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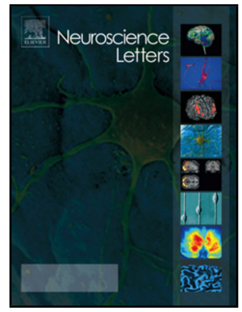

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Perceived timing of active head movement at different speeds

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Highlights

- Active head movement onset must precede sound onset to be perceived as simultaneous
- This perceptual delay for active head movement onset is reduced with head movement speed
- There is a persistent perceptual delay of active head movement onset even at extreme speeds

ABSTRACT

The central nervous system must determine which sensory events occur at the same time.

Actively moving the head corresponds with large changes in the relationship between the observer and the environment, sensorimotor processing, and spatiotemporal perception. Active head movement perception has been shown to be dependent on head movement velocity where participants who move their head fastest require the head to move earlier than comparison stimuli for perceived simultaneity more so 44 than those who move their head slower. Such between-subject results cannot address whether active head movement perception changes with velocity. The present study used a within-subjects design to measure the point of subjective simultaneity (PSS) between active head movement speeds and a comparison sound stimulus to characterize the relationship between the velocity and perception of head movement onset. Our results clearly show that i) head movement perception is *faster* with faster head movements within-subjects, ii) active head movement onset must still precede the onset of other sensory events (average PSS: -123ms to -52ms; median PSS: -42ms to -100ms) in order to be perceived as occurring simultaneously even at the fastest speeds (average peak velocity: 76°/s to 257°/s; median peak velocity 72ms to 257ms). We conclude that head movement perception is slow, but that this delay is minimized with increased speed. These within-subject results are contrary to previous and present study between-subject results and are in agreement with literature where perception of auditory, visual and vestibular stimulus onset is less delayed with increased stimulus intensity.

KEYWORDS

Auditory, Head movement, Multisensory, Stimulus Intensity, Time perception, Vestibular

1. INTRODUCTION

To create an accurate representation of the world, the central nervous system (CNS) processes incoming signals from different sensory modalities and determines how information from these senses relates to each other. The ability to bind sensory information accurately in time is crucial for the CNS to make correct decisions about our environment and our movements in it. Since the same event can stimulate multiple sensory modalities at different absolute times, the CNS must distinguish whether these stimuli originated from the same or separate events. Actively moving the head corresponds with large changes in the relationship between the observer and the environment, sensorimotor processing, and spatiotemporal perception. While quickly detecting the onset of head movement is crucial for reflexive behaviour and rapidly updating the representation of the world around us, past research suggests that perceptual awareness of active head movement onset is slower than passive movement of the head, as well as slower than comparison stimuli such as light, touch or sound[1].

The vestibular system is essential for functions ranging from the perception of self-motion and spatial orientation, to motor coordination for maintaining balance and posture[2]. The physiological response to vestibular stimulation is extremely fast. For example, the vestibulo-ocular reflex (VOR), which is the compensatory movement of the eyes in response to head movement, responds to vestibular stimulation in 5-6ms in monkeys[3]. Despite this fast physiological response, research has surprisingly shown that the perception of vestibular stimulation[4] as well as passive and active head movement[1] is slow compared to other senses[See 5 for a review]. In these studies, participants' vestibular systems are either directly stimulated, participants are passively moved, or actively move their heads and judge whether the perceived onset of head movement occurs before or after a comparison stimulus. Here, the PSS is measured and used to assess whether participants perceive the onset of their head movement as being delayed. Since studies have repeatedly shown that self-motion perception is delayed, here we are interested in how this delay changes with head movement velocity.

Barnett-Cowan and Harris[1] found that increased active head movement velocity results in greater perceptual delays for the perceived timing of active head movement onset. They attributed this to the suppression of vestibular afferent signals which has been shown during higher movement velocities in monkey neurophysiology[6]. It is known that when an efferent signal is sent from the motor cortex to the muscles, a copy of the motor command called an efference copy[7] is routed from the supplementary motor area to the cerebellum and parietal cortex so that the CNS can make comparisons between the predicted movement and the sensory reafference[8]. Semicircular canal related activity in the vestibular nuclei is diminished during an active movement when compared to a passive movement[9–12], an effect that may be driven by an efference copy[13].

Based on this literature, it was thought that this suppression could also affect the perceived timing of active versus passive head movements, where active head movements are perceptually delayed[1]. This "suppression hypothesis", which has also been referred to for active versus passive touch[14,15], was contrasted with an "anticipation hypothesis" where the availability of an efference copy in the CNS prior to movement onset could allow an active head movement to be perceived earlier than a passive one[1]. This anticipation hypothesis was motivated by Blakemore et al[16] who showed that sensory outcomes of our own actions involves highly specific information about when self-generated sensations occur.

The purpose of the present paper was not to assess these suppression and anticipation hypotheses directly, but rather address an issue related to the velocity of active head movement.

An issue with the findings of Barnett-Cowan and Harris[1] was that the results were from between-subjects data, which could not address whether increasing the velocity of active head movement in an individual would lead to a change in the perceptual delay of the movement. Active head movement velocity is variable; a slow velocity for one participant could have the same magnitude as a fast velocity for another participant. The result showing that greater head movement velocities result in greater perceptual delays[1] should really be interpreted as participants who move their head faster than other participants require the head to move even earlier than comparison stimuli for perceptual simultaneity. Here we vary the velocity of an active head movement and analyze the data both between- as well as within-subjects. Participants performed temporal order judgment (TOJ) tasks at different active head movement speeds paired with an auditory stimulus, using a within-subjects design. Our main "velocity hypothesis" is that faster active head movements will lead to a smaller temporal delay in perception when paired with a comparison sound stimulus. We compare our results to the findings of Barnett-Cowan and Harris[1] and discuss our results in the context of literature where the perception of more intense auditory, visual and vestibular stimuli is less delayed.

2. METHODS

2.1 Participants

20 participants (19-25y) who reported having no auditory, visual or vestibular disorders were remunerated $10 for one hour of testing. Three participants were fully removed from the analysis since they had excessively noisy signals in over 20% of the trials within one or more of the original three velocity conditions (see Supplementary Materials). This study was carried out in accordance with the recommendations of Canada's Tri-Council Policy Statement: Ethical

Conduct for Research Involving Humans (TCPS2) by the University of Waterloo's Human Research Ethics Committee with written informed consent from all subjects. All participants gave written informed consent in accordance with the Declaration of Helsinki.

2.2 Procedure

As the general methods, procedure and analysis have been documented previously (c.f. [1]) and replicated here, we provide a brief summary of procedures and analysis here and refer the reader to the supplementary materials section for more information. Participants performed a temporal order judgement task in which they reported whether the onset of their head movement came first, or the onset of the 2000Hz sound stimulus came first. Each trial began with the onset of the low pitch go signal. The duration of the go signal was randomized to prevent participants from predicting the timing of the offset, and anticipating the start of the head movement. At the go signal offset, participants initiated head movement, and due to the response time delay between the go signal offset and the onset of the head movement, the comparison sound stimulus could occur before or after the head movement. Participants responded by pressing the left or right key on the keyboard, where the left key and right key indicated that the onset of head movement or that onset of sound came first respectively. The next trial would begin immediately after the participant responded. A schematic of a typical trial is shown in Supplementary Figure 1.

Participants performed 10 practice trials prior to the experiment, which consisted of three conditions in a block design with 100 trials within each block. Each block took approximately 10 minutes to complete with a break of 5 minutes in between blocks. For the three conditions, participants were asked to move their head at what they considered to be a slow, normal, or fast head movement, the latter being as fast as they could move their head. The order of the conditions across participants was randomized.

2.3 Grouping of data into four categories

Due to the subjective nature of the participants deciding what constitutes a slow, medium and fast head movement and participants poorly replicating their head movement trajectory trial-to-trial, there was significant overlap in the peak velocities for the three conditions. To correct for this, the peak velocities of each participant were artificially stratified into four equally-sized conditions according to increasing peak velocity and renamed velocity 1, 2, 3 and 4 (see Supplementary Material and Supplementary Figure 2 that confirm that the categories are sufficiently different from each other so that they can be used in subsequent analysis).

2.4 Extracting PSS and JND

Stimulus onset asynchronies (SOAs) were determined by calculating the difference between head movement onset and sound onset, with a negative SOA indicating that the head moved prior to the sound. A sigmoidal function (Supplementary Eq. 1; Supplementary Figure 3) was fitted to the participants' responses for all four conditions as a function of SOA using SigmaPlot 12.5, with the inflection points of the sigmoidal function (x_0) taken as the point of subjective simultaneity (PSS) and the slope of the function (b) as the just noticeable difference (JND).

$$y = \frac{a}{1+e^{-\left(\frac{x-x_0}{b}\right)}} \qquad (1)$$

Shapiro-Wilk tests were conducted on the PSS values of each of the four stratified conditions to see whether the data was normally distributed. To compare the PSS of each condition to 0ms and confirm whether head movement must precede a sound stimulus for perceived simultaneity, one sample t-tests were used if the data in each individual condition was normally distributed, and the Wilcoxon signed-rank t-test was used if the data was not normally distributed. To test whether there was a significant difference in PSS between conditions, a one-way repeated measures ANOVA on ranks was conducted between all four striated conditions.

To assess whether people who move their head faster require active head movement onset to occur earlier than a comparison sound stimulus (i.e., replicate[1]), we ran Pearson's r correlations (Spearman's ρ if not normally distributed) between peak head movement velocity and the PSS for each head movement condition, where a significant negative correlation for any head movement condition would replicate[1].

Lastly, to assess the hypothesis that the faster the head moves within-subjects requires active head movement onset to occur earlier than a comparison sound stimulus (i.e., support for suppression hypothesis[1]), a linear regression (Eq. 2) was fitted to each participant's PSS values for each of the four velocity conditions, and the slope and y-intercept was obtained for each participant's regression.

$$y = y_0 + a * x \quad (2)$$

Since the linear regression slopes were not normally distributed as per the Shapiro-Wilk test, an average linear regression line was obtained by taking the median of the slope (a) and y intercept parameters (y_0) for the individual regressions. A Wilcoxon signed rank t-test was applied to the slopes (a) relative to 0 (i.e., no change in the PSS relative to peak head movement velocity). A negative slope would confirm the hypothesis that the faster the head moves within-subject, the earlier active head movement onset must occur than a comparison sound stimulus. A positive slope would support the alternative "velocity hypothesis" that an increase in active head movement speed reduces the PSS.

3. RESULTS

In total, 17 participants were included for analysis. Four artificial, equal-sized conditions were created by sorting the peak velocity of each participant from the lowest to highest velocity and then grouping the trials into four equally-sized conditions. These conditions are referred to as velocity 1 (average: 76.46°/s, s.e.=6.42), velocity 2 (average: 110.42°/s, s.e.=8.13), velocity 3 (average: 167.47°/s, s.e.=12.30), and velocity 4 (average: 256.78°/s, s.e.=19.75). In total, 6.47% of trials were removed due to anticipatory head movement, excessively noisy data, or two peaks being present in the velocity signal.

Supplementary Figure 4a-d shows the results of fitting the sigmoidal curve function to each individual participant's data (grey lines and dots) as well as a representation of the average sigmoidal curve constructed from the average slope and PSS value for each condition (black lines and dots). Figure 1a shows the individual (grey dots) and median (black dot with standard error bars) PSS values for each condition. In the velocity 1 condition, the average PSS was -122.51ms (s.e.=18.32) and significantly before 0ms ($t(16)=-6.688$, $p<0.001$). In the velocity 2 condition, the average PSS was -110.94ms (s.e.=20.60) and significantly before 0ms (Median=-103.5243, Wilcoxon $Z=-3.621$, $p<0.001$). In the velocity 3 condition, the average PSS was -66.57ms (s.e.=22.19) and significantly before 0ms ($t(16)=-3.000$, $p=0.00848$). In the velocity 4 condition, the average PSS was -52.13ms (s.e.=22.76) and significantly before 0ms ($t(16)=-2.290$, $p=0.0359$). The global average PSS value for all four conditions was -88.03ms (s.e.=10.89) and the global median was -84.47ms (iqr = -92.37ms). Together these results replicate previous work showing that the perceived timing of an active head movement is slow compared to a comparison sound stimulus[1,17,18].

To assess the hypothesis that participants who move their head faster require the active head movement to occur with less delay when paired with a comparison sound stimulus, a one-way repeated measures ANOVA (Kruskal-Wallis) indicated a significant difference in PSS values being reduced between subjects ($F(3,67)=9.39$, $p<0.001$) from -122.51ms (V1: ~76 °/s) to -52.13ms (V4: ~257 °/s). Holm-Sidak pairwise comparisons revealed significant differences between V1&V4 ($p<0.001$), V2&V4 ($p=0.002$), V1&V3 ($p=0.003$), V2&V3 ($p=0.020$). A one-way repeated measures ANOVA on ranks revealed no significant difference for the JND values between the four conditions ($\chi 2 = 3.141$, df = 3, $p = 0.370$) (Figure 1b), meaning that the participants' precision did not differ as the velocity of head movement changed.

As previously peak velocity[1] and time to peak velocity[17] were negatively correlated with the PSS between subjects, correlations between peak velocity and time to peak velocity versus PSS were run separately for each velocity condition. Peak velocity had no significant relationship to the PSS for velocity 1 (Pearson's $r=0.157$, $p=0.548$), velocity 2 (Spearman's $\rho=0.061$, $p=0.817$), velocity 3 (Pearson's $r=0.086$, $p=0.741$), or velocity 4 (Pearson's $r=0.068$, $p=0.794$). Neither did the time to peak velocity versus have any significant relationship to the PSS for velocity 1 (Spearman's $r=0.191$, $p=0.461$), velocity 2 (Spearman's $\rho=0.123$, $p=0.639$), velocity 3 (Pearson's $r=0.256$, $p=0.321$), or velocity 4 (Pearson's $r=0.325$, $p=0.203$). Thus we failed to replicate between-subjects effects that support the "suppression hypothesis" previously reported[1,17].

To test whether increasing the peak velocity within an individual participant affects the PSS, linear regressions of peak velocity versus PSS were applied individually for each participant (average r^2: 0.577, s.e.: 0.321), and are shown in Figure 1c. A representative regression line was obtained from the median slopes and y-intercepts of these linear regressions, to describe the overall trend within-subjects (Figure 1d and 1e). The representative regression line had a median slope of 0.892 (interquartile range = 0.906) and a median y-intercept of 192.40 (interquartile range = 172.67). A one-sample signed-rank test confirmed that the regression slopes were significantly different from zero (Wilcoxon Z=2.49, p=0.011). Interquartile ranges revealed one outlier with a slope of -3.54. After removing this outlier, the average regression slope had an even higher median of 0.992 and a median y-intercept of 194.29. These results suggest that within-subjects, an increase in active head movement velocity leads to a reduced PSS, but one still significantly before 0, where the head has to move before a comparison sound by -88ms on average (median = -84ms) in order to be perceived as simultaneous.

4. DISCUSSION

In the present study, we investigated whether the velocity of active head movement will influence the perceived timing of the head movement onset using a within-subjects design. We provide further evidence that the perceived timing of active head movements is slow when paired with a sound stimulus. This delay, which had a global average of -88ms for all conditions is similar to the ~80ms delay previously reported[1,17,18], although it is important to note that previous studies only looked at one active head movement velocity, whereas our study looked at a range of active head movement velocities. Contrary to the predictions of our second hypothesis, the results do not replicate previous between-subjects effects of people who move their head faster[1] or reach peak velocity faster[17] require the head to move earlier than a comparison stimulus for perceived simultaneity. Most importantly, the individual regressions of the within-subjects data revealed that an increase in peak head movement velocity is significantly correlated with a reduction in the delay of the PSS.

Barnett-Cowan and Harris[1] reported an increased lag in the perceived timing of active head movements as the velocity of head movement increased, in a between-subjects design. Our results do not replicate these past findings. We quite convincingly show that higher velocities cause a decrease in the lag of the perceived timing of an active head movement, and not an increase. It should also be noted that two other studies since[1] have also found no effect of active head movement velocity on the PSS between-groups[17,18].

What might explain our results? There is reason to suspect that within-subjects, the perceived delay for head movement onset may be reduced as the head moves faster because of an increase in stimulus (head movement) intensity. To actively move the head, the CNS will plan a motor command in the premotor cortex and the supplementary motor area, and send that information to the primary motor cortex, which generates a motor command. In a yaw rotation, for example, this motor command will activate the sternocleidomastoideus muscle (SCM) opposite to the direction of rotation, and the dorsal neck muscle group on the same side as rotation[19]. To generate fast head movements, an increased number of motor units will be recruited to quickly generate enough force to overcome the inertia of the head over a shorter time period. This leads to external stimulation of the vestibular and proprioceptive organs, primarily the horizontal semicircular canals and the neck muscle spindles and golgi tendon organs. In our study, peak velocity was reached after approximately 200-400ms (frequency of 0.8Hz - 1.6Hz), and this falls within the linear portion of Goldberg and Fernandez'[20] single unit recordings of semicircular canal afferents. Within this range, the hair cells in the semicircular canals encode the speed of velocity with an increase in firing rate. From these results, we can suggest that an increase in active head movement speed corresponds with an increase in vestibular stimulus intensity in the semicircular canals, however as there can be nonlinear responses particularly from low-gain irregular afferents suited for encoding the onset of rapid head movements[21], this will need to be systematically explored in future research.

Most studies that have investigated the effect of stimulus intensity on the perceived timing of sensory stimuli involve audiovisual tasks or comparing two visual events. As early as 1933, Smith[22] reported that stimuli of higher intensity were perceived earlier than lower intensity, in an audiovisual temporal order judgment (TOJ) task where the intensity of stimuli was varied. Roufs[23] showed that bright flashes of light are perceived earlier than synchronous dim flashes. When two flashes were shown simultaneously with different intensities between 10-1000 trolands, observers reported an apparent movement of the flash in the direction of the dimmer flash, due to the longer perceptual delay of the weaker flash. Efron[24] paired a light stimulus with a shock stimulus under four sets of conditions, where either stimuli could be weak or strong. If both stimuli were strong, there was less of a deviation from true simultaneity than if both stimuli were weak. Additionally, if either stimulus was weak, the weaker stimulus had to be presented before the stronger stimulus in order for the observer to subjectively rate them as occurring simultaneously. Neumann and colleagues[25] varied stimulus intensity in an audiovisual task, where for most trials the auditory stimulus had to be presented first in order to be perceived as simultaneous. This effect could be reversed, however, when the intensity of light was decreased, and the intensity of sound was increased. These results suggest that intensity can influence the order in which stimuli from different modalities are perceived. More recent studies confirm that higher intensity stimuli in audiovisual tasks are perceived earlier in time[26], and that higher intensity stimuli are less likely to be reported as synchronous than lower intensity stimuli in simultaneity judgement tasks[27]. With respect to the vestibular system, the only study we are aware of that has used a temporal order judgement task, while varying the intensity of vestibular stimulation, found that the PSS between the onset of passive self-motion and sound is significantly shorter during passive whole-body rotations when the angular velocity increases from 5 to 60°/s (-223 to -90ms at 0.5Hz; -63 to -31ms at 1Hz, respectively)[28]. Note that in addition to reducing the delay of the PSS as a function of velocity, passive head movements in the same frequency range as the active head movements of the present study (~1Hz) are less delayed (~ -63 to -31ms)[28] than active head movements (~ -122 to -52ms), respectively. Taken together, these findings suggest that a greater velocity (stimulus intensity) should result in less time required for the head to move prior to other stimuli to be perceived as simultaneous.

In sum, our within-subjects result that the perceived timing of active head movements becomes less delayed at increasing head velocities are in agreement with other literature on stimulus intensity[22–27]. Here, the timing between stimuli to be perceived as simultaneous is shorter when the intensity is increased. A greater head movement velocity may be considered a more intense stimulus, as it requires the neck muscles to generate a larger force and evoking stronger sensory signals from the vestibular and neck proprioception neurons. This could also explain why we only observe a significant difference in the within-subjects data because we can only compare the varying intensity within individuals, due to the subjective nature of our stimuli. This further supports the hypothesis that the perceived timing of an active head movement can be modulated by the intensity of the stimuli, represented by the velocity of the head movement.

Based on their finding that a greater head movement velocity was correlated with a larger delay in PSS, Barnett-Cowan and Harris[1] postulated that the suppression mechanism described earlier could be velocity-based. Their results were similar to the findings of vestibular suppression of active head movements in monkeys[6]. If increasing speeds of active head movements increase the delay in perception, it would provide further evidence for velocity-based suppression. In our study, increasing the speed of active head movement decreases the delay in perception within-subjects, so our results do not support a velocity-based suppression mechanism for temporal order processing. Why was an effect of velocity on PSS found between-subjects in Barnett-Cowan and Harris[1], but not this study? There are several key differences between these studies. PSS and peak velocity are subjective measures, and a between-subjects design may not have reflected the effect of these parameters. Participants in Barnett-Cowan & Harris[1] were asked to move their head at one speed (as fast as possible), whereas in our study, participants were asked to move their head at slow, medium and fast speeds. As a result, peak velocities in Barnett-Cowan and Harris[1] ranged from 70 °/s – 280 °/s, whereas peak velocities in this study ranged from 34 °/s - 400 °/s. Furthermore, this study had 310 trials, whereas Barnett-Cowan and Harris[1] had 110 trials in total. The effect found in Barnett-Cowan and Harris[1] may be attributable to sampling due to the lower range of peak velocities and lower number of trials. As noted above, two studies since Barnett-Cowan and Harris[1] have found no effect of head movement velocity on the PSS between-groups[17,18]. Further studies should look at the effect of velocity with both active and passive head movement to determine whether the findings of Barnett-Cowan and Harris[1] can be replicated when explicitly controlling for the velocity of the head movement as well as consider alternative psychometric curve fitting with two independent variables[29].

Further support for sampling can be found in Figure 1d, where most linear regression slopes cluster around 0-2, but in the case of two participants there was a negative slope, meaning that as head velocity increased for these two participants, the time needed to perceive the movement also increased. Given that most participants had slopes that were relatively close to one another, we suspect it is possible that the results from these two participants are not indicative of the typical participant. These negative slopes may be a result of the small number of data points that were used to make the linear regressions, a result of the constraints in the number of trials that could be conducted for each participant, and the minimum number of trials that were necessary to create the corresponding sigmoidal functions. Alternatively, there may be characteristics in certain participants that cause them to behave in an opposite way, or they performed the experimental task differently. Indeed, a recent study by Shayman et al.[30] not only found that participants with vestibular deficits had a significantly larger TBW for audio-vestibular simultaneity than normal controls, TBWs for both vestibular patients and controls were positively correlated with vestibular thresholds for self-motion perception. While no differences were found between patients and controls for the PSS and no relationship between the PSS and vestibular thresholds, this work underscores the possible role of individual differences in vestibular sensitivity and the perceived timing of head movement. Subsequent studies should investigate this and other factors, which may be responsible for this individual variability.

From the within-groups analysis, it is suggested that true simultaneity of audio-vestibular stimuli would be reached at around 200°/s. However, it is important to note that the within-groups comparison only contained four data points per participant for each linear regression, for each of the four conditions. This limits any analysis on the dynamics that head movement velocity has on the PSS. We cannot conclude whether the behavior is linear, or non-linear and importantly how these change across individuals. A visual analysis of the within-group regression seems to indicate a more exponential relationship. Future studies could include more trials per participant on multiple testing days to avoid fatigue and habituation so that the velocities can be stratified into more than four conditions, in order to tease apart whether this relationship is linear or non-linear.

5. CONCLUSION

From the results of this experiment, we conclude that the perceived timing of active head movement is slow in comparison to an auditory stimulus, replicating previous research on the perceived timing of active head movements. Furthermore, we conclude that an increased active head movement velocity shortens this perceptual delay within the responses of each individual participant. This is in line with literature where more intense auditory, visual and vestibular stimuli are perceived earlier in time. We failed to replicate the results from Barnett-Cowan and Harris[1] where higher velocities of active head movements are related to an increase in the perceptual delay when paired with a comparison auditory stimulus when examining the data across participants. While our study was not designed to assess the suppression hypothesis directly, our results do not refute the suppression hypothesis that was previously reported, where an efference copy of the active head movement delays the perceived timing of the head movement via suppression of the vestibular afferent signals[1], although we do provide evidence against a velocity-based suppression mechanism. Instead, our results suggest a stimulus intensity effect, where increasing the velocity of the head movement and thus providing greater stimulus intensity, leads to a decrease in the perceptual delay.

Conflict of interest

None.

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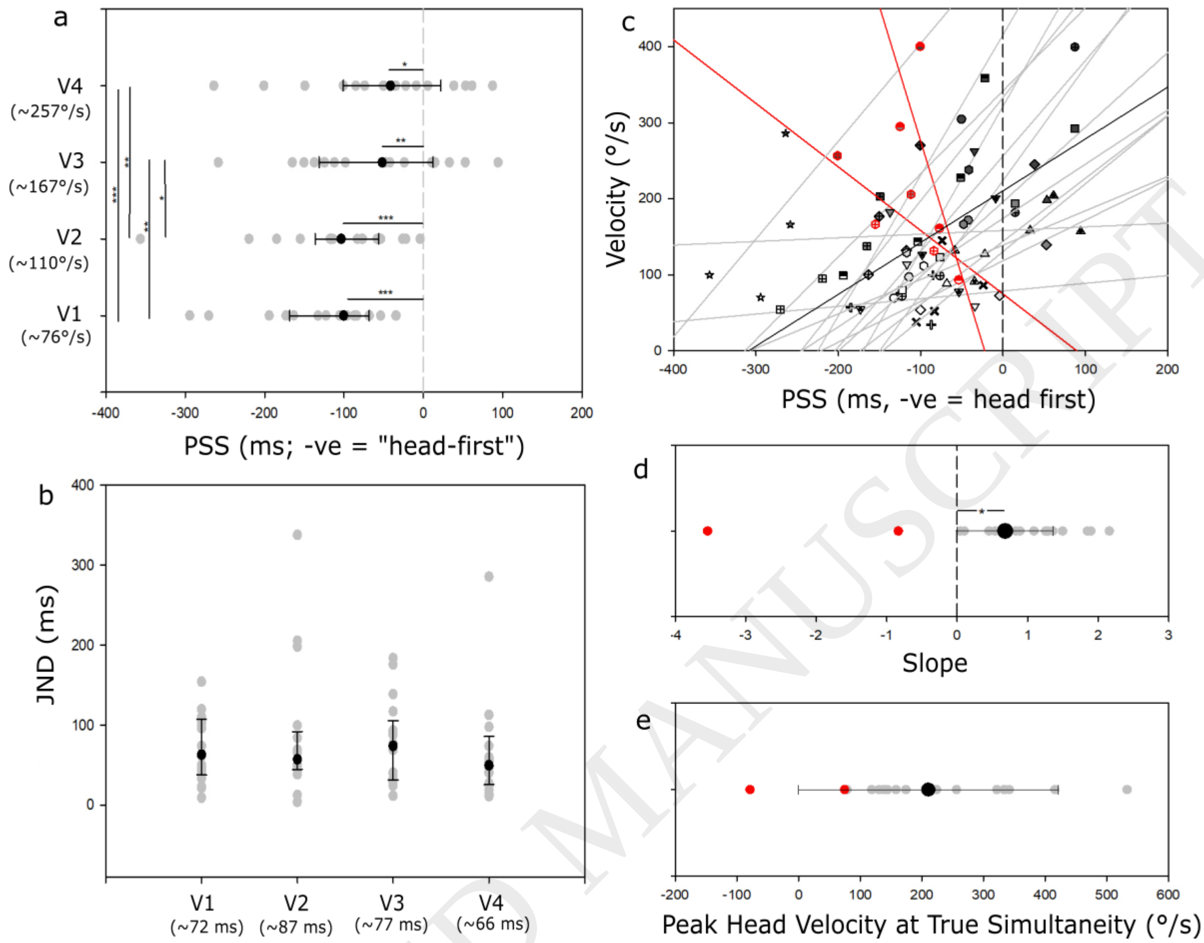

Figure 1. Average TOJ, PSS and JND data for all four stratified velocities. **a.** Average PSS data for all four stratified conditions. Grey dots represent individual participants and black dots represents the median PSS for each condition, with error bars representing the 25% and 75% quartiles. **b.** JND data for all four stratified conditions. Grey dots represent individual participants and black dots represent median JND value for each condition. Error bars are 25% and 75% quartiles. *: p<0.05, **: p<0.01; ***: p<0.001 **c.** Individual linear regressions for each participant for all four velocity conditions. Different symbols represent different participants. Thicker black line is the median linear regression which represents the average participant. Dashed line shows the point of true simultaneity. Red dots and line represent linear regressions

for participants with a negative slope **d.** Slopes and **e.** Peak head velocity at true simultaneity for within-groups linear regressions. Each gray dot represents one participant, the black dot represents the median. Red dots represent participants with a negative slope. Error bars are 25% and 75% quartiles. *: $p<0.05$.