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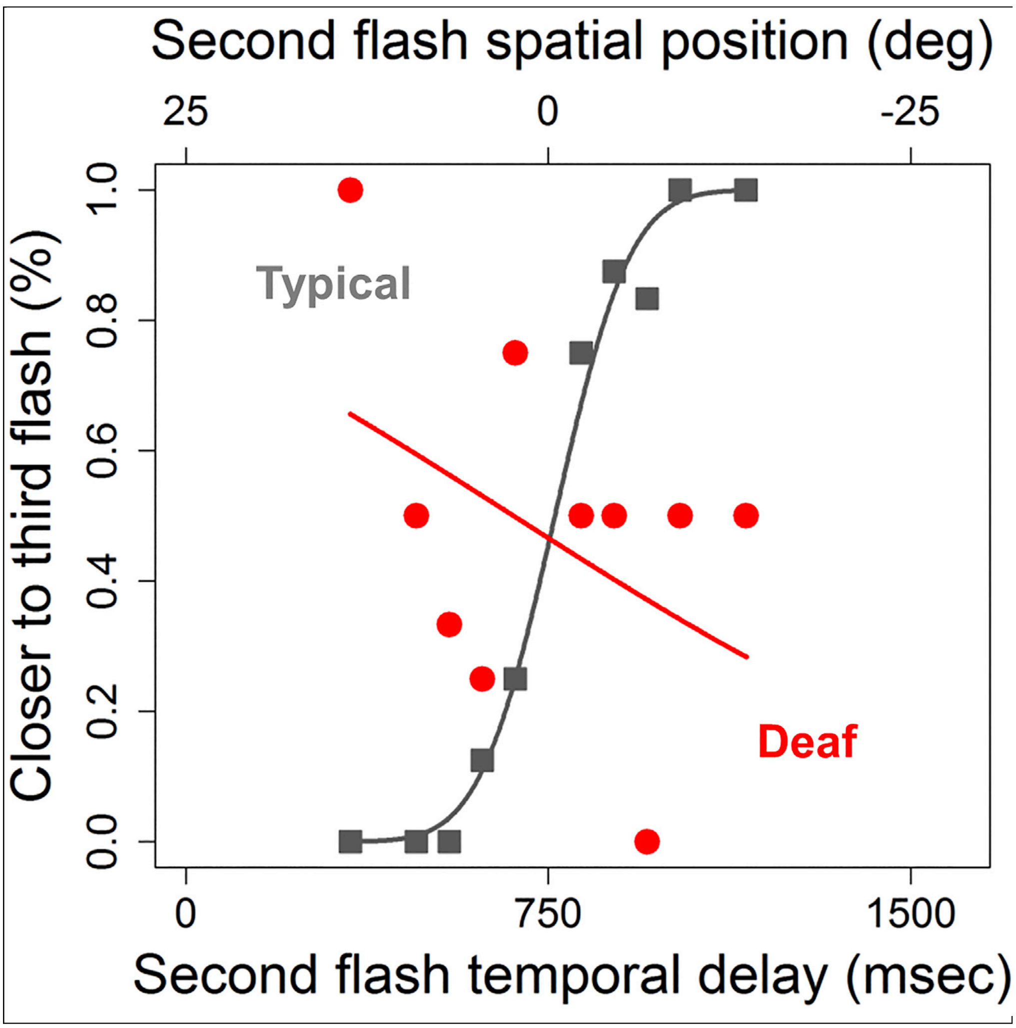

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HIGHLIGHTS

Deaf individuals are not able to build complex temporal representations

Their deficit disappears when coherent temporal and spatial cues are presented

In some cases, deaf people use spatial cues to infer temporal coordinates

There exists a strong interaction between spatial and temporal representation

Amadeo et al., iScience *19*, 369–377
September 27, 2019
https://doi.org/10.1016/j.isci.2019.07.042

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Spatial Cues Influence Time Estimations in Deaf Individuals

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SUMMARY

Recent studies have reported a strong interaction between spatial and temporal representation when visual experience is missing: blind people use temporal representation of events to represent spatial metrics. Given the superiority of audition on time perception, we hypothesized that when audition is not available complex temporal representations could be impaired, and spatial representation of events could be used to build temporal metrics. To test this hypothesis, deaf and hearing subjects were tested with a visual temporal task where conflicting and not conflicting spatiotemporal information was delivered. As predicted, we observed a strong deficit of deaf participants when only temporal cues were useful and space was uninformative with respect to time. However, the deficit disappeared when coherent spatiotemporal cues were presented and increased for conflicting spatiotemporal stimuli. These results highlight that spatial cues influence time estimations in deaf participants, suggesting that deaf individuals use spatial information to infer temporal environmental coordinates.

INTRODUCTION

Time perception is inherently part of everyday life. It occurs while we stare at the hands of the clock slowly moving when we are bored, but also while listening to our favorite song or listening to speech unfolding in time. To perceive a coherent temporal representation and successfully interact with our environment, we need to combine information derived from our sensory modalities. In 1963, Paul Fraisse stated that "hearing is the main organ through which we perceive change: it is considered as the 'time sense'." (Fraisse, 1963). Recent studies support his idea, showing that different sensory modalities are more appropriate to process specific environmental proprieties, and specifically the auditory system is the most accurate one to represent temporal information (e.g., Guttman et al., 2005; Bresciani and Ernst, 2007; Burr et al., 2009; Barakat et al., 2015).

Behavioral results showed that audition prevails in audiovisual temporal tasks. For instance, a single flash is perceived as two flashes when presented with two concurrent beeps (Shams et al., 2000) and the perceived frequency of flickering lights is influenced by an auditory stimulus presented simultaneously at a different rate (Gebhard and Mowbray, 1959; Shipley, 1964). Similarly, neuroimaging studies on hearing individuals highlighted a crucial role of the auditory cortex on time representation. For example, activation of the superior temporal gyrus has been observed during temporal processing of visual stimuli with functional Magnetic Resonance Imaging (Coull et al., 2004; Ferrandez et al., 2003; Lewis and Miall, 2003), and transcranial magnetic stimulation (TMS) over the auditory cortex has been shown to affect time estimation of both auditory and visual stimuli (Kanai et al., 2011), as well as tactile events (Bolognini et al., 2010).

Given the superiority of audition over the other sensory systems for time perception, the auditory modality might offer a temporal background for calibrating other sensory information. Converging evidence suggests that the development of multisensory interactions between audition and other senses depends on early perceptual experience (e.g., Merabet and Pascual-Leone, 2010; Cardon et al., 2012; Lazard et al., 2014) and the lack of auditory experience might interfere with the development of a temporal representation of the environment (Gori et al., 2017).

Deafness is a natural condition that offers valuable insight into the role of audition on temporal representation (see Bavelier et al., 2006; Pavani and Bottari, 2012). Research in both animals and humans suggests that a deficit in one sensory modality, such as audition, can induce compensatory mechanisms leading to increased abilities in spared sensory modalities, such as vision or touch (Strelnikov et al., 2013; Allman et al., 2009; Barone et al., 2013; Lomber et al., 2010). At the neurophysiological level, large-scale reorganization

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https://doi.org/10.1016/j.isci.2019.07.042

occurs after this sensory loss (e.g., Bola et al., 2017; Auer et al., 2007; Finney et al., 2003; Benetti et al., 2017). The auditory cortex deprived of the auditory input starts to be recruited by tactile and visual stimuli (e.g., Finney et al., 2001; Kok et al., 2014; Campbell and Sharma, 2016; Bottari et al., 2014; Karns et al., 2012), and changes within the early visual pathway in the absence of auditory input have also been reported in deaf individuals (e.g., Bottari et al., 2011). However, other studies reported only little change of the auditory neural structures in deaf animals (e.g., Clemo et al., 2016) and very few new connections between visual and auditory cortices as a result of deafness (e.g., Chabot et al., 2015; Butler et al., 2016). Focusing on the abilities to process temporal information in conditions of auditory deprivation, behavioral results are conflicting and seem to vary based on the type of task and stimuli. When asked to estimate and reproduce the duration of visual stimuli, for instance, deaf participants are often found to perform similar or better than controls in the range of milliseconds (Bross and Sauerwein, 1980; Poizner and Tallal, 1987), but not in the range of seconds (Kowalska and Szelag, 2006). However, Bolognini et al. (2012) observed low abilities to reproduce tactile durations in the range of milliseconds. In addition, tactile perceptual thresholds in a simultaneity judgment task are significantly higher in deaf compared with hearing individuals regardless of the spatial location of the stimuli (Heming and Brown, 2005), but opposite results were obtained for a visual temporal order judgment task (Nava et al., 2008).

Developmental results showed that both typical children and adults exhibit strong auditory dominance during audiovisual temporal bisection, which involves judging the relative presentation timings of three stimuli and requires to build complex temporal representations (Gori et al., 2012). Interestingly, deaf children with restored hearing do not show the same auditory dominance (Gori et al., 2017). In light of these findings, here we hypothesized that the lack of audition should affect the development of complex temporal representation underlying visual temporal bisection skills. Moreover, we recently reported a strong interaction between spatial and temporal representation when the visual experience is missing (Gori et al., 2018). Specifically, we showed that when vision is not available, such as in blindness, subjects are not able to build complex spatial representations and are strongly attracted by temporal cues. Based on the evidence showing a strong link between space and time representation in the absence of vision, we hypothesized that when audition is not available, not only complex temporal representations could be impaired but also spatial representation of events could be used to build a temporal metric.

To test our hypotheses, we asked hearing and deaf individuals to perform visual bisection tasks, where conflicting and not conflicting temporal and spatial information was delivered. Participants see three stimuli and need to judge whether the second stimulus is temporally (i.e., temporal bisection) or spatially (i.e., spatial bisection) closer to the first one or the third one. Specifically, the second stimulus was randomly and independently delivered at different spatial positions with different temporal lags, giving rise to coherent (i.e., identical space and time) and incoherent (i.e., opposite space and time) spatiotemporal information, as well as independent spatiotemporal information (i.e. space not informative about time, and vice versa). As predicted, deaf individuals were not able to perform the temporal bisection when only temporal and not spatial cues were informative. However, the temporal bisection deficit disappeared when coherent temporal and spatial cues were presented (e.g., short time associated with short space) and increased when conflicting temporal and spatial information was presented (e.g., short time associated with long space). Our results suggest that deaf individuals rely strongly on spatial cues when inferring temporal metric information. These findings support the idea that the temporal and spatial domains tightly interact, and sensory experience is fundamental for the development of independent temporal and spatial representations.

RESULTS

Seventeen deaf adults (see Table S1 for details) and seventeen age-matched controls performed four visual bisection tasks: three temporal bisection tasks and one spatial bisection task as a control experiment. In the three temporal bisection tasks (*independent space*, *coherent space,* and *opposite space*), aimed to measure thresholds for temporal bisection, three consecutive flashes were presented (see Figure 2, upper panels), and subjects judged whether the second flash was temporally closer to the first (displayed at -25°, left of center) or to the third (+25°, right of center) flash. To evaluate the role of spatial cues on temporal bisection performance of deaf individuals, the spatial distance between the three flashes was manipulated in the three temporal tasks. In the *independent space* temporal bisection task, the three flashes were delivered with the same distance between the first and the second flash and between the second and the third flash (25°, as in previous work, Gori et al., 2014). In this case, only temporal cues were relevant to

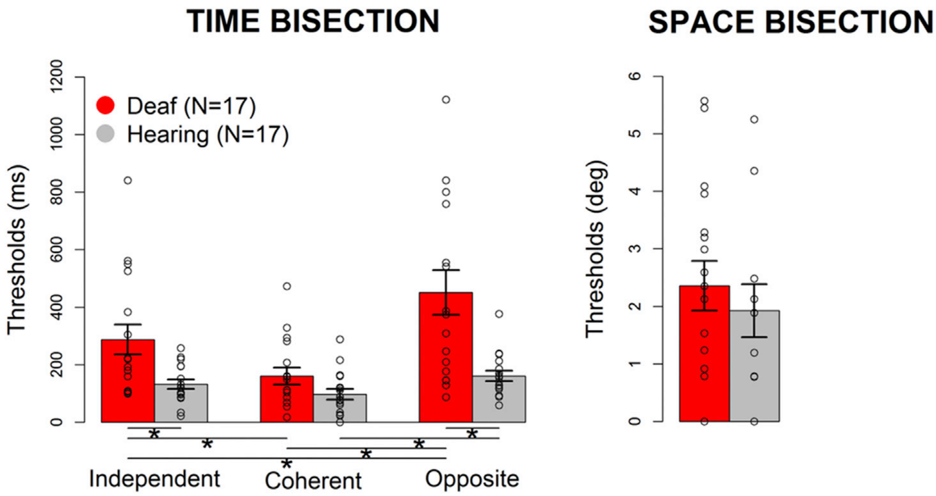

Figure 1. Group Performance in Visual Bisection Tasks

Average thresholds (±SEM) of the three temporal bisection tasks (left panel) and the spatial bisection task (right panel) for deaf (red; see also Table S1) and hearing (gray) participants. Dots represent individual data; *p < 0.01 after Bonferroni correction.

compute the task as the spatial distance between the three flashes was the same and space coordinates were uninformative about time coordinates (Figure 2A top). In the *coherent space* temporal bisection task, temporal intervals and spatial distances between the three flashes were directly proportional: a longer time delay between the first and the second flash was associated with a longer spatial distance between the two flashes, and the reverse for shorter intervals (Figure 2B top). In the *opposite space* temporal bisection task, temporal intervals and spatial distances between the three flashes were inversely proportional: a longer time delay between the first and the second flash was associated with a shorter spatial distance between the two flashes, and the reverse for shorter intervals (Figure 2C top). In the spatial bisection task performed as a control, subjects had to pay attention to three similar flashes but produced with the same temporal delay between the first and second flashes and the second and third flashes and report if the second flash was closer to the first one or to the last one in space, thus using spatial cues.

Averages and individual data for the three temporal bisection tasks and for the spatial bisection task are reported for deaf (in red) and hearing (in gray) individuals in Figure 1. The two-way ANOVA with temporal thresholds as dependent variable shows a significant interaction ($F_{2,64} = 9.39$, $p < 0.001$, generalized eta squared = 0.2) between group (hearing, deaf) and task (*independent space*, *coherent space*, *opposite space*). Post-hoc comparisons were conducted with follow-up one-way ANOVAs and two-tailed t tests, with probabilities treated as significant when lower than 0.05 after Bonferroni correction. Post-hoc t tests reveal that deafness impairs temporal bisection abilities, as evident from the higher thresholds of deaf people in the *independent space* temporal task compared with hearing participants (deaf versus hearing: $t_{19.7} = 2.86$, $p = 0.03$). Moreover, whereas for hearing individuals (in gray) the manipulation of the spatial cue during time bisection slightly influences the response (i.e., similar performance for the three temporal conditions, see Figure 1), it strongly affects the response of deaf participants (in red). Indeed, from follow-up one-way ANOVAs significant differences among tasks emerge for both deaf ($F_{2,34} = 14.96$, $p < 0.001$, generalized eta squared = 0.2) and hearing participants ($F_{2,34} = 6.53$, $p = 0.004$, generalized eta squared = 0.01), but post-hoc t tests reveal only a small difference between the coherent and the opposite conditions for hearing participants ($t_{16} = 2.87$, $p = 0.03$), whereas the performance of deaf individuals results is statistically more impaired in the *opposite space* bisection task compared with the *independent space* ($t_{16} = 3.29$, $p = 0.01$) and *coherent space* ($t_{16} = 4.84$, $p < 0.001$) conditions. These findings indicate a strong reduction of precision in the conflict condition after auditory deprivation. Still, performance of deaf individuals significantly improves from the *independent space* to the *coherent space* condition ($t_{16} = 3.71$, $p = 0.005$), suggesting that deaf individuals benefit from the spatial cue during temporal judgments. The average threshold of deaf participants (red bar) is also higher than that of hearing participants for the *opposite space* time bisection (deaf versus hearing: $t_{17.8} = 3.66$, $p = 0.005$), but average thresholds become low and similar between the groups for the *coherent space* time bisection (deaf versus

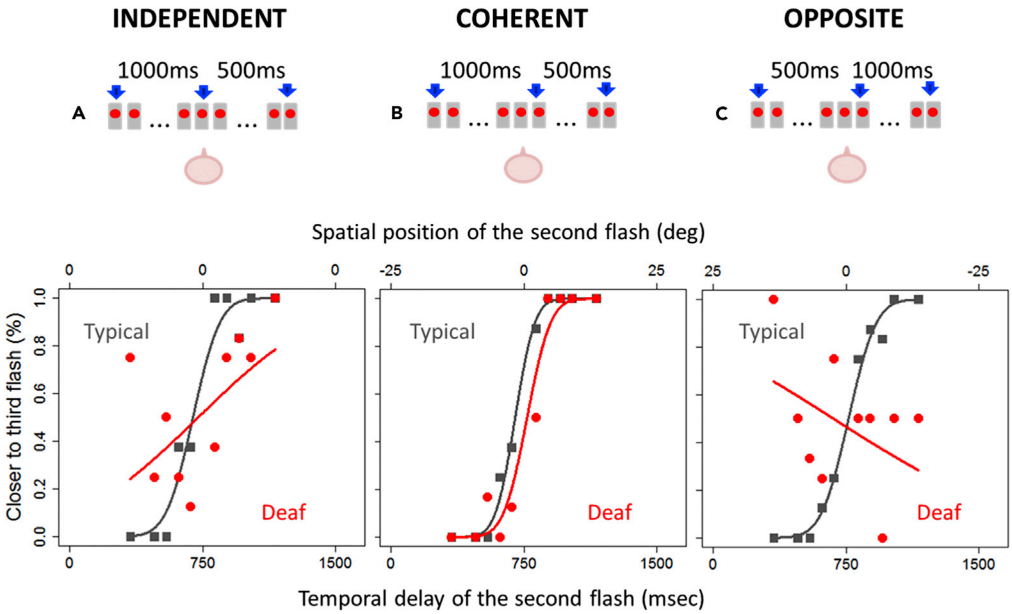

Figure 2. Visual Temporal Bisection Tasks

Results of the three conditions for a deaf participant showing strong spatial attraction (red symbols) and a typical hearing control (gray symbols). Subjects sat in front of an array of 23 light-emitting diodes, illustrated by the sketches above the graphs.

(A) *Independent space temporal bisection*. Top: the space distance between the first (-25°) and the second (0°) flashes was equal to the space distance between the second (0°) and the third (+25°) flashes. Bottom: proportion of trials judged "closer to the third flash source" plotted against the temporal delay for the second flash. Both sets of data are fitted with the Gaussian error function.

(B) *Coherent space temporal bisection*. Top: temporal intervals and spatial distances between the three flashes were directly proportional (e.g., a long temporal interval of 1,000 ms is associated with a longer spatial distance). Bottom: same as for (A).

(C) *Opposite space temporal bisection*. Top: temporal intervals and spatial distances between the three flashes were inversely proportional (e.g., a short temporal interval of 500 ms is associated with a longer spatial distance). Bottom: same as for (A) and (B).

hearing: $t_{26.9} = 1.82$, $p = 0.2$), in which temporal cues can be used by deaf participants to succeed at the task. The timing of sign language exposure does not affect the results of deaf participants, as no significant differences across the tasks emerge between early and late sign language learners from the permutation ANOVA (n. $\text{permutation}_{1,45} = 429$, $p = 0.2$).

As expected, all participants were able to perform the spatial bisection task and similar precision is observed between hearing and deaf groups (Figure 1 right panel; $F_{1,32} = 0.47$, $p = 0.5$, generalized eta squared = 0.01). However, we can exclude that deaf subjects performed better at the *coherent space* temporal bisection task simply because they performed a spatial task using the easier discriminable dimension for them (i.e., space) as no correlation appeared between performance in the *coherent space* temporal bisection and performance in the spatial bisection ($r = 0.11$, $p = 0.7$), and between performance in the *opposite space* temporal bisection and performance in the spatial bisection ($r = 0.11$, $p = 0.6$). Similarly, there is no correlation between the *independent space* temporal bisection task and the spatial bisection task ($r = 0.08$, $p = 0.7$), supporting the interpretation that the spatial cue was not influencing the performance in the *independent space* temporal bisection.

Figure 2 (lower panels) plots the proportion of answer "second flash closer to the third flash" as a function of the temporal delay of the second flash, for one deaf subject (in red) and one age-matched hearing control (in gray). Figure 2A reports the results for the *independent* bisection condition, Figure 2B for the *coherent* bisection condition, and Figure 2C for the *opposite* bisection condition. As suggested by group data, in the *independent* bisection condition (Figure 2A) the hearing individual shows the typical psychometric

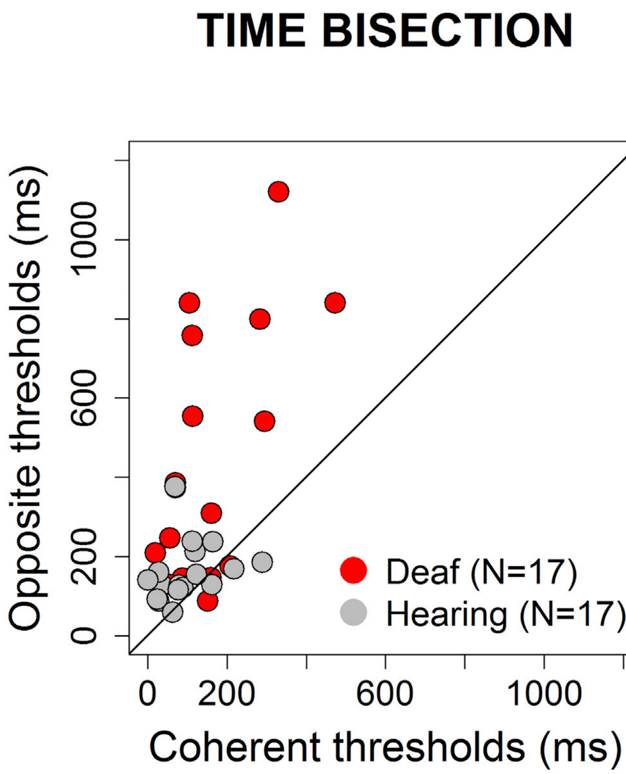

Figure 3. Relationship between Coherent and Opposite Temporal Bisection Tasks
Individual data, plotting opposite thresholds against coherent thresholds (calculated from the width of individual psychometric functions). Red and gray dots represent deaf and hearing individuals, respectively.

function. Contrarily, the deaf subject shows more random responses without a well-shaped psychometric function, reflecting for the first time an impairment of deaf people in this task. As regards the *coherent* bisection task (Figure 2B), the results are quite different: here the psychometric function for the deaf individual is present and as steep as that of the hearing participant, meaning similar precision. This result suggests that a spatial cue can be used by deaf individuals to improve their performance in the time bisection task. In the *opposite* temporal bisection task (Figure 2C), the response of the hearing subject is identical to the response in the other two conditions. In contrast, the deaf individual not only does not show a clear psychometric function but also his pattern of responses is in the opposite direction than expected (in red). The performance of the deaf individual reveals a strong spatial influence for the time bisection task under this condition, suggesting that in this deaf subject, whereas not in the hearing one, the spatial cue is attracting the temporal visual response.

In Figure 3 individual thresholds in the *coherent space* temporal bisection task are plotted against individual thresholds in the *opposite space* temporal bisection task for the hearing (in gray) and deaf (in red) groups. Hearing participants show similar performances for both tasks, with all the individual data laying in the equality line, whereas deaf participants display discrepancies between thresholds in the two tasks. In this latter group, almost all dots lie above the equality line suggesting lower performance for the *opposite space* than the *coherent space* task.

DISCUSSION

Here we studied whether space influences time for individuals with auditory impairment. In particular, we hypothesized that in deaf individuals, for whom the auditory input is missing, the construction of complex temporal metrics could be impaired and spatial cues could be used to determine the temporal relationships of events. Deaf and hearing subjects were tested with a visual task where conflicting and not conflicting temporal and spatial information was delivered. As predicted, deaf individuals showed a deficit in complex temporal representation, and we observed a strong attraction toward spatial cues during time bisection in deaf but not in hearing individuals. Indeed, deaf participants were not able to perform the temporal bisection task when space distances between the flashes were always the same and independent with respect to the time delay (i.e., *independent space* temporal bisection task). However, the temporal bisection deficit disappeared when coherent temporal and spatial cues were presented (i.e., *coherent space* temporal bisection task) and increased for conflicting temporal and spatial stimuli (i.e., *opposite space* temporal bisection task). On the contrary, hearing participants were unaffected by the cross-domain coherence or conflict, showing similar performances for the three conditions.

A first important result from the present study is that deaf participants showed a specific deficit for the temporal bisection task, which required subjects to encode the presentation timings of three flashes, keep them in mind over a period of 1.5 s, extract the relative time intervals between them, and compare these estimates. There was no impairment in the spatial bisection task instead, which required the evaluation of spatial distances between three flashes. This suggests that our results did not originate merely from attentional or mnemonic deficits *per se* and that the effort of deaf subjects did not encompass all aspects of visual processing but was limited to visual temporal representations. Although literature about temporal skills following auditory deprivation is inconsistent (see Introduction), this result is in line with our expectation. The temporal bisection is a complex task in terms of temporal memory and attention; it involves the construction of complex temporal matrices, and we know from previous studies that audition plays a strong dominant role in it. When performing an audiovisual multisensory temporal bisection task, both young children and adults use only auditory information to estimate the multisensory temporal position of the stimulus (Gori et al., 2012). Interestingly, deaf children with restored hearing did not show this auditory dominance during the same task, further confirming that the auditory experience has a crucial influence on temporal bisection skills (Gori et al., 2017). In addition, the temporal bisection deficit we observed in deaf participants is in agreement with existing literature showing that auditory experience is necessary for the development of timing abilities in other modalities. Deaf adults were found to be impaired in estimating visual temporal durations in the range of seconds (Kowalska and Szelag, 2006) and tactile temporal durations in the range of milliseconds (Bolognini et al., 2012).

Most importantly, this study allowed us to describe the influence of spatial features on time estimations in deaf individuals. By naturally combining temporal and spatial representations (as both spatial distances and temporal intervals are determined by the first and the third stimuli and the spatial and temporal coordinates of the second stimulus can be independently modulated with respect to the other two stimuli), the bisection task gives the opportunity to investigate the interaction between space and time. In line with our study in blindness (Gori et al., 2018), the current findings provide further evidence that temporal and spatial representations are strictly linked in the human brain and sensory experience is crucial for the development of independent spatial and temporal representations. Indeed, we have previously demonstrated that the gross deficit of blind people in visual-spatial bisection (Amadeo et al., 2019; Gori et al., 2014; Campus et al., 2019) disappears when coherent temporal cues are delivered, and increases in front of conflicting spatiotemporal information (Gori et al., 2018). As vision is the most apt sense for spatial representation, blind people are impaired in building complex spatial representations and show a temporal attraction of space. Here, we show the opposite: deaf people are impaired in building complex temporal representations and show a spatial attraction of time. Thus the modification of spatiotemporal cues alters temporal and spatial bisection performance in deafness and blindness, respectively, whereas in both tasks control subjects can easily dissociate the spatial and temporal cues.

To better understand the strategy used by deaf participants we run some additional correlational analyses. The lack of correlation between spatial performance (i.e., space bisection) and temporal performance when coherent (i.e., *coherent space* temporal bisection) and conflicting (i.e., *opposite space* temporal bisection) spatiotemporal cues were presented suggests that the improved and impaired temporal performance of deaf individuals under these conditions was not simply due to the use of the spatial cue. Indeed, if they just performed the spatial task with temporal information injecting noise, at least their performance in the *coherent space* temporal bisection should be as good as in the *independent space* temporal bisection. Furthermore, if deaf participants were simply performing a spatial task even though asked about time, in the *opposite space* temporal bisection the psychometric functions should be always perfectly inverted. Instead, in the *opposite space* condition we observed a biased and a not complete inversion, suggesting that the strategy of the group was not exclusively based on the spatial cue but that there exists a dominance of spatial over temporal information. Also, performance in the *independent space* temporal bisection task did not correlate with that in the pure spatial bisection, further supporting the lack of weight assigned to the spatial cue in the *independent space* temporal task. Thus, although we cannot completely exclude that deaf participants used space as it was the easier discriminable dimension, our results suggest that participants were not simply performing a spatial task instead of a temporal judgment.

In the literature, two main theories address how the concepts of space and time are linked in the human mind. According to the Metaphor Theory (MT, Lakoff and Johnson, 1999), temporal representations depend asymmetrically on spatial representations, meaning that space unilaterally affects time, whereas the opposite is not possible. The metaphorical language is mentioned to sustain this hypothesis (Boroditsky, 2000; Clark, 1973), suggesting that spatial metaphors are necessary to think and talk about time. By contrast, Walsh et al. (Walsh, 2003) introduced a different perspective by proposing A Theory of Magnitude (ATOM), which does not predict any cross-domain asymmetry. ATOM states that space and time, together with numbers, are represented in the brain by a common magnitude system and are thus symmetrically interrelated (Bueti and Walsh, 2009; Burr et al., 2010; Lambrechts et al., 2013). At first glance, our results seem to support the MT as we show a spatial attraction on time. However, considering our specular study on blindness too (Gori et al., 2018), there exists a strong interaction between space and time, with space influencing time estimations, and vice versa, which strongly supports the ATOM. Several other behavioral (e.g., Bueti and Walsh, 2009; Dormal et al., 2008) and neuroimaging studies (e.g., Fias et al., 2003; Pinel et al., 2004; Dormal and Pesenti, 2009) agree with this theory, highlighting interferences between the two domains and the overlapping activation of areas in the parietal lobe during magnitude processing.

Our results also provide strong support to previous studies showing that the visual system is fundamental for space perception (Alais and Burr, 2004), whereas the auditory system is essential for temporal discrimination (Burr et al., 2009). In this context, McGovern et al. (2016) recently demonstrated that benefits derived from training on a spatial task in the visual modality transfer to the auditory modality, and benefits derived from training on a temporal task in the auditory modality transfer to the visual modality. As the converse patterns of transfer were absent, they suggested a unidirectional transfer of perceptual learning across sensory modality, from the dominant to the non-dominant sensory modality. In line with this, we previously suggested that, as audition is fundamental for time perception, the temporal sequence of events could be at the base of the development of auditory spatial metric understanding (Gori et al., 2018). Symmetrically, as vision is fundamental for space perception, the spatial relationship of events could be at the base of the development of visual temporal metric understanding. Therefore, on the one hand, temporal metric representations seem to be mediators for the development of auditory spatial metric representations, and the visual experience is crucial for this mediation to occur (Gori et al., 2018). On the other hand, spatial metric representations seem to be mediators for the development of visual temporal metric representations, and the auditory experience is crucial for this mediation too.

However, how space and time are represented in the brain and how different sensory modalities shape the development of these representations is still an open issue. Further research is necessary to better understand whether spatial attraction of time is a general mechanism of time perception in deafness, or it is specific for the temporal bisection task. The present data are also in agreement with the theory of cross-sensory calibration (Gori, 2015), which states that during development the most robust, accurate sensory modality for a given perceptual task (i.e., audition for temporal judgments, Gori et al., 2012) can be used to calibrate the other sensory channels. From our studies in deafness and blindness, we can add that not only sensory modalities interact during development but also the spatial and the temporal domains seem to interact. It might be that the auditory system is used to calibrate visual temporal representation, transferring the visual processing from a spatial to a temporal coordinate system, thanks to a prior of constant velocity, which may represent a channel of communication between the two sensory systems. The brain may implicitly assume the constant velocity of the stimuli and consequently uses spatial maps to solve visual temporal metric analysis. This hypothesis would explain why when the auditory input is absent, such as in deafness, people are attracted by spatial cues to make specific temporal estimations.

These findings open important opportunities for new rehabilitation strategies following sensory loss, and for the development of new sensory substitution devices. If space attracts time estimations when the auditory input is absent, we should think of new techniques where spatial and temporal cues could be simultaneously manipulated to convey richer information, taking advantage of spatial cues to recalibrate temporal representation in deaf individuals.

Limitations of the Study

One limitation of the study is sample size due to difficulties in recruiting deaf individuals.

METHODS

All methods can be found in the accompanying Transparent Methods supplemental file.

SUPPLEMENTAL INFORMATION

Supplemental Information can be found online at https://doi.org/10.1016/j.isci.2019.07.042.

ACKNOWLEDGMENTS

Authors would like to thank Alessia Tonelli for her precious help in data collection and Lucilla Cardinali for her suggestions in discussion. Moreover, the authors thank deaf and hearing adults for their willing participation in this research.

AUTHOR CONTRIBUTIONS

M.G., M.B.A., F.P., and C.C. conceived the study and designed the experiments. M.B.A and C.C. carried out experiments and analyzed data. M.G., M.B.A., F.P., and C.C. wrote the manuscript, prepared figures, and reviewed the manuscript.

DECLARATION OF INTERESTS

The authors declare no competing interests.

Received: April 2, 2019
Revised: July 11, 2019
Accepted: July 26, 2019
Published: September 27, 2019

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ISCI, Volume *19*

Supplemental Information

Spatial Cues Influence

Time Estimations in Deaf Individuals

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Supplemental Information

Participant	Age	Sex	Age at deafness detection	Hearing aid use	Age at sign language first exposure
S01	56	F	From birth	Uses currently	26 years old
S02	42	M	From birth	Uses currently	Unknown
S03	34	F	From birth	Uses currently	6 years old
S04	33	F	From birth	Uses currently	From birth
S05	23	F	From birth	Used in the past	From birth
S06	28	F	7 years old	Uses currently	18 years old
S07	24	F	From birth	Used in the past	15 years old
S08	37	F	5 years old	Uses currently	13 years old
S09	60	M	From birth	Used in the past	From birth
S10	21	F	13 years old	Never used	19 years old
S11	26	F	From birth	Used in the past	From birth
S12	29	M	3 years old	Used in the past	6 years old
S13	21	F	From birth	Uses currently	From birth
S14	37	F	From birth	Uses currently	3 years old
S15	73	M	6 years old	Never used	7 years old
S16	35	M	From birth	Used in the past	6 years old
S17	28	M	From birth	Uses currently	25 years old

Table S1. Demographic information about deaf participants obtained through self-report questionnaires, Related to Figure 1.

Transparent Methods

Participants

A group of 18 deaf participants (mean age±SEM: 35.7±3.5 yo; F=9) and 18 age and gender-matched hearing participants (32.4±1.5 yo; F=9; $t_{21.2}$= 0.86, p=0.4) took part in the study. Deaf participants were recruited at the National Association for Deaf (Ente Nazionale per la protezione e assistenza dei Sordi), in Genova, Italy. One deaf and one hearing participant were excluded from statistical analysis because they were identified as outliers (i.e. score in at least one task differing more than three standard deviations from the mean score of the group), giving rise to a final sample of 17 subjects per group. All participants reported no history of neurological or cognitive deficits, they had normal or corrected-to-normal vision and they were right-handed by self-report. All deaf participants had bilateral moderate to profound hearing loss, and did not receive a cochlear implant (see Table S1 for details). The research protocol was approved by the ethics committee of the local health service (Comitato Etico, ASL3 Genovese, Italy) and conducted in line with the Declaration of Helsinki. Written informed consent was obtained prior to testing.

Stimuli and procedure

Participants were sitting in front of an array of 23 light-emitting devices placed at a distance of 180 cm and spanning ±25° of visual angle (with 0° representing the central device, negative values on the left, and positive values on the right; Fig. 1, upper panels). Their body midline was aligned with the central device position. They performed three temporal bisection tasks, and one spatial bisection task as a control. The order of temporal and spatial blocks was counterbalanced across subjects. In each task, subjects see a sequence of three consecutive flashes (2.3° diameter, 75 ms duration) for a fixed trial duration of 1500 ms. For deaf participants, a hearing person fluent in Italian sign language was involved for instructions and questions. Before testing, participants were warned to maintain a stable head position straight ahead throughout testing. A short training session with feedbacks was conducted to make participants familiar with the task and to be sure they understood it correctly. They were informed from the beginning that the first flash was always produced by a device placed on their left, whereas the last flash by a device on their right. No feedbacks were given during experimental sessions. Procedure was similar to our previous paper investigating auditory spatial bisection abilities in blind participants (Gori et al., 2018).

Temporal Bisection Tasks

In temporal bisection tasks, participants judged verbally whether the second flash (S2) was temporally closer to the first flash (S1; -25°, -750ms considering 0ms the halfway point of the trial duration) or to the third flash (S3; +25°, +750 ms). S2 could occur randomly at an intermediate time point between -750ms (corresponding to the trial start time) and +750ms in time (corresponding to the trail end time), determined through the method of constant stimuli. To evaluate the role of spatial cues in time perception, spatial distances between the three flashes were manipulated to create three different temporal bisection tasks (Fig. 1, upper panels from left to right): *independent space*, *coherent space* and *opposite space* temporal bisection tasks, with spatial distances between visual stimuli which could be independent, coherent or opposite with respect to time intervals respectively. In the *independent space* temporal bisection, S2 was always delivered from 0° in space, which corresponded to the central light-emitting device. To correctly compute this task participant had to rely exclusively on temporal features since the spatial distance between S1-S2 was identical to the spatial distance between S2-S3, making spatial aspects entirely uninformative. Among temporal bisection tasks, the *independent space* one was always performed as the first one, with the order of the other two tasks randomly varying across participants. In the *coherent space* temporal bisection task, temporal intervals between S1-S2 and S2-S3 were directly proportional to spatial distances between the three flashes (e.g. a shorter temporal delay between S1-S2 was associated with a shorter spatial distance between the two flashes). The exact spatial position associated with each temporal delay of S2 is reported in the upper horizontal axis of the central psychometric function in Figure 1. Considering that the total trial duration was 1500ms and the number of speakers was 23, when S2 was for example presented at -682ms (i.e. with a delay of 68ms from S1) it was delivered from the second device on the left; when it was presented at -614ms (i.e. with a delay of 136ms from S1) it was delivered from the third speaker, and so on. In this condition, spatial cues could be used by subjects to infer temporal metric. Instead, in the *opposite space* temporal bisection task time intervals between the three lights were inversely proportional to space distances (e.g. a shorter temporal delay between S1-S2 was associated with a longer spatial distance between the two flashes), making space informative but in the opposite direction with respect to time. Again, the exact spatial position associated with each temporal delay of S2 is reported in the upper horizontal axis of the psychometric function on the right in Figure 1. In the *opposite space* temporal bisection task, S2 was delivered from the second speaker on the left when it was presented at +682ms (i.e. with a delay of 1432ms from S1), it was delivered from the third speaker on the left when it was played at +614ms (i.e.with a delay of 1364ms from S1), and so on.

Spatial Bisection Task

In the *spatial bisection task* (control experiment), participants were asked to verbally report whether S2 was closer to S1 or to S3 in the space domain. Differently to temporal bisection tasks, S2 occurred randomly at an intermediate position from -25° to +25° in space but it was always presented at 0ms (i.e. 750ms after S1, which corresponded to the middle time of the temporal sequence between S1-S3). As for the S2 position in the temporal bisection tasks, the spatial position of S2 in the spatial bisection task was determined using the method of constant stimuli.

Data analysis

For each task, we calculated the proportion of trials where the second flash was perceived as closer to the third flash and data were fitted by cumulative Gaussian functions. Following standard psychophysical procedure (Kingdom and Prins, 2010), PSE and threshold estimates were obtained from the mean and standard deviation of the best fitting function, and standard errors for the bisection PSE and threshold estimates were calculated by bootstrapping (Efron and Tibshirani, 1993). Specifically, we used a custom algorithm that has been previously validated in many published papers involving children (e.g. Gori et al., 2008) and clinical participants (e.g. Gori et al., 2014, Gori et al., 2018) whose performance was far from being optimal and similar deficits in bisection tasks were reported. The algorithm is based on Bootstrap technique; it automatically verifies the goodness of fit of the psychometric function and, when it is not significant, it assigns as threshold the worst value one subject can get (i.e. max threshold). In our case, two subjects were interpolated in the *opposite space* condition, and one subject was interpolated in the *independent space* condition. Moreover, some deaf participants based their answers in the *opposite space* temporal bisection task on spatial features (i.e. when space distances were incoherent with respect to time intervals), resulting in inverted psychometric functions with threshold expressed by negative values (values closer to 0 meaning good precision but in the spatial domain). In order to include these results together with those of deaf individuals who performed the *opposite space* task without inverting the psychometric function, we applied a conversion to negative thresholds as previously in Gori et al. 2018. Given thresholds (t) for the *opposite space* bisection task, negative values t_{neg} were converted to $t'_{neg} = t_{neg} - min(t) + max(t)$. This transformation allowed us to treat thresholds as a continuum, ranging from low thresholds representing good precision in the temporal domain to high thresholds representing poor temporal performance but good precision in the spatial domain.

To investigate temporal bisection precision, statistical comparisons between thresholds were performed with an omnibus two-way ANOVA, considering group (hearing, deaf) as a between-subjects factor, and task (*independent*, *coherent*, *opposite*) as a within-subjects factor. For each group, a follow-up one-way ANOVA was carried out with the task (*independent*, *coherent*, *opposite*) as a within-subjects factor. To control whether an early exposure to sign language was impacting on the performance, deaf participants were also split into early and late based on sign language first exposure (cut-off: three years old) and a permutation ANOVA with group (early, late) as a between-subjects factor, and task (*independent*, *coherent*, *opposite*) as a within-subjects factor was run. To perform this analysis, we applied the *aovp* function of the lmPerm package in R (Wheeler, 2010). For the spatial bisection task, thresholds were analyzed with a one-way ANOVA with group (hearing, deaf) as a between-subjects factor. For both bisection tasks, post-hoc comparisons were conducted with two-tailed t-tests, with probabilities treated as significant when lower than 0.05 after Bonferroni correction.

Moreover, for the group of deaf individuals Pearson correlational analyses were carried out to evaluate the relationship between the performance at the three conditions (*independent space*, *coherent space* and *opposite space*) of temporal bisection task and the performance at the spatial bisection task.

Data and Software Availability

Data and/or code used in the study are available from the corresponding author upon direct request.

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