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Effects of an illusory orientation of the head on straight-ahead pointing movements

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Abstract. Rotation of the head is known to induce a contralateral shift in straight-ahead pointing movements performed in the dark. In order to dissociate the influence of the internal representation from that of the actual position of the head, we used the "return" phenomenon, which consists of the illusion of a slow displacement of the head toward its neutral position whenever it is held in a turned position for several minutes with the eyes closed. Eight subjects underwent a 40° passive rotation of the head in the dark. Zero, 3, 6, and 9 minutes after the rotation, the subjects assessed their head orientation by means of a manual device, and performed 5 pointing movements straight ahead of the trunk. The after-effects of the "return" phenomenon were also assessed with the same measurements after the sustained rotated position, i.e., when the head was passively put back into the sagittal position. The initial head turn immediately induced a contralateral shift in pointing movements. The perceived orientation of the head drifted by 9.5° during the 9 minutes in the rotated position. When back in its neutral position, the head was perceived as turned by more than 15° in the direction opposite to the initial rotation. At that time, straight-ahead pointing had shifted contralaterally to the new perceived orientation of the head.

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Thus, the direction of the straight-ahead pointing movements depended on the internal representation of the head rather than on its actual position. The results are discussed with regard to the body scheme concept, wherein a sensorimotor component and a cognitive component are distinguished.

Key words: Body scheme, head orientation, straight-ahead pointing.

INTRODUCTION

The subjective straight-ahead is the direction where you feel the body midline would project in front of you. The body midline is a functional axis which segments space into the right and left sectors. Pointing straight ahead in darkness can be conceived of as a body-centered task independent of exteroceptive spatial cues. Such an oriented movement defines a vector in the subjective mid-sagittal plane, which has been postulated to be the origin of the egocentric coordinate system in the horizontal plane (Jeannerod, 1988).

The building and updating of this egocentric reference depend on the neural integration of various afferent signals such as visual, vestibular, and proprioceptive input (Andersen, Snyder, Li, & Stricanne, 1993; Karnath, Fetter, & Dichgans, 1996; Stein, 1992). Head position signals play a major role since passive rotation of the head, for instance, induces a shift in straight-ahead pointing in the direction opposite to the rotation (Werner, Wapner, & Bruell, 1953). Similarly, the space representation shifts in the direction opposite to head rotation, as shown by Fookson, Smetanin, Berkinblit, Adamovich, Feldman, and Poizner (1994). The shift was attributed to influences from the neck muscle proprioceptors, which indicate changes in the head position on the trunk (static effect), rather than to vestibular reactions indicating movements of the head (dynamic effect).

The influence of neck muscle proprioception on the subjective straight-ahead direction has been confirmed by vibrating the neck unilaterally, a procedure known to generate neural activity signaling false muscle lengthening. Vibrating the neck on one side produces spindle discharges comparable to the ones elicited in neck muscles when stretched by a head turn toward the opposite side. The effects on the subjective straight ahead appear to be similar to the ones elicited by an actual rotation of the head (Biguer, Donaldson, Hein, & Jeannerod, 1988; Karnath, Sievering, & Fetter, 1994).

Besides their effects on oriented movements, mechanical vibrations applied to muscles have been known to induce body illusions (Goodwin, McCloskey, & Matthews, 1972). Lackner (1988) found that, depending on the position of the vibrated limb in relation to the rest of the body and to its surroundings, it is possible to generate systematic perceptual distortions of the body and changes in its apparent orientation in the absence of any actual movement. Roll, Vedel, and Roll (1989) demonstrated that visual and postural directional effects are induced by vibrations of the eye, neck, and ankle muscles. They argued that since body segments like the head, trunk, and legs connect the eyes with the ground, the proprioceptive input which signals their position sense must be processed in an integrative way to ensure postural regulation and spatial coding of retinal information in terms of egocentric coordinates. In their discussion, Roll et al. (1989), like Lackner (1988), called upon the body scheme concept and suggested its importance in relating the body space to the extrapersonal space where oriented movements are performed.

The body scheme can be broadly defined as the internal model of the body in the central nervous system. Head and Holmes (1911, 1912) introduced the distinction between body image as the conscious representation of the body, and the postural body schema, "a combined standard against which all subsequent changes of posture are measured" and which operates "before the changes of posture enter consciousness". Gallagher (1986) argued that there has been redundant confusion between the two concepts, and proposed several criteria to help differentiate them. He defined the body image as "an inconstant intentional object of consciousness", a conceptual construct of the body influenced by cognitive and emotional factors as well as sensory information. The strictly defined body schema would be a "non-conscious performance of the body", which reflects and determines posture and which organizes the body in its relationship with the environment. Gurfinkel and Levick (1991) distinguished a perceptual component of the body scheme connected with awareness of body position (i.e., body image), from an automatic component thought to deal with the sensorimotor processes that form the basis of postural and motor control. However, the authors claimed that, even if perceptual and automatic components work at different levels, they both contribute to the organization of motor activity.

The rationale for the present study was to further specify the role of the body image in the definition of oriented movements. For this purpose, we used the head "return" paradigm, with which one can dissociate the perceived orientation of the head from its actual position without manipulating proprioceptive information. The so-called head "return" phenomenon was described by Gurfinkel, Popov, Smetanin, and Shlykov (1989; cited in Gurfinkel & Levick, 1991) as the perception of a slow head movement toward its neutral position while the head is kept turned for about 10 minutes with the eyes closed. Moreover, when the head is passively replaced in sagittal position, it is perceived as turned in the opposite direction to its former turned position. The authors studied the effects of these illusions on the bilateral distribution of tonic activity in the legs, and argued that the perceptual illusions and their postural concomitants could not be due to changes in the activity of neck proprioceptors. Rather, they pointed to a drift in the internal representation of the head position toward some subjectively symmetrical position which occurs when no other spatial information is available to calibrate the system. The same conclusions were drawn by Gross, Webb, and Melzack (1974), and more recently by Wann and Ibrahim (1992) from the study of a related illusion. Both studies showed that localization of a static limb during visual occlusion tended to drift over time toward the mid-sagittal plane along the right-left dimension and closer to the body along the near-far dimension. The drift was halted, but not compensated for, by brief glimpses or small movements. Moreover, the illusion was amplified by attention. These observations are not easily accounted for by a peripheral receptor adaptation hypothesis. Here again, a modification in the body image seems to be a better explanation for the illusory displacement of a body segment to some standard usual position.

In the present experiment, we used the "return" phenomenon in order to assess the influence of an inaccurate representation of the head on straight-ahead pointing.

METHODS

Subjects

Eight naive volunteers (six males and two females) aged 18-27 participated in this experiment. All were right-handed, as assessed by

Hécaen's laterality test (1984). All were free of any problem that could have impeded arm movements.

Apparatus

The subject sat in a modified dental chair (Figure 1). His/her shoulders, legs, and feet were strapped to ensure a stable and symmetrical posture throughout the experiment. The head was held up in a semi-rigid helmet which could be fixed at any required orientation.

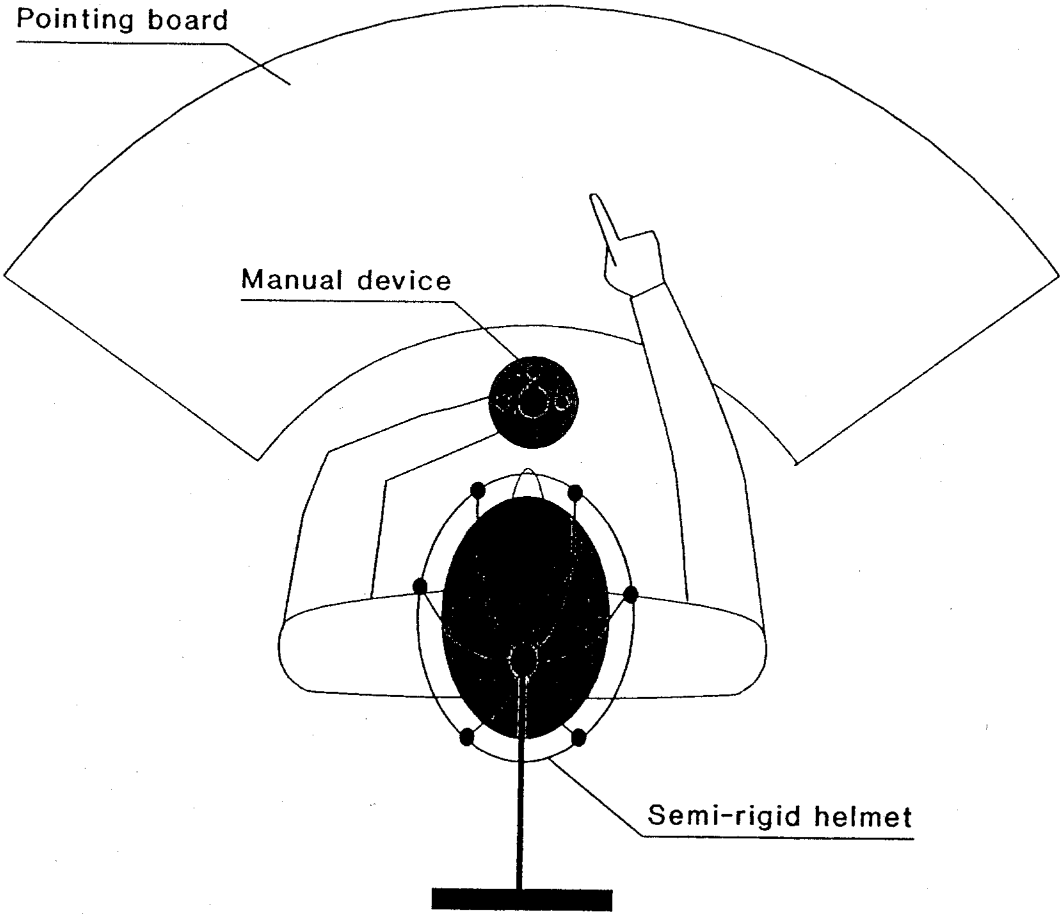

Figure 1. Schema of the apparatus. Head orientation ratings were made using the analogue manual device.

Evaluation of the perceived orientation of the head was achieved using a cylindrical box (which stood for the trunk) topped by a knob (representing the head). The box was held in the subject's left hand and rested on his/her lap. Three orthogonal tactile markers were fastened to the upper part of the box, two symbolizing the shoulders and the third the straight-ahead direction. The knob controlled the axis of a potentiometer enclosed in the box. It was centered relative to these three markers, and had another tactile marker representing the nose. The four markers were close enough to each other to allow the subject to feel them simultaneously with the finger tips while manipulating the knob to reproduce the perceived orientation of the head.

Pointing movements were performed with the right index finger on a 100° ring-shaped horizontal board (80 cm in outer diameter, 40 cm in inner diameter) centered on the subject's spine and resting on three linear strain gauges. The index was covered with a rubber thimble in order to dampen the oscillations of the board at landing time.

After A/D conversion, the output of the potentiometer was used to compute the perceived angular position of the head. Similarly, the forces recorded by the gauges fed a routine that gave the position of the center of pressure. This position was then expressed in polar coordinates relative to the spine.

Procedure

The experiment took place in a dark room. In addition, subjects wore a night mask to allow the use of a flashlight when changing head orientation. The experiment began with a training session in which the subjects had to perform correct pointing movements with and without being able to see their hand. Subjects were instructed about the important features of the task, such as the initial position (arm held horizontally, fist closed next to the chest at the solar plexus level, index finger hooked), the movement itself (fast, at one go, arm straight when hitting the board, no shoulder movement), and contact with the board (about 1 second in duration).

The subjects were then familiarized with the potentiometer device, and used it to do one rating of nine different orientations of the head (sagittal, 10°, 20°, 40°, and 50° to the right, 5°, 15°, 30°, and 45° to the left) in a pseudo-random order. There was no time limit on the ratings. Analysis of this training session showed that all subjects used the device properly, as the correlation coefficient (*r*) between actual and perceived orientation of the head was 0.957 (*df* = 6) for the least efficient subject.

The experiment proper comprised 6 trials, each consisting of one rating of the perceived orientation of the head and 5 straight-ahead pointing movements. On the first trial, control data were obtained with the head in sagittal position. The head was then turned 40° to the right (5 subjects) or to the left (3 subjects) and held in that position for 9 minutes, a duration that seemed sufficient to get close to a full illusory "return" (Gurfinkel & Levick, 1991). The subjects performed four trials at 0, 3, 6, and 9 minutes. Finally, the head was slowly brought back to its neutral position by the experimenter, with the subject's eyes still closed. Rating of head orientation and pointing movements were performed once more (6th trial). The experiment ended with a questionnaire to collect the subject's impressions. The whole experiment lasted about 40 minutes.

RESULTS

In the control condition (first trial), the head orientation ratings resulted in a mean constant error of 4.2° to the left ($t = 1.70$, $df = 7$, ns). The pointing movements were close to the mid-sagittal plane, with a mean constant error of 0.6° to the right ($t = 1.07$, $df = 7$, ns).

For each subject, control values were subtracted from the measures obtained on trials 2 to 6. The sign of the corrected constant errors was changed for the 3 subjects whose head had been turned to the left. A preliminary analysis including the direction-of-rotation factor did not reveal any significant effect of this factor. Consequently, all corrected data were pooled for subsequent analyses. The results are summarized in Figure 2, where positive values stand for head position ratings or pointing errors toward the head rotation side.

Head turn immediately (0 minutes) induced a -3.4° contralateral shift in the pointing movements, $F(1, 7) = 30.97$, $p < .01$. The perceived orientation of the head changed over the 9 minutes in the rotated position, $F(3, 21) = 6.01$, $p < .01$; the amount of drift reached 9.5°. The "return" phenomenon occurred in 7 subjects (range: 7.1° to 18.9°). Analysis of the post-experimental questionnaire revealed that the only subject on whom the effect did not occur reported having struggled

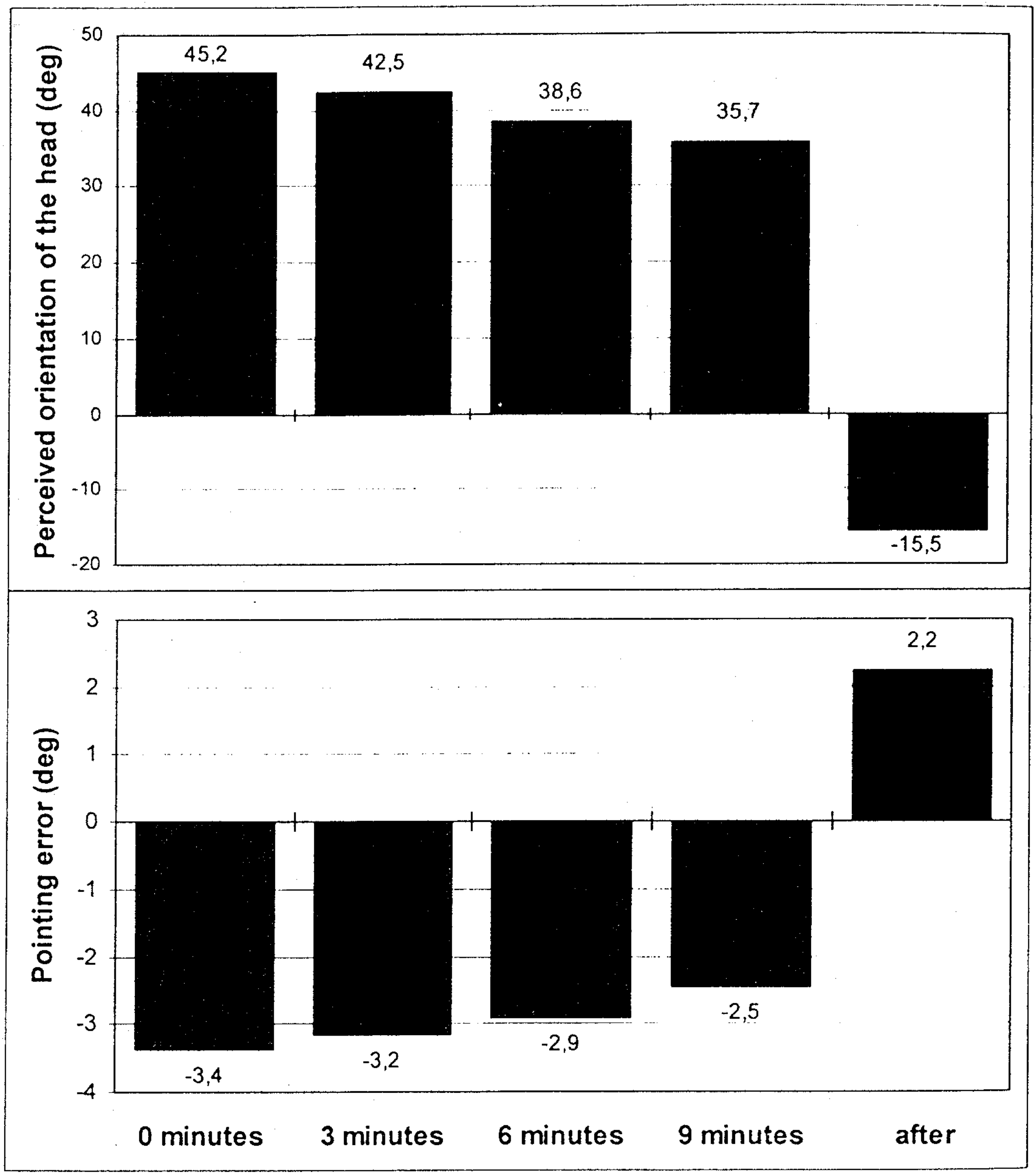

Figure 2. Top: Head orientation rating error as a function of the time elapsed since head rotation. Bottom: Pointing constant error as a function of the time elapsed since head rotation. Measures were obtained 0, 3, 6, and 9 minutes after the rotation, and after the head was replaced in sagittal position. Positive values stand for perceived orientations or pointing errors toward the side of the initial rotation.

against the illusion. In the meantime, the shift in the pointing movements from the median plane, which remained significant at 3, 6, and 9 minutes ($p < .05$), showed a non-significant decrease from -3.4° to -2.4°.

When the experimenter put the head back into the neutral position, the rating of its position differed by -15.5° from the control condition, in the direction opposite to the initial rotation, $F(1, 7) = 16.75$; $p < .01$. At this time, straight-ahead pointing displayed a 2.2° shift contralateral to the new perceived orientation of the head, $F(1, 7) = 6.77$, $p < .05$.

DISCUSSION

Our data showed a shift in straight-ahead pointing movements as a consequence of head turn. No definite explanation is available to account for this shift, but one may consider that the experimental setting does not really represent natural situations, where beyond a certain angular displacement of the head, rotation of the trunk would occur. Indeed, fixing the head in a given position disrupts the synergy of the eyes, head, and hand moving together (Biguer, Prablanc, & Jeannerod, 1984; Rossetti, Tadary, & Prablanc, 1994). However, a systematic shift of the subjective straight-ahead orientation contralateral to a head rotation is a consistent finding (Werner et al., 1953; Fookson et al., 1994).

The head "return" phenomenon did occur. Yet the magnitude of the illusion was less than the one described by Gurfinkel and Levick (1991). This was predictable, as the authors of the original work selected subjects with good responses to muscle vibration and a pronounced Kohnstamm phenomenon, who might be more prone to the head "return" illusion. In order to assess the extent of the illusion in naive subjects, ours were not informed of the expected "return" phenomenon, nor were they instructed to attend to their head orientation throughout the nine minutes. Such instructions probably would have made them more sensitive to the illusion. For instance, Wann and Ibrahim (1992) showed that a drift in perceived arm position could be amplified by asking subjects to attend to the limb position rather than performing a secondary task. Anyway, the incompleteness of the "return" phenomenon could account for the non-significant decrease in the pointing shift while the illusion was taking shape.

The after-effects of the illusion are of particular interest. Indeed, when the head was passively brought back to its neutral position, it was perceived as turned by more than 15° in the direction opposite to the initial rotation. At the same time, straight-ahead pointing shifted contralaterally to the perceived position of the head. Thus, in our experimental conditions, the subjective straight-ahead direction depends on the subjective representation of head position rather than on its real position. Therefore, oriented motor activity does not depend solely on immediately available sensory information, but can also be controlled by the body image.

These results suggest that the components of the body scheme we distinguished in the introduction can be discussed in reference to an analogous dichotomy made by Paillard (1987) regarding the computation of spatial information. This author hypothesized that spatial information is processed in a sensorimotor mode coupled with a cognitive mode. The sensorimotor mode deals with the various afferent signals brought by the local sensorimotor apparatus, and contributes to the continuous updating of a body-centered mapping of the extra-corporeal space. The cognitive mode contributes to the construction of a body-centered space and to the control of spatially-oriented behavior by consulting the internal representations of the relative positions of objects and of the body itself in its spatial environment. Dissociation of the two systems was discovered through numerous neurophysiological, neuropsychological, and behavioral studies (for a review, see Bridgeman, 1996; Paillard, 1991). For instance, Bridgeman (1996) reported that a target whose movement is masked by saccadic suppression is correctly reached at its (unperceived) new location by a pointing hand (Bridgeman, Lewis, Heit, & Nagle, 1979). Spatial information about target displacement was available to the motor system even if it was not consciously perceived. On the other hand, the illusory displacement of a target (verbally assessed) induced by a moving frame was not found to affect pointing (Bridgeman, Kirch, & Sperling, 1981). Thus, a double dissociation occurred: in one condition, a real displacement affected only the sensorimotor mode, and in the other an illusory target displacement affected only the cognitive system. Interestingly, when a responding delay was added, reaching shifted to the illusory position (Wong & Mack, 1981), implying that the sensorimotor system usually works with "on-line" information and must rely on the cognitive system to perform a required movement when cut off from immediate information. Rossetti, Rode, and Boisson (1995) presented the case of a brain-damaged patient who was unable to perceive tactile stimulation on his right arm, but could point to it if instructed. This pointing ability disappeared when the subject had to indicate on a picture of an arm where the stimulus was applied, or when the response was verbalized. The patient seemed only able to process the tactile information at the sensorimotor level. As soon as the task required symbolic spatial representation, the pointing performance went down to the random level. We can also mention the work by Rossetti and Régnier (1995) who studied the endpoint distribution of pointing movements toward two arrays of six targets, one in the form of a line, the other in the form of an arc. They showed that when movements were delayed after target encoding or when a verbal representation of the goal was built, not only was pointing variability greater, but endpoint distribution became contingent upon the target array form. This was not observed when pointing was performed in a reactive mode, suggesting that the cognitive mode can take over sensorimotor processing of spatial information when symbolic representation is needed to perform the task. We hypothesize that the sensorimotor and cognitive modes dissociated in these studies are concepts of the same kind as those of the automatic and perceptual components of the body scheme, as defined by Gurfinkel and Levick (1991). When information signaling the position of the head is reduced, the sensorimotor mode seems to rely on the internal representation of this body part. In our study, the predominance of the cognitive mode over motor responses was perhaps potentiated by the head position rating task, which required symbolic representation.

In conclusion, the internal representation of the head was disturbed by reducing the redundant information flow that usually contributes to the sense of position. The role of the body image in the control of oriented motor activity was manifested in the resulting impairment. This confirms the idea that the body scheme is a valuable concept in the understanding of central processes which relate body space and extrapersonal space. The neural networks involving the parietal posterior cortex could play a major role in these processes, as a lesion of this structure is frequently associated with an alteration of body awareness (Berlucchi & Aglioti, 1997) as well as an impairment of egocentric localization (Mark & Heilman, 1990; Perenin, 1997).

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RÉSUMÉ

En l'absence d'information visuelle, une rotation de la tête induit une déviation contralatérale des mouvements de pointage droit devant. Afin de dissocier l'influence de la représentation interne de la tête et celle de sa position véritable, nous avons utilisé le phénomène de "retour", illusion d'un lent déplacement de la tête vers sa position neutre, lorsqu'elle est maintenue tournée pendant plusieurs minutes, les yeux fermés. Plongés dans l'obscurité, la tête tournée passivement à 40°, huit sujets ont, à 4 reprises (0, 3, 6 et 9 minutes après la rotation), évalué l'orientation de leur tête à l'aide d'un dispositif analogique manuel, et exécuté des pointages manuels droit devant leur tronc. Pour déterminer les effets consécutifs du phénomène de "retour", les mêmes mesures ont été effectuées après la rotation prolongée, une fois la tête passivement ramenée en position sagittale. La rotation de la tête produit immédiatement une déviation contralatérale des mouvements de pointage. L'orientation perçue de la tête dérive de 9,5° pendant les 9 minutes de rotation prolongée. Replacée en position centrale, la tête est perçue comme tournée de plus de 15° dans la direction opposée à la rotation initiale. Les pointages droit devant sont alors déviés contralatéralement à l'orientation perçue de la tête. La direction des mouvements de pointage droit devant dépend donc de la représentation de la tête plutôt que de sa position réelle. Les résultats sont discutés en relation avec le concept de schéma corporel dont les composantes sensorimotrice et cognitive sont distinguées.

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