Vestibular Sense and Perspectival Experience

A Reply to Adrian Alsmith

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To answer Alsmith's questions about the existence of a vestibular sense, we outline in the first part of our reply why we believe the vestibular sense is a true "sixth sense". We argue that vestibular information constitutes distinct sensory events and that absolute coding of body orientation and motion in the gravity-centered space is the important unique feature of the vestibular system. In the last part of our reply, we extend Alsmith's experimental suggestions to investigate the vestibular contribution to various perspectival experiences.

Keywords
Absolute coding | Gravity | Otoliths | Perspective | Self-motion | Vestibular sense | Vestibular thresholds | Vestibular-evoked potentials

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1 Is there a vestibular sense?

The first section of Alsmith's commentary ("Structural vs. taxonomic approaches to vestibular processes") raises an important question: *is there a vestibular sense*? The enduring lack of a clear answer to this seemingly simple question might stem from the old assumption that there are five and only five senses, all of which giving rise to a distinct conscious sensation. The relatively late identification of the anatomical structures that code self-motion (Wade 2003; Lopez & Blanke 2014) has probably further contributed to the neglect of the "vestibular sense" in philosophy and science. We comment below on two questions raised by

Alsmith concerning this debate: (1) *Are vestibular events sensory events?* and (2) *Are vestibular events of a specific kind, i.e., distinct from other sensations?*

(1) Are vestibular events sensory events? Several criteria have been proposed to determine whether an event is sensory or not (Macpherson 2011).[1] Following this type of approach, vestibular events can be described as sensory events because a sensory organ is dedicated to coding gravito-inertial forces and because there is a phenomenal experience associated with vestibular stimulation. Indeed, there are many situations during which passive own-body motions are characterized by distinct self-motion sensations. Imagine, for example, a situation in which we are sitting with eyes closed in the train and feel the departure, or when we are standing with eyes opened in a lift and experience vertical movement of the body. In such situations visual and somatosensory signals do not (or only weakly) contribute, but changes in vestibular signaling result in the conscious perception of self-motion, i.e., of "being translated forward" or "being elevated".

Self-motion perception due to vestibular stimulation is also testable in the laboratory using motorized motion platforms (rotating chairs or translational platforms, see Palla & Lenggenhager 2014): participants are usually tested sitting on a chair, while non-vestibular sensory signals are largely excluded by having the participant's body strapped to the chair and stabilized with cushions, by testing participants with eyes closed, by reducing auditory cues via white noise presented in headphones, and by testing participants with gloves and long sleeves (e.g., Grabherr et al. 2008; Hartmann et al. 2013; Lopez et al. 2013; Macauda et al. 2014; Valko et al. 2012). Participants are able to accurately detect and report self-motion and its direction, which forms the basis for the measurement of *vestibular thresholds*, which are comparable to auditory or tactile thresholds. When accelerations are applied above the threshold of the mechanoreceptors in the inner ear (e.g., above $0.6°/s^2$ for rotations around the vertical axis), a motion sensation emerges in healthy participants, which in our opinion is the sensory event corresponding to the vestibular sensation "I was moved". Such sensory events therefore constitute the basis of what has often been referred to as the "sixth sense" (Goldberg et al. 2012; Wade 2003; Berthoz 2000). Further compelling support comes from patients with dysfunctions of the peripheral vestibular apparatus like benign paroxysmal positional vertigo, vestibular neuritis, or Menière's disease, who experience strong vestibular sensations in the form of vertigo (Brandt 1999).

We acknowledge, however, that in situations where we actively move the head with eyes opened in space, vestibular signals from self-motion do not give rise to such distinct "vestibular" sensation of self-motion. As explained in our target article, in conditions of active, self-generated head movements, vestibular signals are cancelled or strongly attenuated in the vestibular nuclei (Cullen 2011; Roy & Cullen 2004). This is probably why the vestibular sense has been termed a "silent sense" by some authors (Day & Fitzpatrick 2005).

(2) Are vestibular sensory events of a specific kind, i.e., distinct from other sensations? Vestibular sensations are sensations of own-body rotations, translations, and orientation (sensation of whole-body orientation with respect to the vertical) in space. Such sensations may in principle also emerge from the stimulation of other sensory systems, such as the visual, somatosensory and auditory systems. Impressively, illusory self-motion might be evoked by large optic flows, tactile stimulation under the feet, or displacement of auditory stimuli (Berthoz et al. 1975; Dichgans et al. 1972; Lackner & DiZio 2001, 2005; Väljamäe 2009). These findings resulted in Alsmith's claim that "one may begin to seriously consider the possibility that vestibular processing does not constitute a form of sensory processing of its own kind "(this collection, p. 2). Yet if vestibular processing does

1 For example, according to Macpherson, four main approaches to describe the senses can be distinguished: *"the representational criterion," "the phenomenal character criterion," "the proximal stimulus criterion,"* and *"the sense-organ criterion"* (2011).

Figure 1: A) Crise de désinvolture (2003) an artwork by Philippe Ramette. Copyrights: © 2015, ProLitteris, Zurich. All rights are reserved. Reproduction and any other use without permission - except for the individual and private use - is prohibited. B) Drawing of the "haunting sway", a "gravity-defying" device that was originally developed in the US in the 1890s for amusement parks. The visitors had the impression that they were turning with the sway, while actually the room was turning around them.

not constitute a distinct form of sensory perception, to which type of sensory processing does it belong? Some authors have proposed that vestibular processing might relate to *proprioception* (since the vestibular system detects own body motions) or to *exteroception* (since it detects gravitational acceleration), but these propositions link vestibular processing to a function rather than a sensory modality. As recently pointed out by Macpherson (2011), "it is not even clear which sensory modality equilibrioception should be assimilated to, if indeed it should be assimilated to any" (p. 18).

Although vestibular, visual, and somesthetic signals may all support self-motion perception, this does not mean that the phenomenal experience of self-motion based on vestibular signals is similar to the experience based on visual signals. Actually, they may strongly differ in their content since, for example, the vestibular system is specialized in coding high-frequency movements whereas the visual system is tuned to low-frequency movements (see also next paragraph).[2] And even at the neurophysiological level, vestibular signals interact very early with visual and somatosensory signals; yet this does not mean that these signals provide the exact same sensation of body motion and orientation. An analogy might be when we observe a person speaking: both auditory and visual signals from the speaker's lip movements contribute to the experience of listening to a voice; nevertheless both signals provide clearly distinct sensations and experiences. We believe the same holds for vestibular processing. Vestibular sensations might be clearly distinct sensations, but in daily life they are often integrated with other senses, confounding a pure conscious sensation (Angelaki & Cullen 2008; Angelaki et al.

2 We add that while visual, auditory, and somatosensory signals about self-motion can be suppressed, vestibular signals about body accelerations are *necessarily present*.

2009). Vestibular-only neurons are found in the vestibular nuclei, which are not influenced by visual signals or eye movements, suggesting that vestibular signals are not entirely fused with other sensory signals (Goldberg et al. 2012). Similarly, intracranial stimulations in epileptic patients have showed that pure vestibular sensations could be evoked during electrical stimulations of the superior temporal cortex and insula (Penfield 1957; Kahane et al. 2003; Mazzola et al. 2014).

2 A unique feature of the vestibular system: The representation of absolute self-motion and orientation

As mentioned by Alsmith, the vestibular system, unlike other sensory systems, does not code unique properties of sensory inputs such as loudness or hue. Yet, as already argued in the target article, the coding of *absolute* self-motion in space and self-orientation within gravity-related space is unique to the vestibular system. While relative (self-) motion and orientation can be detected by other sensory systems (e.g., vision and proprioception), gravity itself is not directly visible to these senses.[3] Because vestibular organs contain gravito-inertial sensors, they provide a coding of body translations and rotations that is independent from external references (unlike visual, auditory, and somatosensory coding of whole-body motions). For this reason, vestibular organs code self-motion even when the eyes are closed, while we are jumping on a trampoline, or swimming in the sea.

With these properties the vestibular system, especially otolith signaling, also gives us the sensation of an "up" and a "down" by encoding gravitational acceleration. This process might be less accessible to consciousness in normal circumstances, as gravitational pull is constantly acting on vestibular mechanoreceptors. However, there is a large body of data showing that an "internal model of gravity" (predicting how objects move in the physical world according to Newton's laws; McIntyre et al. 2001) which is strongly based on otolith processing, shapes at a preconscious level several aspects of the visual perception of objects, body movements, and structure (e.g., Indovina et al. 2005; Lacquaniti et al. 2013; Lopez et al. 2009; Maffei et al. 2015; Yamamoto & Yamamoto 2006). A further illustration of the importance of the coding of body orientation in a gravity-centered space can be provided by the "tilted room illusion," in which the furniture is aligned in a way that is incongruent with gravitational vertical (see figure 1A for an example by the French artist Philippe Ramette[4]), which has been used in a moving version as well in theme parks (the haunting swing, a "gravity-defying" ride, see figure 1B). Experiments conducted in this type of tilted environment have shown that the participant's perception and posture are biased by tilted visual references, but not totally (Jenkin et al. 2003; Oman 2003). Merleau-Ponty has nicely noted the ambiguity of space-coding regarding the experience of *up* and *down*: "A direction can only exist for a subject who traces it out, and although a constituting mind eminently has the power to trace out all directions in space, in the present moment this mind has no direction and, consequently, it has no space, for it is lacking an actual starting point or an absolute here that could gradually give a direction to all determinations of space" (2012). It is interesting to note Merleau-Ponty's claim that what is missing for the experience of up and down is an "absolute". Merleau-Ponty also explains that "[w]e cannot, then, understand the experience of space through the consideration of the contents, nor through that of a pure activity of connecting, and we are confronted by that '*third spatiality*' that we foreshadowed above, which is neither the spatiality of things in space, nor that of spatializing space [...] We need an '*absolute within the relative*', a space that does not skate over appearances, that is anchored in them and depends upon them" (2012, p. 296–297; our italics). Although Merleau-Ponty did not mention the vestibular system when he described the necessity of a "third spatiality," we now know that the otolithic sys-

3 Of course we can infer about (the direction of) gravity by the relative motion and specific properties of certain objects; however this process is much slower, less intuitive, and not always applicable.

4 To be precise, Ramette does not glue the furniture to the roof or wall, but rather "glues" himself to the wall. His position is thus tilted compared to gravity, not the furniture.

tem provides the "absolute within the relative" he mentions and allows the coding of absolute self-orientation in space (see also Berthoz 2011 for a detailed account).

3 Vestibular system and perspectival experience—Experimental suggestions

In this last part we elaborate on the experimental suggestions provided by by Alsmith, proposed in order to investigate more fine-grained forms of perspectival perceptions and their interaction with vestibular processes. In the target article we used the term first-person perspective (mainly in the context of mental perspective taking and out-of-body experiences) to refer to an egocentric visuo-spatial perspective. Alsmith proposes a subdivision of this perspective into three forms of perspectival structures: "origin," "egocentric frame of reference," and "focal point of sensory flow (egomotion)," which might be differentially influenced by vestibular signals. While we do not necessarily agree on the importance and justification of these (and *exactly these*) components, we appreciate the experimental suggestions, on which we will briefly comment below.

3.1 Experiments I and II: Changing vestibular processes through change in perspective

A common approach to testing the influence of the vestibular system on high-level cognition is to alter vestibular information during a specific task—for example a perspective-taking task. This can be done either by applying galvanic (Lenggenhager et al. 2008) or caloric (Falconer & Mast 2012) vestibular stimulation, by natural vestibular stimulation (Van Elk & Blanke 2014), by exposing participants to microgravity (Grabherr et al. 2007), by changing the body orientation relative to gravity (Arzy et al. 2006), or by testing patients with vestibular dysfunction (Grabherr et al. 2011). What Alsmith describes[5] in the first two experiments mentioned in the commentary is the opposite approach, namely assessing vestibular processing during specific tasks, or bodily states, respectively.[6] We believe that this is a potentially powerful way to better understand vestibular implication in fine-grained aspects of the bodily self and their interrelation—both in experimental work and research in patients with bodily-self disturbances (see e.g., Brugger & Lenggenhager 2014 for a recent review). We would like, however, to point out a few important issues that should be considered.

Alsmith suggests that we measure time-locked vestibular-evoked potentials without stating more precisely what vestibular stimulation to use. However, this is crucial, since there are various ways to test vestibular processing, mostly by stimulating a specific part of the vestibular system (see e.g., Palla & Lenggenhager 2014 for a recent review). One possibility (in the suggested experiment) could be to use sound-induced vestibular-evoked potentials. The advantage of these is that they can be recorded in a static condition, unlike other forms of vestibular stimulation (e.g., rotatory evoked cortical potentials; Keck 1990), which is important for the suggested full-body illusion paradigms. When designing experiments along these lines, it is indispensable to know what part of the vestibular system is stimulated by the used technique. Sound-induced cortical vestibular potentials, for example, represent cortical processing of otolith signals, mainly from the saccule, thus coding preferentially linear movements in the vertical plane (i.e., up and down movements in a standing position). If we rather expect a difference in coding the front-back movement, as proposed in Experiments 1 and 2, a vestibular stimulation of the utricule might be more appropriate (e.g., Todd et al. 2014, using evoked-potentials by impulsive accelerations). Since testing all different aspects in all the proposed conditions is technically impossible, the specific vestibular stimulation should be carefully chosen based on the hypothesis. Alternatively,

5 This idea of measuring vestibular processes during situations of altered sense bodily self evolved in the framework of a grant entitled "Finding Perspective" awarded to Adrian Alsmith, Christophe Lopez and colleagues by the Volkswagen Foundation.

6 A similar approach has been used for other sensory processes such as the measure of body temperature during the rubber hand illusion (Lenggenhager et al. 2014; Moseley et al. 2008) or the full-body illusion (Macauda et al. 2014; Salomon et al. 2013).

more indirect measures could be used to test a vestibular implication, such as changes in posture or stability during various experimentally-induced alterations in the bodily self, e.g., via dynamic posturography using a moving platform, as it is commonly used in clinical settings (e.g., Ghulyan et al. 2005).

3.2 Experiment III: Egocentric perspective

In the third proposed experiment, Alsmith considers which (bodily) reference (e.g., eye, head or body centered) is taken as the egocentric reference frame. The fact that there are multiple bodily frames of reference has been nicely shown in a classical task where ambiguous letters (e.g., d/p) are written on the skin. They are typically perceived differently depending on the bodily location on which they are written (Sekiyama 1991); and interestingly the perspective can be modified by vestibular stimulation (Ferrè et al. 2014). Alsmith here suggests that there is a need to investigate the egocentric perspective both with implicit and explicit measures in a situation where body and head[7] are misaligned, as previously done to test spatial cognition (Schindler 1997) and heading direction during passive motion (Ni et al. 2013). This is a very interesting suggestion; however from the experimental description it is not entirely clear how Alsmith thinks that the vestibular contribution should be investigated. Furthermore, his hypothesis only concerns the respective contribution of head and torso position, but not its vestibular contribution. He suggests that participants might receive galvanic vestibular stimulation or tendon vibration stimulation to investigate "the relative contribution of vestibular processes to egocentric perspective." One way to test this could be to align the participant's head and torso, but use tendon vibration or galvanic vestibular stimulation in order to induce an illusory tilt or turn the participant's head, thus inducing an illusory misalignment of the head and body. By doing the suggested task in such a condition, vestibular or proprioceptive contribution could be isolated. While this is theoretically very interesting, there might be practical difficulties: vestibular and proprioceptive illusions are usually susceptible to huge individual differences, and inducing illusory shift of ±15% could be difficult. Furthermore, in the proposed experiment that misaligns body and head around the yaw axis, gravitational cues do not differ between the position of the torso and the head in the misaligned condition. Adapting the experiment to a lying-down position,[8] where body and head would be at different angles with respect to gravity, could help investigating the otolithic influence on perspective.

4 Conclusion

In response to Alsmith's inspiring theoretical suggestions, we have argued that there is a true vestibular sense, with distinct and important properties. We believe and agree with Alsmith that better understanding its contribution to various aspects of experiential life is crucial and that this might also facilitate taxonomic and structural approaches. Alsmith's response exemplifies, in our view, the mutual benefit of an interdisciplinary dialogue, as his thorough analysis of current experimental data, paired with new theoretical considerations, leads to concrete experimental suggestions, which might reshape theoretical considerations depending on the potential results. In our reply we have pointed out some possible methodological difficulties, some possible ways to overcome these, and some new directions such experimental work could take. In particular, we are optimistic that analyzing vestibular processing in the brain using electrophysiological approaches will provide in the near future important new data about the vestibular contribution to the sense of self. We hope that our reply will help foster interdisciplinary collaborations that further investigate the role of the vestibular system in shaping our mind.

7 Additionally, eye-position could be manipulated.

8 Or generally test various body orientations (e.g., as in Lopez et al. 2009).

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