Final Report
Vestibular updating and the continuity of awareness (grant number: 269/14)

PI: Patrick Haggard, UCL
Co-I: Elisa Ferre, RHUL

1. Vestibular contribution to updating body position in space

The *sense of self* is defined by a spatial unity between the self and perceptual experience. One convincing perspective defines the self as a sensory construct that remains constant as an organism moves through and explores their environment. The vestibular system is essential for successful navigation. Thus, one function of this input might be bridging the self to the world. When an organism moves through his environment, it keeps track of vestibular signals caused by its own movements, in order to localise its own body in environmental space, and to build a coherent representation of the environment from its multiple, viewpoint-dependent perceptual experiences. Here, we hypothesise and test an equivalent vestibular contribution to awareness of one's own body, based on temporal continuity of perceived limb position.

Experiment 1

Fifteen healthy, right-handed volunteers participated in the study. Volunteers place their right hand on the platform of a robotic planar positioning machine (Arrick Robitics) which passively moves the hand and arm in four locations in the horizontal plane. Galvanic vestibular stimulation (GVS) was delivered during the passive movement, potentially interfering with processing of proprioceptive inputs. 1mA square-wave GVS was applied for 6s (Figure 1).

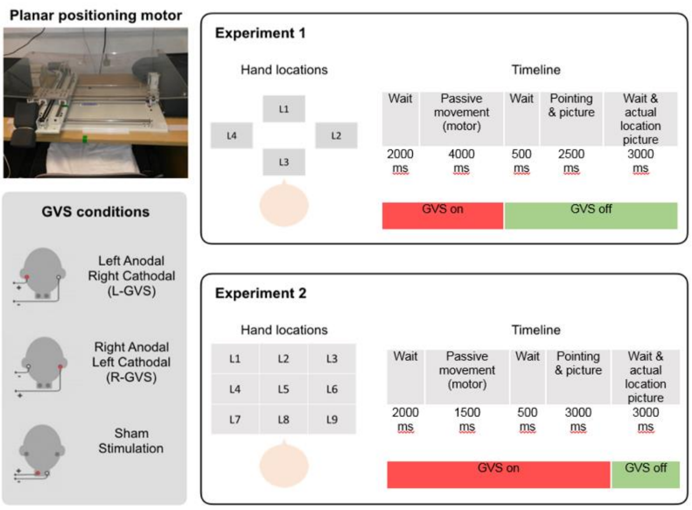

Figure 1

Left anodal/right cathodal GVS and right anodal/left cathodal GVS was delivered at random from the start of each trial until participants' response. As a control condition, a sham stimulation was applied. This produced similar tingling sensations, controlling for non-specific alerting effects, and for the knowledge that an unusual stimulation is occurring. A black planar surface above the participants' hand prevented vision of the hand. After each passive displacement, participants were asked to report the perceived location of their index finger by pointing a laser beam. A webcam was mounted above the setup and took pictures of the real and perceived locations of the hand. A total of 12 trials were administered per block, with each location presented three times per block. Four sequences of movements were randomised with each GVS condition, giving a total of 12 blocks in total.

As dependent measures, we used constant and variable matching errors in the x (left–right) direction and y (distal-proximal) direction for the trials completed by each subject at each target location, within each GVS condition. *Constant error* is computed as the difference between the real and the judged target location. *Variable error* is measured as the standard deviation of repeated trials at the same target location and condition. If vestibular signals interfere with the proprioceptive information, constant and variable error measures should differ between GVS and sham conditions. Further, we hypothesised that GVS might influence the perceived limb position in two distinct ways. First, any activation of the vestibular system might influence limb position independent of polarity and hemispheric effects. To test this generic hypothesis, we compared the average of the L-GVS and R-GVS conditions to the SHAM condition. Second, we hypothesised that the effects of vestibular stimulation could be specific to the hemisphere activated, and would therefore differ between L-GVS and R-GVS conditions.

Paired t-tests on *constant error* measures revealed no significant generic or specific effects at any location. Paired t-tests on *variable error* measures revealed no significant generic or specific effects at location L1, L2, or L3, however significant generic effects were found at L4 for both left–right direction ($p=0.064$) and distal-proximal direction ($p=0.043$). No specific effects were found at this location. Thus, GVS appeared to increase variable error relative to sham stimulation, but only at this leftmost location.

Experiment 2

The lack of GVS-induced effects on limb position might be explain by (1) an update of proprioceptive information during the few milliseconds between the end of GVS and participant's judgement, (2) participants could have learn the

locations of the hand and (3) GVS effects may be more apparent when using the left, as the vestibular system is generally lateralised to the right hemisphere. A further experiment was conducted to address these points.
Fifteen healthy, right handed volunteers participated in this study. The experimental procedure was as Experiment 1 except that participants' hands were passively moved to one of 9 locations and GVS (1mA L-GVS, R-GVS, or Sham) was applied until after that participants made their judgements (Figure 1).
Constant and variable errors for left–right (X) direction and distal-proximal (Y) direction were calculated. Constant error measures showed only significant main effects and interaction between X and Y directions. No GVS main effects or interactions were found. Similarly, variable error showed an effect of direction but no GVS main effects or interactions were found in our variables. GVS did not influence limb position.
Taken as a whole, these experiments suggest that vestibular and proprioceptive systems make independent contributions to bodily spatial awareness. They cast doubt on previous reports of vestibular modulation of proprioceptive information (Schmidt et al., 2013a; Schmidt et al., 2013b). Thus, while the vestibular system clearly plays a role in bodily awareness (Ferre et al., 2011; Ferre et al., 2013), and awareness of the relation of the body to external spatial structures such as gravity, it may not contribute to the spatial representations of the internal structure of the body, such as the position of one body part relative to one another that classically defines proprioception.

2. Disentangling the visual, motor and representational effects of vestibular input

Judging the position of external objects relative to the body is essential for interacting with the external environment. Egocentric representations describe the external world as experienced from an individual's location, according to the current spatial configuration of their body. Consider, for example, a tennis player who must quickly select a forehand or backhand shot based on the ball location relative to their body. A coherent and rapid response to the approaching ball requires combining perceptual information about the ball's trajectory relative to the player with information about the player's ever-changing posture and gaze. Such egocentric representations are thought to be essential in representing the world in relation to oneself

The body midline may provide a basic reference for egocentric representation of external space. Everyday descriptions of spatial locations frequently begin with "on the left..." or "on the right…". The subjective body midline is considered the internal representation of the plane that divides the body in two equal left and right parts. It remains unclear whether the subjective body midline co-ordinates are a static stored representation reflecting primarily semantic knowledge about body morphology, or rather a dynamic, continuously updated sensory datum, perhaps reflecting balance between afferent signals from lateralized receptor organs (left and right eyes, ears etc.), across changing body posture and orientation.

We aimed to clarify whether and how vestibular inputs contribute to egocentric representation in healthy volunteers. In a psychophysical task, participants were asked to judge whether visual stimuli were located to the left or to the right of their body midline. Artificial vestibular stimulation was applied to stimulate the vestibular organs. We hypothesized that vestibular information might play a role in shaping the online perception of the body midline, and thus contribute a basic reference for egocentric spatial representation. Accordingly, we dissociated the vestibular contributions to egocentric spatial representations from those to motor responses (Experiment 1). In a second experiment, we investigated whether GVS-induced bias on body midline could be explained by biases in visual perception, particularly in visual allocentric representation, and found that it could not (Experiment 2). Finally, we showed that effects of GVS on egocentric representation were qualitatively distinct from the effects of GVS on gaze location (Experiments 3 and 4).

Our studies highlighted vestibular contributions to egocentric body representations. Although the role of vestibular signals in egocentric representation has often been suggested, the dependent measures and control conditions used as operational definitions of egocentric representation in previous studies could not rule out other explanations, based on possible vestibular influences on the visual and motor processes used to measure egocentric representation. We have shown that vestibular stimulation biases participants' perception of their body-midline location, shifting it towards the anode. Importantly, we have systematically ruled out alternative explanations based on possible vestibular influences on action selection, action execution, gaze direction, and allocentric visual representation. Thus, our results suggest that vestibular information is involved in the process of egocentric visual localization, necessary for making rapid motor actions. Our results strongly support the idea of a central, cognitive representation of egocentric space, centred on the body midline, and abstracted from specific visual input and from motor output. Vestibular signals provide an ongoing input to the cognitive process which computes and maintains the representation of the body midline.

2. An online vestibular contribution to distance judgement

Whether a visual stimulus seems near or far away depends partly on its vertical elevation. Contrasting theories suggest either that perception of distance could vary with elevation, because of memory of previous upwards efforts in climbing to overcome gravity, or because of fear of falling associated with the downwards direction. In principle, the influence of upward/downward head inclination on distance perception could be based on online information. In particular, under terrestrial conditions, the vestibular system constantly provides signals relating current head orientation to the direction of gravity. Although the vestibular system provides a fundamental signal for the downward direction of gravity, the relation between this signal and depth perception remains unexplored. Here we asked participants to judge the distance of an object presented at different distances on an inclined plane, leading to different head and gaze elevations.

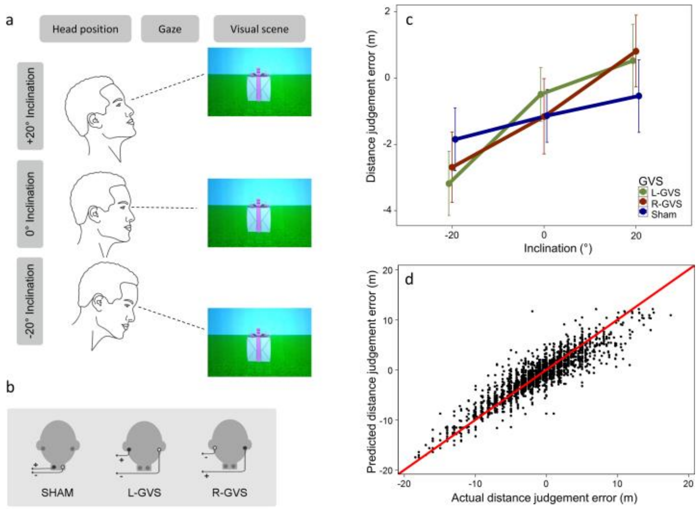

Figure 2

We developed a novel Virtual Reality environment in which neither risks of falling, nor navigational effort were actually present (Figure 2). This minimised confounds such as familiarity, and memory for previous efforts, that could affect previous field-based experiments. Participants were seated in the centre of the CAVE, 1.5m from the front screen. A visual scene was presented on vertical screens and on the floor in order to create a seamless, wide field-of-view immersive display. Participants made absolute judgements about the distance between their own body and an object (a gift box) that appeared in front of them. The positions of the present box were distributed logarithmically between 5m and 25m; thus, the possible distances were 5, 6.9, 9.52, 13.3, 18.2, 25m. The object appeared on a smooth plane that was inclining (+20°), flat (0°), or declining (-20°). The participants' head inclination was systematically varied by asking them to tilt both the head and gaze upwards or downwards to fixate a target object. We could thus directly compare predictions of gravity and evolved navigation theories. Further, we applied event-related galvanic vestibular stimulation (GVS) during each judgement, to investigate whether online vestibular signals indeed affected the distance perception biases.

Relative to distance estimates collected with the object at the level of horizon, participants tended to overestimate distances when the object was presented above the level of horizon and the head was tilted upward and underestimate them when the object was presented below the level of horizon. Distance perception varied significantly across head inclinations ($p < .001$) (Figure 2). Downward distances were underestimated by 1.65m ($SD = 3.50$), while upward distances were overestimated by 1.19m ($SD = 3.90$), compared to ground level. Interestingly, adding artificial vestibular inputs strengthened these distance biases, showing that online multisensory signals, and not only stored information, contribute to such distance illusions. This pattern of results is consistent with an inclination effect generated online by a vestibular signal that is boosted by artificial vestibular stimulation.

Our results suggest that the gravitational modulation of visual distance perception depends on on-line vestibular signals. This elevation distance bias is, therefore, not merely a product of learned contextual associations but rather reflects a specific multisensory integration mechanism.

2. Vestibular contribution to somatosensory vertical

Gravity is the only always-on perceptual signal. One aspect of the experience of gravity is being the right way up. Humans construct and update their sense of verticality by integrating vestibular, proprioceptive, and visual input. Assessment of the verticality of the environment in the upright position needs mainly vestibular and visual inputs. Proprioceptive information is required when the head or the whole body is tilted. Although the mechanisms for the perception of verticality are well know for visual stimuli, no studies have so far investigated how the brain computes verticality judgements for somatosensory stimuli applied on the body. Here we developed a series of experiments to address this question.

Experiment 1: online vestibular signals do not influence somatosensory vertical.

Galvanic Vestibular Stimulation (GVS) was used to artificially stimulate the vestibular organs while participants judged the verticality of somatosensory stimuli applied on their forehead (Figure 3). A bias towards the anode was predicted based on previous reports on visual vertical.
Thirteen right-handed volunteers participated. GVS was applied in bipolar configuration with a boxcar pulse of 2 mA for around 2.5 min. Left-anodal and right-cathodal configuration is named 'LGVS', while the inverse polarity, namely left-cathodal and right-anodal configuration, was named 'RGVS'. A sham stimulation was applied attaching the electrodes on the left and right side of the neck, about 5 cm below the GVS electrodes. A spherical probe (4 mm) attached to an L-shaped extension arm was moved across the forehead using a 3-dimensional force feedback device (PHANToM Premium 1.0, Geomagic Inc., USA). Participants head rested in a fixed position while the probe moved in a straight, up-to-down line along the forehead with a deviation either leftward or rightward from the vertical. Stimulus velocity was 69 mm/s, with smoothly connected rising and falling phases lasting 30 ms each, generating a clear direction sensation. Verticality estimates were obtained with a reversed staircase procedure in which lines were progressively reaching the vertical towards clockwise and counterclockwise directions. At the beginning of each trial, the probe made static contact with the skin for 1 s. The initial position of the probe on the forehead was jittered across trials to prevent participants from judging direction by the final position of the probe only. At the end of the falling phase, the probe was immediately retracted from the skin.
To identify whether generic vestibular input influences the perception of verticality, we compared (LGVS+RGVS)/2 to sham condition. This planned comparison revealed no significant difference in verticality bias ($p=0.467$). To investigate the specific vestibular effect, we directly compared LGVS to RGVS conditions. This contrast was designed to reveal how vestibular projections in each hemisphere might influence verticality. No significant differences were found in bias values ($p=0.482$). Surprisingly, these results suggest that somatosensory verticality is not influenced by online gravitational signals.

Experiment 2: online GVS signals influence visual vertical.
Thirteen right-handed volunteers were administered with a visual verticality perception task combined with GVS. GVS intensity and duration were as in the previous study. A LED light was attached to the L-shaped extension arm of the robotic device, which was drawing lines in the air in a complete dark room. Generic vestibular input did not influence the perception of verticality ($p=0.451$) (Figure 2). However, the direct comparison between LGVS to RGVS conditions revealed, as expected, a shift in the vertical bias towards the anode side ($p=0.003$).

Experiment 3: Somatosensory vertical: gravity or neuraxis?
The neuraxis denotes the direction in which the central nervous system lies. Critically, in bipedal animals, as humans, this direction is aligned to the gravitational vector. Here we dissociated the direction of the neuraxis and gravity by asking participants to tilt their head. Sixteen participants estimated somatosensory vertical of stimuli applied on the forehead while their head was titled 10 degrees to the left, 10 degrees to the right or not tilted. The experimental procedure was otherwise similar to the previous study. Results revealed a reliable bias in verticality judgements towards the direction of the neuraxis ($p<0.001$). Thus, the head tilted towards the left induced a rightward somatosensory verticality bias, while the head tilted tilted towards the right induced a leftward verticality bias. The neuraxis seems to be adopted as reference in computing verticality for stimuli applied to the body.
Importantly, the bias towards the neuraxis is not restricted to body midline: a similar pattern of results was found with somatosensory stimuli applied on the cheek while the head was tilted forward and backward.

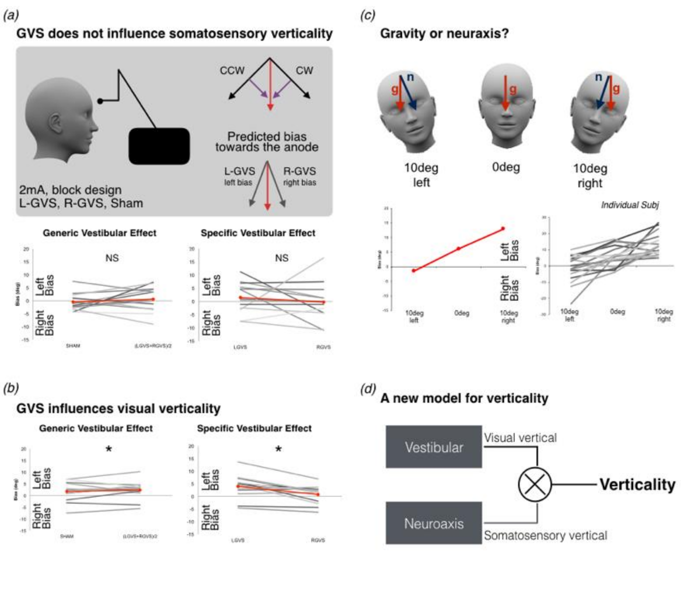

Figure 3

Further, the bias toward the neuraxis is present only if a particular body part is tilted. In a factorial design we combined stimuli delivered on the head or torso while the head or torso were tilted. The bias in somatosensory verticality judgement was present only when the somatosensory stimulus was delivered to a body part that was tilted, while tilt of non-stimulated body parts was irrelevant. This suggests that somatosensory verticality is referred to the *local* major axis of each body part, rather than a global representation of the body as a whole.

Our study provides the first direct evidence of two representations of vertical. While online vestibular signals are essential for computing vertical judgement of exteroceptive stimuli, the neuraxis is adopted for cuteaneous stimuli. Taken together our results suggest that the cutaneous somatosensory vertical is non-vestibular and linked to a local neuraxis representation.

Our results imply that the brain has some source of information about the internal structure of body parts, such as their axes of symmetry. The nature of this information remains unclear, and will be an important focus of interest in our future work.

Taken as a whole, our results converge on a new theory of bodily spatial cognition, based on a clear dissociation between two independent representations. The first is a local representation focussed on individual body parts. Our work shows that this representation includes (a) information about position relative to an adjacent body part, signalled by the proprioceptive system (b) information about the underlying morphological structure of the body part. Crucially, this representation does not integrate central signals such vestibular inputs, and, we believe, makes no reference to external information. The second representation is vestibular in origin, and based on integrating purely central information. This representation defines the relative of the organism to the fundamental features of the *external* environment, notably gravity.
During the remaining period of the project, we plan further experimental testing, and theoretical work, to explore this framework. Outstanding questions include the mechanism for updating these spatial representations with new input, and the computations that link the internal spatial representations of body parts to the representation of the location in external space.

3. A shared gravitational vertical experience

Gravity is the only always-on perceptual signal. One aspect of the experience of gravity is being the right way up. Humans construct and update their sense of verticality by integrating vestibular, proprioceptive and visual input. Assessment of the verticality of environmental stimuli is based not only on vestibular and visual inputs, but also on proprioceptive information about body posture. A compelling demonstration of the role of bodily proprioception in perceiving verticality comes from the “Aubert effect”. Briefly, when participants are asked to first tilt their head or body slightly to one side, and then judge whether a visual stimulus is vertical or not, they show a clear bias towards the body midline (Anastasopoulos et al., 1999; Yardley, 1990). That is, in order to appear vertical, a visual stimulus must be rotated in the direction of their tilted body. Thus, if they are leaning to their right, the object has to be tilted slightly to the right to appear exactly vertical (Figure 4).

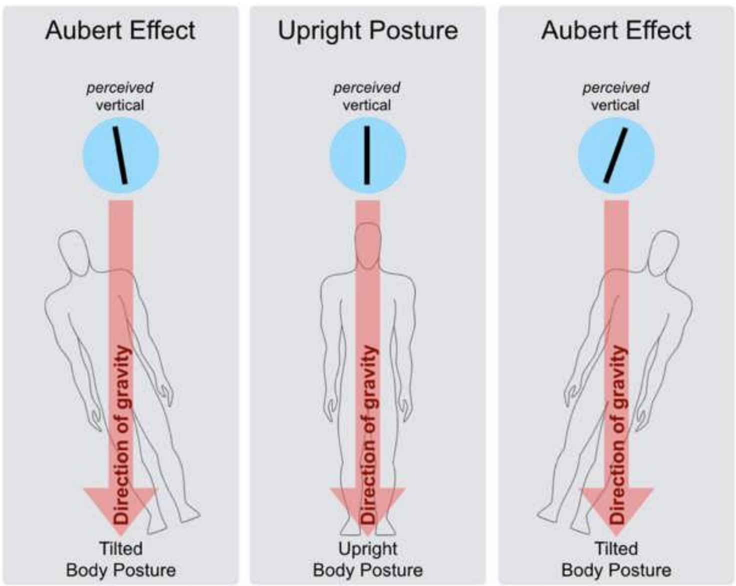

Figure 4

Classical explanations of the Aubert effect suggest that the vestibular-gravitational signal and the proprioceptive signal are placed into conflict, so that the sense of straight up in the outside world depends on body orientation.
Verticality is the distinctive feature of our normal bodily experience: most of us spend most of our lives vertical, and the transition to bipedalism is seen as a key marker in cognitive evolutionary time. Here we measured whether the individual experience of verticality might be automatically updated by the presence of another person.
Sixteen right-handed volunteers were administered with a Subjective Visual Vertical. The method of constant stimuli was used to estimate the subjective perception of verticality: on each trial a line was presented on a visual screen with a different orientation, and participant was asked to judge whether the line was tilted clockwise or counter clockwise.

Participants performed the Subject Visual Vertical judgments in two experimental conditions. In one condition they were asked to lean on a tilted support, while in the other condition the support was replaced by a person (the experimenter). Critically, the participants’ posture was exactly the same in the two conditions.
Our results showed that individual experience of verticality is influenced by the presence of another person (p=0.01). Our results suggest an intriguing modulation by social perspective of the most basic feature of our perceptual experience, namely how gravity itself acts on our own body.

References

Anastasopoulos, D., Bronstein, A., Haslwanter, T., Fetter, M., & Dichgans, J. (1999). The role of somatosensory input for the perception of verticality. Annals of the New York Academy of Sciences, 871(1), 379-383.

Ferrè, E. R., Bottini, G., & Haggard, P. (2011). Vestibular modulation of somatosensory perception. *European Journal of Neuroscience*, *34*(8), 1337-1344.

Ferrè, E. R., Day, B. L., Bottini, G., & Haggard, P. (2013). How the vestibular system interacts with somatosensory perception: a sham-controlled study with galvanic vestibular stimulation. *Neuroscience letters*, *550*, 35-40.

Yardley, L. (1990). Contribution of somatosensory information to perception of the visual vertical with body tilt and rotating visual field. Perception & Psychophysics, 48(2), 131-134.

Schmidt, L., Keller, I., Utz, K. S., Artinger, F., Stumpf, O., & Kerkhoff, G. (2013). Galvanic Vestibular Stimulation Improves Arm Position Sense in Spatial Neglect A Sham-Stimulation-Controlled Study. *Neurorehabilitation and neural repair*, *27*(6), 497-506.

Schmidt, L., Artinger, F., Stumpf, O., & Kerkhoff, G. (2013). Differential effects of galvanic vestibular stimulation on arm position sense in right-vs. left-handers. *Neuropsychologia*, *51*(5), 893-899.