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Ears on the Hand: Reaching Three-Dimensional Targets With an Audio-Motor Device

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4 **Ears on the hand.**

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6 **Reaching three-dimensional targets with an audio-motor device**

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41 **Short title: Ears on the hand**
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4 **Abstract**
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8 Understanding the processes underlying sensorimotor coupling with the environment is
9 crucial for sensorimotor rehabilitation and sensory substitution. In doing so, devices which
10 provide novel sensory feedback consequent to body movement may be optimized in order
11 to enhance motor performance for particular tasks. The aim of the study reported here was
12 to investigate audio-motor coupling when the auditory experience is linked to movements
13 of the head or the hands. The participants had to localize and reach a virtual source with
14 the dominant hand in response to sounds. An electromagnetic system recorded the position
15 and orientation of the participants' head and hands. This system was connected to a 3D
16 audio system that provided binaural auditory feedback on the position of the virtual
17 listener located on the participants' body. The listener's position was computed either
18 from the hands or from the head. For the hand condition, the virtual listener was placed on
19 the dominant hand (the one used to reach the target) in Experiment 1 and on the non-
20 dominant hand, which was constrained in order to have similar amplitude and degrees of
21 freedom as that of the head, in Experiment 2. The results revealed that, in the two
22 experiments, the participants were able to localize a source within the 3D auditory
23 environment. Performance varied as a function of the effector's degrees of freedom and
24 the spatial coincidence between sensor and effector. The results also allowed
25 characterizing the kinematics of the hand and head and how they change with audio-motor
26 coupling condition and practice.
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44 **Keywords:** Sensory substitution, neural plasticity, perceptual adaptation, rehabilitation
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4 **Introduction**

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6 *Sensory substitution*

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8 In the field of perceptual rehabilitation, sensory substitution devices were developed
9 with the aim of compensating one or several functions of a deficient sensory modality. To do
10 so, these devices convert stimuli that are normally accessed through this deficient sensory
11 modality into stimuli accessible by another sensory modality (e.g., Auvray and Myin, 2008;
12 Gallay *et al.*, 2012, for reviews). For instance, these devices can convert visual information
13 into tactile stimuli (e.g., Bach-y-Rita *et al.*, 1969) or sounds (e.g., Hanneton *et al.*, 2010;
14 Meijer, 1992). Studies conducted on sensory substitution revealed an important plasticity of
15 the central nervous system. Behavioural studies revealed that sensory substitution devices
16 allow improving spatial processing in the absence of vision. In particular, users of these
17 systems become able to perform localisation tasks (e.g., Levy-Tzedek *et al.*, 2012; Proulx *et*
18 *al.*, 2008), recognition tasks (Arno *et al.*, 2001; Auvray *et al.*, 2007-a, 2007-b; Pollok *et al.*,
19 2005; Sampaio *et al.*, 2001), navigation tasks (Chebat *et al.*, 2011; 2015) and, to some extent,
20 consolidate a perceptual space that possesses visual characteristics (e.g., Renier *et al.*, 2005).
21 However, the degree to which the use of a sensory substitution device involves visual
22 processes varies from one person to another (Arnold *et al.*, 2017). In parallel, brain-imaging
23 studies have shown that the use and practice of visual-to-tactile (Ptito *et al.*, 2005) and
24 visual-to-auditory (e.g., Striem-Amit and Amedi, 2014) devices result in increased activation
25 in blind people’s visual cortex (for reviews, see Proulx *et al.*, 2014; Ptito *et al.*, 2018).
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42 *Sensory substitution, learning, and body kinematics*

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44 Effective use of sensory substitution devices is largely dependent upon the users’
45 ability to master their different features and the amount of training required to do so. In most
46 cases, users are able to approximate objects’ location and shape in a short amount of time
47 (i.e., one or two hours with the Tongue Display Unit, Kaczmarek and Haase, 2003). However,
48 to gain precision in these tasks and to perform more complex ones, more intensive training is
49 required. The length of the training is estimated at around 10 to 15 hours with visual-to-
50 auditory devices (Auvray *et al.*, 2007) and around eight hours with visual-to-tactile devices
51 (Kaczmarek and Haase, 2003). It is estimated that further time still would be required to
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4 achieve a high level of expertise, for instance to be able to recognize facial expressions with
5 visual-to-auditory devices (Striem-Amit *et al.*, 2012).
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9 Another crucial characteristic of learning is the ability to generalize, that is, the
10 ability to extend the acquired perceptual abilities to both new stimuli and new perceptual
11 conditions. With tactile devices, it has been shown that learning transfers across body
12 surfaces, both for surfaces represented in adjacent and non-adjacent areas of the
13 somatosensory cortex (Arnold and Auvray, 2014). This result provides behavioural support
14 for the claim that training in sensory substitution results in a relative independence from the
15 stimulated body surface. In addition, transfer of learning to novel stimuli has been
16 documented for both tactile (Arnold and Auvray, 2018; Kim and Zatorre, 2010) and auditory
17 devices (Kim and Zatorre, 2008). This ability to generalize to new symbols depends on the
18 number of stimuli to learn and on feature variability (Arnold and Auvray, 2018). These
19 results are in line with the reverse hierarchy theory (RHT) of perceptual learning (Ahissar
20 and Hochstein, 2004), according to which the degree of specificity depends on the difficulty
21 of the perceptual task and on the level of cortical processing that is required to perform the
22 task.
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35 Finally, performance and experience with sensory substitution devices depend on
36 each person’s abilities (see Arnold *et al.*, 2017, for a review). For instance, Brown *et al.*’s
37 (2011) study showed that people with good musical abilities learned a visual-to-auditory
38 device faster than people with low musical abilities, although they did not reach better
39 abilities with the device. Haigh *et al.*’s (2013) study found that musicians had a better
40 “visual” acuity (tested with Snellen E) when using the visual-to-auditory conversion system
41 The vOICE than non-musicians. Note that regarding visual abilities, Brown *et al.* (2011)
42 found no influence of individual visual imagery abilities (measured with VVIQ, Marks,
43 1973) on the learning of the vOICE. On the other hand, in a study by Hanneton *et al.* (2015),
44 performance reached by the participants on a task based on the auditory conversion of a
45 visual video game was found to be correlated to the scores the participants obtained in a
46 visual mental rotation test (Vandenberg, 1971). It thus seems that performance with sensory
47 substitution devices is related to only some visuo-spatial abilities. Overall, these results
48 suggest that perceptual strategies will differ as a function of people’s specificities and
49 cognitive style which, in some tasks, affects people’s performance.
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4 The studies described above showed people’s ability to learn how to use sensory
5 substitution devices. These studies focused on the sensory aspects, leaving the motor changes
6 involved in learning undocumented. With other devices, learning the new sensory
7 consequences of body movements has been shown to increase motor performance and to
8 induce an evolution of body movement characteristics. In particular, as adaptation
9 progresses, movements become less segmented, smoother, more rapid and fluid, with an
10 increase in the amplitude of joint motion (e.g., Novak *et al.*, 2003; Rand *et al.*, 2004). Our
11 study aimed at investigating such motor consequences of perceptual learning in the case of
12 sensory substitution.
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22 *Aim of the study*

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24 The first aim of the study reported here was to investigate the changes in kinematic
25 parameters while learning a novel auditory device. To do so, the participants had to learn to
26 intercept a static auditory target within a 3D immersive auditory environment. Motion
27 capture sensors were placed on the participants’ head and hand, and their kinematics were
28 analysed while adapting to this new system. In addition to success rate and reaching duration,
29 the kinematics of hand and head movements, and in particular the number of velocity peaks,
30 the direct distance followed by the hand and head during reaching, the cumulative length of
31 the trajectories, and the cumulative rotations were analysed.
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39 The second aim of the study was to investigate if performance with the device is
40 influenced by the location of the sensors. In particular, one hypothesis raised by sensorimotor
41 theories of perception is that the use of a head-mounted camera shares more sensorimotor
42 resemblance with vision than the use of a hand-held camera (e.g., O’Regan, 2011; O’Regan
43 and Noë, 2001). As a consequence, according to this theory, the use of a head-mounted
44 camera might favour an association between perception with the device and the visual
45 sensory modality as compared with the situations in which the camera is hand-held. Thus,
46 two modes were investigated in our experiment, the head mode and the hand mode. In the
47 head mode, the head sensor was used to drive the position and orientation of the virtual
48 listener in the 3D auditory display. In the hand mode, the position and orientation of the
49 virtual listener was driven by the sensor fixed on the hand. Consequently, in this condition,
50 the target’s sound is perceived through “ears” on the participant’s hand.
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4 Thirdly, in order to further investigate the influence of body kinematics on the use of
5 the device, our experiments studied the extent to which the differences in performance
6 obtained with the hand and head is attributable to differences in amplitude of movement and
7 degrees of freedom. Thus, in the first experiment, hand movements were not constrained,
8 whereas in the second experiment, the movements of the non-dominant hand wearing the
9 listener were constrained in order to have similar amplitude and degrees of freedom as that of
10 the head.
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19 **Experiment 1**

20 **Materials and methods**

21 *Participants*

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24 12 participants (4 females and 8 males, age range: 25-50 years) took part in this
25 experiment which lasted approximately 40 minutes. All were students or faculty members
26 at Paris Descartes University. Inclusion criteria were being aged between 18 and 50 years
27 with no self-reported neurological disorder nor auditory impairment. The participants were
28 naive as to the hypotheses under investigation. The experiment was performed in
29 accordance with the ethical standards laid down in the 1991 Declaration of Helsinki.
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37 *Experimental set-up*

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39 An electromagnetic device (Fastrak Polhemus) was connected to the 3D audio
40 system OpenAL that provides auditory feedback on movements. The Polhemus system
41 acquires 6D motion data with a 30 Hz sample frequency. This electromagnetic system
42 gives real time position (X, Y, Z) and orientation (Euler angles: azimuth, elevation, and
43 roll) of two sensors, allowing a distinction between changes in position and orientation.
44 The body-auditory coupling system is thus made of a listener (sensor) placed on the
45 participants' body and a virtual audio source. The perceived sounds depend on the position
46 and orientation of the listener relative to the position of the source (see Figure 1). More
47 precisely, a «buzzing» sound similar to a fly with significant harmonics between 100 and
48 2000 Hz varied in intensity and frequency as a function of the position and orientation of
49 the listener (see below for the modelling and equations used).
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4 In the “head mode”, the listener was attached to the head and the perceived sound
5 was sensitive to the position and orientation of the head with respect to the sound source.
6 It corresponded to a relatively natural situation since the positions of the “virtual ears”
7 were located close to the real ears. In the “hand mode”, the listener was attached to the
8 hand used to reach the fly and the perceived sound was sensitive to the position and
9 orientation of the hand relative to the presented sound source (see figure 1).
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19 *Sound spatialisation modelling*

20 The binaural sound generated by the audio device (SoundMax integrated digital
21 audio by Analog Devices Inc.) was computed from the relative position and orientation
22 between the listener and the virtual source (see figure 1). The 3D audio system was based
23 on the library OpenAL¹, used in video games, which allows 3D sound spatialisation.
24 OpenAL uses both interaural intensity differences (IIDs) and interaural time differences
25 (ITDs), which are combined to code for the target’s distance and direction. As a sound
26 source does not have the same distance between the two ears, the sound arrives faster to
27 the closest ear (ITDs) and with a higher intensity (IIDs). Regarding IIDs, according to the
28 specifications of OpenAL library, the intensity decreases and the sound is slightly muffled
29 as the listener moves away from the source. This models reality in which air absorbs high
30 frequency waves more rapidly than low frequency ones. Within 5 cm from the source, the
31 sound remains at a constant maximum volume. Beyond a maximal distance of 40 cm, the
32 amplitude is held constant. Between these two limits, the intensity of the sound is
33 computed as a function of distance, for each hear, according to the following equation:
34 $G(d)=D_{ref}/(D_{ref}+R*(d-D_{ref}))$. where d is the distance to the source, G is the gain applied to
35 the sound, R (= 1.3) is the Roll-off factor, and D_{ref} (= 5 cm) is a reference distance
36 corresponding to the distance that gives a unitary gain.
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54 *Procedure*

55 For each of the two modes (head and hand), the participants were instructed to catch
56 the fly, i.e. to reach the static virtual sound source, with their dominant hand. The
57 participants sat in front of a table. They were blindfolded, fitted with headphones, and two
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4 sensors were fixed with specific double-sided tape on the back of the hand and on the
5 headphones. A geometrical transformation was applied in order to place the virtual listener
6 either on the centre of the hand or on the centre of the head, midway between the ears. At
7 the start of each trial, the dominant hand, used to reach the source, was placed on the
8 sternum near the xyphoid process. The participants were instructed to start to move as
9 soon as they heard the sound. The trial was considered as being successful (i.e., the “fly”
10 was caught) when the centre of the hand approached within a distance smaller than 5 cm
11 of the static sound source. In this case, the recording stopped and a synthetic applause was
12 played. The participants were able to give their responses up to 31s after the end of the
13 stimulus.
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22 The virtual source could be presented at 9 possible locations within the
23 participants’ workspace: 1 in the middle and 8 in the corners of a virtual parallelepiped
24 rectangle (20 cm on the right or the left of the participants’ midline, at 5 or 25 cm from of
25 their sternum and at 15 or 35 cm above the table). The order of presentation of the 9
26 targets was randomized within blocks. Blocks of 9 trials were repeated three times for
27 each of the two modes, with the participants completing 54 trials in total. Half of the
28 participants began with the hand mode while the other half began with the head mode.
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37 *Statistical analyses*

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39 The computed dependent variables were the success rate (percentage of catches
40 before cut-off) and reaching duration (time to reach the target). The kinematics of hand
41 and head movements during successful trials were characterized by the number of velocity
42 peaks, the direct distance followed by the hand and head during reaching (3D distance
43 between their starting and final positions), each sensor’s cumulative length of trajectories
44 and cumulative rotations. The cumulative length of the trajectories corresponds to the sum
45 of all the elementary 3D displacements performed during each 33 ms time sample. The
46 cumulative rotations were obtained after calculating the 3D rotation matrix at each time
47 sample, then the change in 3D orientation during one time sample. The rotation angle
48 performed during each time sample was computed using the axis-angle formalism. Then,
49 the obtained elementary rotations were summed during the whole trial to obtain the
50 cumulative rotations of the hand and head.
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4 The distribution of the variables was verified with Mauchley's Sphericity test.
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6 Repeated measures ANOVAs were conducted to analyse the dependent variables with the
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8 factors Session (2 levels), Mode (2 levels: hand and head), and Block (3 levels). The
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10 results were averaged across targets. Post Hoc comparisons were performed with
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12 Bonferroni tests. A Multivariate approach of ANOVA was used when the conditions for
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14 ANOVA were not fully met, completed with Friedman non-parametric analysis, when
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16 relevant. Additional statistics were performed using Chi-squared test.
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18 **Results**

19 *Success rate*

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21 The success rate appeared to be variable across participants and conditions. The
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23 mean success rate in the three blocks ranged between 51.8 and 100% in the hand mode
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25 and between 26 and 100% in the head mode. The success rate did not vary with the Order
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27 of sessions and there was no interaction with Mode (Pearson's Chi-squared test, $p=0.18$
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29 and $=0.38$, respectively). Given this, results were pooled across sessions for the subsequent
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31 analyses.
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33 An ANOVA conducted with the factors Mode and Block showed a significant effect
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35 of Mode ($F[1,11]=15.03$, $p=0.002$). The success rate was higher in the hand mode ($75.93 \pm$
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37 4.79 %, mean \pm sem) than in the head mode (71.3 ± 7.58 %) (Figure 2A). The sphericity
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39 condition was not fully met for the Block factor (Mauchley's test $p=0.044$). Non
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41 parametric statistics (Friedman test) showed a significant effect of Block in the head mode
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43 ($p= 0.011$) but not in the hand mode ($p=0.30$).
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45 (Fig. 2 about here)

46 47 *Trial duration*

48 An ANOVA conducted with the Factors Mode and Block on trial duration did not
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50 show any significant main effect, nor interaction between Mode and Block (all $ps>.05$).
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52 Numerically, trial duration was $11.59 \pm 1.03s$ in the hand mode and $12.37 \pm 1.02s$ in the
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54 head mode (see Figure 2B).
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57 58 *Hand and head kinematics*

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4 An ANOVA conducted with the Factors Mode and Block on the direct distance
5 followed by the hand during reaching did not show any effect of Mode nor Block ($F_s < 1$),
6 confirming that movement execution during successful trials was reproducible across
7 conditions (see Figure 3A). The trajectories followed by the head and hand did not follow
8 a single path, but several of them, suggesting a behaviour of exploration. As a
9 consequence, cumulative trajectories and cumulative rotations of the head and hand were
10 used as dependent variables. Figure 3 shows the kinematic variables of the reaching hand:
11 cumulative trajectories (Figure 3B) and cumulative rotations (Figure 3C). The observation
12 of the graphs suggests that the participants followed longer exploratory movements of the
13 reaching right hand, with more cumulative rotation in the head mode than in the hand
14 mode. Interestingly, the variability was more important in the head mode, and in particular
15 regarding the cumulative hand rotations. ANOVAs were conducted with the factors Mode
16 and Block on the dependent variables describing reaching hand trajectories: cumulative
17 trajectories, number of velocity peaks, and cumulative rotations of the reaching hand
18 trajectory. The results for cumulative trajectories failed to show any significant effect of
19 Mode ($F[1,11]=4.28$, $p=0.062$) or Block ($F[2,22]=1.12$, $p=0.34$). Similarly, the results on
20 number of velocity peaks failed to show any significant main effect of Mode
21 ($F[1,11]=0.45$, $p=0.51$) or Block ($F[2,22]=2.35$, $p=0.11$). The results on cumulative
22 rotations of the reaching hand trajectory showed a significant effect of Mode ($F[1,11]=5.8$,
23 $p=0.034$), no effect of Block ($F[2,22]=0.6$, $p=0.55$), and no interaction between Mode and
24 Block ($F[2,22]=0.71$, $p=0.50$). There were more cumulative rotations of the reaching hand
25 trajectory in the head mode than in the hand mode (see Figure 3C).

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The direct distance followed by the head and its kinematic variables: cumulative
trajectories and cumulative rotations are shown on Figure 3D-F. The direct distance
followed by the head during reaching showed a significant effect of Mode ($F[1,11]=82.06$,
 $p < 0.0001$), no effect of Block ($F[2,22]=1.18$, $p=0.32$), and no interaction between these
two factors ($F[2,22]=1.86$, $p=0.17$). The distance was 9.76 ± 2.01 cm in the hand mode
and 32.75 ± 3.03 cm in the head mode (see Figure 3D). The cumulative trajectories and
rotations of the head were greater in the head mode (171.9 ± 8.65 cm and $319.2 \pm 16.7^\circ$,
respectively) than in the hand mode (44 ± 2.74 cm and $74.5 \pm 3.38^\circ$, respectively), with a
higher variability in the head mode (see Figure 3E and 3F). The conditions for ANOVA

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4 were not fully met (sphericity test $p= 0.002$). Multivariate analysis was used with the
5 factors Block and Mode on the cumulative trajectories. The analysis showed a significant
6 effect of Mode ($p<0.0001$), no effect of Block ($p=0.1$), and no interaction between these
7 two factors ($p=0.06$). Two factors ANOVA for cumulative rotations (Figure 3F) showed a
8 significant effect of Mode ($F[1,11]=48.36$, $p<0.0001$), no effect of Block ($F[2,22]=0.98$,
9 $p=0.39$), and no interaction between these two factors ($F[2,22]=0.39$, $p=0.68$).

16 17 *Learning and adaptation:*

18 As was described above, there was no effect of the session and the effect of Block
19 appeared to be complex. Numerically, the success rate increased with Block (Figure 2A)
20 but the statistics were difficult to interpret, in particular, a borderline sphericity test
21 ($p=0.044$) weakened the results of the ANOVA. Non parametric Friedman analysis
22 showed an effect of Block in the head mode ($p=0.011$) but not in the hand mode ($p=0.30$).
23 It is likely that an important inter-individual variability contributed to this complexity. A
24 possible interpretation is that the lack of significant effect in the hand mode is due to a
25 saturation of the success rate (8 out of 12 participants succeeded in at least 89% of the
26 trials) inducing a ceiling effect, which did not occur in the head mode.

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35 (Fig. 3 about here)

36 37 38 39 *Discussion of Experiment 1*

40 In Experiment 1, the participants were able to use auditory feedback in order to
41 guide reaching movements. In addition, there was a significant improvement in success
42 rate in the head mode and a ceiling effect in the hand mode. This result indicates that the
43 participants were able to adapt to a new audio-motor environment and to learn efficient
44 motor strategies. However, most of the kinematic variables did not vary with blocks. A
45 possible explanation is that the participants used quite different individual strategies when
46 completing motor tasks. For example, some of the participants performed relatively direct
47 reaching movements, but most of them used various oscillatory exploratory movements
48 that cannot be easily compared between them.

49 The second main result from Experiment 1 is that the success rate was higher in the
50 hand mode than in the head mode. In addition, the kinematic analysis of the reaching
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4 dominant hand showed that the target was reached after a simpler movement trajectory
5 characterized by less cumulative rotations in the hand mode than in the head mode. This
6 result indicates that when using a sensory substitution device, or any other technology, the
7 idea that sensory organs would benefit from staying at their usual location is not
8 necessarily true, given that here, the most unnatural condition was the most efficient.
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13 It should however be underlined that there were two main differences between the
14 hand mode and the head mode. First, in the hand mode, there was a spatial coincidence
15 between the sensor and effector that was not there in the head mode. Second, the
16 amplitude of possible movements was greater in the hand mode than in the head mode. As
17 a consequence, a second experiment was conducted in order to investigate if these two
18 differences account for the better performance in the hand mode then in the head mode.
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26 **Experiment 2**

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28 The better performance in the hand mode than in the head mode obtained in
29 Experiment 1 can be due to the fact that the head condition involved more complexity and
30 less amplitude of movements. First, in the hand condition, the sensor (the virtual listener)
31 was located on the hand which was also used to catch the fly. Second, head movements
32 have less amplitude than hand movements. To investigate the effect of these differences on
33 participants' performance, in Experiment 2, in the hand condition, the listener was placed
34 on the non-dominant hand while the dominant hand was used to reach the target. In
35 addition, the participants' non-dominant hand displacements were constrained in order to
36 have similar amplitude and degrees of freedom as that of the head.
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46 **Materials and methods**

47 *Participants*

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50 18 new participants (9 females, age range: 20-50 years), recruited at the Paris
51 Descartes University, completed Experiment 2. Inclusion criteria were being aged between
52 18 and 50 years with no self-reported neurological disorder nor auditory impairment. This
53 experiment was conducted in accordance with the ethical standards laid down in the 1991
54 Declaration of Helsinki.
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4 *Experimental set-up and procedure*
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6 The same devices and methods as in Experiment 1 were used in Experiment 2, but
7 this time three sensors were used and placed on the two hands and the head, respectively.
8 The reaching movements were again performed by the dominant hand. The listener was
9 defined as the head sensor (head mode, as in Experiment 1) or as the non-dominant hand
10 sensor (non-dominant hand mode). As in Experiment 1, the perceived sounds varied as a
11 function of the sensor's position and orientation with respect to the sound source. In the
12 non-dominant hand mode, the participants were instructed to lean their elbow on a
13 homemade backing fixed on the armrest of the chair, with their forearm elevated so that
14 the hand was at the shoulder's height. This posture aims at limiting the non-dominant
15 hand's degrees of freedom, so that they are similar to those of the head. The conditions of
16 presentation of each auditory target was the same as in Experiment 1: 9 different target
17 positions were presented in each block, in a randomized order. There were 3 successive
18 blocks for each of the two modes with the participants completing 54 trials in total.
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31 *Performance and motion analyses*
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33 The same dependent variables as in Experiment 1 were computed: success rate, trial
34 duration, kinematics of head and both hands.
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39 **Results**
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41 *Success rate*
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43 The success rate ranged between 14.8 and 77.8% in the hand mode and between
44 37.0 and 88.9% in the head mode (mean \pm sem 55.93 ± 4.11 %, in the hand mode; $55.35 \pm$
45 3.54 % in the head mode). As in Experiment 1, there was no effect of Order of sessions
46 (Pearson's Chi-squared test, $p=0.60$) and the results were pooled across sessions.
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50 Figure 4A illustrates the evolution of Success rate in the two modes. An ANOVA
51 with the factors Mode and Block showed a significant of Block ($F[2,32]=15.7$, $p<0.0001$),
52 no effect of Mode ($F[1,16]=1.31$, $p=0.27$), and no interaction between these two factors
53 ($F[2,32]=1.04$, $p=0.36$). A Bonferoni Post-Hoc test showed that the success rates in Blocks
54 2 and 3 were significantly higher than in Block 1 ($p<0.001$).
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Trial duration

For Trial duration, the conditions for the ANOVA were not met and a Multivariate analysis failed to show any significant effect of Mode and Block ($p > 0.5$), nor interaction between these two factors ($p = 0.19$). The numerical trend (illustrated in Figure 4B) indicated a slight decrease in trial duration with Block, with an increased variability.

Kinematics of the reaching right hand

Figure 5A-C illustrates the kinematic variables of the reaching dominant hand during the task. As in Experiment 1, the direct distance followed by the reaching hand did not vary with the factors Mode and Block, confirming that movement execution during successful trials was reproducible across conditions (see Figure 5A). The cumulative trajectories and cumulative rotations are shown in Figure 5 B,C. An ANOVA conducted with the factors Block and Mode on the cumulative trajectories indicated a borderline effect of Block ($F[2,32] = 3.23$, $p = 0.052$), no significant effect of Mode ($F[1,16] = 3.27$, $p = 0.08$), and no interaction between these two factors ($F[2,32] = 1.0$, $p = 0.037$). An ANOVA conducted with the factors Block and Mode on the cumulative rotations of the reaching hand did not reveal any significant effect of Mode ($F[1,16] = 0.43$, $p = 0.8$), nor Block ($F[2,32] = 1.6$, $p = 0.21$), nor interaction ($F[2,32] = 0.18$, $p = 0.83$). However, the ANOVA conducted on the number of velocity peaks showed a significant effect of Mode ($F[1,16] = 8.36$, $p = 0.01$), without any effect of Block ($F[2,32] = 1.49$, $p = 0.23$), nor interaction between these two factors ($F[2,32] = 0.46$, $p = 0.63$). The number of velocity peaks was higher in the head mode (18.2 ± 1.76) than in the hand mode (13.8 ± 1.44).

Kinematics of the listener

The listener was the head or the non-dominant hand as a function of the condition. The kinematics of the listener are shown in Figure 5D-F. A two factors ANOVA on the direct distance followed by the listener (Figure 5D) showed a significant effect of Mode ($F[1,16] = 8.48$, $p = 0.01$), no effect of Block ($F[2,32] = 0.14$, $p = 0.63$), and no interaction between these two factors ($F[2,32] = 0.611$, $p = 0.54$). The non-dominant hand (blue line) moved 14.6 ± 1.37 cm and the head (red line) moved 21.7 ± 1.91 cm.

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4 An ANOVA with the factors Mode and Block showed that the listener's
5 cumulative trajectories (Figure 5E) did not vary with Mode ($F[1,16]=0.11$, $p=0.74$), nor
6 with Block ($F[2,32]=0.24$, $p=0.79$), and there was no interaction ($F[2,32]=0.95$, $p=0.39$). A
7 two factors ANOVA showed that the cumulative rotations of the listener did not vary with
8 Mode ($F[1,16]=1.55$, $p=0.23$) nor with Block ($F[2,32]=0.46$, $p=0.62$), however, there was
9 a significant interaction between Block and Mode ($F[2,32]=3.93$, $p=0.03$). This suggests
10 that the cumulative rotations decrease with Block only when the listener is fixed on the
11 head (Figure 5F). This interaction was confirmed by Multivariate analysis ($p=0.019$).
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21 *Discussion of Experiment 2*

22 Experiment 2 revealed that the participants were able to adapt their motor
23 behaviour to a novel audio-motor environment that involves a new sensorimotor
24 coordination between the two hands. In this experiment, there was no significant
25 difference between the head mode and the hand mode, neither for the success rate nor for
26 trial duration. These results suggest that the higher performance obtained in the hand mode
27 in Experiment 1 was due to the spatial coincidence between the effector and the sensor.
28 Surprisingly, the head mode that was supposed to be very close to a natural condition (for
29 the human species, the ears are on the head) is not significantly better than the hand mode,
30 and improvements are slower. As in Experiment 1, even if performance seems to be
31 similar in the two modes, the participants moved their virtual ears with smaller amplitudes
32 in the hand mode.
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44 **General discussion**

45 The study reported here investigated adaptation to a novel audio-motor
46 environment. An electromagnetic system recorded the position and orientation of the
47 participants' head and hand and it was connected to a 3D system that provides auditory
48 feedback on movements. The participants' task was to reach an auditory target. The
49 target's sound was perceived by using virtual ears (the listener) located either on the
50 participants' hand (hand mode) or on their head (head mode). In Experiment 1, the
51 participants' hand position was unconstrained and the listener was placed on the same
52 hand as the one used to reach the target. To control for the role of spatial coincidence and
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4 movement amplitude, in Experiment 2, hand movements were constrained in order to have
5 similar amplitude and degrees of freedom as those of the head. In addition, the listener was
6 placed on the other hand than the one used to reach the target.
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10 The first main result to emerge from our study was that the participants were able
11 to localize a source within the 3D auditory environment. This result indicates that people
12 are able to learn new efficient motor strategies and to adapt to a new audio-motor
13 environment (see also Safstrom and Edin, 2006). The second main result to emerge from
14 our study was the higher performance obtained when the sensor was located on the hand
15 used to reach the target. This was the case in Experiment 1, in which performance was
16 better in the hand mode than in the head mode. It should be underlined here that in the
17 head mode, the task is mainly a binaural 3D sound source localization task; the reaching
18 component of the task is secondary. The binaural localization of a virtual sound source is
19 critically dependent on the algorithm used for spatialisation. In the present study it was not
20 optimal since it was not personalized by Head Related Transfer Function (HRTF, see
21 Simon *et al.*, 2016). On the other hand, auditory feedback in the hand mode is similar to
22 movement sonification acting as a guide for the reaching hand toward the target
23 (Bevilacqua *et al.*, 2016). In this hand mode, the task resembles more a guided approach
24 task than a pure reaching task. In Experiment 2, the sensor was placed on the other hand
25 and its movements were constrained to be similar to those of the head. The head mode was
26 supposed to be closer to a natural condition, approximately the position of ears. However,
27 performance was similar in the hand mode and in the head mode and improvements were
28 slower in the head mode.
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44 This result contradicts some hypotheses from sensorimotor theories of perception
45 according to which the use of a head-mounted camera shares more sensorimotor
46 resemblance with vision than the use of a hand-held camera and thereby might favour
47 better performance (e.g., O'Regan, 2011; O'Regan and Noë, 2001). However, it might be
48 the case that sensorimotor resemblance influences experience on a phenomenological
49 rather than at the behavioural level. It would be interesting to further investigate those
50 factors differentially influencing the behavioural and phenomenological components of the
51 task, as well as the individual differences potentially at play. Indeed, the extent to which
52 the use of a sensory substitution device induces supplemental visual, auditory, tactile, or
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4 cognitive processing varies from one user to another (e.g., Auvray et al., 2007-a; see also
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6 Arnold *et al.*, 2017, Deroy and Auvray, 2014, for discussions on this topic). Thus, in our
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8 study, performance appeared to be less linked to the natural aspect related to sensor
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10 location than to the spatial coincidence between the body part performing the motor task
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12 and the origin of the audio-motor coupling. These results have practical implications,
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14 suggesting that under degraded perceptual situations (real or virtual), it could be more
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16 efficient to use spatially coincident sensors and effectors.

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18 The third main result from our study concerns the kinematic data, which allow
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20 investigating the quality of movement associated with task success. Overall, the
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22 kinematics of the reaching hand is not more informative than the success rate. However,
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24 the kinematics of the head and non-dominant hand allows a better understanding of the
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26 listener's behaviours of active exploration to perform the perceptual task. More precisely,
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28 in Experiment 1, the analysis of head movements confirmed that the reaching task was
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30 executed differently in the two modes. In the hand mode, the head moved around 10 cm
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32 during reaching with relatively small cumulative trajectories and rotations. This
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34 displacement can be at least partially explained by the known contribution of the upper
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36 trunk to reaching movements (Mark *et al.*, 1997). In contrast, in the head mode, the head
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38 roamed the workspace with much larger cumulative trajectories and rotations. The direct
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40 3D displacement of the head at the end of reaching attained 30 cm which is a strikingly
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42 large distance. This observation suggests that in the head mode, the function of the head is
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44 not that of a stable egocentric reference frame for planning and executing reaching
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46 movement (see also Crawford *et al.*, 2004; Paillard, 1991). Rather, it suggests that head
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48 movements, guided by the auditory feedback, are primarily used to explore the 3D
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50 workspace in order to ease target detection. We hypothesize that head movements simulate
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52 hand movements toward the target. Then, the position and orientation of the head toward
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54 the target (heading) can be secondarily used to perform target-directed hand reaching
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56 movements (see also Boyer *et al.*, 2013).

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58 Although the two experiments involved differences in terms of constraints on
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60 movements and location of the listener, the kinematics of the listener had similarities in
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62 the head during head mode in Experiment 1, the head, and the non-dominant hand in
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64 Experiment 2, which have similar constraints in terms of amplitude. Indeed, in these three
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4 situations, there were large cumulative trajectories and rotations, contrasting with the
5 relatively limited movements of the right reaching hand in hand mode in Experiment 1. In
6 Experiment 2, the kinematics of the head and non-dominant hand are similar. However,
7 the direct distance followed during reaching is smaller when the listener is fixed on the
8 non-dominant hand (around 15 cm) than when it is fixed on the head (around 22 cm). This
9 is quite paradoxical since the movement of the non-dominant hand is free (elbow and wrist
10 degrees of freedom) and probably less effortful than the trunk and neck movements
11 needed to move the head listener. These results suggest that the role of the head to explore
12 space and to indicate target direction (heading) does not transfer easily to the hand.
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21 Participants' performance suggests that the paradigm used in our study can provide
22 useful 3D auditory feedback. This can be applied to a broad range of situations. In the field
23 of sensory substitution, our results are in line with many other studies investigating the
24 relevance of using audition to convey visual information (e.g., the vOICe, Meijer, 1992;
25 Vibe, Hanneton et al., 2010; the EyeMusic, Levy-Tzedek et al., 2014; the See ColOr;
26 Bologna et al., 2009). They additionally suggest that we can step away from reproducing
27 the conditions of natural perception and rather take into account how motor performance
28 relates the best to changes in sensory information. A similar audio-motor coupling could
29 also be used to compensate proprioceptive deficits, for which tactile devices have been
30 mainly used so far (e.g., see Danilov et al., 2007; Diot et al., 2014). In addition, augmented
31 auditory feedback in a game-like situation may be a useful tool for rehabilitation of
32 sensory-motor functions (Schmitz *et al.*, 2018). The hand mode could thus be used as a
33 way of providing augmented feedback to patients with movement disorders such as
34 hemiparesis following stroke. Indeed, due to the strong link between sensory inputs and
35 motor outputs, augmented auditory feedback can be a useful tool in rehabilitation. This
36 paradigm can also be used to train specific technical skills such as minimally invasive
37 surgery which relies now on virtual reality simulators with enhanced sensory feedback
38 (see Papanikolaou *et al.*, 2019, for a review). Finally, audio-motor feedback can be useful
39 in the field of perceptual augmentation, in which devices are developed to improve access
40 to visual information in a variety of situations, for instance when there is an excess of
41 visual information to process, like when driving a car (e.g., Ho and Spence, 2008) or when
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4 conditions of perception are degraded, as can be the case for those involved in firefighting
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6 (Carton and Dunne, 2013) or military operations (Jones et al., 2009).
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15 0004-02.
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23 **Footnote**

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25 1. See IA-SIG Interactive 3D Audio Rendering and Evaluation Guidelines (Level 1) and
26 OpenAL Documentation for details: <https://www.openal.org/>
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4 **Figure captions**

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6 **Figure 1.**

7 Schematic representation of the experimental set-up. The auditory target is represented by
8 a fly. For each mode, the sensor (or listener) is represented by a black square placed either
9 on the dominant hand (A) or on the head (B). The schema illustrates how the participants'
10 hand or head orientation relative to the sound source is used to produce spatialised
11 auditory feedback.
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19 **Figure 2.**

20 Success rate and trial duration in Experiment 1. The graphs show the evolution of the
21 success rate (A) and trial duration (B) during the three successive blocks for the two
22 modes: hand mode (in blue) and head mode (in red). The symbols and vertical lines
23 represent the mean and standard error to the mean.
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30 **Figure 3.**

31 Kinematics of the reaching hand and of the head in the hand mode (in blue) and head
32 mode (in red). The left part of the figure shows the kinematic variables of the reaching
33 hand: 3D direct distance (A), cumulative trajectories (B), and cumulative rotation (C). The
34 right part of the figure shows the kinematic variables of the head: 3D direct distance (D),
35 cumulative trajectory (E), and cumulative rotation (F). The symbols and vertical lines
36 represent the mean and standard error to the mean.
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45 **Figure 4.**

46 Success rate and trial duration in Experiment 2. The graphs show the evolution of the
47 success rate (A) and trial duration (B) during the three successive blocks for the two
48 modes: hand mode (in blue) and head mode (in red). The symbols and vertical lines
49 represent the mean and standard error to the mean.
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56 **Figure 5.**

57 Kinematics of the reaching hand and of the head in the non-dominant hand mode (in blue)
58 and in the head mode (in red). The left part of the figure shows the kinematic variables of
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the reaching hand: 3D direct distance (A), cumulative trajectories (B), and cumulative rotations (C). The right part of the figure shows the kinematic variables of the listener: 3D direct distance (D), cumulative trajectories (E), and cumulative rotations (F). The symbols and vertical lines represent the mean and standard error to the mean.

Figure 1

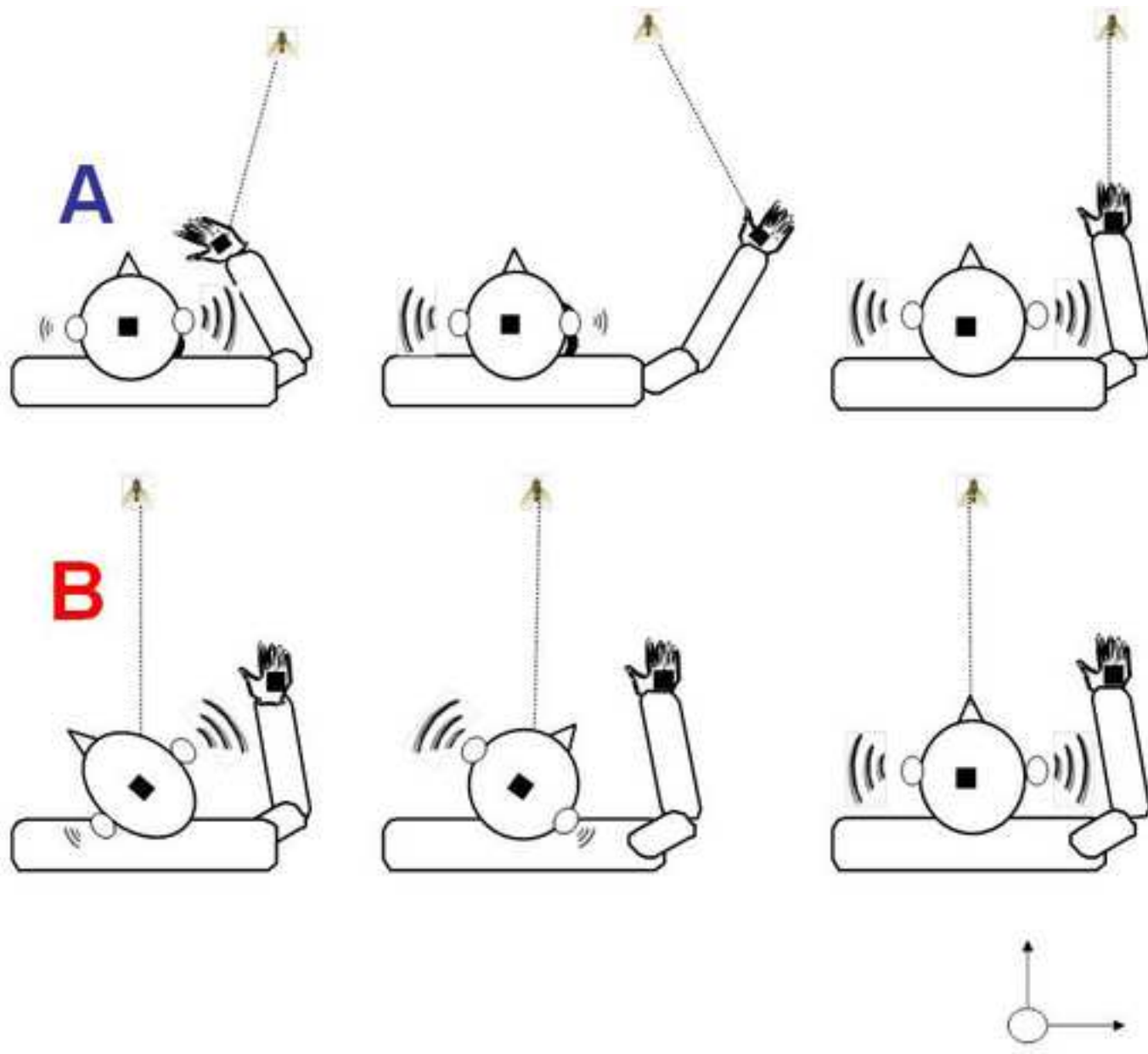


Figure 2

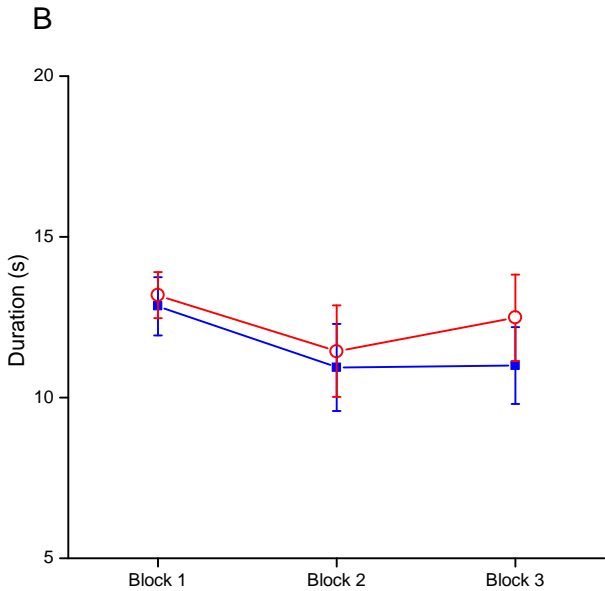
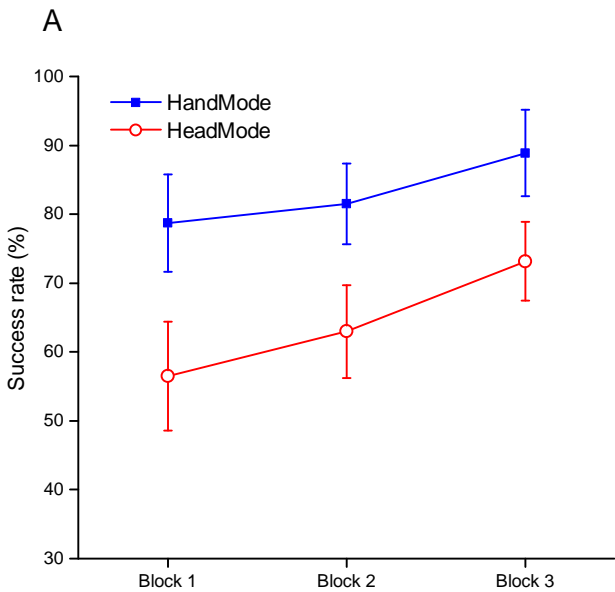


Figure 3

Reaching hand

Head

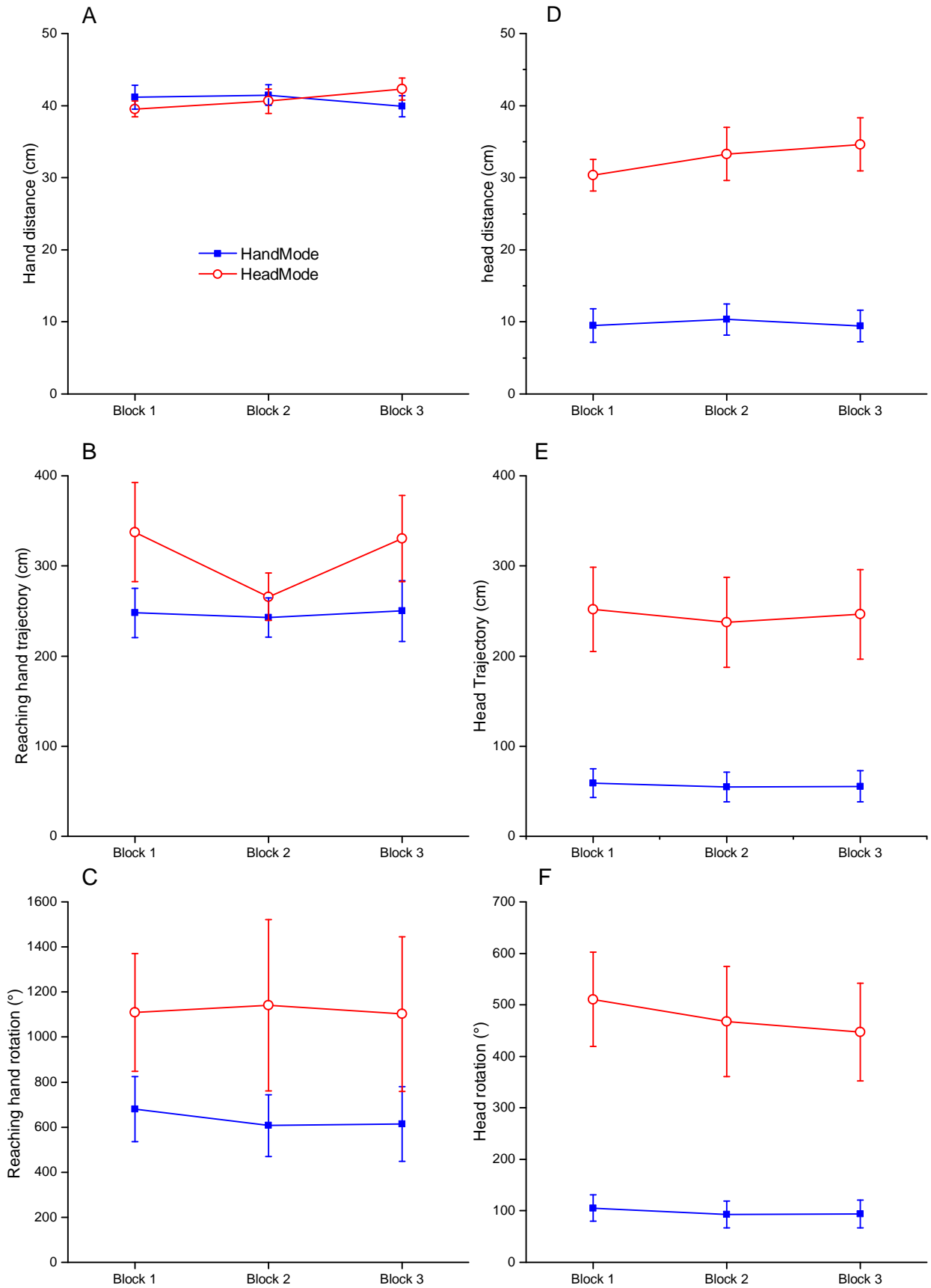


Figure 4

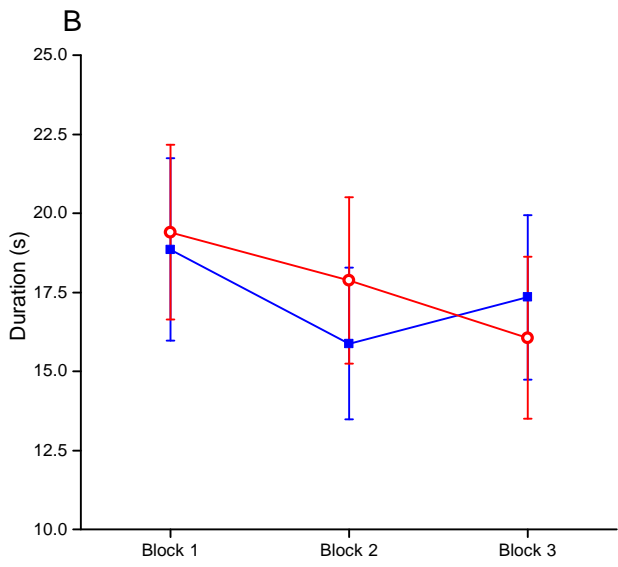
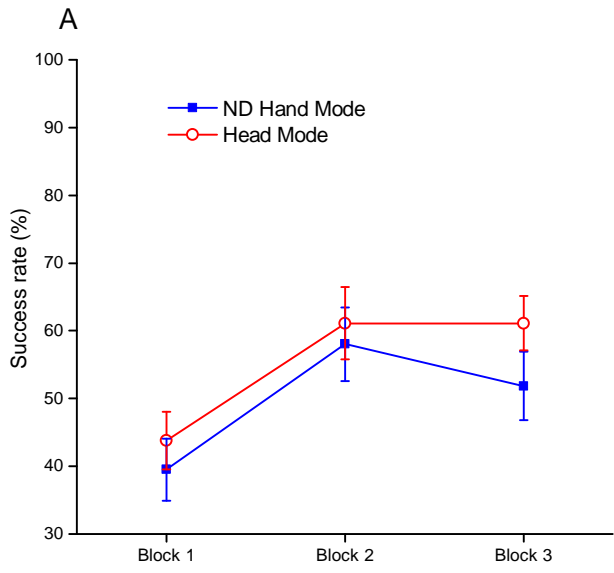
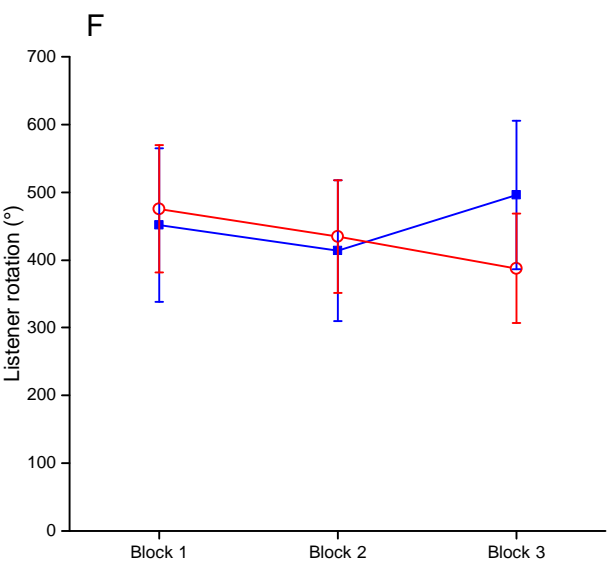
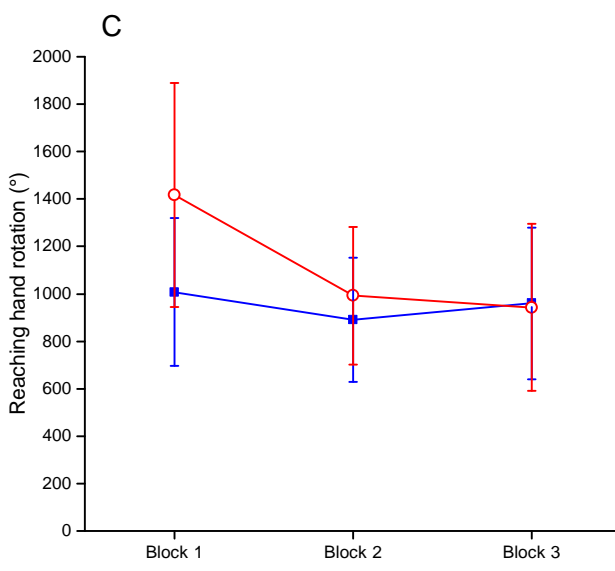
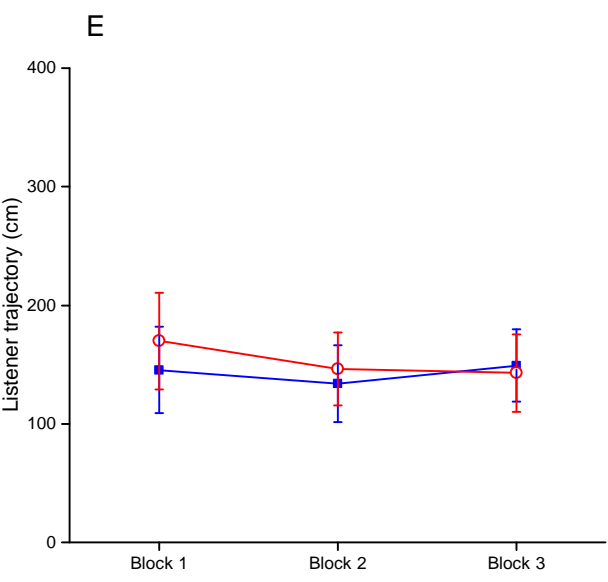
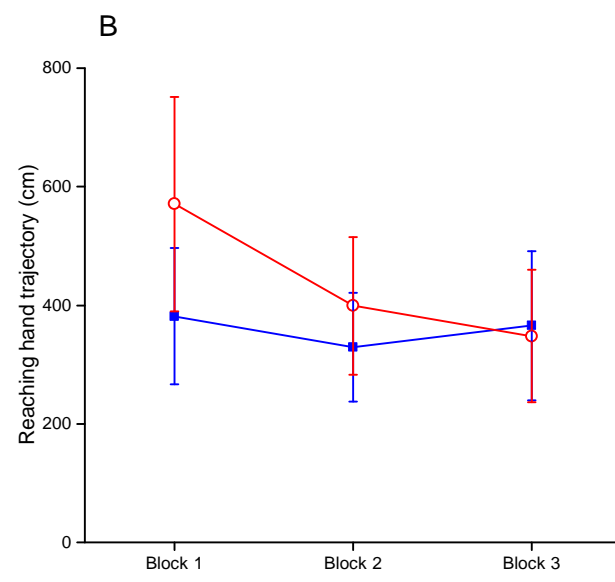
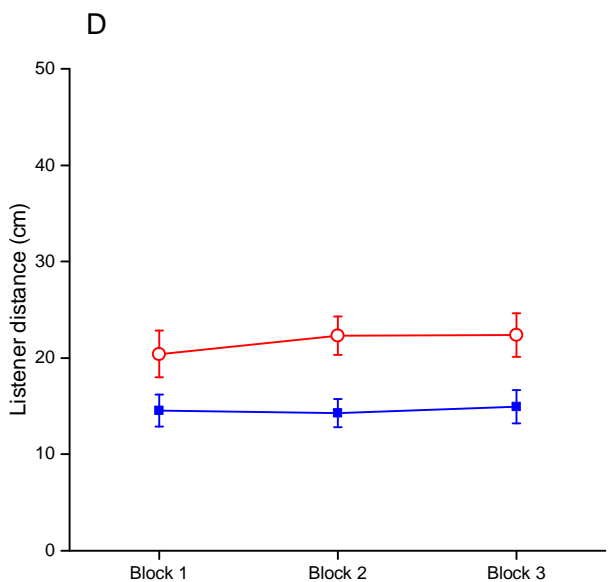
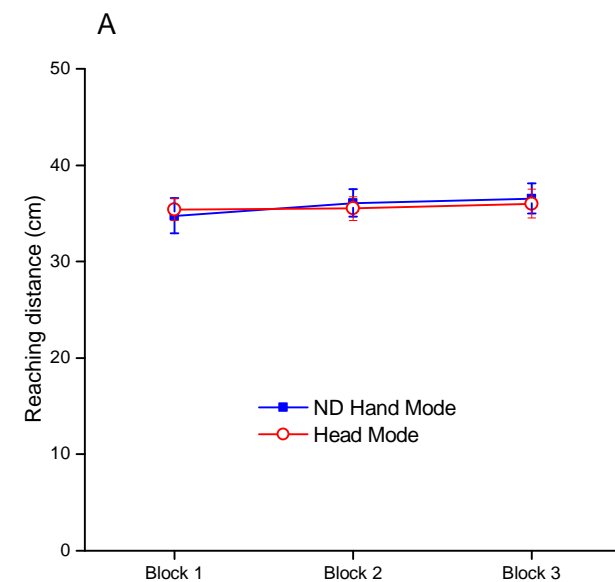


Figure 5

Reaching hand

Listener



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