
Why Encode Limb and Body Displacements in the Velocity Domain? Neurophysiological and Behavioral Evidence

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Abstract

Performing voluntary actions often requires using more than one sensory modality. However, different modalities provide information in different domains. For example, vision primarily gathers information in the positional domain while the inner ear primarily encodes information in the acceleration domain. This chapter presents neurophysiological and behavioral evidence for the use of visual and vestibular information in the velocity domain during perceptual and sensorimotor activities. Specifically, for activities of daily living requiring the use of visual and vestibular information, it is argued that the central nervous system preferentially converts sensory cues into the velocity domain prior to implementing the multisensory combination and integration processes relevant to perception and action.

Keywords: speed; perception; action; vision; vestibular

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Introduction

Reaching for a cup of coffee involves much more than planning a spatial trajectory or a final position. Once visual information about the target to be attained has been encoded, the central nervous system must often compute sensorimotor transformations involving modalities other than vision. However, different modalities gather information in different domains (i.e., position, velocity, acceleration). The core idea in the following sections is that sensorimotor transformations may be optimally computed in the velocity domain.

When reaching to a target object with the upper-limb, the central nervous system must consider the spatial arrangements between the eye, head, trunk and limb (see Crawford, Medendorp, & Marotta, 2004; Flanders, Helms Tillery, & Soechting, 1992; Henriques, Klier, Smith, Lowy, & Crawford, 1998). The position of the target on the retina must be contrasted with input from the muscle spindles of oculomotor muscles to encode the eye orientation relative to the head. In turn, muscle spindles of neck muscles provide information about the head orientation relative to the trunk. In addition, because visual information is not sufficient by itself to determine absolute head location in space (see Blouin, Labrousse, Simoneau, Vercher, & Gauthier, 1998; Cohen, 1961; Vaitl, Mittelstaedt, Saborowski, Stark, & Baisch, 2002), vestibular information is also used to successfully reach for targets in our environment (see Figure 1).

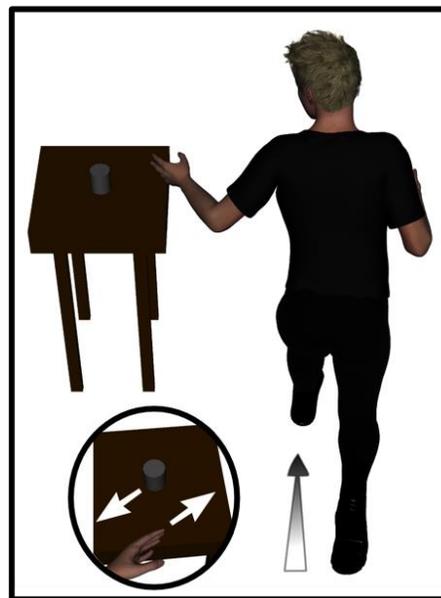


Figure 1. A depiction of a situation where visual and vestibular information must be contrasted to disentangle motion of the target in space vs. motion of the head relative to the target. Resolving such ambiguity is necessary to successfully reach for an object in the depicted dynamic condition. Inset: the relative visual motion of the hand and the target. This original figure was inspired by Gomi (2008) Figure 1.

Thus, being able to reach to a target presented on the retina requires contrasting visual and vestibular information to disentangle motion of the target in space vs. motion of the head relative to the target (e.g., Bresciani, Blouin, Popov, Bourdin, Sarlegna, Vercher, & Gauthier,

2002). As a result, one constraint facing the central nervous system is to perform multisensory comparisons from modalities that provide information in different domains (i.e., position vs. velocity¹ vs. acceleration).

The retina provides information in the positional domain. Retinal cells primarily respond to the presence of light on specific locations of the retina (e.g., Meister & Tessier-Lavigne, 2013). As a result, visual information is fundamentally in the positional domain. To provide a contrast, the vestibular system provides information in the acceleration domain. The hair cells of the semi-circular canals and the otoliths respond to changes in linear and angular head accelerations (e.g., Goldberg, Walker, & Hudspeth, 2013). Interestingly, there is neurophysiological and behavioral evidence supporting the idea that visual and vestibular information are processed in the velocity domain to perform voluntary sensorimotor behaviors. Further, such processing of multisensory information in the velocity domain extends to perceptual processes.

Visuomotor Processing and the Velocity Domain

Neurophysiological Evidence of Visuomotor Processes

Bullock, Cisek, and Grossberg (1998) forwarded a cortical model primarily designed to explain the use of proprioceptive information when dealing with obstacles or perturbations during voluntary arm movements. Recognizing the imperative of visuomotor transformations when performing voluntary actions, they proposed that a visual input is used to generate a difference vector (see also Buneo & Andersen, 2006; Prablanc, Echallier, Jeannerod, & Komilis, 1979; Vindras & Viviani, 1998). For example, according to Bullock et al. (1998), positional information about a target location, which is obtained via visual information, is used to compute a difference vector (i.e., in Brodmann's area 5). The next processing step in that model is to use the difference vector to compute a desired velocity vector (e.g., in Brodmann's area 4). Such desired velocity vector is the sole source of signals that are transmitted to the dynamic gamma motor neurons. That is, visual information from the spatial / position domain must be transformed into the velocity domain before being used to initiate a voluntary arm movement. Such a view has been corroborated by other neurophysiological evidence.

Ashe and Georgopoulos (1994) performed multiple linear regression analyses between cell discharge activity and four characteristics of reaching movements: target direction, hand position, hand velocity, and hand acceleration. The cells analyzed were from the primary motor cortex (i.e., Brodmann's area 4) and Brodmann's area 5 from monkeys. While the target direction was most strongly associated with activity in these cortical areas (i.e., Brodmann's area 5: see also Buneo, Jarvis, Batista, & Anderson, 2002), the second most important characteristic was hand velocity. Specifically, for 55 and 57% of the cells in Brodmann's areas 4 and 5, the first ranked movement parameter was target direction,

¹ The term velocity will be employed throughout this chapter while the term speed will be avoided. This is primarily for brevity purposes but also because of the association of neurophysiological processes with vector information processing (e.g., vector-integration-to-endpoint model: see Bullock, Cisek, & Grossberg, 1998; Bullock & Grossberg, 1988).

respectively. In contrast, for 27 and 25% of the cells of the same areas, the first ranked movement parameter was hand velocity. Finally, for the same areas, hand position was the first ranked parameter for only 17 and 18% of the cells. This led Ashe and Georgopoulos to conclude the existence of a “strong relation of both areas to target direction and movement velocity, less to position, and even less to acceleration” (p. 599). Referring to the thesis of the current chapter, it is also important to note that direction is not solely associated with the positional domain as the velocity domain can include both a direction and a magnitude (cf. speed). Nevertheless, the evidence brought forward by Ashe and Georgopoulos is in line with the model from Bullock et al. (1998: see also Cisek, Grossberg, & Bullock, 1998). As well, more recent neurophysiological evidence provided direct support for the importance of the velocity domain for the control of neuromotor behaviors.

Churchland, Santhanam, and Shenoy (2006) provided compelling evidence for the importance of the velocity domain in neuromotor processing through the manipulation of limb velocity of voluntary reaching movements. Monkeys were taught to perform a three-stage trial type. First, the hand has to be stabilized on a start position for 400-500 ms. Second, a target appeared and was “jittered” to instruct the monkey to wait before initiating the reach. During that period, the target and a central cue were either green or red, instructing the monkey whether the reaching movement had to be slow or fast, respectively. Third and last, the target became stable and the central cue disappeared, which was the cue to initiate the reaching movement. The training period allowed the monkey to associate a peak limb velocity criterion with a successful trial and a reward. The velocity criteria were set according to the reaching distances (i.e., 3 to 12 cm). The main analyses of their study were related to neural activity recordings from cells in the primary motor and dorsal premotor cortices (i.e., Brodmann’s areas 4 and 6, respectively). The novel finding of that study was that activity in the measured cortical areas during the movement preparation period was strongly associated with the velocity of the to-be-performed reaches and not necessarily associated with spatial characteristics (e.g., distance, direction). Such results further support the importance of the velocity domain for the preparation of voluntary movements.

Overall, both neurophysiological theoretical modeling and empirical evidence have supported the concept that limb velocity represents a core movement preparation component. Albeit limited to specific areas of the monkey brain, a theoretical model and neurophysiological evidence provide a clear rationale for converting visual signals into the velocity domain prior to sending commands to the motor neurons. Corroborating evidence can be extracted from neuro-behavioral investigations performed with humans.

Behavioral Evidence of Visuomotor Processes

The seminal work of Woodworth (1899) provided evidence that humans perform upper-limb movements in distinct phases. Based on sensory information available prior to movement initiation, the first phase of the trajectory (i.e., ballistic or initial impulse) propels the limb towards the target. Then, based on sensory information gathered during the ballistic phase, the second phase of the trajectory (i.e., current control) implements amendments to bring the limb onto the target. Of particular relevance to this chapter are the kinematic criteria employed to segregate the ballistic and current control phases of a movement.

Meyer, Abrams, Kornblum, Wright, and Smith (1988) employed a series of kinematic criteria to segregate the primary submovement (i.e., ballistic phase) and secondary submovements (i.e., current control phase). The velocity of a wrist rotation movement was employed to identify the start of the primary submovement. Then, the end of the primary submovement could be identified with a zero crossing in the velocity profile or a re-acceleration (i.e., with or without a zero acceleration crossing). As a result, the first increase in velocity was deemed to be the start of the primary submovement. Subsequently, a zero crossing in the velocity profile or a subsequent increase in velocity after reaching peak limb velocity was deemed to represent secondary submovements. Increases in velocity were thus deemed as central components for the parsing of iterative trajectory submovements, even if the idea of iterative trajectory amendments has been subsequently challenged.

Elliott, Carson, Goodman, and Chua (1991) asked participants to make reaching movements of the upper limb with a stylus. The experimental conditions included reaches made with and without vision under instructions to emphasize accuracy or speed. Participants exhibited more discrete trajectory amendments for movements performed with the instructions to be accurate than with the instructions to go fast. However, there were no reliable differences in the number of submovements for reaches made with than without vision. Instead, it was the time between peak limb velocity and movement end that reliably differed between the trials with and without vision. Elliott et al. (1991) suggested that voluntary movements may be comprised of many overlapping trajectory amendments that are not necessarily detectable via increases in limb velocity but still yield longer times between peak limb velocity and movement end. Overall, these behavioral studies indicate that information about the phases of a limb movement can be reliably parsed using the velocity profile of a movement (see also Chua & Elliott, 1993; Elliott, Hansen, Grierson, Lyons, Bennett, & Hayes, 2010; Jeannerod, 1988). Therefore, despite arguments regarding the sequencing of online trajectory amendments between Meyer et al. (1988) and Elliott et al. (1991), both lines of investigations emphasize the importance of limb velocity in extracting information about online control mechanisms.

Notably, the above lines of research employed vision withdrawal manipulations that took place immediately after the velocity of the limb or the effector departed from zero. If sensorimotor processes are performed in the velocity domain, manipulating vision before the limb velocity significantly departs from zero (0) could in fact minimize the chances of detecting sensorimotor processes that depend on limb velocity. In contrast, manipulating vision at different limb velocity criteria rather than time or position could prove a useful method to assess sensorimotor mechanisms.

Using vision manipulations as a function of limb velocity during upper-limb reaching movements, Tremblay, Hansen, Kennedy, and Cheng (2013) supported the idea that some portions of the trajectory do not significantly contribute to the control of movement endpoint (e.g., Carlton, 1992). Vision was manipulated via liquid-crystal goggles on the basis of the real-time limb velocity (i.e., goggles changed state within 10 ms of the limb meeting a velocity criterion). In the first experiment, vision could be made available or not during the entire movement (i.e., Vision or No-Vision), or available above or below a limb velocity criterion of 0.8 m/s (i.e., VHigh or VLow) (see Figure 2). The endpoint precision or variable error (i.e., standard deviation of endpoint distribution) contrasts were as follows: Vision ~ VHigh < No-Vision ~ VLow. That is, seeing when the limb travels at velocities above 0.8 m/s yields comparable endpoint precision than seeing throughout the movement. In contrast,

seeing when the limb travels at velocities below 0.8 m/s did not yield any better endpoint precision than not seeing throughout the movement. Further, endpoint precision was significantly better when seeing the limb travelling above than below 0.8 m/s. In the second experiment of Tremblay et al. (2013), real-time limb velocity criteria ranging from 0.8 to 1.2 m/s were employed.

The endpoint variability results yielded support for the idea that amendments to the initial impulse (i.e., impulse regulation processes: see Elliott et al., 2010) are made when the limb travels between 0.8 and 0.9 m/s, while amendments based on contrasts between limb and target positions (i.e., limb-target regulation processes: see Elliott et al., 2010) are made when the limb travels above 1.0 m/s. Considering that commands sent to motor neurons presumably require transformations of the visual signals into the velocity domain (Bullock et al., 1998; Cisek et al., 1998), it is possible that information in the velocity domain is relevant for both the planning (e.g., Churchland et al., 2006) and the online control of upper-limb movements (re.: results of Tremblay et al., 2013). Nevertheless, these results provided further evidence for the importance of the velocity domain when assessing sensorimotor functions. Be it more, such importance of real-time limb velocity for sensorimotor processes extends to perceptual processes.

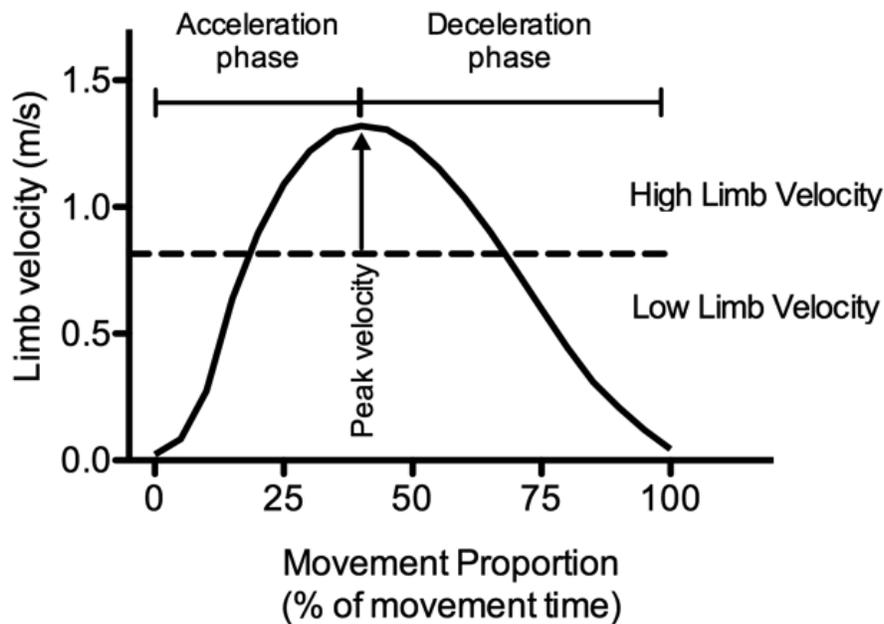


Figure 2. A depiction of the vision at high (VHigh) and low (VLow) limb velocity conditions from Tremblay et al. (2013). The above plot depicts a smoothed average velocity profile over proportions of movement time, peak velocity as well as the acceleration and deceleration phases. In the VHigh condition, vision was provided when the limb velocity was above 0.8 m/s, whereas in the VLow condition, vision was provided when the limb velocity was below 0.8 m/s.

Using an audio-visual illusion wherein one or two beeps influence the perception of one or two flashes (see Andersen, Tiippana, & Sams, 2004; Shams, Kamitani, & Shimojo, 2000; Shams, Kamitani, & Shimojo, 2002), Tremblay and Nguyen (2010) showed that the relative contribution of visual and auditory information to the perception of visual events is

modulated as a function of real-time limb velocity. Typically, the presentation of a single beep with two flashes yields the perception of a single flash (i.e., fusion illusion: see Andersen et al., 2004). By presenting one or two beeps with one or two flashes at various times relative to movement onset (0-250 ms), Tremblay and Nguyen (2010) showed that the strength of the fusion illusion was weaker when the stimuli were presented at the times corresponding to the higher limb velocities (see Figure 3). Specifically, higher limb velocities at the stimulus midpoint were associated with a decreased likelihood of being influenced (i.e., fooled) by the number of beeps when judging the number of flashes. In an unpublished experiment, these results were replicated and expanded, showing that: 1) the fusion illusion was strongest in a control condition wherein no movements were required (i.e., at rest); and 2) the control condition and presentation conditions associated with the lowest limb velocities yielded comparable fusion illusion strengths.

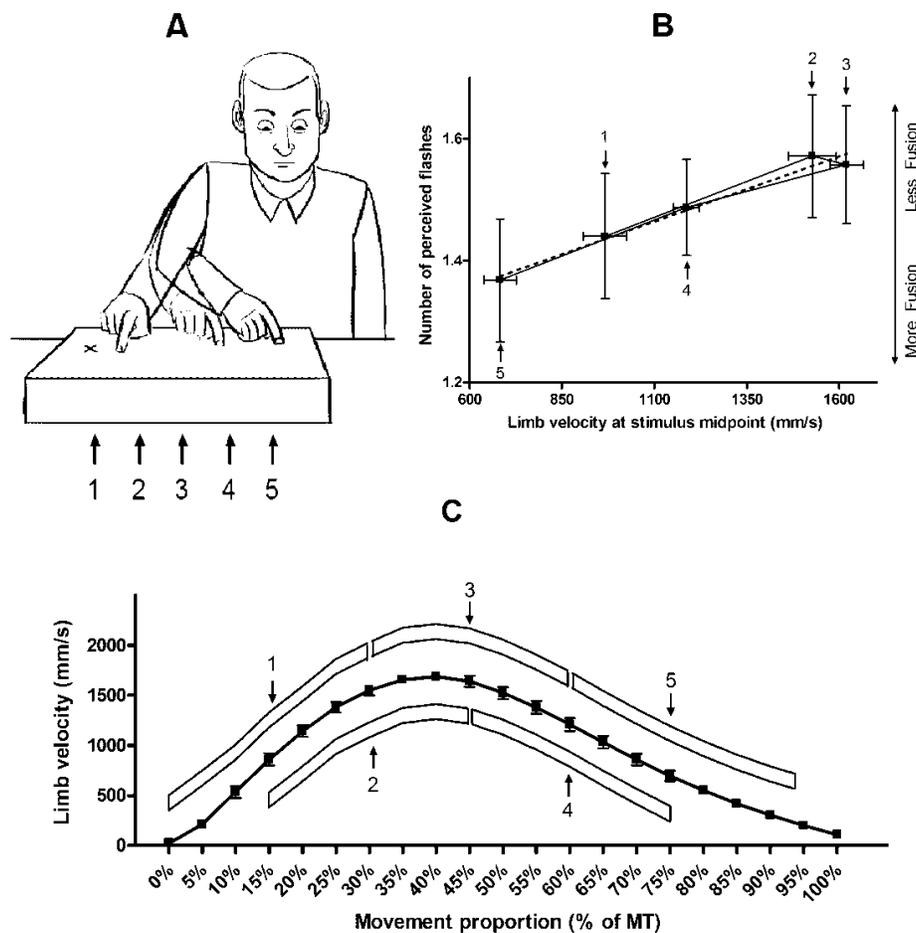


Figure 3. Experimental Task, Limb Velocity vs. the Fusion Illusion, and Average Velocity Profile. Reproduced from Tremblay and Nguyen (2010), licensed under CC By 3.0. (doi:10.1371/journal.pone.0008952.g002). Panel A: Depiction of the experimental task. Panel B: Mean number of perceived flashes for the 2 flashes and 1 beep condition (i.e., fusion illusion stimulus) at the different stimulus midpoints. Panel C: Average limb velocity profile with depiction of stimuli presentation (white boxes) and stimuli midpoints (arrows). The stimulus onset conditions are numbered as follows: 1 = 0 ms, 2 = 50 ms, 3 = 100 ms, 4 = 150 ms, and 5 = 200 ms relative to movement onset.

Altogether, there is a decreased susceptibility to be influenced by an audio-visual illusion at the high velocity stages of a movement. These results further support the above-mentioned proposal that processing sensory information in the velocity domain is important before (e.g., Churchland et al., 2006) and during a movement (e.g., Tremblay et al., 2013).

The importance of information in the velocity domain for the control of a voluntary upper-limb movement clearly extends to the perception of visual events. While the behavioral research cited above needs further replications and investigations, it emphasizes the importance of the velocity domain for central nervous system processing because it allows for the evaluation of multisensory contributions to optimal perceptual estimates (e.g., Ernst & Bühlhoff, 2004). Interestingly, the vestibular system offers parallels to the above-mentioned contributions of the visual system.

Vestibulomotor Processing and the Velocity Domain

Neurophysiological Evidence of Vestibulomotor Processing

Ventre-Dominey (2014) provided a review of the neural pathways involved in the processing of vestibular information. Two main pathways were emphasized in that review. One pathway includes the temporal cortex, which processes visual and vestibular information to encode the velocity of self-motion. This first pathway is deemed to be most relevant for the encoding and processing of head accelerations into the velocity domain, to implement vestibulo-ocular control processes. The need to convert the head acceleration into the velocity domain is justified considering that vestibular inputs must ultimately be employed to send commands to static (i.e., alpha) or dynamic (i.e., gamma) motor neurons, which implies position or velocity commands, respectively. The second pathway highlighted by Ventre-Dominey projects through the parietal cortex and contributes to the “storage” of velocity information. Such pathway is deemed to be involved in extrapersonal and self-referential space encoding. Because the head acceleration (i.e., vestibular) signals are ultimately encoded to identify body position relative to objects and/ or in space, the conversion of head accelerations into the velocity domain is mathematically necessary before being able to encode position. Altogether, the model forwarded by Ventre-Dominey presents neurophysiological arguments as to how information from the vestibular system, which encodes head accelerations, must be converted into the velocity domain information in order to be used for eye movement control and body position encoding in space.

Behavioral Evidence of Vestibulomotor Processing

The suggestion made by Ventre-Dominey (2014) is substantiated by the behavioral literature. For example, Pulaski, Zee, and Robinson (1981) tested the vestibulo-ocular reflex response at various angular velocities of the head. The participants exhibited strong relationships between the head and the eye velocity, up to an individual velocity limit. On average, the head angular velocity was strongly related to the eye angular velocity, until

approximately 350 degrees per second. This relationship between head and eye velocity represents further empirical evidence of the vestibular pathway involving the temporal cortex (Ventre-Dominey, 2014).

In terms of the vestibular pathway involving the parietal cortex and contributing to the perception of the body in space (Ventre-Dominey, 2014), support for the “storage” of velocity information was reported by Tremblay, Kennedy, Paleressompouille, Borel, Mouchnino, and Blouin (2013). Participants were passively rotated and asked to reproduce the perceived rotation with a manipulandum (see Figure 4). Symmetric and asymmetric angular acceleration profiles were employed (i.e., shape of acceleration phase being the same / symmetric or different / asymmetric than shape of deceleration phase). One main finding was that the gains between the perceived and actual body rotations were significantly greater before than after the maximum angular velocity of the body (see Figure 4).

It is likely that these greater gains observed before than after peak velocity of the body rotation were due to velocity storage mechanisms. As highlighted by Ventre-Dominey (2014; see also Raphan, Matsuo, & Cohen, 1979), the central nervous system can accumulate velocity information by integrating acceleration signals over time. Because natural head acceleration profiles tend to be symmetric, the acceleration phase is highly predictive of the deceleration phase. It is thus efficient for the central nervous system to prioritize the use of acceleration information over time through velocity storage mechanisms to encode body rotation information. Indeed, the angular velocity of the body was more associated with the perceptual judgments of body rotation than the angular acceleration, providing further empirical support for the notion that vestibular signals need to be encoded in the velocity domain in order to be used for encoding body position in space.

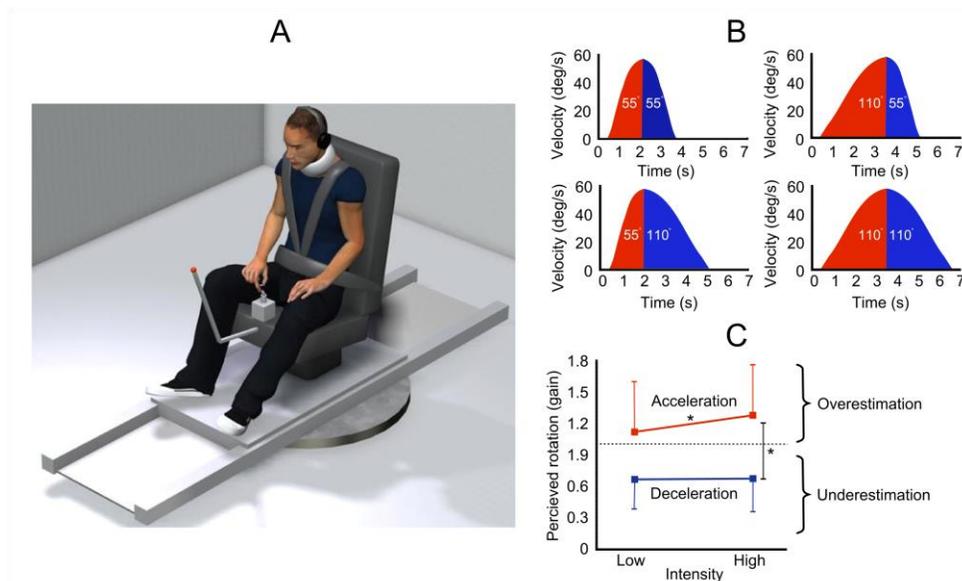


Figure 4. Amalgamation and adaptation of figures originally published in Tremblay et al. (2013b). Biases in the perception of self-motion during whole-body acceleration and deceleration. *Frontiers in Integrative Neuroscience*, 7(90), 1–10. Panel A: Depiction of the experimental setup. Panel B: Chair angular velocity profiles. Panel C: Gains between the perceived and actual body rotations during the acceleration and deceleration phases.

Moreover, the segregation of different phases of vestibular information encoding prior to and after peak velocity is analogous to the phases of online visuomotor regulation (e.g., Elliot et al., 1991). Together, the above lines of evidence prompt the need for the central nervous system to make multisensory contrasts when performing some activities of daily living.

Multisensory Combination, Integration and Conclusion

Information from the visual and vestibular systems must be compared to make optimal multisensory judgments. One model that helps predict how sensory signals are integrated to optimize perceptual and motor performance is the Maximum Likelihood Estimator (MLE) model (see Ernst & Banks, 2002; Fetsch, DeAngelis, & Angelaki, 2010; Knill & Saunders, 2003; Ghahramani, Wolpert, & Jordan, 1997). Mathematically, this model was presented as:

$$\text{Estimate} = \sum_i (w_i \times \hat{S}_i) \quad \text{with} \quad w_i = \frac{1/\sigma_i^2}{\sum_j (1/\sigma_j^2)} \quad (\text{Eq. 1})$$

where \hat{S}_i represents the estimate of a particular modality, and w_i represents the weight associated with it. This weight, (i.e., w_i), is computed as the proportional inverse variance of the estimate relative the total (i.e., the linear sum) of the inverse variances associated with all (i.e., j) contributing estimates (see Equation 1). If the estimates are combined in accordance to the MLE, then the variance of the combined estimate is lower than the variance of individual estimates alone (see Equation 2).

$$\sigma_{AB}^2 = \frac{\sigma_A^2 \times \sigma_B^2}{\sigma_A^2 + \sigma_B^2} \quad (\text{Eq. 2})$$

To support this model, Ernst and Banks (2002) manipulated visual and haptic signals to ascertain the contribution of both modalities to the perceived dimension of a graspable object. The relative contribution of visual and haptic information was significantly altered based on the amount of noise present in the visual signal, which was introduced via depths displacements of dots. More importantly, in order “to be integrated, the sensory estimates must be in the same units” (Ernst & Bühlhoff, 2004, p. 163). Although estimates of a target location or an object size should intuitively be performed in the positional domain, encoding position and acceleration information when our body moves into space could be optimally integrated by transforming the visual and vestibular information into the velocity domain.

It is important to note that the thesis of this chapter does not challenge the idea that position, direction, distance, and other spatial characteristics can also be crucial domains of multisensory integration for the preparation and execution of voluntary movements (e.g., Ashe & Georgopoulos, 1994; Messier & Kalaska, 2000; van Beers, Wolpert, & Haggard,

2002). As such, the proposal that multisensory integration may be performed in the velocity domain might be limited to situations when the body is subject to accelerations and when vestibular signals are crucial to making a perceptual estimate or performing a goal-directed movement. That is, multisensory integration processes performed in the velocity domain would likely yield optimal performance if the encoding of head position (i.e., via vestibular inputs) is processed relative to other relevant information (e.g., step or door handle height) that requires afferent inputs in the position domain (e.g., via visual inputs). Such an approach would surely yield better performance than integrating the vestibular acceleration signals twice or, even worse, differentiating the visual position signals twice.

The use of whole body movements presents methodological challenges (e.g., motion capture), which could explain the relatively common use of transient and non-moving stimuli in scientific investigations. However, stable stimuli requiring minimal motor responses may fail to elicit all multisensory combination and integration capacities of the brain. For example, if a stimulus is not moving, there may be no need to process vestibular information and disentangle stimulus motion from self-motion. As a result, neurophysiological and behavioral studies employing stable stimuli without body or arm movements may be investigating a rather limited proportion of the brain's capabilities. Indeed, many activities of daily living require head rotations/ displacements in addition to limb movements, which would thus prompt visual-vestibular comparisons that may be optimally performed in the velocity domain.

Overall, it is suggested that the optimal integration of visual and vestibular information is made in the velocity domain, at least when making upper-limb reaching movements that includes head motion. It is acknowledged that such a view does not negate the existence of multisensory contrasts performed in other domains (i.e., position and acceleration) as well as other mechanisms influencing basic motor functions (e.g., grasping a tennis ball vs. a light bulb: see Marteniuk, MacKenzie, Jeannerod, Athenes & Dugas, 1987; see also Buckingham, Cant, & Goodale, 2009). Simply, the importance of the velocity domain for perceptual and sensorimotor functions is clearly supported by neurophysiological and behavioral evidence.

Acknowledgments

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References

- Andersen, T.S., Tiippana, K., & Sams, M. (2004). Factors influencing audiovisual fission and fusion illusions. *Brain Research*, *21*(3), 301–308.
- Ashe, J., & Georgopoulos, A.P. (1994). Movement parameters and neural activity in motor cortex and area 5. *Cerebral Cortex*, *4*(6), 590–600.

- Blouin, J., Labrousse, L., Simoneau, M., Vercher, J., & Gauthier, G.M. (1998). Updating visual space during passive and voluntary head-in-space movements. *Experimental Brain Research*, *122*, 93–100.
- Buckingham, G., Cant, J.S., & Goodale, M.A. (2009). Living in a material world: how visual cues to material properties affect the way that we lift objects and perceive their weight. *Journal of Neurophysiology*, *102*(6), 3111–3118.
- Bullock, D., Cisek, P., & Grossberg, S. (1998). Cortical networks for control of voluntary arm movements under variable force conditions. *Cerebral Cortex*, *81*(1), 48–62.
- Bullock, D., & Grossberg, S. (1988). Neural dynamics of planned arm movements: Emergent invariants and speed-accuracy properties during trajectory formation. *Psychological Review*, *95*(1), 49–90.
- Bresciani, J.P., Blouin, J., Popov, K., Bourdin, C., Sarlegna, F., Vercher, J.L., & Gauthier, G.M. (2002). Galvanic vestibular stimulation in humans produces online arm movement deviations when reaching towards memorized visual targets. *Neuroscience Letters*, *318*(1), 34–38.
- Buneo, C.A., & Andersen, R.A. (2006). The posterior parietal cortex: Sensorimotor interface for the planning and online control of visually guided movements. *Neuropsychologia*, *44*(13), 2594–2606.
- Buneo, C.A., Jarvis, M.R., Batista, A.P., & Andersen, R.A. (2002). Direct visuomotor transformations for reaching. *Nature*, *416*(6881), 632–636.
- Carlton, L. (1992). Visual processing time and the control of movement. In L. Proteau, & D. Elliott (Eds.), *Advances in Psychology: Vision and Motor Control* (pp. 3–32). Amsterdam: North-Holland.
- Chua, R., & Elliott, D. (1993). Visual regulation of manual aiming. *Human Movement Science*, *12*(4), 365–401.
- Churchland, M.M., Santhanam, G., & Shenoy, K.V. (2006). Preparatory activity in premotor and motor cortex reflects the speed of the upcoming reach. *Journal of Neurophysiology*, *96*(6), 3130–3146.
- Cisek, P., Grossberg, S., & Bullock, D. (1998). A cortico-spinal model of reaching and proprioception under multiple task constraints. *Journal of Cognitive Neuroscience*, *10*(4), 425–444.
- Cohen, L. A. (1961). Role of eye and neck proprioceptive mechanisms in body orientation and motor coordination. *Journal of Neurophysiology*, *24*, 1–11.
- Crawford, J.D., Medendorp, W.P., & Marotta, J.J. (2004). Spatial transformations for eye-hand coordination. *Journal of Neurophysiology*, *92*(1), 10–19.
- Elliott, D., Carson, R., Goodman, D., & Chua, R. (1991). Discrete vs. continuous visual control of manual aiming. *Human Movement Science*, *10*, 393–418.
- Elliott, D., Hansen, S., Grierson, L.E.M., Lyons, J., Bennett, S.J., & Hayes, S.J. (2010). Goal-directed aiming: two components but multiple processes. *Psychological Bulletin*, *136*(6), 1023–1044.
- Ernst, M.O., & Banks, M.S. (2002). Humans integrate visual and haptic information in a statistically optimal fashion. *Nature*, *415*(24), 429–433.
- Ernst, M.O., & Bühlhoff, H.H. (2004). Merging the senses into a robust percept. *Trends in Cognitive Sciences*, *8*(4), 162–169.

- Fetsch, C.R., DeAngelis, G.C., & Angelaki, D.E. (2010). Visual-vestibular cue integration for heading perception: Applications of optimal cue integration theory. *The European Journal of Neuroscience*, *31*(10), 1721–1729.
- Flanders, M., Helms Tillery, S.I., & Soechting, J.F. (1992). Early stages in a sensorimotor transformation. *Behavioral and Brain Sciences*, *15*, 309–362.
- Ghahramani, Z., Wolpert, D.M., & Jordan, I. (1997). Computational models of sensorimotor integration. In P. Morasso, & V. Sanguineti (Eds.), *Advances in psychology: Self organization, computational maps, and motor control* (pp. 117–147). Amsterdam: North-Holland.
- Goldberg, M.E., Walker, M.F., & Hudspeth, A.J. (2013). The vestibular system. In E.R. Kandel, J.H. Schwartz, T.M. Jessel, S.A. Siegelbaum, & A.J. Hudspeth (Eds.) *Principles of Neural Science* (pp. 917-934), New York: McGraw-Hill.
- Gomi, H. (2008). Implicit online corrections of reaching movements. *Current Opinion in Neurobiology*, *18*(6), 558–564.
- Henriques, D.Y.P., Klier, E.M., Smith, M.A., Lowy, D., & Crawford, J.D. (1998). Gaze-Centered Remapping of Remembered Visual Space in an Open-Loop Pointing Task. *The Journal of Neuroscience*, *18*(4), 1583–1594.
- Jeannerod, M. (1988). *The neural and behavioural organization of goal-directed movements*. Oxford: Oxford University Press.
- Knill, D.C., & Saunders, J.A. (2003). Do humans optimally integrate stereo and texture information for judgments of surface slant? *Vision Research*, *43*(24), 2539–2558.
- Marteniuk, R.G., MacKenzie, C.L., Jeannerod, M., Athenes, S., & Dugas, C. (1987). Constraints on Human Arm Movement Trajectories. *Canadian Journal of Psychology*, *41*(3), 365–378.
- Messier, J., & Kalaska, J.F. (2000). Covariation of primate dorsal premotor cell activity with direction and amplitude during a memorized-delay reaching task. *Journal of Neurophysiology*, *84*, 152–165.
- Meister, M., & Tessier-Lavigne, M. (2013). Low-level visual processing: The retina. In E.R. Kandel, J.H. Schwartz, T.M. Jessel, S.A. Siegelbaum, & A.J. Hudspeth (Eds.) *Principles of Neural Science* (pp. 577-601), New York: McGraw-Hill.
- Meyer, D.E., Abrams, R.A., Kornblum, S., Wright, C.E., & Smith, J.E. (1988). Optimality in human motor performance: Ideal control of rapid aimed movements. *Psychological Review*, *95*(3), 340–370.
- Prablanc, C., Echallier, J.E., Jeannerod, M., & Komilis, E. (1979). Optimal response of eye and hand motor systems in pointing at a visual target: II Static and dynamic visual cues in the control of hand movement. *Biological Cybernetics*, *35*, 183–187.
- Pulaski, P.D., Zee, D.S., & Robinson, D.A. (1981). The behavior of the vestibulo-ocular reflex at high velocities of head rotation. *Brain Research*, *222*, 159–165.
- Raphan, T., Matsuo, V., & Cohen, B. (1979). Brain Velocity Storage in the Vestibulo-Ocular Reflex Arc. *Experimental Brain Research*, *248*, 229–248.
- Shams, L., Kamitani, Y., & Shimojo, S. (2000). What you see is what you hear. *Nature*, *408*, 788–788.
- Shams, L., Kamitani, Y., & Shimojo, S. (2002). Visual illusion induced by sound. *Cognitive Brain Research*, *14*(1), 147–152.
- Tremblay, L., Hansen, S., Kennedy, A., & Cheng, D.T. (2013). The utility of vision during action: multiple visuomotor processes? *Journal of Motor Behavior*, *45*(2), 91–99.

- Tremblay, L., Kennedy, A., Paleressompouille, D., Borel, L., Mouchnino, L., & Blouin, J. (2013). Biases in the perception of self-motion during whole-body acceleration and deceleration. *Frontiers in Integrative Neuroscience*, *7*(90), 1–10.
- Tremblay, L., & Nguyen, T. (2010). Real-time decreased sensitivity to an audio-visual illusion during goal-directed reaching. *PLoS ONE*, *5*(1), 1–4.
- Vaitl, D., Mittelstaedt, H., Saborowski, R., Stark, R., & Baisch, F. (2002). Shifts in blood volume alter the perception of posture: further evidence for somatic graviception. *International Journal of Psychophysiology*, *44*(1), 1–11.
- Van Beers, R.J., Wolpert, D.M., & Haggard, P. (2002). When feeling is more important than seeing in sensorimotor adaptation. *Current Biology*, *12*(10), 834–837.
- Ventre-Dominey, J. (2014). Vestibular function in the temporal and parietal cortex: distinct velocity and inertial processing pathways. *Frontiers in Integrative Neuroscience*, *8*(53), 1–13.
- Vindras, P., & Viviani, P. (1998). Frames of reference and control parameters in visuomanual pointing. *Journal of Experimental Psychology. Human Perception and Performance*, *24*(2), 569–591.
- Woodworth, R.S. (1899). The accuracy of voluntary movement. *Psychological Review*, *3*(2), 1–114.