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Perception of audio-visual synchrony is modulated by walking speed and step-cycle phase

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Abstract

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Investigating sensory processes in active human observers is critical for a holistic understanding of perception. Recent research has demonstrated that locomotion can alter visual detection performance in a rhythmic manner, illustrating how a very frequent and natural behaviour can influence sensory performance. Here we extend this line of work to incorporate variations in walking speed, and test whether multi-sensory processing is impacted by the speed and phase of locomotion. Participants made audio-visual synchrony judgements while walking at two speeds over a range of stimulus onset asynchronies (SOAs). We find that sensitivity to multi-sensory synchrony decreases at slow walking speeds and is accompanied by an increase in reaction times, compared to when walking at a natural pace. A further analysis of the shortest SOAs was conducted to test whether subjective synchrony modulated over the step cycle. This revealed that synchrony judgements were quadratically modulated with perceived synchrony being higher in the swing phase of each step and lower when both feet were grounded during stance phase. Together, these results extend an earlier report that walking dynamically modulates visual sensitivity by contributing two new findings: first, that walking speed modulates perceived synchrony of audio-visual stimuli, and second, that modulations within the step-cycle extend to multisensory synchrony judgements which peak in the swing phase of each step.

Introduction

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Movement characterises our experience of the environment, as we shift our gaze, adjust our posture, and move about the world to achieve our behavioural goals (Noë, 2004). Despite this interplay between the sensory and motor systems, the vast majority of past research within experimental psychology and perception has focused on highly restrained experimental settings. These settings have been critical for building our understanding of human perception, but they cannot provide a complete account of how our senses function during dynamic real-world behaviour. The present study addresses this deficit by examining a critical perceptual challenge – that of judging multisensory synchrony – while engaged in one of the most common natural behaviours: locomotion. Specifically, we compare audio-visual synchrony perception while walking at a natural walk speed or at a slower speed, and we test for systematic changes in synchrony perception occurring at different phases within the step cycle.

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Audio-visual events are commonly encountered in natural behaviour and careful evaluation of the relative timing of each modality's response is essential in a multisensory brain. It is needed to determine whether two sensory signals arriving at a similar time are linked to a common external cause and should be integrated, thereby speeding reaction times and improving precision (Ernst & Bühlhoff, 2004). This has clear functional benefits and can be critical for survival. For example, integrating the sound and location of an approaching car helps optimise the safe crossing of a busy road; and weak unimodal signals that may have gone unnoticed become salient when integrated. Equally importantly, however, is signal segregation. If two signals are sufficiently offset in time, it suggests they arise from distinct external causes and thus they should be kept segregated to avoid spurious binding of unrelated signals that could lead to maladaptive behavioural responses.

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Accurately determining the relative timing of external auditory and visual events is not a trivial problem. There is a series of temporal factors, both external and internal, that differentially affect each modality (Alais et al., 2010). First, the travel time of the physical stimulus from source to peripheral receptors is very sluggish in the case of sound (~3 ms per metre) but it is near-instantaneous for light. Second, once a signal arrives at the receptors, transduction times differ for vision and sound. In addition, the physical-to-neural transduction is very rapid (1-2 ms: (Corey & Hudspeth, 1979; King & Palmer, 1985)) whereas visual transduction is much slower by a factor of ~20x (Lamb & Pugh, 1992; Rodieck, 1998). In the case of vision, latencies are further modulated by adaptation, intensity and duration (Lennie, 1981). As these asymmetries are not fixed, they require that temporal integration windows for perceived simultaneity remain flexible, for example by accommodating for auditory travel time in the case of distant audio-visual events (Alais & Carlile, 2005; Kopinska & Harris, 2004; Sugita & Suzuki, 2003).

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Another factor affecting the perceived simultaneity of audio-visual stimuli is attention. Previous work has demonstrated that simultaneity perception can be flexibly biased by attention, such as when spatially attending to a visual event leads to a speeded response to the attended signal (Kanai et al., 2007; Spence et al., 2001; Zampini et al., 2005). Thus, a given perceptual or behavioural task could alter perceived synchrony if it requires focusing on one component of the multisensory pair. Other factors affecting audio-visual synchrony

80 perception include the content of the signals, binding windows differ when using simple
81 tones/flashes compared to audio-visual speech (Eg & Behne, 2015). The richness of the
82 stimulus environment also raises the difficulty of synchrony perception by increasing the
83 number of potential distractors and raising the likelihood of misbinding (Cary et al., 2024).

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85 In the current paper, we examine whether audio-visual synchrony perception might also be
86 influenced by another factor: the simple act of walking. Recent work has used time-resolved
87 perceptual probes to demonstrate that visual sensory processing undergoes continual
88 dynamic change during locomotion (Davidson et al., 2024). More specifically, visual
89 detection performance was shown to oscillate in a rhythm entrained to the phases of an
90 individual's stride cycle. During the swing phase of the stride, there was an increase in
91 sensitivity and faster reaction times to visual stimulus probes. During the stance phase, the
92 pattern was reversed with poorer sensitivity and slower response times. Here, we extend this
93 approach to investigate audio-visual synchrony perception. Specifically, we test whether
94 synchrony perception varies when comparing natural and slow walking speeds, and whether
95 synchrony modulates within the dynamic phases of each step. Recent work has shown that
96 the speed of self-movement can interact with timing judgements (De Kock et al., 2021;
97 Wiener et al., 2019). Consequently we also predict that the propulsive actions involved with
98 each step will modulate synchrony judgements as actions executed close in time to an
99 audio-visual stimulus affect both subjective synchrony and the width of the synchrony
100 window (Arikan et al., 2017; Benedetto et al., 2018).

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102 To preview our results, we find that walking slowly increases overall synchrony
103 judgements and the width of the synchrony window, demonstrating a reduction in the
104 precision of audio-visual perception compared to when walking at a natural pace. Synchrony
105 perception also decreased around the stance phase of the step cycle, with a greater
106 likelihood of perceiving synchrony during the swing phase of each step.

108 **Methods**

109 ***Participants***

110 We recruited 23 healthy volunteers via convenience sampling from The University of
111 Sydney's undergraduate psychology cohort. All participants had normal or corrected to
112 normal vision, and provided informed consent before receiving either 20 AUD or course
113 credit for their time. All research procedures were approved by the University of Sydney
114 Human Research Ethics Committee (HREC 2021/048). Two participants were excluded for
115 failure to understand the task, resulting in a final sample of 21 volunteers (13 female, Mean
116 age 23.0 years, SD= 4.9).

117 ***Apparatus and virtual environment***

118 We built a virtual environment in Unity (version 2020.3.14f1), with the SteamVR plugin (ver
119 2.7.3, SDK 1.14.15), displayed using a DELL XPS 8950, with a 12th Gen Intel Core i7-
120 12700K 3.60 GHz processor, running Microsoft Windows 11. The environment was similar to
121 our previous studies investigating the effects of walking on visual perception (Davidson et
122 al., 2023, 2024), and consisted of an open woodland, through which participants walked a

123 9.5 m path at two predetermined walking speeds. Participants walked the 9.5 metre path at
124 ~ 0.65 m/s in the slow condition or ~ 1.1 m/s in the natural speed condition. Both speeds were
125 chosen after extensive pilot testing, to be consistent with our prior work and previous
126 research estimating preferred natural walking speeds over unfamiliar terrain (Davidson et al.,
127 2024; Hausdorff et al., 1996; Matthis et al., 2018). Participants were wearing the HTC Vive
128 Pro Eye head mounted display (HMD), which contains two 1440 x 1600-pixel (3.5" diagonal)
129 AMOLED screens (110 degree FOV, refresh rate 90 Hz). Participants carried two wireless
130 hand-held controllers to submit responses and self-pace trial progression, as well as the
131 wireless adapter kit (130 gram weight) and a lightweight shoulder bag with a battery that
132 powered the wireless device. Five HTC base stations (v 2.0) were used to record the three-
133 dimensional position of the HMD while walking, which was used in offline analysis to
134 determine step-cycle phase.
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136 ***Procedure***

137 After providing informed consent at the start of the experiment, each participant was
138 familiarised with the VR apparatus and virtual environment before beginning a first practice
139 block which contained 5 stationary trials, as well as a sequence of easy trials (alternating
140 easy "same" and "different" types, at 40 and 400 ms SOA respectively) to familiarise the
141 participants with the response mapping. On all trials, participants were instructed to respond
142 "same" or "different", via right or left click of the index finger on the wireless controllers. On
143 all trials, audio-visual stimulus pairs were presented at one of seven fixed stimulus-onset-
144 asynchronies (SOAs). These were -320, -140, -50, +40, +130, +220, +400 milliseconds, with
145 negative representing auditory leading stimuli, positive for visual leading stimuli. These
146 values were selected after pilot testing to finely sample the centre of the synchrony function,
147 with easy trials at the extrema to enable reasonable Gaussian fits to the data. To arrive at
148 these SOAs, we began with a set defined as $[\pm 360 \pm 180 \pm 90 \ 0]$ ms and then added an
149 offset of 40 ms. The reason for this was to align the centre of the SOA set closer to the true
150 point of subjective synchrony, which typically occurs when vision has a lead of about 30-40
151 ms relative to audition (Arrighi et al., 2005; Galton, 1885, 1899; Welford, 1980) owing to the
152 longer transduction and latency of vision and it has been shown that auditory signals activate
153 midbrain neurons faster than visual signals by about 50 ms (King & Palmer, 1985). Thus,
154 setting the middle value of the set of SOAs to 40 ms provides a good estimate of the true
155 point of subjective synchrony.
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157 Each experimental block contained 20 trials, within which all trials were the same
158 walking pace (either slow or natural speed). There were 3 slow walking and 6 natural
159 walking blocks, and the entire experiment was completed in ~ 1 hour. Each trial required the
160 participants to walk the 9.5 m path over 9 seconds in the normal speed condition (velocity =
161 $1.06\text{m/s} \approx 1$ m/s), or 15 seconds in the slow speed condition (velocity = $0.63\text{m/s} \approx 0.6\text{m/s}$,
162 approximately 60% of the speed of the normal condition), while performing the task.

163 ***Stimuli***

164 On all trials participants were positioned behind a walking guide (10 cm x 10 cm
165 cube) at approximate waist height, which traversed the length of the virtual path at either the

166 slow or natural walk velocity. The walking guide served to ensure participants walked at a
167 near constant velocity during walking trials, and determined the location of the visual
168 stimulus on all trials. The visual stimulus was a large (5 cm radius) disc located 10 cm above
169 the walking guide, which changed colour - flashing white (RGB: 1,1,1) for 20 ms. Auditory
170 stimuli were bursts of white noise 20 ms duration, ramped over 2 ms at onset and offset. In
171 each walking trial, Participants were presented with a maximum of 6 audio-visual stimulus
172 pairs in the normal speed condition, and maximum of 10 pairs in the slow walking condition,
173 such that the time allowed to respond between presentations was constant across
174 conditions. We wish to note that both stimuli were easily perceivable, suprathreshold flashes
175 and tones, and our main dependent variable is the perceived synchrony of these audio-
176 visual stimulus pairs.
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178 ***Verification of SOA's***

179 To verify the onset of auditory and visual stimuli, the output of a photodiode attached
180 to the HMD screen was compared to the analogue output driving the in-built HTC-Vive Pro
181 Eye headphones, recorded concurrently using analogue inputs on a Focusright Scarlett
182 Audio Interface. The voltage time-series were then compared using Audacity to confirm
183 stimulus-onset timing and adjust for consistent delays. Before data collection, a significant
184 but stable delay of 77 ms \pm 12 ms was found on the audio stream relative to the visual
185 stimuli, and so a latency correction was applied in the Unity scripting to account for this, after
186 which the empirically observed SOA's were found to be reliably correct to approximately \pm 11
187 ms (where 11 ms is the frame duration of the 90 Hz visual display).
188

189 ***Gait extraction from head position data***

190 To test whether the phase of an individual's step-cycle influenced synchrony
191 judgements, we applied a peak detection algorithm to the time-series of head position data.
192 We first detected troughs in the vertical head position data which correspond to the double
193 support stance phase when both feet are on the ground (Gard et al., 2004; Hirasaki et al.,
194 1999; Moore et al., 2001; Pozzo et al., 1990). We next epoched individual steps based on
195 the trough-to-trough time-points and normalised step-lengths by resampling the time-series
196 data to 200 data points (0-100% stride-cycle completion, incrementing in steps of 0.5%).
197 Stimulus onsets were then allocated into their respective step-cycle quintiles, corresponding
198 to whether the first stimulus in an audio-visual pair was shown in the 1-20%, 21-40%, 41-
199 60%, 61-80%, 81-100% resampled percentile bins. To increase the trial counts per quintile
200 trials were aggregated from both walking speeds.

201 ***Model fitting***

202 To assess the sensitivity of synchrony judgements while walking, we applied a two-
203 step procedure. First, the proportion "same" responses for each SOA were quantified per
204 participant per walking speed, before a Gaussian model was fit to the individual level data.
205 We fit using the standard Gaussian function:
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$$207 \quad f(x) = a * e^{-(x-b)^2/2c^2}$$

208 Where a is a constant, e is Euler's number, b is the SOA at peak of the synchrony
209 distribution and c is distribution's standard deviation. For each participant, we fit a Gaussian
210 to their average per SOA using a non-linear least squares method (max 2000 iterations), and
211 retained the peak centre (b) and standard deviation (c) for statistical comparisons between
212 walking speeds. To improve fit strength and focus on our parameters of interest (mean and
213 standard deviation), we normalised the height of each participant's synchrony function to 1,
214 by dividing by their maximum proportion of "same" responses.

215 We additionally performed a series of asymmetric Gaussian fits to quantify whether
216 the auditory leading or visual leading stimulus pairs interacted with walking speed. These
217 used the same equation, but separately quantified the standard deviation for the left-hand
218 side relative to the Gaussian mean (LHS, auditory leading), or right-hand side relative to the
219 Gaussian mean (RHS, visual leading) of each participant's data.

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221 ***Mixed-effects analyses***

222 We investigated the effect of step-cycle phase on synchrony judgements, focussing
223 on changes to the proportion of 'same' responses at the shortest SOAs (-50ms, +40ms). We
224 focussed on these short SOAs to ensure that the entire stimulus sequence would be
225 approximately 60-70 ms in duration (e.g. 20 ms flash, 20 ms gap, 20 ms tone for the 40 ms
226 SOA, with 60 ms total duration), thus enabling an analysis of how relatively brief step-cycle
227 phases would influence performance.

228 Owing to the few number of targets at this subset of SOAs we combined both walk
229 speeds to increase the statistical power of our analysis (Combined speeds, total trials at
230 SOA -50 ms $M = 192.04$, $SD = 10.95$; SOA +40ms, $M = 195.90$, $SD = 13.97$). Assigning
231 these short SOA trials into step-cycle quintiles resulted in approximately 36 trials per step-
232 cycle quintile (SOA -40 ms Mean across quintiles = 36.11, $SD = 1.07$; SOA +50 ms, $M =$
233 36.69 , $SD = 1.37$).

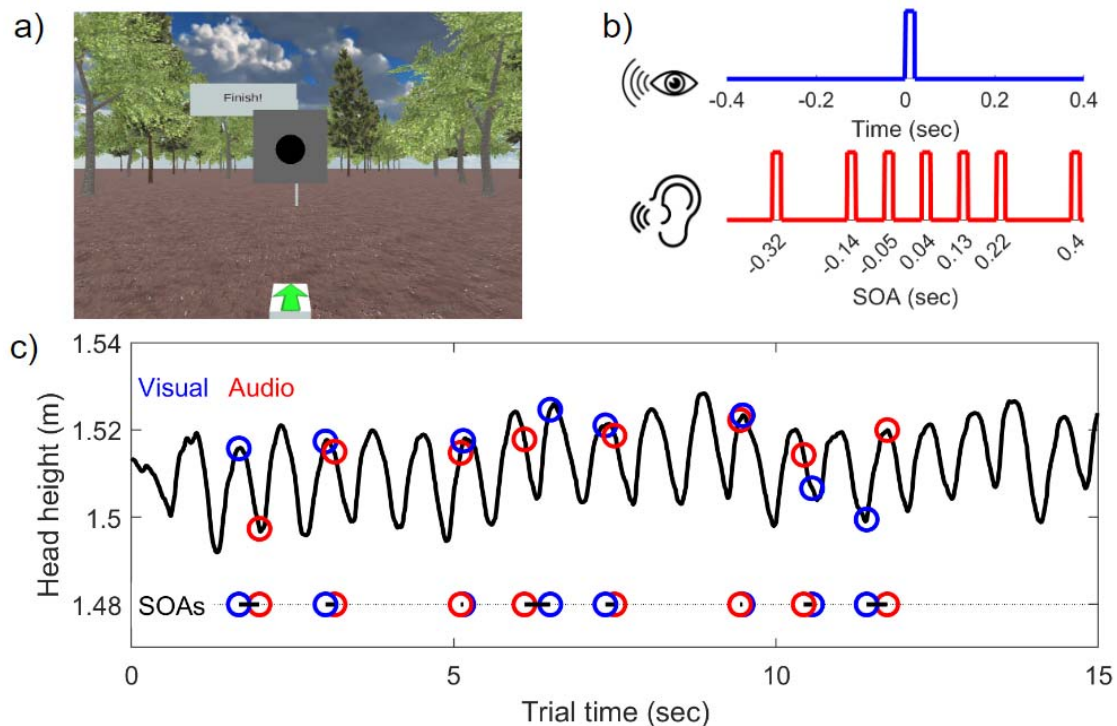
234 We observed quadratic trends in the proportion of 'same' responses at these short
235 SOAs depending on step-cycle quintile, and formally tested for quadratic effects using
236 stepwise mixed-effects analyses. This analysis compared whether models including only a
237 linear effect ($P(\text{same}) \sim \text{step quintile} + (1|\text{Participant})$) or additional quadratic fixed effect
238 ($P(\text{same}) \sim \text{step quintile}^2 + \text{step quintile} + (1|\text{Participant})$) were better than a simple model
239 including only random effects (intercepts) per participant ($P(\text{same}) \sim 1 + (1|\text{Participant})$). We
240 compared the goodness-of-fit of each model using likelihood ratio tests, and report when the
241 quadratic or linear model was a significantly better fit than the basic model, including
242 coefficients for fixed effects (β), their 95% Confidence Intervals (CIs).

243

243 **Results**

244 We quantified audio-visual synchrony judgements during walking at slow and natural
245 speeds to investigate the impact of everyday actions on multisensory perception. **Figure 1**
246 displays a representation of the basic virtual environment and task design.

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Figure 1 - Audio-visual synchrony judgements while walking at natural and slow speeds. *a)* First-person view of the 3D environment participants walked through while providing synchrony judgements. *b)* Example stimulus timing showing the stimulus onset asynchronies used in the present experiment, ranging from -0.32 seconds (audio leading visual), to 0.4 seconds (visual leading audio). *c)* Example change in head position recorded during a single trial at slow walking speed. Vertical head height displays a roughly sinusoidal pattern where the peaks and troughs correspond to the approximate swing and stance phases of the stride-cycle (solid black line). Visual onsets are shown with blue markers, auditory onsets are shown with red markers, overlaid on the head position to display their occurrence in various phases of each step. The SOA is displayed on the horizontal line at bottom.

261 **Slow walking reduces the sensitivity of auditory-visual synchrony judgements**

262 In studies of multisensory synchrony, plotting the proportion of synchronous percepts
263 per SOA typically results in a Gaussian bell-shaped function (Vroomen & Keetels, 2010).
264 The mean (or peak) of the function represents the point of subjective simultaneity (PSS), and
265 the width of the function – particularly the slope of the rise and fall – provides a measure of
266 the sensitivity of synchrony judgements. A very narrow function represents a tight SOA
267 range at which two stimuli will be perceived as simultaneous, and thus higher sensitivity.
268 Conversely, a wider function represents a broader range at which two sequential stimuli are
269 perceived to be simultaneous, and reduced sensitivity.

270 The average proportion of synchronous percepts when walking at a slow and natural
271 pace are displayed in **Figure 2A**. On visual inspection, a wider function is observed for the
272 slow walking condition which we formally quantified by comparing the standard deviation of
273 the Gaussian fits obtained per participant at both walking speeds. Synchrony functions were
274 significantly wider when walking slowly, compared to when walking at a natural speed ($t(20)$)

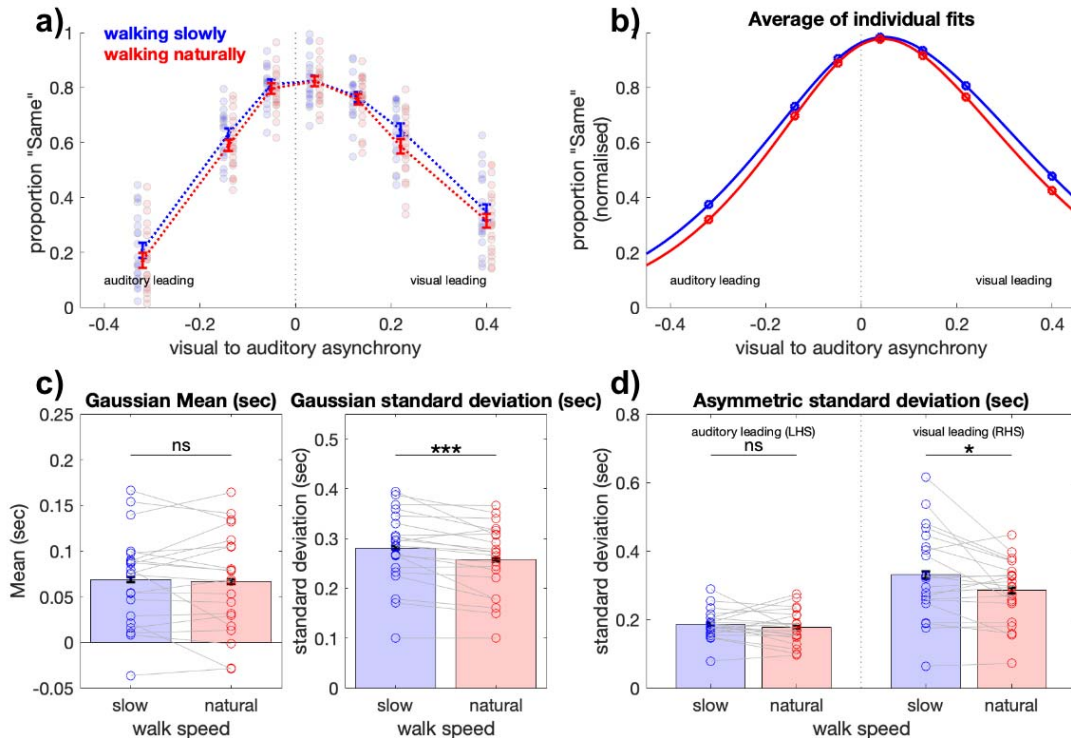
275 = 3.88, $p < .001$, $d = .85$). There was no significant difference between the mean (PSS) of
276 the synchrony functions at both walking speeds ($t(20) = .4$, $p = .7$, $d = .09$). We also
277 conducted a 2 x 7 repeated-measures ANOVA to assess the overall proportion of
278 synchronous percepts in the natural and slow walk speeds over the seven SOAs. This
279 revealed a significant main effect of walk speed ($F(1,20) = 11.674$, $p = .003$, $\eta_p^2 = 0.369$), with
280 slow walk speed producing a higher proportion of “same” responses. As is clear from **Figure**
281 **2A**, the main effect of SOA was also significant ($F(6,120) = 110.643$, $p < .001$, $\eta_p^2 = 0.847$).
282 The walk speed x SOA interaction was not significant.

283 We additionally calculated the standard deviation of Gaussians fit to either the left
284 hand side (LHS) or right hand side (RHS) of the Gaussian mean at both walking speeds.
285 This analysis serves to quantify any asymmetry in the Gaussian profile, which represents an
286 interaction between walking speeds and the type of leading stimulus (auditory leading or
287 visual leading stimulus pairs on the left and right, respectively). These tests of asymmetric
288 fits revealed that on average, the synchrony functions were significantly wider to the right of
289 the Gaussian mean (i.e., vision leading stimuli: RHS standard deviation $M = 0.30$, $SD = .09$)
290 compared to the left of the Gaussian mean (i.e., auditory leading stimuli: LHS $M = 0.18$, SD
291 $= .04$; $t(20) = -6.76$, $p < .001$, $d = -1.48$). A 2x2 repeated measures ANOVA (slow/natural
292 speed x auditory leading/visual leading standard deviation) indicated significant main effects
293 for the left/right asymmetry ($F(1,20) = 39.75$, $p < .001$, $\eta_p^2 = 0.67$), and walking speed
294 ($F(1,20) = 12.59$, $p = .002$, $\eta_p^2 = .39$), with no significant interaction ($F(1,20) = 2.17$, $p = .16$).
295 Post-hoc tests revealed the main effect of walking speed was driven by a change to the
296 width on the RHS of the Gaussian ($t(20) = 3.10$, $p = .02$, $d = 0.2$; Bonferroni corrected for
297 comparing a family of 6).

298 In summary, audio-visual synchrony judgements are biased by whether the visual or
299 auditory stimulus was leading in the pair, with visual leading stimuli perceived with poorer
300 sensitivity. All stimulus pairs were impaired when walking slowly compared to when walking
301 at a natural speed, an effect that was driven by an increase in the width of the synchrony
302 function at slow walking speeds for visual-leading stimuli.

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307 **Figure 2. Walking at slow speed decreases the sensitivity of synchrony judgements.**
 308 **a)** Group average proportion 'same' responses per SOA. Blue and red colours represent
 309 slow and natural walking speeds respectively. Error bars represent ± 1 SEM, corrected for
 310 within participant comparisons (Cousineau, 2005). **b)** Average of participant-level Gaussian
 311 fits at slow and natural walking speeds. Each fit was performed after normalising to the
 312 maximum proportion 'same' per participant, to improve the fit strength for the Gaussian
 313 mean and standard deviation parameters of interest. **c) Left:** Gaussian mean per participant
 314 was not significantly different at slow and natural walking speeds. **Right:** Gaussian width per
 315 participant significantly reduced when walking at natural speeds. **d)** Asymmetric Gaussian
 316 fits (fitting the LHS and RHS separately) show the visual leading stimuli on the RHS were
 317 significantly affected by walking speed. *** $p < .001$, * $p < .05$ Bonferroni corrected

318 **Slow walking increases reaction times**

319 We next analysed whether walking speed and the modality of the leading stimulus
 320 also affected reaction times. While overall performance and reaction times often correlate in
 321 speeded tasks such as ours, they can offer unique and complementary information capturing
 322 distinct aspects of cognitive processes (De Boeck & Jeon, 2019). For example, a change in
 323 sensitivity without a change in reaction time could imply an objective increase in response
 324 error with no change in the perceived difficulty of the task (such as the misattribution of
 325 button-presses). Alternatively, a change in sensitivity and increase in reaction times could
 326 imply that walking slowly altered the perceived difficulty of the task, inducing a reaction time
 327 delay.

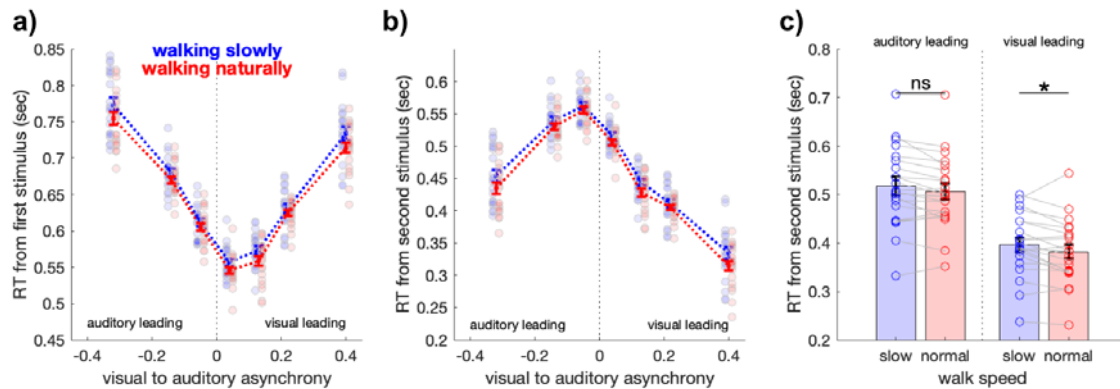
328 **Figure 3A** displays the overall reaction time from the first stimulus per SOA when
 329 walking at slow and natural speeds. Like the proportion 'same' responses, reaction times
 330 displayed a roughly symmetrical Gaussian shape, although interestingly, reaction times were

331 fastest overall for the stimuli with shortest SOAs. This pattern was despite the large
332 suprathreshold asynchrony presented at maximum SOAs, and our instructions to
333 participants that were to respond as quickly as possible. Responses could be made before
334 the onset of the second stimulus during these larger SOAs, yet clearly that was not the
335 dominant strategy. One explanation for this result is that participants may have waited for
336 both stimuli prior to committing to a response. If this were the case, then large SOAs may
337 have also primed a rapid response when measured relative to the onset of the second
338 stimulus. **Figure 3C** displays the reaction times from the second stimulus, (i.e. subtracting
339 the absolute SOA from the reaction times in **Figure 3A**), from which several interesting
340 features emerge.

341 First, reaction times were fastest overall for stimuli with larger SOAs, implying a
342 priming of rapid responses in those trial types. Second, the shortest SOAs, for which the
343 maximum proportion of 'same' responses were observed, resulted in longer reaction-times.
344 There was also a clear asymmetry in reaction-time behaviour for auditory leading compared
345 to visual leading stimulus pairs, despite the symmetrical pattern of response-times when
346 measured relative to the first stimulus (cf. **Figure 3A**). Large differences in reaction times
347 were also clear between visual leading and auditory leading stimulus pairs, despite
348 objectively similar absolute SOAs. For example, for auditory leading SOAs of -0.14 sec,
349 reaction times ($M = 0.53$, $SD = .08$) were over 100 ms slower than visual leading SOAs of
350 +0.13 sec ($M = 0.42$, $SD = .07$), despite an objective difference in absolute SOA of only 10
351 milliseconds ($t(20) = 11.82$, $p < .001$, $d = 2.58$).

352 We proceeded by quantifying the effects of walking speed on these reaction times
353 with a 2x2 repeated measures ANOVA (slow/natural speed x visual/auditory lead). There
354 was a significant main effect for the modality of the leading stimulus ($F(1,20) = 322.19$, $p <$
355 $.001$, $\eta_p^2 = 0.94$), and walking speed ($F(1,20) = 9.71$, $p = .005$, $\eta_p^2 = .33$), with no significant
356 interaction ($F(1,20) = 0.12$, $p = .74$). Post-hoc tests revealed the main effect of walking
357 speed was significant only for the RHS visual leading stimuli ($t(20) = 2.87$, $p = .04$, $d = .59$;
358 LHS, $p = .1$; Bonferroni corrected for comparing a family of 6).

359 Overall, these results indicate that slower reaction times accompany the decrease in
360 sensitivity that occurs when walking slowly (cf. **Figure 2**). When measured from the first
361 stimulus in a pair, reaction times were fastest when SOAs were minimal (**Figure 3A**). On
362 average, however, participants withheld their responses until after both stimuli had been
363 presented, resulting in fastest reaction times for larger SOAs when measuring reaction times
364 from the second stimulus in a pair (**Figure 3B**). There was also a significant advantage for
365 visual leading stimulus pairs, which were responded to faster than auditory leading
366 alternatives. However, responses to visual leading stimuli were significantly slower when
367 walking slowly.



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371 **Figure 3. Walking slowly increases reaction times.** a) Group average reaction times
372 measured from the onset of the first stimulus. Blue and red colours represent slow and
373 natural walking speeds respectively. Error bars represent ± 1 SEM, corrected for within
374 participant comparisons (Cousineau, 2005). b) Group average reaction times when
375 measured from the onset of the second stimulus. c) Average reaction times in b, when
376 walking slowly (blue) or naturally (red), when the stimulus pair was auditory leading (SOAs -
377 320, -140, -50 ms) or visual leading (SOAs +40, +130, +220, +400 milliseconds). Error bars
378 represent ± 1 SEM, participant data shown with circles, and connected per participant with
379 grey lines. * $p < .05$ Bonferonni corrected
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381 **Step-cycle phase modulates synchrony judgements at shortest SOAs**

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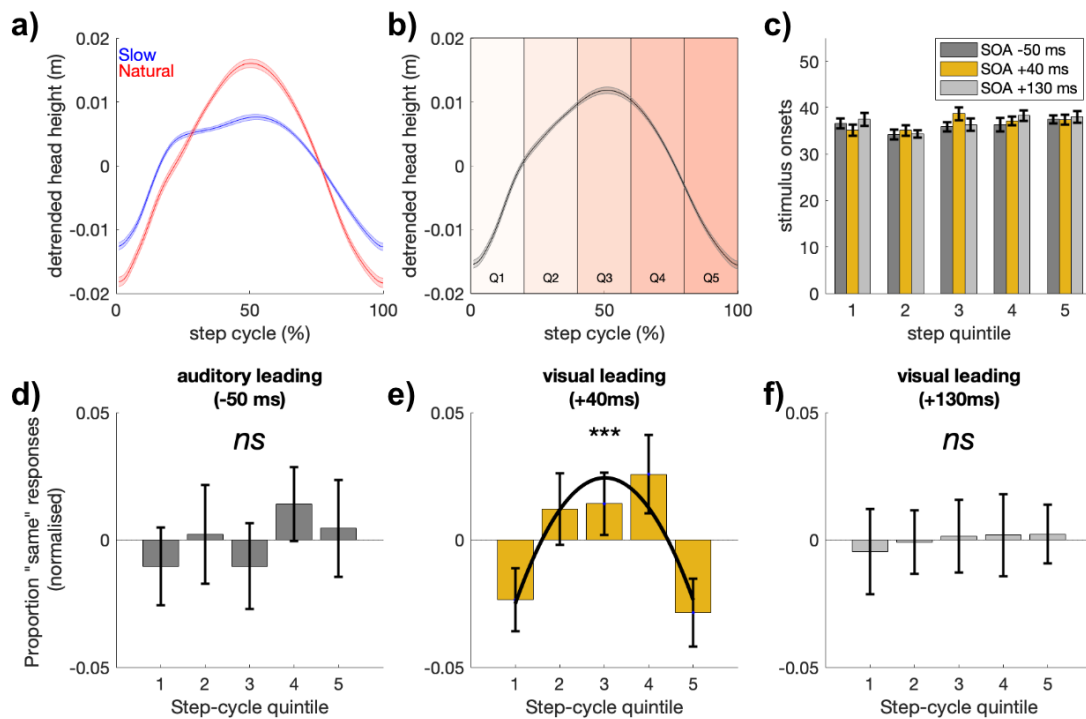
383 Recent evidence has demonstrated that visual detection performance is rhythmically
384 altered throughout the step-cycle. In this previous work, changes in head position while
385 walking in wireless VR were used to define the approximate swing and stance phases of
386 locomotion. Here, we sought to extend this line of work to investigate whether step-cycle
387 phase would also impact upon judgements of audio-visual synchrony. For this analysis, we
388 divided each participant's step-cycle into five quintiles (binning according to the 1-20%, 21-
389 40%, 41-60%, 61-80% and >80% step-cycle percentiles) and focused on the shortest SOA
390 condition (+40 ms) which was closest to the point of subjective simultaneity (PSS), and
391 ensured that the entire stimulus sequence would be 60 ms in duration (e.g. 20 ms visual
392 flash, 20 ms gap, 20 ms auditory click = 40 ms SOA, 60 ms total duration). This focus
393 ensured that both stimuli would be shown in either a single step-cycle quintile or
394 neighbouring step-cycle quintiles (see Methods), facilitating an analysis of how step-cycle
395 phase may impact perceived simultaneity judgements. We note that analysing the impact of
396 step-cycle phase for longer SOAs is also possible but problematic to interpret, as the
397 asynchronous stimuli will be presented in separate phases or steps as SOAs increase. For
398 comparison, we present changes in simultaneity judgements across the three shortest SOAs
399 (-50, +40, +130; **Figure 4**).

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401 **Figure 4** displays the proportion of 'same' responses for these shortest SOAs,
402 including SOA +40 ms which was closest to the point of subjective simultaneity. At this SOA
403 the proportion of 'same' responses decreased around the time of footfall. We formally tested
404 for this quadratic trend using mixed-effects models and likelihood ratio tests, and found a

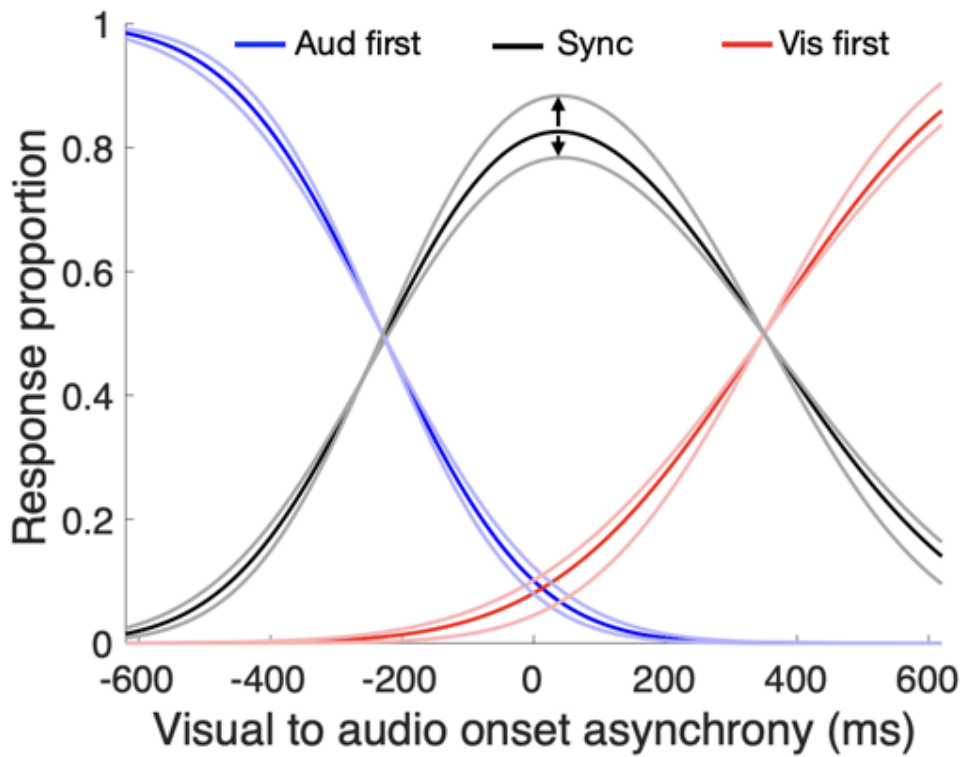
404 quadratic model (with random intercepts per participant) was a significantly better fit than the
 405 basic model that included only random intercepts per participant (quadratic vs basic: $\chi^2(2) =$
 406 11.11 , $p = .004$, $\beta = -0.012$ [-0.02, -0.005]) as well as a simple linear model (quadratic vs
 407 linear: $\chi^2(1) = 11.10$, $p = 8.6 \times 10^{-4}$). The two neighbouring SOAs (auditory leading -50 ms,
 408 visual leading +130 ms) demonstrated no impact of step-cycle quintile on synchrony
 409 judgements, as neither the linear or quadratic models were a better fit than the basic model
 410 ($ps > .4$).

411 In summary, at the shortest SOAs closest to the point of subjective simultaneity,
 412 synchrony judgements are altered by step-cycle phase in a quadratic manner. Judgements
 413 of synchrony for SOAs at the point of subjective simultaneity decrease around the time of
 414 footfall.
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Figure 4. Proportion 'same' responses at short SOAs are modulated by step-cycle quintile. **a)** Grand average detrended change in head-height at slow (blue) and natural (red) walking speeds during a single step. Note to facilitate step-cycle comparisons, each step is normalised to 1-100% step cycle completion. **b)** Average head-height using both speeds over a single step, with step-cycle quintiles overlaid. **c)** Average trial count per step-cycle quintile for the three shortest SOAs (-50, +40, +130 ms, shown in dark-grey, yellow, light-grey, respectively). **d-f)** Proportion same responses per this selection of SOAs. Only the shortest SOAs closest to the PSS (+40 ms) were significantly modulated by step-cycle quintile.



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431 **Figure 5. A modulation of proportion synchronous responses driven by changing**
 432 **auditory and visual timing precision over the step cycle.** Based on independent
 433 channels models (e.g., (Sternberg & Knoll, 1973)) commonly used to explain relative timing,
 434 variations in the slope of component psychometric functions will alter the peak synchrony
 435 value. If component slopes were steepest during the swing phase of the step cycle, as
 436 implied by previous results (Davidson et al., 2024), then peak synchrony judgements would
 437 also modulate with the step cycle and peak in the swing phase, as observed in **Figure 4E**.

438

Discussion

440 Here we investigated perception of audio-visual synchrony during locomotion, testing
441 whether synchrony perception would be affected by walking speed and whether it would vary
442 with the phase of the stride cycle. Participants walked at slow and natural walking speeds in
443 a wireless virtual-reality environment indicating whether pairs of audio-visual stimuli were
444 synchronous or not, responding as quickly as possible. We compared the proportion of
445 'synchronous' judgements and reaction-times to stimuli presented at randomly jittered
446 intervals as participants walked a straight and level path. Overall, the effect of slow walking
447 was to increase the probability of 'synchronous' judgements and to increase reaction time.
448 An asymmetry was also observed such that walking slowly most strongly affected the visual-
449 leading rather than auditory-leading stimulus pairs. To examine whether synchrony
450 perception modulated with the phases of the step cycle, we analysed the shortest SOA
451 which corresponded closely to the point of subjective simultaneity and found that the
452 proportion of synchronous responses rose and fell across the course of a single step. Step
453 cycle phase modulated responses in a quadratic manner, with synchronous responses being
454 lower around the time of footfall at the start and end of each step and higher in the swing
455 phase. Together these results reveal that walking speed and step cycle phase both affect
456 the perception of multisensory synchrony and extend recent unisensory work showing that
457 visual detection is modulated by the stride cycle while walking at a natural speed (Davidson
458 et al., 2024).

459 ***Walking at slow speed impairs audio-visual synchrony judgements***

460 A key finding was that synchrony perception depended on walking speed, with the
461 width of Gaussian functions fit to the proportion of synchronous responses being broader
462 when walking slowly. The overall proportion of synchronous percepts was also higher, and
463 reaction times slower during the slow walk condition. This broadening of the synchrony
464 function in slow walking is effectively a decrease in sensory precision arising from a
465 degraded ability to distinguish the offset of the visual and auditory events.

466 What might underlie this change in sensory precision during walking? Relative timing
467 judgements have previously been explained by independent component models (Sternberg
468 & Knoll, 1973). In these models, a change in synchrony width would be modelled by
469 shallower psychometric functions for the auditory and visual components respectively (see
470 **Figure 5**). In our analysis, there was no difference in the point of subjective simultaneity (i.e.
471 the Gaussian mean) between slow and natural walk speeds, meaning the effect of slow
472 walking was confined to a change in the slope of the component psychometric functions,
473 rather than a shift in their means.

474 The main factors that cause a broadening of psychometric functions, and thus
475 degraded precision, are a poorer signal-to-noise ratio in the stimulus or a reduction in
476 attentional resources applied to the task. The act of locomotion likely creates a degree of
477 noise and disruption to perception, and this would apply similarly to slow and natural
478 walking. The explanation of the broader synchrony function during slow walking may have to
479 do with increased attentional demands and effort required to walk at a slower than natural
480 pace.

481 Indeed, humans exhibit a remarkably narrow distribution of step rate when walking at
482 a natural speed that is centred on a mean value close to two steps per second,
483 corresponding to a peak in biomechanical efficiency (McNeill Alexander, 2002; Zarrugh et

484 al., 1974). Walking faster than this preferred rate requires more effort and, on a naïve view,
485 slow walking would seem to require less effort than the preferred rate. Curiously, however,
486 this is not the case. There is a U-shaped function of effort over walk speed, with both slow
487 and faster speeds requiring more effort (Ralston, 1958) When walking slowly, the attraction
488 to this inherently efficient and preferred speed must be overcome by a wilful, top-down
489 inhibition of the low-level, spinal circuits that drive the walking oscillation (Schubert et al.,
490 1999). We speculate that this effort draws away cognitive resources that would otherwise be
491 free to be deployed on the synchrony judgement. The effect of deploying less cognitive
492 resources could reduce sensitivity on the task either by broadening the component
493 psychometric functions (as shown in **Figure 5**) or by reducing signal salience. For example,
494 participants have shown a greater propensity to judge stimuli as synchronous at low intensity
495 than at high intensity, thus affecting the width of the synchrony function (Krueger Fister et al.,
496 2016). Consistent with these accounts, reaction times were also slower in the more effortful
497 condition of slow walking. Future experiments could arbitrate between the attentional and
498 effort accounts by measuring synchrony perception during locomotion employing a 2x2
499 factorial design, comparing low/high task demands with low/high efforts of locomotion.
500

501 ***Broad synchrony functions during action***

502

503 It is notable that our estimates for audio-visual synchrony derived from Gaussian fits
504 are broader than is typically reported. In this study, we fitted an asymmetric Gaussian to the
505 normalised mean data per participant (i.e., separate standard deviation estimates were fitted
506 to the left and right sides of the synchrony function, see **Figure 2B**) based on findings
507 showing that the left and right sides of the synchrony function often show a considerable
508 asymmetry (García-Pérez & Alcalá-Quintana, 2012; Yarrow et al., 2011). We therefore
509 defined the temporal band width of perceived synchrony as the sum of the left- and right-side
510 Gaussian standard deviations. Using this metric, we find full-width estimates of 457 ms and
511 520 ms for the natural and slow walk speeds, respectively. These values are large when
512 compared to the majority of other studies of audio-visual synchrony conducted with passive
513 participants. A survey of passive studies shows a mean synchrony window (twice the
514 Gaussian standard deviation) of about 335 ms, although values vary with task. It is inferred
515 to be about 200 ms by varying asynchronies in the McGurk effect (van Wassenhove et al.,
516 2007), as high as 400 ms using the stream/bounce illusion (Shimojo & Shams, 2001), 300-
517 400 ms using a standard flash/click stimulus (Alais et al., 2017; Lennert et al., 2021; Noel et
518 al., 2018; Van der Burg et al., 2018), and 300 ms using realistic dynamic audio-visual events
519 (Eg & Behne, 2015). Our values of 457 ms and 520 ms are considerably higher than other
520 reports.

521

522 The most salient feature to explain this key point of difference is our use of active
523 participants. This appears to be critical, as the only other study to measure the perception of
524 audio-visual synchrony in an active context reported a similarly large value of 520 ms (Arikan
525 et al., 2017). In that study, the effect of action upon synchrony percepts was assessed by
526 triggering audio-visual stimuli by a button press. They found that a contiguous action
527 broadened the window of perceived synchrony and that introducing a delay between the
528 action and the stimuli caused the window to become narrower. Based on this observation, it
529 appears that action around the time of a near-synchronous audio visual stimuli increases the

530 likelihood that they will be judged as synchronous. Here we can extend this result by
531 applying a similar interpretation to our participants, who made synchrony judgements during
532 the continuous action of walking. Thus, the only two studies of audio-visual synchrony in
533 active observers agree in reporting larger windows for perceived synchrony than is typical of
534 passive studies (reviewed above, with a mean of 335 ms). It remains to be seen whether this
535 effect on audio-visual synchrony judgements during locomotion would generalise to
536 synchrony of other multisensory stimuli such as tactile-vision and tactile-auditory stimuli.
537

538 Why would action impair synchrony perception? Executing an action is known to
539 produce periods of degraded perception around the time of the action. This is clear from the
540 literature on saccades which has demonstrated strong suppression of vision around the time
541 of saccades as well as distortions of perceived space and time (Ross et al., 2001). The
542 phenomenon of tactile suppression is similar and well established – a loss of tactile
543 sensitivity that occurs when reaching for objects or making other goal-directed movements.
544 This effect is also known as ‘movement-related gating’ and its time-course suggests that it
545 serves to suppress movement-related feedback during action, with suppression released in
546 time for contact and grasping so that perception is optimised when needed (Chapman et al.,
547 1987; Juravle et al., 2010). Walking also involves goal directed actions, yet much less is
548 known about how the act of locomotion impacts on perception. One recent study used a new
549 method to probe perception continuously over the stride cycle and found visual sensitivity
550 modulated approximately sinusoidally, peaking in the swing phase and reaching a minimum
551 during stance (Davidson et al., 2024). Although focused more on visual-motor control,
552 another recent study continuously measured reaching accuracy to a visual target over the
553 stride cycle and found similar modulations, with greater error in swing than stance phase
554 (Davidson et al., 2023). Overall, given the many ways action interacts to constrain
555 perception, it is not surprising that audio-visual synchrony during action would be less
556 precise than in passive observers, even if the precise causes are not clear at this stage.
557

558 ***Perceived synchrony modulates over the step-cycle***

559 The final observation of interest was that the point of maximum synchrony modulated
560 over the step cycle in a quadratic fashion, with peak synchrony occurring in the middle of the
561 swing phase (**Figure 4**). Based on the independent channels models commonly used to
562 explain relative timing (Sternberg & Knoll, 1973), variations in the slope of the component
563 psychometric functions will alter the peak synchrony value, as illustrated in **Figure 5**. Given
564 the prior evidence of visual performance modulating within the step cycle (Davidson et al.,
565 2024), and data forthcoming from our lab showing similar oscillations in auditory sensitivity
566 (Davidson et al., *in prep*), we propose that a steepening of component slopes during the
567 swing phase is what underlies the peak of perceived synchrony in the swing phase, as
568 observed in **Figure 4E**.
569

570 A final point to note is that more recent versions of the independent-channels model
571 (Sternberg & Knoll, 1973) have revised it to include a fourth parameter so that separate
572 estimates can be obtained of the width of the synchrony function on the left and right side of
573 the mean (García-Pérez & Alcalá-Quintana, 2012; Yarrow et al., 2011). For this reason, we
574 fit an asymmetrical Gaussian function with separate left and right side standard deviations
575 (see **Figure 2d**). The results revealed a significantly larger standard deviation on the right

576 side in the slow walk condition, which ties the reduced sensitivity to the right side that is
577 governed by visual timing precision. From these data we can conclude that there is a loss in
578 sensitivity to synchrony perception in general during slow walking relative to natural walk
579 speed, and, more specifically, that this loss is due to impaired sensitivity to visual timing
580 when walking slowly.
581

582 ***Conclusions***

583
584 Overall these data extend recent efforts to move from the seated tradition of laboratory
585 experiments into more ecologically plausible dynamic environments. By testing audio-visual
586 synchrony perception during a frequent everyday behaviour, we have revealed that recent
587 modulations in unisensory vision within the stride-cycle also extend to the perception of
588 multi-sensory timing.
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