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4	Hemisphere-Specific Properties of the Ventriloquism Aftereffect
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16	Running Title: Hemisphere-Specificity of Ventriloquism
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### ABSTRACT (100 words max)

Visual calibration of auditory space requires re-alignment of representations differing 24 in 1) format (auditory hemispheric channels vs. visual maps) and 2) reference frames (head-25 26 centered vs. eye-centered). Here, a ventriloquism paradigm from Kopčo et al. [J Neurosci, 29, 27 13809-13814] was used to examine these processes in humans for ventriloquism induced within 28 one spatial hemifield. Results show that 1) the auditory representation can be adapted even by 29 aligned audio-visual stimuli, and 2) the spatial reference frame is primarily head-centered, with 30 a weak eye-centered modulation. These results support the view that the ventriloquism 31 aftereffect is driven by multiple spatially non-uniform, hemisphere-specific processes.

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#### 38 **1. Introduction**

39 Vision plays an important role in calibration of auditory spatial perception. In the 40 "ventriloquism aftereffect" (VAE), repeated presentations of spatially mismatched visual and 41 auditory stimuli produce a shift in perceived sound location that persists when the sound is 42 presented alone (Canon, 1970; Recanzone, 1998; Woods and Recanzone, 2004; Bertelson *et* 43 *al.*, 2006). The brain mechanisms that support this process are mysterious because spatial 44 representations seem to differ in vision and in hearing in two ways.

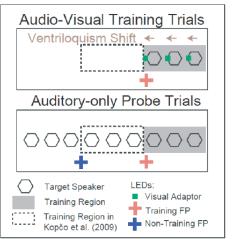
First, visual space is initially encoded relative to the direction of the eye gaze, while the cues for auditory space are first computed relative to the orientation of the head (Groh & Sparks, 1992). A means of reconciling this discrepancy in reference frames (RF) is necessary to achieve correct recalibration. Our previous study suggests that a mixture of eye-centered and head-centered RFs are associated with recalibration in the central region of the audiovisual field (Kopco *et al.*, 2009).

51 Second, there is growing evidence that, in mammals, auditory space is encoded non-52 homogeneously, based on two (or more) spatial channels roughly aligned with the left and 53 right hemifields of the horizontal plane (Grothe *et al.*, 2010; Groh, 2014). This is markedly 54 different from visual spatial codes, in which the retinal surface provides a map of the position 55 of stimuli in the environment.

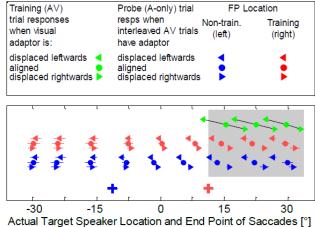
Thus, the process of using visual information to recalibrate auditory space is multifaceted, and may operate differently in different portions of the environmental scene. Indeed, differential patterns of adaptation across auditory space have been observed (Phillips and Hall, 2005; Maier *et al.*, 2010), suggesting that the auditory code in humans likely employs the same two-channel scheme that has been observed in animal species (Salminen *et al.*, 2009).

Here, we tested whether the spatial characteristics of the ventriloquism aftereffect
induced in the audiovisual periphery (i.e., in a single hemifield) differ from those occurring

63 when the aftereffect is induced in the central region (i.e., covering both hemifields; Kopco et 64 al., 2009). Persistent visually driven biases in perceived sound location were induced. As in Kopco et al. (2009), we presented mismatched (5°-shifted) audio-visual (AV) stimuli in only 65 66 a subregion of space (Fig. 1A, top panel), but this time the training region was peripheral, 67 rather than central, to the fixation point used for these trials. We evaluated the effects of this pairing on saccade accuracy for interleaved auditory-only trials both from that fixation point 68 69 and a non-training fixation point in the opposite hemifield (Fig. 1A, bottom panel). As was the case for our previous study involving central training, the pairing of a displaced 70 71 visual stimulus induced a local aftereffect in the peripheral trained region. Contrary to the 72 previous study, this aftereffect appeared to be mostly in the head-centered reference frame, as 73 the contribution of an eye-centered component was not readily apparent. However, we also 74 observed biases related to the location of the fixation point, even when the AV stimuli were 75 aligned. Together, these findings confirm the contribution of multiple signals related to 76 different reference frames and representational formats across the horizontal space.



#### A) Audio-Visual Display



### B) Raw Saccade Endpoints

Figure 1: Experimental set-up and raw experimental data. A) Audiovisual display used to present 79 the AV training stimuli in one experimental block. At the beginning of each AV training trial (top), the 80 subject had to fixate on the same initial fixation point (FP); then, the training stimulus was presented from

81 one of three locations lateral to the FP, keeping the direction of the induced shift the same within a block 82 (by consistently presenting the visual adaptor displaced to the left, to the right, or aligned with the target 83 speaker). On the auditory-only probe trials (bottom), the same nine speaker locations and two FPs were 84 used in all blocks. The probe trials were randomly interleaved among the training trials and the FP and 85 target locations varied randomly from trial to trial. Dashed frame indicates the central training region 86 used in Kopco et al. (2009). B) Raw saccade endpoints of the responses to the AV training stimuli and 87 auditory-only probe stimuli as a function of the actual target speaker location, collapsed across time. The 88 symbols represent across-subject mean responses (+/-1 SEM indicated by horizontal lines) in different 89 audiovisual conditions (see legend), separately for the training trials (green), probe trials starting at the 90 training fixation (red), and probe trials starting at the non-training fixation (blue). Graphs for each 91 measurement type are plotted in one row, vertically offset from data for other types, for visual clarity. The 92 A-only data corresponding to each target location are approximately aligned with that target location. For 93 the AV data, the dashed lines connect symbol triplets for the same auditory target when presented with 94 one of the three different visual adaptors (the AV-aligned data are located approximately at the 95 corresponding target location). 96

### 97 **2. Methods**

98 All procedures and equipment closely matched those used in Kopco *et al.* (2009). 99 General methods. Experiments were performed in an experimental lab in the Boston 100 University Hearing Research Center. Subjects made eye movements from a visual fixation 101 point to a broadband noise delivered from loudspeakers in darkness. On training trials (Fig. 102 1A, top), visual stimuli were presented simultaneously with the sounds, using light-emitting 103 diodes (LEDs) displaced from the locations of the speakers or aligned with them. On 104 randomly interleaved probe trials (Fig. 1A, bottom), only the auditory stimuli were presented. 105 Subjects. Seven young adults with normal hearing by self-report participated. The 106 experimental protocols were approved by the Boston University institutional review 107 committee.

Setup. Subjects were seated in a quiet darkened experimental room in front of an array of speakers and LEDs (Fig. 1). To keep the head-centered RF fixed, the subjects' heads were restrained by a chin rest. Subjects' behavior was monitored and responses were collected by an infrared eye tracker, calibrated using visually guided saccades to selected target locations at the beginning of each session.

113 Stimuli. Sounds were 100-ms broadband noises (0.2–6 kHz) with 10 ms on/off ramps 114 presented at 70 dBA from speakers mounted in the horizontal plane ~1.2 m from the center of 115 the listener's head. Spacing between speakers was 7.5°. For the training AV stimuli, only the 116 speakers at the locations 15°, 22.5°, and 30° were used (Fig. 1A). The LEDs for the AV 117 stimuli were mounted so that they were either horizontally aligned with the speakers or 118 displaced (either to the left or to the right) by 5°. They were turned on and off in synchrony 119 with the corresponding speakers. Two additional LEDs 10° below the speaker array served as 120 fixation locations (azimuths of  $\pm 11.8^{\circ}$ ).

121 Procedures. Trials began with the onset of one of the two fixation LEDs. After
122 subjects fixated the LED for 150 ms, the fixation LED was turned off and the AV or A-only
123 stimulus was presented. The subjects performed a saccade to the perceived location of the
124 stimulus. The saccade end point was recorded at the saccade end, i.e., when the eye fixation
125 was sustained at the same location for 150 ms, at which point the experiment continued with
126 the next trial. In both AV and A-only trials, the subjects were instructed to look to the location
127 of the auditory component of the stimulus.

Training (AV) and probe (A-only) trials were randomly interleaved at a ratio of 1:1. Training stimuli were presented from one of the 3 training locations while the subject fixated the training fixation point (FP; top panel of Fig. 1A). Probe stimuli were presented from one of the 9 speakers, while the subject fixated either the training or the non-training FP (bottom panel of Fig. 1A).

Trials were run in sessions with a consistent AV pairing (leftward, rightward, or no shift). Each session started with a pre-adaptation reference measurement (18 A-only trials from the training fixation point), followed by 720 trials in which the training fixation point and the AV shift direction was fixed. Each subject performed 12 sessions (2 fixation points x 3 shift directions x 2 repeats) in order that was randomized across the subjects.

138 Data analysis. Data from the first quarter of each session were excluded to remove 139 transitory values observed during the initial buildup of VAE. Within-session averages were 140 computed from the remaining data separately for each combination of target location, training 141 FP location, fixation position, and condition. Since no large left-right differences were 142 observed, data with training FP on the left were mirror-flipped and combined with the data 143 with training FP on the right (see Table 1). All data are presented as across-subject means and 144 standard errors of the mean, with the training FP always shown on the right and the non-145 training FP on the left. Repeated measures ANOVAs were used to assess statistical 146 significance of the observed effects.

147 **3. Overall Design and Results** 

148 As in Kopco et al. (2009), we presented paired visual-auditory stimuli in a subregion 149 of audiovisual space, fixed in both eye- and head-centered coordinates. We used one initial 150 eye fixation position on training trials and presented the discrepant audiovisual stimuli from a 151 restricted spatial range that was lateral with respect to the fixation point (see Fig. 1A, top). 152 Because the visual training was local, we could test the spatial attributes of the resulting 153 recalibration by shifting fixation on probe trials. Specifically, on interleaved auditory-only 154 probe trials, we varied initial eye position (FP) with respect to the head (which was fixed) and 155 presented sounds from all target locations spanning both the same head-centered locations and 156 the same eye-centered locations as on the training trials (see Fig. 1A, bottom). We first

157 consider the effects observed on the AV training trials themselves before turning to aspects of
158 how the effects generalize to the auditory-only conditions across both the trained and
159 untrained regions of space as a function of eye-referenced vs. head-referenced fixation
160 position.

161 3.1 Ventriloquism effect

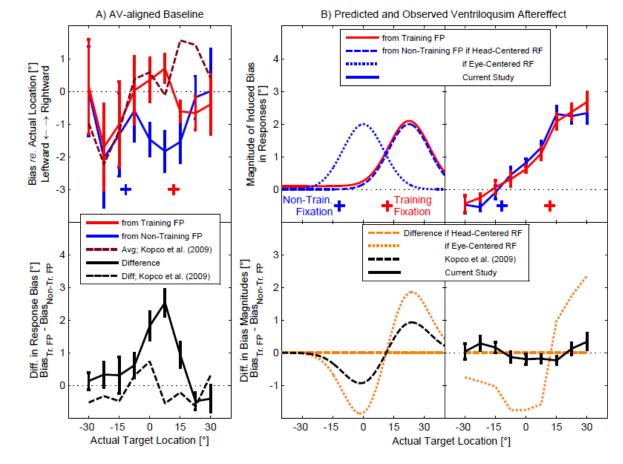
162 A strong ventriloquism *effect* – or capture of the auditory stimulus location by the 163 visual stimulus on combined AV trials - was observed. Green symbols in Fig. 1B show the 164 raw responses. When the AV stimuli were aligned, the average responses were not biased at 165 all. The relative strength of the ventriloquism effect was evaluated as percent of shift in 166 responses towards the visual (V) component re. the A-component on misaligned AV trials, 167 which was for each A target location and V-component shift computed as (resp V-misalign - resp168  $V_{v-align}$  / (stim  $V_{v-misalign} - stim _{v-align}$ ), where stim is the actual location of the V-component. The 169 strength ranged from 96% for the target at 15° to 82% for the target at 30° (averaged across 2 170 directions of induced shift). Even though there was a slight decrease in the strength of the 171 ventriloquism effect for the most lateral targets, it was expected that, as in Kopco et al. 172 (2009), this strong ventriloquism *effect* would be associated with a clear local ventriloquism 173 aftereffect.

174 3.2 Gaze-dependent Effects During AV-aligned Baseline

We next assessed the auditory-only responses interleaved with the spatially aligned AV stimuli. The red and blue circles in Fig. 1B show these responses. Overall, the pattern of results shows that the subjects accurately localized the auditory targets, showing a systematic displacement of the responses with the actual target locations. To analyze the impact of the visual training in more detail, the top panel of Fig. 2A shows the biases in these responses relative to the actual target location, separately for the two fixation points. A gaze-directiondependent adaptation is seen when comparing the responses from the training FP (red) to

182 those from the non-training FP (blue). Specifically, the responses to the targets at azimuth of 0°-15° were biased to the left by 1°-2.5° when performed from the non-training FP (blue "+" 183 184 symbol) compared to the responses from the training FP (red "+" symbol). A dashed line in 185 this panel represents the same data from the central-adaptation experiment of Kopco et al. 186 (2009), averaged across the two FP locations as no large FP-dependent differences were 187 observed in that study. A solid black line in the bottom panel of Fig. 2A shows the difference 188 between the red and blue lines from the top panel, while the dashed line represents the 189 difference from the central-adaptation experiment of Kopco et al. (2009). These panels show 190 that responses to auditory-only stimuli from AV-trained locations that are lateral and near the 191 training FP differ depending on whether eyes fixate within the same hemifield or the opposite 192 hemifield. On the other hand, when the AV training locations are in the center, covering both 193 hemifields, no such differential effect of fixation location is observed (dash-dotted line). A 194 one-way repeated measures ANOVA performed on the difference data showed a significant 195 effect of target location ( $F_{8,48} = 9.45$ , p < 0.001). This effect of eye fixation direction is strong, 196 of size comparable to the VAE (see next section); thus, there is some eye-gaze-dependent 197 contribution to responses to auditory-only stimuli even when vision is not used to induce any 198 recalibration of the auditory spatial representation. However, this contribution is only visible 199 if the AV stimuli are presented within one spatial hemifield. Overall, the pattern of results in 200 the top panel of Fig. 2A for both experiments is that, independent of FP location, the 201 responses are mostly accurate in the trained region (all errors are much smaller than 1°, except 202 for the blue data point at 15°), while they tend to be biased away from the training region 203 outside of it (except for the left-most data point). This bias away is observed in all the non-204 training subregions for both FPs and both experiments, with the exception of the trained-FP 205 data in the central region in the current experiment (3 red central targets in Fig. 2A are

206 approximately at 0°). Thus, the gaze-specific adaptation, which is observed in the same 207 region, is likely caused by this lack of repulsion in the trained-FP central data.



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210 Figure 2. Adaptation induced by AV stimuli. A) Average bias in A-only responses in the AV-211 aligned baseline condition as a function of the actual target location. Top panel shows mean response 212 biases (±SEM) when eyes are fixated at the training FP (red) and the non-training FP (blue). In addition, 213 the across-FP average data for central adaptation from Kopco et al. (2009) are shown for comparison 214 purposes (dashed line). The solid line in the bottom panel shows the difference between responses from 215 training FP and the non-training FP. The dashed line shows the difference for taken from Kopco et al. 216 (2009). B) Predicted and observed ventriloquism aftereffect. The top left panel plots the expected pattern 217 of biases induced in the A-only probe responses when preceding AV trials are presented in the training 218 region (15° - 30°). Red line shows predictions when the eyes fixate the training FP (i.e., the FP location 219 used during AV training trials). Dash-dotted blue line shows expected results from the non-training FP if 220 the RF of adaptation is head-centered, while dashed blue line shows expected results for an eye-centered

221 **RF.** The bottom panel shows the differences between the expected bias magnitudes from the training 222 versus the non-training FPs in the two RFs in orange. For comparison, the black dashed line sketches the 223 results corresponding to the mixed RF observed after VAE was induced in the central region in (Kopco et 224 al., 2009). Top right panel shows the across-subject mean (±SEM) difference between the auditory 225 saccade end point locations when interleaved with spatially displaced AV stimuli vs. when interleaved 226 with AV-aligned stimuli, collapsed across the direction of the AV displacement. The solid black line in the 227 bottom right panel shows the effect of initial fixation position on the magnitude of the induced shift as the 228 across-subject mean (±SEM) difference between the shifts from the training and non-training FPs (i.e the 229 difference between the red and blue lines). Orange lines show the predictions of the difference for the two 230 reference frames based on the training FP data (red) from the top right panel.

231

## 232 3.3 Ventriloquism Aftereffect and its Reference Frame

233 The expected pattern of ventriloquism aftereffect, and the predictions about the 234 reference frame based on it, are illustrated in the left-hand panels of Fig. 2B. The red line in 235 the top left panel shows the predicted magnitude of the aftereffect induced by the AV stimuli, 236 peaking in the trained region  $(15^{\circ} - 30^{\circ})$  when assessed with eyes fixating the training FP. If 237 visually induced spatial plasticity occurs in a brain area using a head-centered RF, then shifts 238 in perceived sound location should occur mainly for sounds at the same head-centered 239 locations (in Fig. 2B, dash-dotted blue line matches the red line). Conversely, if plasticity 240 occurs in an eye-centered RF, then visually induced shifts should occur mainly for sounds at 241 the same eye-referenced locations (dotted blue line is shifted to the left of the red line by the 242 same displacement as the non-training FP is shifted relative to the training FP). The bottom 243 left panel summarizes the predicted results if evaluated as a difference between the responses 244 from the training and non-training FPs. The dash-dotted orange line shows the difference between the red and dash-dotted blue lines, corresponding to the expected results if the 245 246 reference frame is head-centered. The dashed orange line shows the difference between the

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red and dashed blue lines, corresponding to the expected results if the reference frame is eyecentered. The dashed black line shows the predicted difference in the biases expected if the
RF is mixed, as observed in Kopco *et al.* (2009), in which case it should fall approximately in
the middle of the predictions of the two RFs shown in orange.

251 We assessed the auditory-only responses interleaved with the spatially mis-aligned AV 252 stimuli against these predictions. The red and blue triangles in Fig. 1B show the raw 253 responses in the conditions in which the ventriloquism aftereffect was induced in a leftward 254 direction (leftward-pointing triangles) or rightward direction (rightward-pointing triangles). 255 Overall, exposure to spatially mismatched AV stimuli resulted in a shift of responses to 256 sounds in the direction of the previously presented visual stimuli (compare the corresponding 257 triangles to the respective circles). To allow a detailed analysis of the results comparable with 258 the predictions of Fig. 2B, the red line in the top right panel of Fig. 2B plots the magnitude of 259 the bias in responses measured with eyes fixating the trained FP (red plus sign) re. no-shift 260 baseline from Fig. 1B, as a function of target location and averaged across the two directions 261 of induced shift (note that no main effect or interaction involving the direction factor were 262 significant in the ANOVA analysis, supporting this way of collapsing the data for 263 visualization; Table 1). The effect was strongest for the three right-most targets, i.e., in the 264 trained region, reaching approximately 2.3° (51% of the ventriloquism effect strength). It was 265 also location-specific, decreasing quickly toward zero outside of the trained region. These 266 results are consistent with the results of Kopco et al. (2009), confirming that the VAE can be 267 induced locally, so that it can be used to assess the VAE RF.

The reference frame of the VAE was examined by shifting the initial FP to a new location and examining how the observed VAE changed. The blue line in the top right panel plots the bias in responses measured with eyes fixating the new, non-trained FP (blue plus sign), shifted by approximately 23° to the left from the trained FP. There was very little

difference in the measured VAE for the two FPs (blue line lies approximately on top of the
red line). Thus, the observed results are consistent with visual–auditory recalibration
occurring in a predominantly head-centered coordinate frame.

To compare the current results more directly to the predictions of the two models and to the data of Kopco *et al.* (2009), a difference between the shift magnitudes from the two FPs was computed (bottom right of Fig. 2B, black traces) and compared with predictions based on the two models (orange traces). Again, the results are very close to the predictions of the head-centered RF.

280 These results were confirmed by performing a 4-way repeated-measures ANOVA with 281 the factors of target speaker location (nine levels), fixation point of the trials (training vs. non-282 training FP), AV-trial fixation point location (left vs. right), and the direction of induced shift 283 (left vs. right). The results of this analysis, summarized in Table 1, show that the main effect 284 of location was always significant, confirming that the ventriloquism aftereffect is spatially 285 specific and does not automatically generalize to the whole audiovisual field. The location by 286 FP interaction was also significant, showing that the reference frame of visual-auditory 287 recalibration is not purely head-centered, even though the eye-centered modulation is 288 relatively small.

# 289 **4. Discussion and Conclusions**

The current study examined the spatial properties of the ventriloquism aftereffect induced by AV stimuli presented in only one spatial hemifield in the peripheral audio-visual field. The goal was to ascertain how the ventriloquism aftereffect unfolds as a function of multiple different spatial attributes: fixation position, generalization in head- vs. eye-centered coordinates, and training within one spatial hemifield in contrast to training in both hemifields (as in Kopco et al., 2009). The results indicate that the ventriloquism aftereffect is a

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multifaceted process, dependent on both the format of the neural representation of space inhearing and vision, and on the reference frame used by the two senses.

298 In terms of the representational format, the location of the fixation position impacted 299 the pattern of adaptation induced by the AV stimuli, even when the AV-stimuli were 300 presented from matching locations and no VAE was induced. This unexpected adaptation was 301 not observed in the previous central-adaptation study (Kopco et al., 2009). And, it is difficult 302 to identify its cause, since a baseline measurement with no AV stimulation was not 303 performed. However, a comparison of the central-adaptation and peripheral-adaptation data 304 suggests that adaptation away from the training region was observed in the AV-aligned data 305 in both experiments. Such expansion of space is consistent with previously observed inherent 306 biases towards the periphery (Razavi et al., 2007). The current data shows that the inherent 307 biases might be more correctly described as biases away from the AV-training region, rather 308 than towards the periphery, and that the biases might be modulated by eye-gaze direction. 309 Specifically, in the current experiment in which the AV-aligned stimuli were presented in the 310 periphery, there was no repulsive bias in the central region when the gaze was fixated to a 311 point in the training hemifield, but it was observed if the gaze was fixated in the opposite 312 hemifield. At least three other factors of the current experimental design might also contribute 313 to the effect. First, the effect might be a result of adaptation to the auditory stimulus-314 distribution, which becomes skewed when the training stimuli are included since all of them 315 come from one side (e.g., similar to adaptation reported by Dahmen et al. (2010). Second, the 316 visual signal might be causing some global ventriloquism-like adaptation outside the training 317 region, such that the auditory-only responses are shifted towards the region from which the 318 visual stimuli are frequently presented, but only when the FP is in the hemifield ipsilateral to 319 the AV stimulation (and such shift towards the training region cancels out the repulsion 320 observed otherwise). Whatever the specific mechanism, this adaptation effect shows that there

is a hemifield-specific integration of visual and auditory spatial signals that differs from the
integration occurring when the stimuli are presented centrally, covering both spatial
hemifields.

324 Regarding reference frames, the current results together with those of Kopco et al. 325 (2009) show that in humans the RF of VAE is a mixture of eye-centered and head-centered 326 coding. In the central region, the effect is a fairly even mixture of these two reference frames, 327 whereas in the periphery, the pattern more closely fits the head-centered predictions, but also 328 shows an interaction with eye position. This shows that the transformation of the visual and 329 auditory signals into an aligned reference frame, thought to be necessary for the ventriloquism 330 aftereffect to work, is non-uniform. While it is not immediately clear what form of non-331 uniformity might be causing this pattern of results, it may be related to the hemispheric-332 difference channel models of auditory space representation (Salminen et al., 2009; Grothe et 333 al., 2010; Groh, 2014).

334 Kopco et al. (2009) performed the central-adaptation ventriloquism experiments in 335 two rhesus monkeys in addition to the humans (footnote 1). In the monkeys, the RF was 336 mixed between head- and eye-centered frames, consistent with most neurophysiological 337 observations in the same species (Moriya et al., 2013). Overall, these differences across 338 training regions (and, possibly, across species) suggest that the locations in the brain that are 339 recruited to accomplish this recalibration of auditory space may be widely varied. Some are 340 likely head-centered, some are eye-centered, some may involve the position of the eyes in the 341 orbits per se. These sites of plasticity may be recruited differently depending on the training 342 region and whether it spans both head-centered hemifields or is contained within one.

Additional experimental and/or modeling studies are needed to test alternative
explanations about the different reference frames of the ventriloquism aftereffect as well as
about the unexpected AV-aligned adaptation effect. However, the current results demonstrate

346	that there are hemisphere-specific adaptation processes in visual recalibration of auditory
347	space, resulting in different FP-dependent patterns of adaptation depending on the region in
348	which adaptation is induced.
349	
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356	
357	Footnotes
358	<sup>1</sup> The current experiments were also performed in two rhesus monkeys. A detailed treatment
359	of these effects can be found in the bioRxiv preprint BIORXIV/2019/564682.
360	
361	References and links
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- 391 392

Factor	d.f.	F	Signif
Speaker Location (1 to 9)	8, 48	33.87	***
A-only Fixation Point (Tr. vs. Non-Tr.)	1, 6	0.99	
Direction of Induced Shift (L vs. R)	1,6	0.43	
AV Fixation Point (L vs. R)	1, 6	0.27	
Speaker Location X A-only FP	8,48	0.79	*
Speaker Location X AV FP	8,48	2.28	
A-only Fixation Point X AV FP	1, 6	0.42	
Speaker Location X Direction	8,48	0.56	
AV Fixation Point X Direction	1,6	2.16	
A Fixation Point X Direction	1, 6	0.1	
Speaker Loc. X AV FP X A-only FP	8,48	0.31	
Speaker Loc. X AV FP X Direction	8, 48	0.52	
Speaker Loc. X A-only FP X Direction	8, 48	1.69	
AV FP X A-only FP X Direction	1, 6	0.12	
Loc. X AV FP X A-only FP X Direct.	8,48	1.16	

**Table 1**. Four-way repeated-measures ANOVA of the VAE magnitude data.

395 Significance levels are as follows: \* p < 0.05, \*\*\* p < 0.005.

#### **397 Figure Captions**

398 Figure 2: Experimental set-up and raw experimental data. A) Audiovisual display used to present 399 the AV training stimuli in one experimental block. At the beginning of each AV training trial (top), the 400 subject had to fixate on the same initial fixation point (FP); then, the training stimulus was presented from 401 one of three locations lateral to the FP, keeping the direction of the induced shift the same within a block 402 (by consistently presenting the visual adaptor displaced to the left, to the right, or aligned with the target 403 speaker). On the auditory-only probe trials (bottom), the same nine speaker locations and two FPs were 404 used in all blocks. The probe trials were randomly interleaved among the training trials and the FP and 405 target locations varied randomly from trial to trial. Dashed frame indicates the central training region 406 used in Kopco et al. (2009). B) Raw saccade endpoints of the responses to the AV training stimuli and 407 auditory-only probe stimuli as a function of the actual target speaker location, collapsed across time. The 408 symbols represent across-subject mean responses (+/-1 SEM indicated by horizontal lines) in different 409 audiovisual conditions (see legend), separately for the training trials (green), probe trials starting at the 410 training fixation (red), and probe trials starting at the non-training fixation (blue). Graphs for each 411 measurement type are plotted in one row, vertically offset from data for other types, for visual clarity. The 412 A-only data corresponding to each target location are approximately aligned with that target location. For 413 the AV data, the dashed lines connect symbol triplets for the same auditory target when presented with 414 one of the three different visual adaptors (the AV-aligned data are located approximately at the 415 corresponding target location).

416

417 Figure 2. Adaptation induced by AV stimuli. A) Average bias in A-only responses in the AV-418 aligned baseline condition as a function of the actual target location. Top panel shows mean response 419 biases (±SEM) when eyes are fixated at the training FP (red) and the non-training FP (blue). In addition, 420 the across-FP average data for central adaptation from Kopco et al. (2009) are shown for comparison 421 purposes (dashed line). The solid line in the bottom panel shows the difference between responses from 422 training FP and the non-training FP. The dashed line shows the difference for taken from Kopco et al. 423 (2009). B) Predicted and observed ventriloquism aftereffect. The top left panel plots the expected pattern 424 of biases induced in the A-only probe responses when preceding AV trials are presented in the training 425 region (15° - 30°). Red line shows predictions when the eyes fixate the training FP (i.e., the FP location

426	used during AV training trials). Dash-dotted blue line shows expected results from the non-training FP if
427	the RF of adaptation is head-centered, while dashed blue line shows expected results for an eye-centered
428	RF. The bottom panel shows the differences between the expected bias magnitudes from the training
429	versus the non-training FPs in the two RFs in orange. For comparison, the black dashed line sketches the
430	results corresponding to the mixed RF observed after VAE was induced in the central region in (Kopco et
431	al., 2009) . Top right panel shows the across-subject mean (±SEM) difference between the auditory
432	saccade end point locations when interleaved with spatially displaced AV stimuli vs. when interleaved
433	with AV-aligned stimuli, collapsed across the direction of the AV displacement. The solid black line in the
434	bottom right panel shows the effect of initial fixation position on the magnitude of the induced shift as the
435	across-subject mean (±SEM) difference between the shifts from the training and non-training FPs (i.e the
436	difference between the red and blue lines). Orange lines show the predictions of the difference for the two
437	reference frames based on the training FP data (red) from the top right panel.