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TEMPORAL INTEGRATION OF AUDITORY AND VESTIBULAR STIMULI

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Abstract

Objective—Integration of balance-related cues from the vestibular and other sensory systems requires that they be perceived simultaneously despite arriving asynchronously at the central nervous system. Failure to perform temporal integration of multiple sensory signals represents a novel mechanism to explain symptoms in patients with imbalance. This study tested the ability of normal observers to compensate for sensory asynchronies between vestibular and auditory inputs.

Study Design—Double-blinded experimental design.

Methods—We performed whole-body rotations about the earth-vertical axis following a raised-cosine trajectory at 0.5 and 1.0 Hz to several peak velocities up to a maximum of 180 deg/sec in five normal subjects. Headphones were used to present a diotic auditory stimulus at various times relative to the onset of the rotation. Subjects were required to indicate which cue occurred first.

Results—The vestibular stimulus needed to be presented 61 ms before the auditory stimulus (at a stimulus frequency of 0.5 Hz) and 19 ms (at 1.0 Hz). Stimuli presented within a window of 300 ms (at 0.5 Hz) and 200 ms (at 1.0 Hz) were judged to be simultaneous.

Conclusion—The central nervous system must accommodate for delays in perception of vestibular and other sensory cues. Inaccurate temporal integration of these inputs represents a novel explanation for symptoms of imbalance.

Level of Evidence—4

Keywords

Multisensory; Temporal; Vestibular; Auditory; Integration

INTRODUCTION

Maintaining balance requires visual, auditory, vestibular, and proprioceptive input. Cues from individual sensory systems are synergistically combined in several areas of the central nervous system to improve function beyond what each individual system can provide^{1–3}. Related cues must coincide both in space and in time for this combinatorial process to be maximally effective^{4–8}.

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The process of combining information from multiple sensory systems is complicated by relative delays in the perception of simultaneously presented sensory cues. For example, a match being struck is actually heard before it is seen. This offset arises from differences in the time required to complete peripheral and central neurological processes involved in perceiving the signal^{9,10}. The amount of time by which one sensory input must be delayed in order for it to be perceived most convincingly as simultaneous with the other input is termed the “point of subjective simultaneity,” or PSS^{10,11}. For example, a visual stimulus must be presented before an auditory stimulus by somewhere between 8 and 65 ms for the two to be perceived with the greatest degree of certainty that they occurred simultaneously^{12–15}. Similarly, a visual stimulus must be presented before a tactile cue by about 10–40 ms^{16–18}. The variability among these values can be related to stimulus parameters such as amplitude, complexity, and context. For example, increasing amplitude leads to a shorter PSS^{10,19}.

Despite the delay in perception between two stimuli that are presented simultaneously, we typically do not sense any time lag between them. The brain is able to integrate stimuli into a single experience if they are perceived within a period of time that has been termed the “temporal binding window” (TBW)^{9,20–22}. Events occurring within this window are perceived as simultaneous, and those outside the window are perceived as non-simultaneous. Typical examples of TBW widths for visual and auditory pairs are 64 ms¹⁴, 95 ms¹², and 300 ms²³. TBW widths for visual and tactile stimuli have been found to be 106 ms⁹ and 210 ms¹⁸. Variability in the TBW depends on the characteristics of the stimulus, becoming shorter as stimulus intensity increases.

Abnormal prolongation of the TBW could be expected to cause an observer to blur two sensory experiences that are not actually linked into the inaccurate perception that they derive from a single event. Conversely, inappropriate shortening of the TBW could cause an observer to perceive two sensations as being unrelated when they were actually generated simultaneously. This would lead us to experience the world around us much like a movie with its sound out of synchronization to the picture. Either a prolonged or shortened TBW could be expected to lead to perceptual confusion and poorer execution of tasks that involve the combination of multiple sensory inputs. Abnormal prolongation of the TBW, for example, has been observed in several conditions including autism, dyslexia, and aging^{24–27}. Similar perceptual confusion would be likely to accompany changes in the PSS.

Given the critical nature of sensory combination involving vestibular inputs for maintaining balance, it is surprising that the timing relationships of stimuli involving the vestibular system are poorly quantified. Here, we used a novel experimental paradigm to determine the PSS and TBW involving the vestibular system and to test the hypothesis that these values vary inversely with vestibular stimulus intensity.

METHODS

The appropriate human studies committee approved this study. Each subject was seated comfortably in a rotational chair designed to minimize perception due to proprioceptive cues^{28–31}. The head was secured with Reid’s plane 20 degrees chin-down to orient the horizontal canals in the earth-horizontal plane³². Light was excluded using a blindfold and the subject was shielded from air currents with a fabric cover. Noise-attenuating earmuffs (FM Basic 26000, MSA Sordin, Värnamo, Sweden) fitted with internal headphones providing white noise generated by MATLAB (The MathWorks, Natick, MA) were used to eliminate external auditory cues.

The chair was mounted on a motor (Kollmorgen Goldstar DDR D063M7, Danaher Motion, Radford, VA) oriented to rotate about the earth-vertical axis. Chair trajectories were

generated by custom-written software in MATLAB and output to the chair controller via the MATLAB Data Acquisition Toolbox in conjunction with a National Instruments data acquisition device (BNC-2090, Austin, TX).

Each trial consisted of a rotation with a velocity following a raised-cosine stimulus followed by the identical trajectory but in the opposite direction (Fig. 1). The second cosine of the pair was included to counteract the effect of the velocity storage mechanism, which would otherwise have prolonged the sense of rotation provided by the first and unnecessarily lengthened each trial³³. Stimuli were provided at a frequency of 0.5 Hz with peak velocities of 5, 10, 20, 40, 60, 90, 120, and 180 deg/s and 1.0 Hz with peak velocities of 5, 10, 20, 40, and 60 deg/s.

Each trial consisted of a self-paced, single-interval 2-alternative forced-choice task. A method of constant stimuli was used (Macmillan and Creelman 2004). At 0.5 Hz, 195 trials were presented at each of the velocities of 5, 10, 20, and 40 deg/s, and 140 trials were presented at each of the velocities of 60, 90, 120, and 180 deg/s. In each trial, a tone burst (10 ms duration, 800 Hz) was presented at various stimulus onset asynchronies (SOAs) ranging from 100 to 700 ms (vestibular leading auditory) for lower velocities (5, 10, 20, and 40 deg/s) and -100 (auditory leading vestibular) to 450 ms (vestibular leading auditory) for higher velocities (60, 90, 120, and 180 deg/s). Negative numbers represented the auditory stimulus preceding the onset of rotation and positive numbers represented the auditory stimulation following the rotation. At 1.0 Hz, SOAs ranged from -100 ms to 350 ms and 100 trials were presented at each of the velocities of 5, 10, 20, 40, and 60 deg/sec. The order of presentation was randomized among trials. The timing of the stimulus presentations were chosen based on preliminary experiments and published data³⁴.

After each trial, the subject performed a temporal order judgment task, choosing whether the vestibular or auditory stimulus occurred first. These responses were fit with a cumulative Gaussian distribution to construct a psychometric curve. The PSS at each frequency and velocity was defined as the SOA where the subjects performed at chance; that is, at the 50% point (the point of inflection) on the psychometric curve. Each subject was oriented to the equipment and experimental paradigm before testing began and underwent several practice runs. Subjects took rest breaks as desired.

We defined the temporal binding window (TBW) as extending from the -1 SD to the +1 SD on the psychometric curve. These limits result in a range of times within which the perception of simultaneity was strong enough that subjects never had more than a 68% chance of guessing the order correctly (with 68% of the area of a Gaussian distribution lying between -1 and +1 SD).

In addition to temporal parameters, vestibular detection thresholds were obtained using an adaptive paradigm. Each trial consisted of a single horizontal rotational movement along a raised cosine presented at 0.5 and 1.0 Hz. White noise was presented through the same sound-attenuating ear muffs as described before throughout the duration of each trial. Subjects indicated whether the rotational stimulus was moving to the left or to the right³⁵. The order of the trials was randomized, with a total of 30 trials in each direction. A maximum-likelihood-estimation technique was used to generate a psychometric curve (Prins, N & Kingdom, F. A. A. (2009) Palamedes: Matlab routines for analyzing psychophysical data. <http://www.palamedestoolbox.org>). We designated 79% as the threshold level for sensation of the vestibular stimulus.

RESULTS

Five volunteer test subjects (age range: 20–22 years) were paid for their participation in the study. None of the subjects reported a history of vestibular or auditory disease and all passed a screening audiogram (thresholds better than 20 dB HL at 250, 500, 750, 1000, 1500, 2000, 3000, 4000, 6000, and 8000 Hz). One subject (age 18) with confirmed bilateral vestibular areflexia also participated.

Point of Subjective Simultaneity (PSS)

The PSS for all subjects are plotted with respect to the peak angular velocity of the stimulus in Fig. 2. Curves for individual subjects were noted to be qualitatively similar. At 0.5 Hz (top), the PSS decreased as angular velocities increased from 5 to 60 deg/s. At the lowest angular velocity tested (5 deg/s), the PSS was 223 ± 26 ms (mean $\pm$ SD). At the highest angular velocity tested (180 deg/s), the PSS was 90 ± 26 ms. The PSS for each subject tended to maintain a similar relationship to those of the other subjects across all stimulus paradigms. At most velocities, for example, the PSS for subject A was smaller than for any of the other subjects. Two-way ANOVA confirmed the main effects of both velocities (ANOVA, $F=14.03$, $p<0.0001$) and subjects (ANOVA, $F=20.88$, $p<0.0001$) on PSS.

At 1.0 Hz (Fig. 2, bottom), the PSS values tended to lower than for the same peak velocities at 0.5 Hz. At the lowest angular velocity tested (5 deg/s), the averaged PSS was 63 ± 24 ms. At the highest angular velocity tested (60 deg/s), the average PSS occurred at 31 ± 7 ms. Two-way ANOVA showed that the PSS was significantly different among subjects (ANOVA, $F=20.52$, $p<0.0001$) and among the velocities tested (ANOVA, $F=11.51$, $p=0.0001$). The PSS for subject A was consistently lower than the other participants at 1.0 Hz, as it had been at 0.5 Hz. The PSS was dependent both on frequency (ANOVA, $F=56.21$, $p<0.0001$) and velocity (ANOVA, $F=6.98$, $p=0.0002$).

To confirm that subjects did not obtain extr vestibular cues for detecting the vestibular stimulus, we tested a subject with profound bilateral vestibular loss (confirmed on caloric, cVEMP, and rotational chair testing). The subject performed at the 50% level across the range of SOAs, indicating an inability to determine temporal order at any frequency or amplitude. Even at double the highest amplitude tested in normal subjects, the subject was unable to produce a reliable psychometric curve. This confirmed that the psychometric curves generated in this study were derived from vestibular perception alone and did not include substantial contributions from other sensory modalities such as proprioception.

Detection Threshold and PSS

A suprathreshold auditory stimulus can be generated almost instantaneously, but a vestibular stimulus requires a substantial amount of time to rise beyond a subject's detection threshold. To accommodate for this, we measured the threshold rotational velocity for each of our subjects and calculated an "estimated time to reach threshold," or how long it would take to reach this threshold velocity during each paradigm. We then adjusted each subject's experimentally measured PSS by this time.

A regression of each subject's adjusted PSS at each frequency and velocity, as a function of the estimated time to reach threshold, is shown in Fig. 3. Plotted this way, the y-intercept represents the estimated PSS if the vestibular stimulus were instantaneous. This value ranged from -56 to 130 ms (mean = 61 ms, SD = 70 ms) at 0.5 Hz. At 1.0 Hz, the value was always closer to zero, with a range of -11 to 43 ms (mean = 19 ms, SD = 22 ms). For four of five subjects, the Y-intercept was positive indicating that the vestibular stimulus needed to be presented before the auditory stimulus for the two to be sensed simultaneously. In all

subjects, the slope of the regression line at both frequencies was less than unity. The mean slope was 0.53 at 0.5 Hz and 0.44 at 1.0 Hz.

Temporal binding window (TBW)

For stimulation at 0.5 Hz, two-way ANOVA indicated that TBW widths were significantly affected by both stimulus velocity (ANOVA, $F=3.16$, $p=0.0137$) and across subjects (ANOVA, $F=9.74$, $p<0.0001$) (Fig. 4, top). At 1.0 Hz, TBW widths were significantly different across subjects (ANOVA, $F=7.78$, $p=0.0011$), but not across velocities (ANOVA, $F=0.64$, $p=0.6405$) (Fig. 4, bottom). In determining the relationship between TBW widths and frequencies and velocities, two-way ANOVA showed that frequency affected the TBW significantly ($F=11.62$, $p=0.0015$) but velocity did not ($F=1.63$, $p=0.185$). The subject with bilateral vestibular loss performed at chance across all stimulus frequencies and velocities tested, rendering his TBW too wide to calculate.

DISCUSSION

We found that an instantaneous vestibular stimulus must be presented before an auditory stimulus for the two stimuli to be perceived simultaneously. This relationship is dependent on frequency, so that the PSS is 61 ms during a 0.5 Hz stimulus and 19 ms during a 1.0 Hz stimulus. These findings represent an extension and confirmation of results presented in the three previous papers that have examined the relationship between vestibular and other sensory modalities, although they had significant methodological differences. In one, the PSS was found to be 172 ms, with the vestibular stimulus leading the auditory stimulus, but the vestibular input was delivered galvanically rather than mechanically³⁶. In another, the PSS was reported as 265 ms, but this number may have been an overestimate due to the very slow stimulus trajectory³⁴. In the third, the head rotation needed to precede the auditory stimulus by approximately 45 ms to be considered simultaneous. The onset of rotations in this case was quite rapid, but the paradigm involved a head-on-body rotation incorporating both a vestibular and proprioceptive stimulus³⁷.

An unexpected finding was that certain study subjects tended to have smaller PSS values and others tended to have larger PSS values over most or all stimulus paradigms than others. For example, subject A's PSS values were smaller at both 0.5 Hz and 1.0 Hz. These results are consistent with the idea of a "personal equation," a concept that was introduced to explain systematic differences in temporal perception among individuals observing astronomical transits³⁸. More recent studies have also demonstrated the concept of a "personal equation" for describing judgments of synchrony^{13,39}. Our finding that subjects demonstrate consistent differences in PSS among themselves suggests that the PSS might be a good metric for detecting pathologic conditions involving vestibular inputs or characterizing each person's innate ability to process vestibular stimuli.

The variability of the PSS in our normal subjects is presumably due to small differences in the ability of their central nervous system to process multiple stimuli in the temporal domain. However, the performance of our vestibular-deficient subject indicates that peripheral vestibular dysfunction alone may also lead to a prolonged PSS and widened TBW. In the case of subjects with decreased vestibular function, a rotational stimulus takes much longer to reach threshold, requiring a much longer lead ahead of the auditory stimulus to be perceived as simultaneous and lengthening the PSS. Similarly, the prolonged climb of a vestibular stimulus toward the elevated threshold of a subject with vestibular dysfunction would make it difficult to determine exactly when the vestibular stimulus occurred and widen the TBW. This secondary effect of vestibular hypofunction on temporal integration may be an important and previously unrecognized cause for imbalance in patients with

vestibular loss. It also indicates that a severely prolonged PSS or widened TBW may be a novel indicator of peripheral vestibular loss.

Changes in the PSS or TBW may be especially problematic in certain populations. In the elderly, an extended temporal binding window might be particularly clinically important given their difficulty in processing multiple streams of information simultaneously⁴⁰. In fact, older adults who are prone to falls may have a wider TBW for combinations of auditory and visual stimuli than younger adults²⁵. It remains to be determined whether alterations in these timing relationships are directly causal to imbalance or whether they are associated with imbalance due to linkages with a common source of anomalous central processing of sensory inputs.

It is important to note that the PSS and the TBW are dependent on stimulus characteristics, and the results presented here could be quite different under different experimental conditions. The PSS is shorter when stimuli are relatively realistic (such as when they are presented from the same location in space) than when they are more artificial (such as presented from different places). In one study, a visual and tactile stimulus were found to have a PSS of 10 ms when presented from the same location and a PSS of 24 ms when presented from separate locations on the opposite side of the body. The same study found that a visual and auditory stimulus had a PSS of 10 ms when presented ipsilaterally and a PSS of 30 ms when presented contralaterally¹⁶. In another study, visual and auditory information presented ipsilaterally had a PSS of 60 ms while presented contralaterally had a range of PSS from 69–80 ms¹⁴. This effect seems to be dependent on the degree of spatial separation: in a single experiment, the PSS of auditory and visual cues decreased from 48 to 46 to 39 ms as the spatial separation between the cues increased from 0 to 20 to 40 degrees¹². Given that our auditory stimulus was presented diotically, which is inconsistent with what one would expect during a natural head rotation in the presence of an external auditory source, the PSS may be longer here than under other circumstances.

The TBW is also dependent on stimulus characteristics and tends to be wider when stimuli are more realistic. In one study of auditory-visual integration, the TBW was found to be 106 ms when the stimuli were presented ipsilaterally versus 83 ms when presented contralaterally¹⁶. In another experiment using the same stimuli, the TBW ranged from 60–66 ms when presented ipsilaterally and 44–46 ms when presented contralaterally¹⁴. The effect of concordant cues widening the temporal binding window persists even in more complicated stimulus paradigms, such as the McGurk effect⁴¹. Hence, we expect that with more realistic stimuli (such as an auditory cue that varied in amplitude between the ears to match the rotation of the chair) the TBW might be wider than reported here.

Differences in timing perception among subjects may due to environmental factors such as hobbies, occupation, or even daily routines. This suggests that training may be able to affect the temporal relationships of vestibular stimuli to improve balance function. Further work will be required to determine if these differences may predict athletic performance, susceptibility to motion sickness or the development of neurodegenerative conditions; or whether training can affect them in ways meaningful for long-term performance⁴². Better knowledge of timing relationships among separate sensory channels may be useful for the development of sensory interfaces such as games, warning systems, and medical devices.

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Figure 1. Stimulus profile. Thick black line: chair trajectory, 0.5 Hz with peak amplitude of 20 deg/sec. Thick gray vertical line: auditory stimulus. Dashed gray vertical lines: range of stimulus onset asynchronies (SOAs) over which the auditory stimulus was presented (−100 to +700 ms).

Figure 2. Point of subjective simultaneity (PSS). Thin colored lines: results of individual subjects (A–E). Thick black lines: mean $\pm$ SD. Top: results at 0.5 Hz; bottom: results at 1.0 Hz.

Figure 3.

Point of subjective simultaneity as a function of estimated time to reach threshold. Circles and dashed regression lines: 0.5 Hz data; triangles and solid regression lines: 1.0 Hz data. For each paradigm, the x-axis represents the estimated time required for each subject (A–E) to reach the vestibular perceptual threshold. Y-intercepts for each subject during the 0.5 and 1.0 Hz stimulus indicate the estimated PSS if the vestibular stimulus were “instantaneous.”

Figure 4. Temporal binding window (TBW). Thin colored lines: width of the temporal binding window (in ms) for individual subjects (A–E). Thick black lines: mean $\pm$ SD.