system 'prefers' to use binocular information for object size or volume determination, but can fall back on retinal information under monocular viewing conditions. These two opposite observations argue in favour of an independent treatment of shape and localisation [34].

As the possible neural substrates for such integration of retinal and extraretinal signals in the context of reaching movement, the dorsal stream originating from the visual cortex (V1) and directed into the posterior parietal cortex is a brain region implicated in spatial perception and visuomotor performance [1,22]. Interactions between gaze related signals and the discharge of light sensitive cells have been observed in the prestriate areas of the occipital lobe like V1 and V3a, in the parieto-occipital (PO) area, in the MT, MST complex, as well as in the 7a and LIP regions of the parietal cortex (see [22] for a review). In particular, PO receives direct projections from V1, V2, V3, and MT [14], and provides visual information to the rostral part of the premotor cortex [36]. Furthermore, neurones in V6 and V6a regions of PO area are capable of combining retinal, eye-position and oculomotor signals in order to encode the position of a visual stimulus with respect to the body [21]. Neurones in these regions are also involved in the computation of motor commands from sensory input. Thus, these regions might be where the influence of background information carried out by the retinal signals is the most likely to occur. However, these studies have focussed their investigation mainly on the directional coding of visual target, and it remains speculative to generalise these findings to distance coding. Furthermore, no influence of the activity of light sensitive cells on extra-retinal signal as been documented yet, and the issue of a putative site for such influence remains to be properly addressed.

5. Conclusion

The relationship between retinal and extra-retinal is very complex and depends seemingly upon the spatial constraints of the task. Considering distance coding, the present study strongly suggests that the prevailing source of spatial information is attached to retinal signals, which, in the presence of a rich environment, enables accurate relative position coding and calibration of ocular (vergence) signals. These findings are quite crucial for people investigating spatial perception in real or artificial visual environment for two reasons. First, they clearly establish retinal signals as a prevailing source of information for distance perception, indicating that tests about visual perception could be widely influenced by the environmental context. Second, because the calibration process was found to be effective for a short period following visual occlusion, studying visuo-motor coordination in various but randomly presented visual environments may introduce a source of error, which needs to be considered.

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