## Internal models and spatial orientation

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**Abstract:** Aspects of "emulation theory" have been seminal to our understanding of spatial orientation for more than 50 years. Sometimes called internal models, existing implementations include both traditional observers and optimal observers (Kalman filters). This theoretical approach has been quite successful in helping understand and explain spatial orientation – successful enough that experiments have been guided by model predictions.

First, a correction is warranted. Typically, the feedback signal from a Kalman filter to a controller is not the estimated noise-free measurement, $I^*(t)$, as shown in Figure 6 of the target article. Because one has the freedom to choose the state variables that are most interesting for a specific control problem, it is standard to choose the state variables $r(t)$ and $r^*(t)$, such that they include the primary states that one is interested in controlling. Therefore, these are generally used for such feedback control. For example, one could choose to make position (e.g., eye position) a state variable for control problems that require accurate control of position (e.g., saccades to a stationary target) but could also choose to make velocity (e.g., eye velocity) a state variable for those problems that require control of velocity (e.g., smooth pursuit or vestibulo-ocular reflexes). One seldom has the same freedom to choose sensors. For example, the semicircular canals cannot directly indicate angular position instead of angular velocity.

More importantly, while agreeing that motor control has been well served by frameworks related to Grush's emulation theory, I vehemently dispute the notion that "motor control is the only area in which this framework has the status of a major or dominant theoretical player" (sect. 6.4, Conclusion, para. 3). Kalman filtering, observers, and other closely related concepts have been hypothesized to contribute to aspects of human spatial orientation (i.e., balance control, vestibulo-ocular reflexes, and perception of motion and orientation) for more than 50 years. There is no question that these "internal models" have contributed substantially to our understanding of spatial orientation and are major theoretical players on this stage.

Because space considerations prevent comprehensive coverage, I will briefly introduce some models used to understand human spatial orientation. The original authors can be allowed to speak for themselves via extensive citations. Von Holst (1954) proposed a concept, springing from spatial orientation experiments performed in collaboration with Mittelstaedt (von Holst & Mittelstaedt 1950), that has come to be known as "efference copy." The concept was that efferent commands are copied within the central nervous system (CNS) and used to help distinguish re-afference – afferent activity due to internal stimuli (e.g., self-motion) – from ex-afference – afferent activity due to external stimuli. A similar hypothesis was proposed by Sperry at about the same time (Sperry 1950); some credit von Uexkull (1926) for publishing a similar hypothesis almost 30 years earlier.

Later, while studying adaptation to sensory rearrangement (Hein & Held 1961), Held (1961) recognized a shortcoming in von Holst's original formulation – that efference copy and the re-afference generated by self-motion cannot be compared directly because one signal has the dimensionality of a motor command whereas the other has dimensions of sensory feedback. Held proposed that efference copy must proceed to a hypothetical neural structure called correlation storage, with the output from the correlation storage compared to the sensory afferent. (The similarity between Held's "correlation storage" and the process model in Grush's Figs. 5 and 6 is striking, as is the similarity between Held's comparator and Grush's sensory residual difference calculation.)

Reason (1977; 1978) noted that earlier theories had looked at sensory conflict as an incompatible difference between different sensory afferents and emphasized that sensory conflict is more accurately defined when sensory inputs differ from the expected sensory pattern that we expect, based upon our previous exposure history. These concepts were later included in Oman's thoroughly considered observer theory model of motion sickness (1982; 1990; 1991). Because Kalman filters, discussed in detail by Grush, are simply observers (Luenberger 1971) whose feedback gains are optimally chosen based on noise characteristics, Oman's observer formulation and that presented by Grush are indistinguishable.

In parallel with these efforts, Young and some of his colleagues were developing and implementing models of human spatial orientation. Following a study of the interaction of rotational motion cues from the semicircular canals and vision, Zacharias and Young (1981) modeled their responses with the inclusion of an internal model of the canals. This model was later followed by a model (Borah et al. 1988) based on optimal observer theory (Kalman filtering) that was developed to explain and model how the nervous system combined and processed sensory information from several sensory systems (vision, semicircular canals, and otolith organs).

More recently, we (Merfeld 1995a; 1995b; Merfeld et al. 1993; Merfeld & Zupan 2002) have implemented a series of models that most closely follow in the trail blazed by Oman's observer-theory approach to explain both vestibulo-ocular reflexes and perceived motion and orientation. Another model (Glasauer 1992), making similar predictions and addressing similar questions and problems, was developed in parallel with the above approach. At almost the exact same time, a third group developed a similar approach using what they referred to as coherence constraints (Droulez & Cornilleau-Peres 1993; Droulez & Darlot 1989; Zupan et al. 1994). This approach used internal models, not unlike those used by Merfeld and Glasauer, and might be accurately characterized as a thoroughly considered implementation of Held's correlation storage and comparator discussed previously. More recently, the observer and coherence constraint approaches have been combined in a comprehensive model of sensory integration (Zupan et al. 2002). In parallel with all of these efforts, a model has been developed to explain and model human postural control using optimal observers (Kuo 1995). This postural model implements internal models of both sensory and motor systems.

Given this lengthy and illustrious history, including implementations of both traditional observers and optimal observers (Kalman filters), it is our opinion that the lack of general acceptance is *not* due to the lack of a formal theoretical or modeling framework, but rather, on account of *too little cross-disciplinary communication* (such cross-disciplinary communication is fostered by *BBS*) and *the lack of direct experimental evidence and experimental investigations specifically targeted to prove or disprove the hypothesized "internal models."* To address the latter problem we have recently begun performing experimental investigations (Merfeld et al. 1999; Zupan et al. 2000; Zupan & Merfeld 2003) specifically designed to prove or disprove aspects of the internal model hypotheses.

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