1 **The human cerebellum is essential for modulating perceptual sensitivity based on temporal**

2 **expectations**

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4 SHORT TITLE: Cerebellar control of temporal attention

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14   Abstract

15   A functional benefit of attention is to proactively enhance perceptual sensitivity in space and time.

16   Although attentional orienting has traditionally been associated with cortico-thalamic networks,

17   recent evidence has indicated that individuals with cerebellar degeneration (CD) show reduced

18   reaction time benefit from temporal cues that entail an interval-based representation. While this

19   deficit might merely reflect impairment in anticipatory motor preparation, it is also possible that

20   the cerebellum contributes to the temporal modulation of perceptual sensitivity. To examine this,

21   we tested CD participants on a non-speeded challenging perceptual discrimination task, asking if

22   they benefit from temporal cues. Strikingly, the CD group showed no duration-specific perceptual

23   sensitivity benefit when temporal orienting relied on isolated interval representation, while

24   showing a comparable benefit to controls when the cues were defined by rhythmic sequences. This

25   dissociation further specifies the functional domain of the cerebellum, establishing its role in the

26   attentional adjustment of perceptual sensitivity in time.

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Introduction

Adaptive behavior is facilitated by an attentional system that can proactively modify the state of perceptual systems. While the majority of research on the underlying mechanisms has focused on spatial orienting, the brain is also anticipatory in time [1]. Temporal predictions for forthcoming sensory events are used to adjust attention in time, manifest in increased perceptual sensitivity at expected compared to unexpected times [2,3]. This form of anticipation has been associated with left inferior parietal and ventral premotor cortices [4–6], a network that overlaps with frontal-parietal components of the cortico-thalamic network implicated in attentional orienting in space [7–9].

Recently, we reported that individuals with cerebellar degeneration (CD) fail to exhibit reaction time benefits from temporal cues on a simple detection task [10,11]. These findings implicate the cerebellum in temporal preparation, and raise the possibility that it is involved in temporal control of attention to proactively modulate perception. However, reaction time benefits in speeded detection tasks from temporal cues may result from a change in perceptual sensitivity or from a change in motor preparation [3,12,13]. Given the well documented role of the cerebellum in precisely timed movement [14,15], the impairments we observed in the CD group may reflect a novel manifestation of the cerebellar role in the temporal control of motor preparation [16]. Determining the functional domain of the cerebellum in attention is critical to both models of attention and cerebellar function.

To address this question, we compared the ability of individuals with cerebellar degeneration (CD) and age-matched healthy controls to use temporal cues to benefit performance in a difficult non-speeded perceptual discrimination task. Participants judged the orientation of a briefly presented visual target. In each trial, a temporal cue indicated that the interval between the

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51   target and a preceding warning signal (WS) would either be 600 or 1000 ms (Figure 1A). Targets

52   mostly appeared at the cued time (valid trials) and rarely at the uncued time (invalid trials). The

53   target contrast was titrated to near-threshold level to make the task perceptually demanding and

54   participants could only respond after a substantial delay following target offset, eliminating the

55   need for motor preparation. With these manipulations, we assume that the expected performance

56   advantage on valid compared to invalid trials ('validity effect' [2,4,17–19]) will reflect temporally-

57   focused enhancement of perceptual sensitivity. If the cerebellum has a causal role in temporal

58   orienting at a non-motor, attentional level, the validity effect should be reduced in CD patients

59   relative to controls.

60   In addition to manipulating the validity of the temporal cue, we also varied the manner in

61   which this information was presented. In our previous work, we found that the cerebellar

62   involvement was limited to when temporal anticipation required encoding and recalling an isolated

63   interval, but not when temporal anticipation could emerge via synchronization with a stream of

64   rhythmic sensory events. We employ a similar manipulation in the present study, comparing

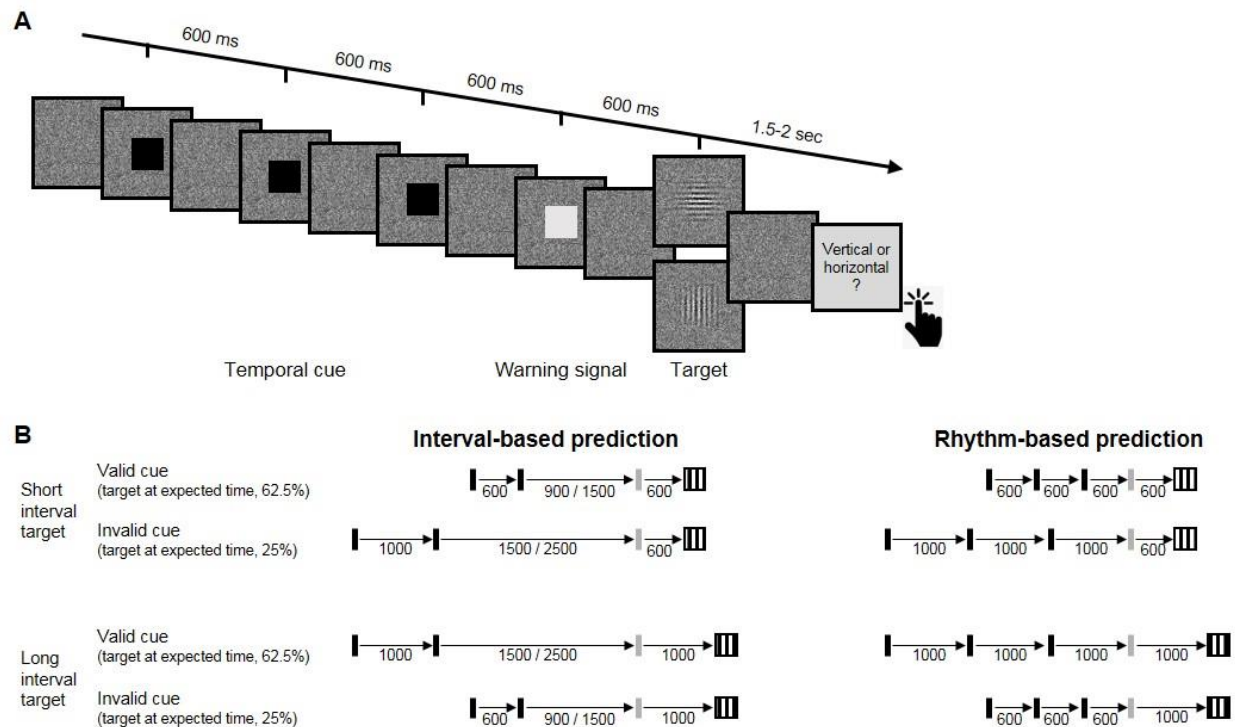65   attentional benefits from interval and rhythmic temporal cues (Figure 1B).

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Figure 1. Experimental task. A. Trial sequence, depicting a trial with the faster rhythmic temporal cue. Participants viewed a visual stream of black squares (temporal cue), followed by a white square (warning signal, WS), and then a luminance-defined Gabor grating (target). Participants made a delayed, non-speeded judgment of the orientation of the grating. Continuous dynamic masking was generated by a white noise visual stimulus mask that changed at 60 Hz. Whereas the black and white squares were highly visible when superimposed on the mask, the target was embedded in the noise, reducing its visibility. The target contrast was set on an individual basis using an adaptive procedure. **B.** Temporal cue conditions. The target could appear at a short (600 ms, top) or long (1000 ms, bottom) interval after the WS. Left: Interval task. Two black squares were separated by either the short or long interval, with a random non-isochronous interval between the second black square and the WS. On valid trials (62.5%), this interval matched the WS-target interval; on invalid trials (25%), it matched the other interval (with the remaining 'catch' trials containing no target). Right: Rhythm task. Three black squares and the WS appeared with identical SOA (short / long). Valid and invalid trials were as in the Interval task.

5

83   Results

84   Perceptual sensitivity was quantified using d', a measure derived from signal-detection

85 theory [20]. The benefits of temporal orienting or validity effect would be manifest as a larger d' on

86 valid trials compared to invalid trials. A 4-way omnibus analysis of variance (ANOVA) revealed

87 a significant validity effect across groups, tasks and target intervals (main effect of Cue Validity:

88 $F(1,23)=13.79$, $p=0.001$, $\eta_p^2=0.37$). Prior work has shown that the validity effect is less robust, or

89 even absent for late targets [17,21]. Thus, we developed an a priori analysis plan that focuses on the

90 early target trials to increase sensitivity for detecting attenuation of the validity effect (see

91 Methods). As expected, the validity effect was larger when the target appeared at the early onset

92 time (Cue Validity X Interval interaction: $F(1,23)=3.59$, one-tailed $p=0.035$, $\eta_p^2=0.14$). Indeed,

93 neither group showed a significant validity effect in either task for the late onset targets (all p's >

94 0.1).

95   Analysis of the d' values for early onset targets revealed a significant validity effect (3-

96 way ANOVA, $F(1,23)=14.74$, $p=0.001$, $\eta_p^2=0.39$). Across tasks, the validity effect was larger in

97 the Control compared to the CD group ($F(1,23)=5.05$, $p=0.034$, $\eta_p^2=0.18$), but this effect was

98 qualified by a significant Cue Validity X Group X Task interaction ($F(1,23)=4.52$, $p=0.044$,

99 $\eta_p^2=0.16$). We used a series of planned contrasts to evaluate the validity effect within each task.

100 For the Interval task (Figure 2A), the validity effect was significantly smaller in the CD group

101 relative to the Control group (2-way ANOVA, Cue Validity X Group interaction: $F(1,23)=7.11$,

102 $p=0.014$, $\eta_p^2=0.24$). The Control group showed a higher mean d' for valid compared to invalid

103 trials ($t(11)=3.08$, $p=0.01$, Cohen's d=0.89), while d' values in the CD group were not significantly

104 different, and even numerically higher on invalid trials ($t(12)= -0.43$, $p=0.67$, $BF_{10}=0.21$, moderate

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105   evidence against a directional hypothesis of a validity effect). Thus, the CD group failed to show

106   an enhancement in perceptual sensitivity from an interval-based temporal cue.

107   A different pattern was observed on the Rhythm task (Figure 2B). Here, the magnitude of

108   validity effect did not differ between the two groups (F(1,23)=0.09, p=0.77, η_p^2<0.01, BF$_{10}$=0.3).

109   The Control group again showed a validity effect (t(11)=2.69, p=0.021, Cohen's d=0.78).

110   However, unlike in the Interval task, the CD group also showed a validity effect (t(12)=3.36,

111   p=0.006, Cohen's d=0.93). Thus, the ability to increase perceptual sensitivity at a specific time

112   point based on a rhythm cue was preserved in the CD group. Furthermore, the presence of the 3-

113   way interaction implies that the attenuation of the validity effect in the CD group relative to

114   controls was significantly larger in the Interval task than in the Rhythm task.
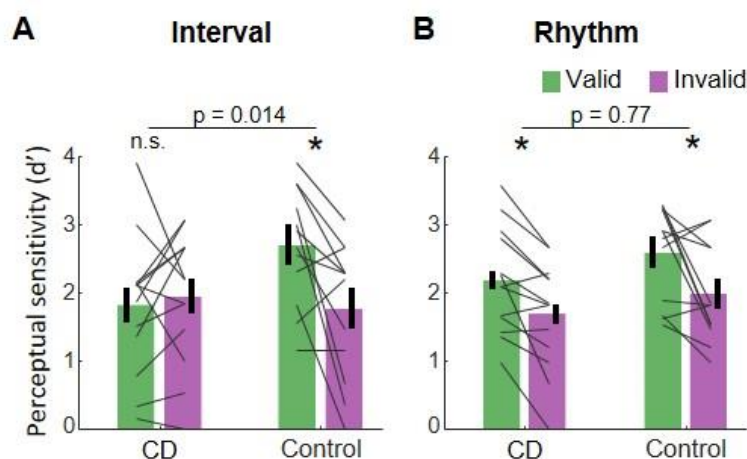
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118   Figure 2. Absence of validity effect in individuals with cerebellar degeneration in interval-based temporal
119   anticipation. A. Interval task. Mean d' for temporally expected (valid) and unexpected (invalid) for the CD
120   and Control groups. Unlike the controls, the CD group showed no increase in d' when the target appeared
121   at the expected time. B. Rhythm task. Both groups show a similar increase in d' on valid trials. * p<0.05.
122   In both A and B, error bars represent one standard error of the mean (SEM). Gray lines depict individual
123   subject data.

7

124   Discussion

125   Our results provide compelling evidence that the integrity of the human cerebellum is

126   necessary for proactive modulation of perceptual processing based on temporal expectations. The

127   ability to use a temporal cue to enhance perceptual sensitivity at specific times was abolished in

128   individuals with cerebellar degeneration when prediction was based on an interval cue. In contrast,

129   the CD group showed a comparable benefit to controls when temporal orienting was based on a

130   rhythmic cue. Critically, the use of a non-speeded, challenging perceptual discrimination task

131   argues strongly against the idea that the impairment is related to motor preparation processes.

132   Rather, the results point to an essential context-specific role of the cerebellum in the temporal

133   control of visual attention, adding to the substantial literature highlighting cerebellar involvement

134   in a broad range of cognitive functions beyond the motor domain [22].

135   These findings point to the need for an expanded picture of the neuroanatomical network

136   involved in attentional control. Attention research has traditionally emphasized cortico-thalamic

137   networks, and in particular, dorsal and ventral fronto-parietal networks associated with top-down

138   and stimulus-driven attention control, respectively [7–9]. For attention in the time domain, human

139   imaging studies consistently reveal activations of the left inferior parietal cortex and the ventral

140   premotor cortex [4–6]. Similarly, neural signatures of temporal anticipation identified in human

141   electrophysiology studies have been localized to cortico-thalamic circuits [23,24]. In general, the

142   cerebellum has not featured in this work (but see, for example [25]). This might reflect the difficulty

143   in neuroimaging studies to separate the effects of temporal prediction on neural activations from

144   the effects of other task parameters, or the difficulty of electrophysiology studies to measure

145   cerebellar sources.

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146   Our neuropsychological approach provides a more direct method to evaluate the

147   contribution of the cerebellum to attention. Previous work, focusing on the spatial domain, has

148   proven inconclusive. Some studies have found that individuals with focal cerebellar lesions show

149   reduced benefits from cues indicating the spatial location of a forthcoming stimulus [26,27]. However,

150   it has been proposed that these impairments may be motoric in nature, with the tasks confounding

151   attentional demands with demands on eye movements and/or response preparation [28,29]. These

152   concerns do not apply to the current study given that the spatial aspects of the task were fixed and

153   the motor requirements were minimal, delayed until well after stimulus offset. We note that the

154   current results do not address the question of whether the cerebellum, in addition to its role in

155   temporal attention, is also involved in other spheres of attention.

156   The dissociation between the impairment in the interval task and the preserved

157   performance in the rhythm task in the CD group has two important implications. First, a

158   longstanding debate in the timing literature concerns whether temporal anticipation in a rhythmic

159   context is mediated by rhythm-specific mechanisms (e.g., entrainment) or by the repeated

160   operation of an interval-based mechanism [19,30,31]. Our results are at odds with the latter hypothesis

161   given that the CD group failed to benefit from the interval cues yet showed normal benefits from

162   the rhythm cues.

163   Second, selective contributions of the cerebellum in interval-based but not rhythm-based

164   timing have been observed in multiple timing domains, including duration judgments, timed

165   movement, and timed motor preparation [10,11,32,33]. Our findings extend this functional specificity

166   to the attentional domain, pointing to a generalized role for the cerebellum in interval timing, at in

167   the sub-second range. Notably, while inferences from single dissociations such as that observed in

168   the present study can be limited by concerns about differences in task difficulty, this concern is

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169   alleviated by the comparable benefits observed in healthy controls from interval- and rhythm-

170   based cues [10,11,19] (also observed in current dataset: Cue Validity X Task interaction within the

171   Control group, F(1,11)=0.81, p=0.39, η_p^2=0.07).

172   Computationally, how might the cerebellum contribute to the control of attention in time?

173   Given the cerebellar involvement in interval-based timing across timing domains, an intuitive

174   hypothesis is that the cerebellum is necessary for the representation of isolated intervals [14,34]. By

175   this view, predictive processing in non-cerebellar circuits relies on cerebellar interval

176   representations to parameterize the temporal dimension of the prediction. In rhythm-based

177   orienting, an interval-based mechanism would not be required as the temporal parameters are

178   contained within ongoing neural dynamics. However, a broader hypothesis is that the interval-

179   based prediction itself is formed within the cerebellum, part of the cerebellar role in prediction in

180   the motor domain and beyond [22,35,36]. By this view, these cerebellar temporal predictions guide

181   proactive modulation in non-cerebellar circuits according to task goals (e.g., to prepare perceptual

182   or motor systems). In rhythm-based orienting, dedicated prediction mechanisms are not necessary

183   due to the self-sustaining limit-cycle properties of the putatively entrained oscillatory dynamics.

184   Future work should aim to explore the separability of timing and prediction, identifying the

185   cerebellar computations that provide the essential information for temporal orienting.

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187   Materials and Methods

188   **Participants**

189   15 individuals with cerebellar degeneration (CD) and 14 neurotypical control individuals

190   were recruited for the study. The data from two individuals from each group were discarded: One

191   was unable to perform the task, two showed no convergence on the staircase procedure used to

192   determine the perceptual threshold, and one asked to terminate the session prematurely. Thus, the

193   final sample size was 13 CD and 12 control participants. All participants provided informed

194   consent and were financially compensated for their participation. The study was approved by the

195   Institutional Review Board at the University of California, Berkeley.

196   Participants in the CD group 9 females, 12 right-handed, mean age=56.2 years, sd=11.1)

197   had been diagnosed with spinocerebellar ataxia, a slowly progressive adult-onset degenerative

198   disorder in which the primary pathology involves atrophy of the cerebellum. We did not test

199   patients who presented symptoms of multisystem atrophy. Eight individuals in the CD group had

200   a specific genetic subtype (SCA3=2, SCA6=3, SCA17=1, SCA35=1, AOA2=1) and the other 5

201   individuals had CD of unknown/idiopathic etiology. All of the CD participants provided a medical

202   history to verify the absence of other neurological conditions, and were evaluated at the time of

203   testing with the Scale for the Assessment and Rating of Ataxia (SARA, Schmitz-Hübsch et al.,

204   2006). The mean SARA score was 13.5 (sd=6.3). Control participants (8 females, 11 right-handed,

205   mean age=59.1, sd=10.2) were recruited from the same age range as the CD group, and, based on

206   self-reports, did not have a history of neurological or psychiatric disorders. The CD and Control

207   groups did not differ significantly in age (p=0.52).

208   All participants were prescreened for normal or corrected-to-normal vision and intact color

209   vision. We also screened for professional musical training or recent amateur participation in

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210   musical activities (e.g., playing a musical instrument or singing in a choir), with the plan to exclude

211   individuals with such experience (none did). All of the participants completed the Montreal

212   Cognitive Assessment (MoCA) as a simple assessment of overall cognitive competence. Although

213   we did not select participants to provide a match on this measure, there was no significant group

214   difference (CD: mean=26.7, Control: mean=27.5, p=0.32).

215

216   **Stimuli and task**

217   For the experimental task, participants discriminated the orientation of a masked visual

218   target, whose timing was cued on each trial (Figure 1). The target was a grayscale, luminance-

219   defined sinusoidal Gabor gratings (size: 400 x 400 pixels, 11 x 11 cm, 10° visual angle; spatial

220   frequency = 1 cycle/degree; Gaussian standard deviation = 2.5°) that was either oriented

221   horizontally or vertically. The target was embedded in a dynamic, white noise mask. This mask

222   was a square (size: 400 x 400 pixels) in which each pixel was randomly assigned a luminance

223   value between 0.25 to 0.75 (with 0 and 1 being black, RGB: [0,0,0] and white, RGB: [255,255,255]

224   respectively). The luminance value for each pixel in the mask was updated every 16.6 ms (once

225   per monitor refresh cycle) throughout the trial. The contrast of the target relative to the background

226   noise was adjusted for each participant (see below). Temporal cues were provided by black squares

227   (size: 200 x 200 pixels, 5.5 x 5.5 cm, 5° visual angle). All stimuli were created in MATLAB

228   (MathWorks, Natick, MA) and presented using the Psychtoolbox v.3.0 package for MATLAB

229   [38,39]. The stimuli were presented foveally on a gray background (RGB: [128,128,128]) on a 24-in

230   monitor (resolution: 1920 x 1080 pixels, refresh rate: 60 Hz) at a viewing distance of ~65 cm.

231   The dynamic noise mask remained visible throughout the duration of the trial. The other

232   stimuli were superimposed on this mask. The suprathreshold temporal cue involved the serial

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233   presentation of two or three black squares (100 ms duration each), with the first black square

234   always appearing 750 ms after the onset of the dynamic mask. The black squares were followed

235   by a suprathreshold white square, the warning signal (WS, also 100 ms duration), which was

236   followed in turn by the near-threshold target (50 ms duration) after either 600 ms (early target) or

237   1000 ms (late target). Note that given the screen refresh rate, the 50 ms target was successively

238   embedded in three different masks.

239   The dynamic noise mask remained visible until 1700 ms after WS onset regardless of the

240   target timing (1100 ms after early target onset, 700 ms after late target onset). 400-900 ms

241   (randomly jittered) after the termination of the dynamic mask, the participant was cued to make a

242   non-speeded response, indicating the perceived orientation of the target (e.g., *"vertical (press X)*

243   *? horizontal (press M)"*). Responses were made with the X and M keyboard keys, assigned

244   randomly for each participant and fixed for the entirety of the experiment.

245   Two types of sequences, tested in separate blocks, were used to provide temporal cues. In

246   the Interval task, the sequence consisted of two black squares, with a stimulus onset asynchrony

247   (SOA) of either 600 ms (short cue) or 1000 ms (long cue). The SOA between the second black

248   square and WS was randomly set on each trial to be either 1.5 or 2.5 times the cue interval on that

249   trial (short cue trials: 900 / 1500 ms; long cue trials: 1500 / 2500 ms), strongly reducing any

250   periodicity between the timing of the cue and target [19]. In the Rhythm task, the sequence consisted

251   of three black squares, presented periodically with an SOA of 600 ms (short cue, equivalent to

252   1.66 Hz) or 1000 ms (long cue, 1 Hz). The SOA between the third black square and WS was the

253   same duration as the cue SOA for that trial. Thus, the WS fell on the "beat" established by the

254   temporal cues.

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255   In both tasks, the SOA between the WS and target was either the same SOA as defined by

256 the temporal cue (valid trial, 62.5% of trials) or the non-cued SOA (invalid trials, 25% of trials).

257 This ratio was selected to incentivize the participant to use the temporal cues to facilitate

258 performance on this challenging task. On the remaining 12.5% of the trials, no target was

259 presented. We included these catch trials to discourage participants from re-orienting their

260 attention in time to the long interval when they failed to detect an early onset target.

261

262 **Procedure**

263   Upon arrival, all participants provided consent, demographic information, and completed

264 the MoCA. The CD participants also provided their clinical history and were evaluated with the

265 SARA.

266   The experiment was conducted in a quiet, dimly lit room. The session began with a

267 familiarization stage, in which participants performed four practice trials with 100% target contrast

268 followed by four with 40% target contrast. The latter were included to demonstrate to the

269 participants how difficult it could be to make a simple orientation judgment when the contrast of

270 the target was similar to that of the mask.

271   Following this familiarization phase, we used an adaptive method to determine, on an

272 individual basis, the target contrast level expected to produce discrimination accuracy of ~79%

273 (descending staircase procedure, 3 down 1 up, step size = 2%, 10 reversals [40]). We opted to target

274 79% accuracy to provide sufficient room to detect improvement (to a ceiling of 100%

275 performance) or impairment (to a floor of 50% performance). Importantly, for this adaptive

276 procedure only rhythmic temporal cues were used, and the target always appeared at the expected

277 time (valid). Our reasoning here was that if the CD group were able to use the temporal cues to

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278   modulate perception, it is more likely to occur in this task (and have a similar threshold value as

279   controls) given previous work showing that these individuals are not impaired in utilizing rhythmic

280   temporal cues [10]. In this way, we would be positioned to ask if the CD group showed an impaired

281   validity effect in the Rhythm task as well as overall performance (valid and invalid trials) on the

282   Interval task. The contrast level identified from the adaptive procedure for a given individual was

283   used in the main experiment for both tasks. Consistent with our expectation, the mean contrast

284   level did not differ between groups ($t(23)=0.83$, $p=0.41$).

285   In the main experiment, participants preformed four blocks of each task, alternating

286   between Rhythm and Interval blocks (8 blocks total). Each block consisted of 32 trials, 16 with

287   the short temporal cue and 16 with the long temporal cue. Of these 16 trials, the target appeared at

288   the cued time on 10 trials (valid), the uncued time on 4 trials (invalid), and did not appear on 2

289   trials (catch). When present, the target was horizontal on 50% of the trials and vertical on the other

290   50% of the trials. Short breaks were provided between each block.

291   To ensure that the target contrast fell in a range that would be optimal for detecting a

292   validity effect, we calculated the averaged performance on valid trials across the two tasks after

293   each pair of blocks. If the value was higher that 95%, we reduced the target contrast for subsequent

294   blocks by 4%, and if it was lower than 60%, we increased it by 4%. Block pairs in which

295   performance was above 95% or below 60% were not included in the d' analyses (8 excluded blocks

296   across all participants; exclusion had no impact on the statistical tests).

297   Prior to the first block for each task, the experimenter demonstrated the trial sequence and

298   then conducted practice trials until the participant could describe how the cues were predictive of

299   the onset time of the target. For subsequent blocks, the participant first completed two practice

300   trials as a reminder of the format for the temporal cues in the forthcoming block. Participants

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301   received feedback on their performance after these practice trials (but not after any of the staircase

302   or experimental trials).

303

304   **Statistical analysis**

305   To quantify discrimination performance, we calculated for each participant a d-prime (d')

306   score separately for each combination of task, target interval and cue validity. These values were

307   calculated by subtracting the z-score of the percentage of hits from the z-score of the percentage

308   of false alarms (referring to vertical and horizontal categories as "stimulus present" and "stimulus

309   absent", respectively, in classic signal detection terminology). As the "hit" category was arbitrarily

310   assigned to one orientation and the two orientations were equally probable, we did not calculate or

311   analyze the criterion index. An increase in perceptual sensitivity due to temporal anticipation

312   should be manifest as an increase in d' when the target appeared at the expected time compared to

313   when it appeared at the unexpected time (validity effect).

314   Previous work indicates that validity effects from temporal cues in two-interval designs

315   such as that used here are usually attenuated for late onset targets, either due to re-orienting of

316   attention in time or foreperiod effects [21]. As such, our *a priori* plan was to focus on the short

317   interval trials to increase sensitivity for detecting attenuation of the validity effect. To confirm that

318   this pattern was present in our data, d' values were analyzed using an omnibus 4-way mixed

319   ANOVA with a between-subject factor Group (CD / Control), and within-subject factors Task

320   (Interval / Rhythm), Target Interval (Early / Late) and Cue Validity (Valid / Invalid). As expected

321   (see Results), we observed a significant interaction of Cue Validity and Target Interval, and post-

322   hoc comparisons showed that the validity effect was only significant in the Early Interval

323   condition.

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324 The d' values for short interval targets were analyzed using a mixed ANOVA with a

325 between-subject factor Group (CD / Control), and within-subject factors Task (Interval / Rhythm)

326 and Cue Validity (Valid / Invalid). To assess the effect of cue validity within each group and task,

327 we used within-subject t-tests. To compare the cue validity effect between groups within each task,

328 we used a mixed ANOVA with factors Group (CD / Control) and Cue Validity (valid / invalid).

329 Finally, to assess context-specificity within the CD group, we performed an orthogonal contrast,

330 comparing the cue validity effects between tasks using a repeated-measures ANOVA with factors

331 Task (Interval / Rhythm) and Cue Validity. In all analyses, effect sizes were estimated using

332 Cohen's d and partial eta-squared (η_p^2).

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