# Rationale of the study

The aim of this research project is to investigate in the healthy subject the linkage between two spatial cognitive processes: the perception of object position related to the body in the horizontal plane, and the gravity perception in the frontal plane.

Both egocentric and gravitocentric spatial perceptions appeared to be both abnormally biased after right hemisphere stroke (RHS) (Brandt et al., 1994; Molenberghs et al., 2012; Perennou et al., 2008). RHS patients can experiment spatial neglect, the inability to react to and orient to stimuli presented in the contralesional hemi-space. Spatial neglect is most of the time egocentric, that is, centred on body parts such as the eyes, the head, or the trunk (Kerkhoff, 2001).

This egocentric spatial bias is often assessed through the subjective straight ahead (SSA) task, in which subjects are usually asked to point toward an imaginary line cutting their body and the external space in two parts. In neglect patients the SSA was found to be translated (Richard et al., 2004), or rotated (Karnath, 1994a, 1994b; Schindler et al., 2006) toward the ipsilesional side, in comparison with their objective body midline.

In addition to these egocentric spatial biases along the horizontal plane, spatial neglect is also associated with a multimodal distortion of gravity perception in both frontal plane (Baier et al., 2012; Brandt et al., 1994; Karnath et al., 2000; Kerkhoff, 1999; Kerkhoff & Zoelch, 1998; Lafosse et al., 2004; Perennou et al., 2008) and sagittal plane (Funk et al., 2010; Utz et al., 2011). These vertical biases are most of the time orientated in the counterclockwise direction in both frontal and sagittal planes (Perennou et al., 2008). In addition, the magnitude of the contralesional vertical bias is highly correlated with visual neglect severity (Baier et al., 2012; Funk et al., 2010; Kerkhoff, 1999; Yelnik et al., 2002).

These results raise the possibility that spatial neglect and verticality misperception arise from a common pathological cognitive process. In this view, Pérennou (2006) proposed that an inappropriate integration of somatosensory inputs from the left hemi-body would induce a double deficit: a lateralized deficit affecting awareness of the left hemi-body along the horizontal plane, usually referred to as body neglect, and a graviceptive deficit affecting the orientation of body midline in the frontal plane, oriented toward the contralesional side. More broadly, Kerkhoff and Zoelch (1998) suggested that neglect might reflect lesions affecting two partially common networks: one dedicated to attention and “spatial exploration” in the horizontal plane, and one dedicated to “visual-spatial orientation” in the frontal plane. Alternatively, the strong link between spatial neglect and verticality misperception might result from lesions affecting a broad range of egocentric, allocentric, and graviceptive coordinate systems, underlid by very close neural correlates (Kerkhoff & Zoelch, 1998).

Of interest, the constant clinical association between these egocentric and gravitocentric biases raises the question of a common cognitive processing underlying two 3D representations in the healthy subject. At the one hand, body position or orientation could be coded in 3D relative to the visual space (horizontal plane) and gravity (vertical planes). At the other hand, position or orientation of external objects could be coded in 3D relative to the body (horizontal plane) and gravity (vertical planes). Thus, we hypothesize that the cognitive system might integrate lateralized and graviceptive multi-sensory signals together to represent the multiple body-object relationships (egocentric or allocentric) in a common, gravity-centred, 3D representation. Alternatively, the body-object relationships and gravity representations might rely on independent cognitive processes each dedicated to the independent integration of lateralized or graviceptive sensory signals.

In relation with this hypothesis, recent studies have described in the rodent the activity of neurons coding for 3D body orientations (Angelaki et al., 2020; Finkelstein et al., 2015, 2016). Angelaki et al. (2020) have studied the activity of heading cells in the navigation network of the mouse (in the retrosplenial cortex and the antero-dorsal thalamic nuclei). The mice were submitted to passive 3D rotations. Some heading cells coded the orientation of the mouse in multiple planes, in gravity (vertical planes) and visuo-allocentric (horizontal plane) frames of reference. This experiment suggested that, at least in rodent, spatial navigation might rely on a “3D allocentric neural compass” computing the orientation of body related to gravity and external landmarks in multiple planes. More generally, this field of research shows that some neurons are able to integrate 3D multimodal signals.

For our purpose, an emerging question is whether the human cognitive system can code external objects related to both body and gravity in an integrated or dissociated fashion, possibly by relying on neural resources tuned to both lateralized and graviceptive sensory signals.

To investigate this hypothesis, we plan to submit healthy participants to prism adaptation, a visuo-motor adaptation training known to bias egocentric spatial perception (Prablanc et al., 2020). Error pointing due to a leftward optic shift triggers an adaptation process that realigns proprioceptive coordinates of the hand and visual coordinates of the retina rightward (Bastian, 2008). SSA is systematically shifted rightward after leftward prism adaptation, reflecting a rotation of the body midline coordinates in the direction opposite to the optic shift.

According to our hypothesis, the recalibration of the body-object relationship in the horizontal plane should recalibrate the body-gravity and object-gravity relationships in the frontal plane. Of note, prism adaptation modifies the coordinates of the visual surrounding, and thereby the coordinates of the visual space with respect to the body. At variance, prism adaptation is not known to affect body representation *per se*. Thus, we predict that prism adaptation should bias the visual vertical (VV) but not the postural vertical (PV). Indeed, object-in-gravity estimate is thought to rely on visuo-vestibular inputs, whereas body-in-gravity estimate is thought to strongly rely on somatosensory inputs of the trunk (Barra & Pérennou, 2013; Bringoux et al., 2016; Dakin & Rosenberg, 2018; Pérennou et al., 2014).

Crucially, we aim to test the reverse prediction that a bias of gravity perception should in turn affect egocentric space perception in the horizontal plane. In this view, we plan to expose the same healthy participants to a virtual environment tilted 18° leftward in the frontal plane This paradigm is perfectly suited to bias the VV (Odin et al., 2018; Witkin & Asch, 1948). According to our hypothesis, we should observe a rotation of the SSA rightward after a sustained immersion of the subject in the virtual tilted-room. The recalibration of the object-in-gravity orientation should result in the recalibration of the object-in-body positional coding. If the visual space is remapped rightward in the horizontal plane after the immersion in virtual reality, we should then observe a rotation of the SSA rightward.

Finally, we will test whether the two “trans-dimensional” after-effects —effect of prism adaptation on VV; effect of virtual room tilt on SSA— are correlated within the same participants. Indeed, if egocentric and gravitocentric spatial representations rely on the same cognitive process, we expect that a “large” trans-dimensional after-effect in one direction should result in a similar “large” trans-dimensional after-effect in the other direction.

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