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Mechanisms of learning and plasticity across sensory modalities: insights from bilateral deafness and intense visual training

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ABSTRACT

Interacting with the external environment is an inherently multisensory experience. Therefore, understanding how unisensory deprivations occurring early in life affect this interaction has always been a hot topic of research. In this thesis I aim to contribute to this prolific debate by further investigating the effects on behavior exerted by early-acquired bilateral deafness. In the past decades many studies have extensively investigated this topic, focusing mainly on explaining the changes occurring within the visual modality of deaf people, ultimately aiming at understanding to what extent the intuitive assumption that deaf adults 'see better' than hearing controls is really true. This approach proved highly informative, yet many fundamental aspects of behavior remained largely overlooked. The aim of this thesis was to identify these missing aspects and try to address them as systematically as possible. In particular I focused on four critical domains: (i) the investigation of the behavioral reorganization that occurs within the tactile modality of deaf adults (**Chapter 2, Study 1; Study 2**); (ii) the possible modifications of the interactions between two intact sensory systems (i.e., vision and touch) as a consequence of auditory deprivation (**Chapter 3**); (iii) the finer-grained definition of which mechanisms of visual attention are modified by bilateral deafness (**Chapter 4, Study 1; Chapter 5**); (iv) the further understanding of the role of extensive visual training in driving the behavioral improvements reported in the deaf population compared to hearing controls (**Chapter 2, Study 3; Chapter 4, Study 1; Study 2; Chapter 5**). This set of results highlight that deafness-related plasticity exerts multifaceted effects on behavior, which extend selectively to certain functions but not to others, and that even produced selective aspects of impaired behaviors. Importantly, these data also provide initial evidence that vision and touch might to a certain extent, reorganize independently from one another as a consequence of early bilateral deafness and that also the way they interact with each other shows some modified aspects. Finally, the majority of the behavioral modifications I documented in this thesis depended from deafness per se and was not ascribable to training-related effects. Unexpectedly but very interestingly, what clearly emerged from this set of results is the remarkable flexibility of which are capable the reorganized sensory systems, and in particular the reorganized visual system of deaf adults.

CHAPTER 1:

General Introduction

1.1 Theoretical background: Crossmodal plasticity

The perception of the external environment is unavoidably linked to our sensory systems. It is then quite straightforward to imagine that a unisensory deprivation such as bilateral deafness or blindness will impact the way we perceive and ultimately interact with the world around us. This intuitive awareness fostered a prolific debate on how unisensory loss would affect the remaining and intact sensory modalities. In particular, over the years, two opposing views have developed and have contrasted each other. One proposal is generally referred to as the perceptual deficiency hypothesis and it predicts that as a consequence of a unisensory deprivation occurring early in life, also the other perceptual systems would be irreparably impaired, preventing any efficient interaction with the external environment (e.g., Quittner et al., 2007; Voss, Collignon, Lassonde & Lepore, 2010). The other proposal, instead, is generally referred to as the compensatory hypothesis and it predicts that in unisensory deprived people, the remaining sensory modalities would be potentiated, eliciting improved behaviors compared to the control population, or at least equally efficient behaviors (e.g., Röder & Neville, 2003; Théoret, Merabet & Pascual-Leone, 2004). This latter proposal has been always considered as more appealing than the former one, mainly due to the frequent observation that sensory deprived individuals appear perfectly capable of interacting with the external environment, thus making the perceptual deficiency hypothesis less probable. Moreover, the literature is full of anecdotal reports of sensational abilities that developed as a consequence of sensory loss, especially for what it concerns blindness, with reports dated back to several centuries ago (Diderot, 1749; James, 1890). The French philosopher Denis Diderot, for instance, in his ‘Letter on the blind’ (1749) reported the case of a blind mathematician who was able to disentangle real from fake money simply by touching them. The famous American psychologist William James instead described the incredible ability of blind people to navigate in the environment without bumping into potential obstacles (James, 1890). Overall, then, the notion that the remaining and intact sensory modalities are improved following unisensory deprivations, found a prolific environment to sediment in people’s minds.

In the last two decades, the field of cognitive neuroscience has witnessed a renewed interest toward the compensatory effects that unisensory deprivations (as bilateral deafness or blindness) exert on behavior. This was predominantly due to the growing corpus of evidence reporting *crossmodal plasticity* in bilateral deaf or blind people, as the mechanism underlying many of the documented behavioral enhancements (see for reviews Dormal & Collignon, 2011; Frasnelli, Collignon, Voss & Lepore, 2011; Merabet & Pascual-Leone, 2010; Pavani & Röder, 2012; Voss & Zatorre, 2012). The term crossmodal plasticity generally refers to the adaptive reorganizations of neurons or of brain regions involving the intact perceptual systems as a consequence of sensory deprivation. In particular it refers to the reorganization occurring in the deprived sensory system, due to the recruitment of these brain regions by the remaining and intact sensory modalities. For instance, several studies reported the recruitment of visual cortices of blind people by auditory stimuli (e.g., Bedny, Konkle, Pelphrey, Saxe, & Pascual-Leone, 2010; Collignon, Vandewalle, Voss, Albouy, Charbonneau, Lassonde, & Lepore, 2011; Poirier, Collignon, Scheiber, Renier, Vanlierde, Tranduy, Veraart, & De Volder, 2006; Renier, Arunova, De Volder, Carlston, VanMeter & Rauschecker, 2010; Wolbers, Zahorik, & Giudice, 2011) as well as by tactile stimulations, even though to a lesser extent if compared to results on audition (e.g., Sadato, Okada, Honda & Yonekura, 2002; Stilla, Hanna, Hu, Mariola, Deshpande & Sathian, 2008; see for a review Sathian & Stilla, 2010). Similarly, auditory cortices of deaf people have been shown to be recruited by tactile (Auer, Bernstein, Sungkarat & Singh, 2007; Karns, Dow & Neville, 2012; Levänen, Jousmäki & Hari, 1998) as well as by visual stimulations (in humans: e.g., Cardin, Orfanidou, Rönnberg, Capek, Rudner & Woll, 2013; Fine, Finney, Boynton & Dobkins, 2005; Finney, Fine & Dobkins, 2001; Vachon, Voss, Lassonde, Leroux, Mensour, Beaudoin, Bourgouin, & Lepore, 2013; in deaf cats: Lomber, Meredith & Kral, 2010; Meredith, Kryklywy, McMillan, Malhotra, Lum-Tai, & Lomber, 2011; Wong, Chabot, Kok & Lomber, 2013). These findings revolutionized the whole field of the research on perception, by dramatically challenging the notion of the unimodal intrinsic nature of these sensory cortical areas (see for a review Pascual-Leone, Amedi, Fregni & Merabet, 2005) and consequentially they enormously fostered this branch of research. One of the most influential works guiding this turning point, was a study on short-term visual deprivation, in which sighted participants were blindfolded for five days and subsequently showed strong crossmodal recruitment of occipital areas for both tactile and auditory tasks (Pascual-Leone & Hamilton, 2001). This pioneering work demonstrated that sensory cortices are not devoted to the exclusive processing of information conveyed by specific sensory modalities, but they rather are much more flexible cortical areas than previously conceived, capable of dealing with information coming from different senses. Furthermore, what made these findings particularly interesting for the whole field of cognitive neuroscience was the fact that the recruitment of visual areas by auditory and tactile modalities rapidly disappeared following the removal of the blindfold (Pascual-Leone & Hamilton, 2001). This latter result ultimately strengthens the proposal of the supramodal intrinsic nature of sensory cortices by suggesting that this recruitment was not based on the creation of new connections but rather on the uncovering of pre-existing connections, which were normally overpowered by visual pervasiveness (Pascual-Leone et al., 2005; see for instance Amedi, Malach, Hendler, Peled & Zohary, 2001; Pietrini, Furey, Ricciardi, Gobbini, Wu, Cohen, Guazzelli, & Haxby, 2004; Zangenehpour & Zatorre, 2010, for converging results in the control population).

Later studies of crossmodal changes in blindness corroborated this proposal and even extended it by demonstrating that in early visually deprived people the recruitment of the deafferented visual system is not random, but it follows the same functional organization reported for those occipital regions in the control population (e.g., Amedi, Raz, Pianka, Malach & Zohary, 2003; Collignon et al., 2011; Ptito, Fumal, de Noordhout, Schoenen, Gjedde & Kupers, 2007; Reich, Szwed, Cohen, & Amedi, 2011; Röder, Stock, Bien, Neville & Rösler, 2002). Instead, evidence supporting a functional crossmodal recruitment of the auditory deprived cortices following bilateral deafness are much more scant. In fact, a functional maintenance of the auditory cortices organization has been demonstrated in deaf humans only for higher-order cognitive abilities, such as language, when sign language was tested (e.g., Petitto, Zatorre, Gauna, Nikelski, Dostie & Evans, 2000; Emmorey, Grabowski, McCullough, Damasio, Ponto, Hichwa & Bellugi, 2003; Emmorey, Metha & Grabowski, 2007; Mayberry, Chen, Witcher & Klein, 2011; see MacSweeney, Capek, Campbell & Woll, 2008 for a review), whereas for what it concerns lower-order abilities, evidence are much more ambiguous (e.g., Cardin et al., 2013; Fine et al., 2005; Finney et al., 2001; Karns et al., 2012; Vachon et al., 2013). However, in congenitally deafened cats a clear functional recruitment of the deafferented auditory cortices has been revealed for the localization of peripheral visual stimuli and for visual motion direction (Lomber et al., 2010; Meredith et al., 2011; Wong et al., 2013).

Beside crossmodal recruitment, unisensory deprivation has been shown to lead to two other types of plastic neural changes, which until now provided more straightforward results in explaining deafness-related plasticity. The first type of mechanism is intramodal plasticity, namely, those modifications occurring within the intact sensory modalities. For instance, in bilateral deaf people, increased electrophysiological activity of primary and secondary visual cortices has been shown to underlie the faster detection of abrupt visual stimuli reported for deaf adults compared to hearing controls (Bottari, Caclin, Giard & Pavani, 2011). Furthermore, Codina, Pascalis, Mody, Toomey, Rose, Gummer & Buckley (2011) showed a correlation in deaf adults between the ability to detect peripheral moving stimuli in a kinetic perimetry task and the dimensions of the neural rim areas of the optic nerve. These authors also reported a reorganization of the retinal nervous fibers' layer in the deaf group, with a higher concentration of fibers in the region that typically serves the most peripheral areas of the visual field.

The other type of plasticity concerns the reorganization occurring in inherently multisensory regions, such that clusters of multisensory neurons in these brain regions lose their multisensory nature and they are instead recruited to process exclusively information conveyed by one intact sensory modality. For instance, using fMRI, Bavelier, Tomann, Hutton, Mitchell, Corina, Liu & Neville (2000) and also Bavelier, Brozinsky, Tomann, Mitchell, Neville & Liu (2001) have shown an increased activation of the superior temporal sulcus (a multisensory integration regions) of deaf adults compared to hearing controls when passively viewing peripheral moving stimuli. This increased activation might mediate the improved ability of deaf individuals to discriminate peripheral motion (e.g., Hauthal, Sandmann, Debener & Thorne, 2013; Neville & Lawson, 1987,b).

However, it surely needs further investigation the fact that in humans the properties underlying crossmodal recruitment of visual cortices as a consequence of blindness are much clearer than the properties underlying crossmodal recruitment of auditory cortices as a consequence of deafness (see for instance Dormal & Collignon, 2011; Voss & Zatorre, 2012). Interestingly, a growing corpus of evidence is now suggesting that in deaf adults the deafferented auditory regions, and in particular the primary auditory cortex, are predominantly recruited by the somatosensory modality (Auer et al., 2007; Karns et al., 2012; Levänen et al, 1998), possibly due to its functional similarity and also to its structural proximity to the auditory cortices. However, it is not clear to what extent this recruitment follows the functional organization of hearing auditory cortices or whether it entails any benefit for actual performance (e.g., Bolognini, Cecchetto, Geraci, Maravita, Pascual-Leone, Papagno, 2012; Karns et al., 2012). Indeed, there is some evidence suggesting that crossmodal recruitment of auditory regions by the somatosensory modality might lead to impaired behaviors in the deaf population (Bolognini et al., 2012). Importantly, these findings open the possibility that some aspects of crossmodal recruitment might be maladaptive, producing, in turn, behaviors falling within the predictions of the perceptual deficiency hypothesis.

From this brief overview, it clearly emerges that the principles guiding the multifaceted type of plasticity exerted by bilateral deafness are more ambiguous compared to what it is known about brain plasticity related to blindness. In order to further characterize deafness-related plasticity, it is essential to carefully define the cognitive functions that reorganized as a consequence of early auditory deprivation. Indeed, a lot of research had been done already on the consequences of deafness for behavior, reporting plastic reorganization for several visual functions (see Bavelier, Dye & Hauser, 2006; Pavani & Bottari, 2011; Pavani & Röder, 2012 for reviews). However, there are also many relevant aspects that still lack a systematic investigation. The aim of the present thesis is to identify these missing pieces and address them as systematically as possible.

I am first going to briefly discuss the existing research on the effects of bilateral deafness for behavior, highlighting the critical points I identified in the literature that deserved a further investigation. Then I am going to present in detail the data that I have acquired and the results I have obtained.

1.2 The effects of bilateral deafness on behavior

Profound or severe bilateral deafness (hearing loss > 81 dB in the better ear; hearing loss > 61 dB in the better ear, respectively) is a unisensory deprivation affecting 250 millions of people in the whole world (World Health Organization estimates, 2002). In Italy, it affects 1-2/1000 new-borns every year (Cadoni e Quaranta, 2011). The majority of the studies addressing the consequences of auditory deprivation for everyday life activities have mainly examined the impact of deafness on linguistic abilities (e.g. Marschark, 2006; Caselli, Maragna & Volterra, 2006 for reviews) or on the development of an efficient linguistic system in the brain (e.g., MacSweeney, Waters, Brammer, Woll & Goswami, 2008; Mayberry et al., 2011; Mayberry & Lock, 2003; Penicaud, Klein, Zatorre, Chen, Witcher, Hyde & Mayberry, 2012; see Hickok, Bellugi & Klima, 1998; MacSweeney et al., 2008 for reviews). However, being a bilateral deaf person it impacts also the way in which individuals interact with the external environment and it is therefore fundamental to understand exactly in which way deafness modifies behaviors. Given that humans are mainly visual animals, it is not surprising that a greater emphasis is generally given on the effects of blindness for behavior. And indeed, bilateral deafness is generally and informally referred to as ‘the invisible handicap’. However, there are many situations in everyday life in which we rely on audition in order to promptly implement the correct behavior. Imagine for instance, that you are driving in traffic. If for example an ambulance is approaching, you will hear the noise of the siren, and you immediately know that you have to move your car to let the ambulance pass through. However, if you are a bilateral deaf driver, you cannot rely on this auditory cue to alert your-self to promptly react to the situation (i.e., move your car). There are two possible outcomes to this circumstance: one possibility is that indeed, as a deaf driver, you do not realize that the ambulance is approaching until it arrives right behind you, and you will be blocking the ambulance way, eventually moving your car too late (perceptual deficiency hypothesis). The other possibility is that as a consequence of deafness you have potentiated your ability to monitor the surrounding visual environment by for instance being more prone to detect visual abrupt onsets (e.g., the light of the siren) or by being better in localizing or in discriminating visual objects (e.g., the ambulance), or by devoting more attentional resources to visual events all around you (e.g., the behaviors of the other cars). This may ultimately lead the deaf driver to be as good as, or even better than all the other hearing drivers in promptly dealing with this particular situation (compensation hypothesis). In line with the latter, research investigating the effects of early bilateral deafness on behavior reported visual behavioral improvements in deaf individuals compared to hearing controls exactly for the domains highlighted in the example above, namely, reaction to abrupt visual onsets (e.g., Bottari, Nava, Ley & Pavani, 2010; Loke & Song, 1991; Reynolds, 1993), visual discrimination abilities (e.g., Hauthal et al., 2013; Neville & Lawson, 1987, b), visual localization abilities (e.g., Dye, Hauser & Bavelier, 2009) and visual attention (e.g., Bavelier et al., 2000; 2001; Chen, He, Chen, Jin & Mo, 2010; Chen, Zhang & Zhou, 2006; Proksch & Bavelier, 2002).

Indeed, the majority of research addressing the consequence of bilateral deafness for behavior focused on the visual modality, aiming at understanding whether or not deaf individuals ‘see better’ than hearing controls (see Bavelier et al., 2006). In particular, all this research primarily focused on populations of profound or severe bilateral deaf adults, which were either congenitally deaf individuals or deaf persons that acquired deafness before the age of three years (early bilateral deafness). Often deaf adults in these studies were also native signers, namely, they had acquired a sign language as their first language (e.g. Bavelier et al. 2000; 2001; Chen et al., 2010; Neville and Lawson, 1987, b; Proksch & Bavelier, 2002). In other studies instead, the deaf sample was not defined in terms of their linguistic background (e.g., Chen et al., 2006) or they were categorized as *signing* based on self-reports of participants without specifying for instance, whether deaf participants were native signers or not (e.g., Bottari et al., 2010; Hauthal et al., 2013).

Overall, the research addressing the visual reorganization as a consequence of deafness firmly disconfirmed the perceptual deficiency hypothesis and embraced instead the compensation hypothesis as the best explanation for describing how deaf people interact with the visual external environment. Importantly, the main conclusion from these studies was that deafness-related behavioral changes are impressively selective, not involving all visual behaviors but only certain visual functions (e.g., Pavani & Bottari, 2012; Pavani & Röder, 2012; see below for examples of unaltered aspects of visual perception).

The following sections will provide a brief overview of the existing literature on the behavioral changes regarding bilateral deafness focusing on the visual modality. I will also highlight within each section the limits of previous research and especially the specific aspects I addressed in my Ph.D. project. In particular, my work dealt with four main concerns: (i) the further investigation of the behavioral reorganization that occurs within the tactile modality of deaf adults. Research on touch in the deaf population is much less well-established than the research on vision. Moreover, it produced much more contrasting results, with some reports documenting impaired tactile behaviors in deaf adults compared to hearing controls (e.g., Bolognini et al., 2012; Frenzel, Bohlender, Pinsker, Wohlleben, Tank, Lechner, Schiska, et al., 2012; Heming & Brown, 2005;). My intent was to provide further evidence on the behavioral changes involving the tactile modality as a consequence of bilateral deafness, ultimately aiming at better defining to what extent touch-related modifications fall within the compensatory or the perceptual deficiency hypothesis. In addition, I was also interested in (ii) the further investigation of the possible modifications of the interactions between two reorganized sensory systems (i.e., vision and touch) as a consequence of auditory deprivation. (iii) The further investigation of visual-related plasticity exerted by early auditory deprivation. In particular, my main focus was on better defining which mechanisms of visual attention are modified by bilateral deafness. Indeed, the existing literature on deafness-related changes generally proposes that the broader behavioral reorganization as a consequence of hearing loss concerned specifically visual attention mechanisms (see for instance Bavelier et al., 2006). However, as will be clarified in the following sections, many aspects of visual attention still lacked a systematic investigation. (iv) To test to what extent the behavioral improvements observed in the deaf population compared to hearing controls are the result of extensive visual training in the deprived group. In particular I identified two types of training, which could dramatically influence deaf behaviors. The visual training linked to the intensive use of a sign language to communicate, and the visual training due to the everyday experience with a mainly visual world. In an attempt to isolate the first training aspect, I collected when possible, quantitative data on the linguistic proficiency of deaf participants, which I then correlated with actual performances to the tasks I used. In an attempt to isolate the second training aspect, I tested when possible, also a group of hearing action videogame players (AVGPs) in the same tasks I used for deaf adults. Indeed, hearing AVGPs undergo an intensive visual training for many aspects similar to the one required to deaf adults to orient themselves in the external environment, without though, being sensory deprived. Indeed, in action videogames, the player is for instance required to constantly monitor a complex visual scene that it is always changing, and to promptly react to abrupt events. In the last ten years many works showed impressive improvements in visual tasks in this population compared to non-gamers (see Bavelier, Green, Pouget & Schrater, 2012 for a review). In addition, investigating plasticity effects in hearing AVGPs also permit to directly compare (i) plasticity effects exerted in a sensory deprived brain with those exerted in a non-sensory deprived brain and (ii) plasticity effects developed since infancy with those developed only during adulthood.

1.2.1 Sensory thresholds

Sensory thresholds represent one first example of an aspect of visual perception that does not seem to be modified by bilateral deafness. Sensory thresholds are the perceptual thresholds below which a sensory stimulus is not consciously perceived. Research addressing these visual abilities consistently reported comparable sensory thresholds between deaf and hearing individuals for many visual features, such as colors discriminability (e.g. Heider & Heider, 1940), luminance change (Bross, 1979), flicker-fusion (Bross & Sauerwein, 1980; Poizner & Tallal, 1987), two-points discrimination (Poizner & Tallal, 1987), temporal order judgment thresholds (Nava, Bottari, Zampini & Pavani, 2008; Poizner & Tallal, 1987), motion velocity thresholds (Brozinsky & Bavelier, 2004).

Furthermore, no difference has been observed between deaf and hearing adults for tactile frequency discrimination thresholds (Levänen & Hamdorf, 2001).

At the moment, the only exception to these reports is represented by the works by Stevens & Neville (2006) and Buckley, Codina, Bhardwaj & Pascalis (2010) on the dimensions of the visual field in deaf individuals. Using a kinetic perimetry task, these authors demonstrated that deaf adults detected visual stimuli moving from the periphery toward the center of the visual field at more peripheral locations compared to hearing individuals. These results suggested a larger extension of the visual field in deaf participants compared to hearing controls. Moreover, Buckley's research group (Codina et al., 2011), using Optic Coherence Tomography (OTC), tested a group of deaf adults and a group of hearing controls in the same kinetic perimetry task and they reported, only in the deaf group, a correlation between the larger extension of the visual field observed in the kinetic perimetry task, and the dimensions of the neural rim areas of the optic nerve. Importantly, deaf adults also showed a reorganization of the retinal nervous fibers' layer, with a higher concentration of fibers in the region that typically serves the most peripheral areas of the visual field. These results are particularly relevant because they document intramodal plastic changes at extremely early stages of visual processing in the deaf population.

1.2.2 Reaction to the environmental stimuli

The ability to react to environmental events has been extensively investigated in the deaf population using clearly supra-threshold stimuli (see Pavani & Bottari, 2012 for a review). One of the most solid findings in the literature on deafness-related behavioral changes is indeed the robust reaction time advantage in deaf adults compared to hearing controls reported when simple detection of abrupt peripheral (e.g. Loke & Song, 1991) as well as of abrupt central or peri-foveal static visual stimuli was required (e.g. Reynolds, 1993; Bottari, Nava, Ley & Pavani, 2010).

A recent study by Bottari and colleagues (2011) investigated the neural correlates of this enhanced visual ability using electroencephalography (EEG). They tested a group of deaf adults and hearing controls in a simple visual detection task while registering electroencephalographic activity. The authors found a correlation, present only in the deaf group, between the P1 amplitude (i.e. an early component of visual processing which has a peak typically observed between 100-130 ms following stimulus presentation) and the reaction time advantage observed for both peri-foveal and peripheral static visual stimuli: the ampler the P1 component, the faster deaf participants detected abrupt visual stimuli. These results led the authors to propose that the reaction time advantage for the detection of abrupt visual stimuli in the deaf population might rely on intramodal plastic changes occurring at early stages of visual processing. In other words, these results might suggest the selectivity for vision of this reaction-time advantage in the deaf population.

To further investigate the nature of this behavioral improvement as well as to test to what extent behavioral effects of auditory deprivation are similar across intact sensory modalities, we tested whether or not this visual reaction time advantage extended also to the tactile modality in a group of deaf adults compared to hearing controls (**see Chapter 2, Study 1**).

In addition, I presented the same behavioral task also to a group of hearing action videogame players (VGPs) and compared their performance to a group of hearing non-gamers (NVGPs; **see Chapter 2, Study 3**). The rationale for running this study in AVGPs was the consideration that this hearing population undergoes a visual training for many aspects similar to the visual training deaf individuals constantly experience while interacting with the external world, without though, being sensory deprived. Therefore, testing hearing AVGPs in the same task used for deaf adults also permits to indirectly investigate to what extent the plasticity exerts by avid action videogame playing acts upon the same mechanisms recruited by plastic changes related to bilateral deafness. Interestingly, reaction time improvement in response to abrupt visual events is also one of the most solid finding reported in hearing AVGPs compared to NVGPs (e.g., Castel, Pratt & Drummond, 2005; see Dye, Green & Bavelier, 2009a for a review). However, it has never been tested whether this reaction time advantage could extend also to the tactile modality. Importantly, touch is the sensory modality, which receives the poorer training in the gaming environment, because it is very little involved in action video games. Therefore, investigating whether or not the visual reaction time advantage would extend also to the untrained tactile modality in hearing AVGPs, will provide insight into the level of information processing on which this form of training-related plasticity acts upon (**see Chapter 2, Study 3**).

1.2.3 Localizing, discriminating and recognizing environmental stimuli

Another aspect of visual perception, which received considerable attention within the research on the effects of bilateral deafness on behavior, concerns the abilities to localize, discriminate and recognize visual stimuli in the external environment. Generally, in discrimination tasks participants are asked to take a perceptual-decision on some specific visual feature, such as the spatial position, or the shape of visual objects. The work investigating visual discrimination abilities in deaf adults compared to hearing controls revealed a multifaceted scenario. For instance, one study that contrast sensitivity (Finney & Dobkins, 2001) discrimination of luminance changes (e.g. Bavelier et al., 2000; 2001) resulted comparable in deaf and hearing adults, both in terms of speed and in terms of the accuracy of the responses. In addition, recent data on the tactile modality suggest that also the ability to discriminate the spatial length of vibrotactile stimuli is comparable between deaf adults and hearing controls (Bolognini et al., 2012).

Instead, in other visual discrimination tasks, such as in discrimination of visual-motion direction tasks (Hauthal et al., 2013; Neville & Lawson, 1987, a,b) and in one temporal-order judgment task (Nava, et al., 2008), a reaction time advantage in the deaf group has been reported while accuracy between the two groups was comparable. In addition, in a discrimination of moving direction changes (Bosworth & Dobkins, 2002) and in a visual shape discrimination task (Bottari et al., 2010) a small speed-accuracy trade off (i.e. faster reaction times paired with lower accuracy) has been reported in deaf adults compared to hearing controls. These latter results have been generally interpreted in terms of greater impulsivity in releasing a response in deaf adults compared to hearing controls (e.g., Parasnis, Samar & Berent, 2003). Furthermore, Dye and colleagues (2009) reported better performance in deaf adults compared to hearing controls in an adapted version of a useful field of view task, in which participants were instructed to discriminate a central-presented visual face while at the same time localizing the spatial position of a peripheral visual stimulus embedded among distractors.

Finally, a specific set of discrimination abilities seem to be impaired in deaf adults compared to hearing controls. This is the case of time-related abilities (e.g., Bolognini et al., 2012; Heming & Brown, 2005; Kowalska & Szelag, 2006). For instance, in a recent work Bolognini and colleagues (2012), tested deaf adults and hearing controls in a temporal tactile discrimination task (i.e. discrimination between long vs. short vibrotactile stimulations released on the index finger of the right hand) and reported worse performance in deaf adults compared to hearing controls. This result is particularly relevant because it strengthens the possibility that abilities typically ascribed to the auditory system, as time perception (Julesz & Hirsh, 1972; Miller & Taylor, 1948), could not developed adequately in the deaf population, suggesting the possibility that indeed some aspects of deafness-related plasticity follow within the perceptual deficiency hypothesis rather than within the compensatory hypothesis. However, results on different aspects of time-related abilities within the visual modality have produced contrasting results (e.g., Heming & Brown, 2005; Kowalska & Szelag, 2006; Nava et al., 2008; Poizner & Tallal, 1987).

To further investigate this intriguing aspect of deaf cognition, I presented to deaf adults and hearing controls a duration discrimination task that was very similar to the one used by Bolognini and colleagues (2012), albeit presenting the stimuli not only in the tactile modality but also in the visual modality (**see Chapter 2, Study 2**). My aim was to investigate whether the impairment of temporal processing was indeed more pronounced for touch compared to vision as the existing literature seemed to suggest, or whether it was instead supramodal, namely, equally affecting both sensory modalities.

Finally, I also tested a group of hearing action videogame players (AVGPs) and a group of non-gamers (NVGPs) in the same task I used for deaf adults (**see Chapter 2, Study 3**). The aim of this study was again to provide indirect evidence on whether or not AVGPs related plasticity acts upon the same mechanisms of deafness-related plasticity. Interestingly, as in the deaf population, plasticity effects in AVGPs compared to NVGPs involving spatial processing have been much more investigated than plasticity effects related to temporal processing of stimuli (see Bavelier et al., 2012 for a review). This is probably due to the fact that in action video games temporal features are very poorly trained, as these games predominantly require allocating attention to spatial features of visual stimuli rather than to temporal features.

1.2.4 Control and orientation of visual attention in space

The consequence of bilateral deafness on the mechanisms of visual attention has been extensively investigated (for reviews see Bavelier et al., 2006; Dye & Bavelier, 2010). What predominantly fostered this prolific research, were the findings of early seminal studies reporting differences between deaf adults and hearing controls selectively under conditions of voluntarily-directed attention (endogenous attention) and particularly when visual attention was deployed in the peripheral visual field (e.g., Bavelier et al., 2000; 2001; Finney et al., 2001; Fine et al., 2005; Neville & Lawson, 1987,b; see Bavelier et al., 2006 for a review). Later works mainly focused on investigating the deployment of visual attention in deaf adults through covert attention tasks. One of the most influential works addressing this issue is the study by Proksch & Bavelier (2002) in which the authors presented deaf adults and hearing controls with a flanker-compatibility task. In this task participants were required to individuate a target shape within increasing attentional-load conditions, ignoring concomitant distractors. Distractors could be either compatible (same target shape) or incompatible (different target shape) with respect to the target and they could appear either centrally or peripherally. The interference in the responses caused by the appearance of the incompatible distractors was used as a measure of attentional resources: the more incompatible distractors interfered with the task, the more attentional resources the participants were allocating to that portion of the visual field (Lavie, 1995; Lavie & Cox, 1997; Maylor & Lavie, 1998; Rees, Frith, & Lavie, 1997). Results showed that deaf participants were more distracted by peripheral compared to central distractors, while the opposite was true for hearing controls. Moreover, this pattern of results emerged particularly strongly in high attentional-load conditions (Proksch & Bavelier, 2002). The authors interpreted these findings as evidence for increased endogenous attentional resources devoted to the peripheral visual field in the deaf population compared to hearing controls.

However, results from other works suggest that also the automatic (exogenous) component of visual attention might be involved in deafness-related attentional changes (Armstrong, Neville, Hillyard & Mitchell, 2002; Bottari et al., 2011; Chen et al., 2006; Colmenero, Catena, Fuentes & Ramos, 2004; Parasnis & Samar, 1985). Two EEG studies have documented differences in the evoked-responses of deaf adults compared to hearing controls, when attention was captured automatically by the abrupt appearance of a visual stimulus (either peri-foveal or peripheral; Bottari et al., 2011) as well as when stimuli, which were not even the target of the experimental task, were presented (Armstrong et al., 2002; Bottari et al., 2011). In addition, other studies testing covert attentional orienting in deaf adults suggest faster redirecting of visual attention towards visual stimuli appearing abruptly in the visual field, in the deaf population compared to hearing controls (e.g. Chen et al., 2006; Colmenero et al., 2004; Parasnis & Samar, 1985). In these paradigms, participants are typically required to detect as fast as possible the appearance of a peripheral visual stimulus, which is preceded by a visual cue indicating the spatial position of the target. The cue can be either valid (i.e. the target appeared in the cued spatial position) or invalid (i.e. the target appeared in a different spatial position; e.g. Posner, Snyder & Davidson, 1980). If the cue is invalid participants generally pay a cost in redirecting their attention to the correct position, which is reflected in slower reaction times for detecting the target. Interestingly, when deaf adults were tested in this type of tasks, they paid less cost than hearing controls in detecting targets in invalidly cued trials, possibly indicating a faster automatic redirection of attention towards abrupt visual stimuli (e.g. Colmenero et al., 2004; Chen et al., 2006 with peripheral stimuli; Parasnis & Samar, 1985 for results in the same direction with peri-foveal stimuli).

Furthermore, a recent study on overt attention mechanisms suggests that also oculomotor behavior is modified by bilateral deafness. Bottari, Valsecchi & Pavani (2011) presented to a group of deaf adults and to a group of hearing controls an anti-saccade task (Everling & Fischer, 1998; Hallett, 1978). In the pro-saccade condition participants were asked to make a direct eye-movement (saccade) to a target-stimulus appearing in the visual scene, whereas in the anti-saccade condition, observers were required to direct the eye-movement in the opposite direction with respect to the delivered visual stimulus. In the work by Bottari and colleagues (2011), participants were instructed in each trial whether they would have to produce a pro-saccade or an anti-saccade. Results showed more mistakes in the anti-saccade trials and faster eye-movements in repeated pro-saccade trials in deaf participants compared to hearing controls. Bottari and colleagues interpreted these findings as initial evidence for a prominent role of overt attention-capture mechanisms in the deaf population. In other words, this work suggested a dominance of automatic eye-movements (repeated pro-saccade trials) over voluntarily controlled eye movements (anti-saccade trials).

To sum up all these studies, it appears clear that the contribution of the different mechanisms of visual attention to plastic changes exerted by bilateral deafness is quite complex, and several aspects still need further investigation. For instance, it is still not clear, whether deafness-related changes involve predominantly either the endogenous or the exogenous components of visual attention or the two components are both similarly modified by early auditory deprivation. Furthermore, while covert attention has been studied quite extensively, overt-attention mechanisms in bilateral deaf adults have not been systematically investigated and therefore it is still uncertain to what extent early auditory deprivation affects oculomotor behavior.

To clarify this important domain of deafness-related research, I specifically focused on defining the consequences of auditory deprivation for the relative contribution of the automatic vs. voluntary components of visual attention in the interaction with the external environment. In particular, I was interested in describing the temporal dynamics of the interplay between these two components of visual attention. To this aim, I took advantage of an overt target-selection task repeatedly adopted in the hearing population (e.g., Donk & van Zoest, 2008; van Zoest, Donk & Theeuwes, 2004; van Zoest & Donk, 2005; 2008; see for a review van Zoest, Hunt & Kingstone, 2010). In particular, by manipulating the relative saliency of stimuli presented in search displays, these works demonstrated the critical role of time for successfully disentangling the contribution of automatic vs. voluntary components of visual attention to performance: fast responses following scene onset predominantly show automatic attentional capture to salient stimuli, independently of whether or not these salient elements are relevant for the task; instead it takes time for voluntary, intentional strategies to be efficiently implemented in behaviors (e.g., Donk & van Zoest, 2008; van Zoest et al., 2004; van Zoest & Donk, 2005; 2008).

My aim was to characterize the temporal dynamics of automatic vs. voluntary deployment of overt visual attention in the deaf population, ultimately investigating whether one of the two components was predominantly modified by auditory deprivation (**see Chapter 4, Study 1**). In this study I also carefully controlled for linguistic abilities of deaf participants. In collaboration with the ISTC-CNR in Rome we developed a set of linguistic tests for assessing the proficiency of deaf participants both in Italian and in Italian Sign Language (LIS). For this particular work, I focused only on the results obtained in the tests assessing LIS proficiency and I correlated them with the performance to the overt target-selection task. My aim was to carefully investigate to what extent performances of deaf participants could be explained by linguistic proficiency (**see Chapter 4, Study 1** for the description of the tests).

Following a similar logic to the one presented for the previous studies, I also used the same task to characterize the temporal dynamic of automatic vs. voluntary components of attention as a consequence of intensive action videogame playing (**see Chapter 4, Study 2**). My aim was to test to what extent intensive visual training that is not paired with a sensory deprivation exerted the same type of reorganization on visual attention mechanisms as intensive visual training as a consequence of early auditory deprivation.

1.2.5 Visual attention to social cues

As described in the section 1.1.4, a number of studies have been conducted to characterize orienting of covert attention in deaf people (e.g., Chen et al., 2006; Colmenero et al., 2004; Parasnis & samar, 1985). One aspect that remained unexplored, however, is how deaf adults deploy covert visual attention when social cues are into play. To specifically address this issue and to further investigate the modifications involving covert attentional mechanisms in deaf adults, I tested covert attentional-orienting properties when complex, social cues were presented. In particular, I presented to a group of deaf adults and to a group of hearing controls a gaze-cue paradigm (e.g., Driver, Davis, Ricciardelli, Kidd, Maxwell & Baron-Cohen, 1999; Friesen & Kingstone, 1998; 2003; Friesen, Ristic & Kingston, 2004; Khurana, Habibi, Po & Wright, 2009; Quadflieg, Mason & Macrae, 2004; Tipples, 2005) in which participants were required to ignore the direction of gaze of a central face, while performing a peripheral shape discrimination task (**see Chapter 5**). The rationale of this study stemmed from the intuitive assumption that in the deaf population, given the reduced or absent auditory input, gaze-shifts might represent the preferential way to direct attention on the same object and location attended by the social partner. Furthermore, in deaf people gaze-shifts might convey important information about the surrounding visual environment, while their primary orienting modality (vision) is absorbed by social interactions. For instance, deaf people may follow gaze-shifts of their social partners as an alerting cue for events occurring in the surrounding space. We therefore predicted that gaze-cues might be particularly strong attentional-cues for deaf adults. Furthermore, previous eye-movement research has documented a predominant exploration of the eye-area of the face in deaf native signers compared to hearing beginning signers, when performing comprehension tasks on signed narratives (Emmorey, Thompson & Colvin, 2009) or when evaluating static faces for their emotional valence (Watanabe, Matsuda, Nishioka & Namatame, 2011). Therefore, we hypothesized that in the deaf population life-long sign language experience might further modulate the effect of gaze-cues on performance. To control for this latter prediction, in this study we administered to deaf participants the same set of linguistic tests used in the overt-attention task (see **Chapter 5, Additional Materials**).

1.2.6 Interaction among intact sensory modalities

An important limit of the literature on the effects of unisensory deprivations on behavior concerns the fact that typically it has investigated changes in cognitive functions examining one remaining sensory modality at a time. Although, this approach clearly proved highly informative, it largely overlooked possible changes in the interactions between reorganized sensory systems, ultimately limiting our understanding of the impact of unisensory loss on perceptual processing (but see for blindness: Hötting & Röder, 2004; Van der Lubbe, Van Mierlo & Postma, 2010; see Occelli, Spence & Zampini, 2013 for a review; for deafness: Karns et al., 2012).

The only study, which addressed multisensory interactions between vision and touch in bilateral deaf adults, is a recent study by Karns and colleagues (2012). The authors recorded fMRI activity while congenitally deaf adults and hearing controls performed a task where a somatosensory double-flash illusion was induced; this is a phenomenon that is experienced when a single flash of light paired with two or more somatosensory stimuli, is perceived as multiple flashes of lights (e.g., Lange, Oostenveld & Fries, 2011; Violentyev, Shimojo & Shams, 2005; see Shams, Kamitani & Shimojo, 2000; Mishra, Martinez, Sejnowski, Hillyard, 2007 for a double-flash illusion elicited by auditory stimuli). In particular, the task of the participants was to detect rare visual target events (20% of trials) consisting of two consecutive shorter stimuli compared to the repeatedly presented visual stimuli (80% of trials), while ignoring a concomitant tactile streams of events also composed of repetitive and rare stimulations. Clearly this task taps on temporal abilities (i.e., the ability to detect a deviation from a continuous rhythmic stream of events). Predictions for the outcome of this task were based on the maximum-likelihood estimation (MLE) approach applied to multisensory perception (Ernst & Banks, 2002). As claimed by this approach, sensory information is *weighted* according to the relative precision of the information conveyed by each sensory modality. The sensory modality that *weights* more in a particular context, will dominate behavior. Therefore the idea behind this illusion is that given that touch has higher temporal precision than vision, for the maximum likelihood estimation model, tactile information would *weight* more than visual information, thus leading to the wrong detection of tactile rare and to-be-ignored events as targets, instead of detecting only the correct visual targets. Furthermore, as a control task, Karns and colleagues (2012) presented also the opposite condition to participants (i.e., detect rare tactile events, while ignoring the concomitant visual stream), in which, given the lower temporal precision of the visual modality, no illusion was predicted. Results showed that only the deaf group was susceptible to the somatosensory double-flash illusion. Indeed, only deaf participants incorrectly responded to deviant tactile stimulations, in the condition in which they were instead required to respond only to visual deviant stimulations and to ignore the concomitant tactile stream. Instead, as predicted, in the control condition in which participants had to attend to touch and ignore vision, both groups did not perceive the illusion. Moreover the strength of the illusion in deaf participants positively correlated with the activation of the rostrolateral portion of the Heschl's gyrus. The authors concluded that these results suggest enhanced reliance on the tactile modality for temporal precision in deaf adults compared to hearing controls. Nonetheless, this proposal is not in line with other behavioral results, which reported impaired tactile temporal abilities in the deaf population (Bolognini et al., 2012; Heming & Brown, 2005; see **Chapter 2, Study 2** for a further discussion of this issue), ultimately questioning the adaptive valence of the sensitivity to the somatosensory double-flash illusion reported in deaf adults by Karns and colleagues (2012).

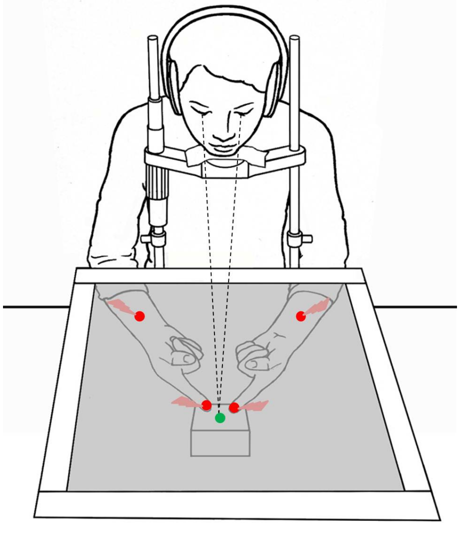
In addition, as already mentioned in the previous sections, unisensory approaches to the study of crossmodal changes in early bilateral deafness suggest an imbalance in the reorganization occurring in vision and touch. Reorganization in vision has been repeatedly documented in both brain and behavior, and some of the observed behavioral advantages have been linked to neuroanatomical changes starting from the very early stages of visual processing (Bottari et al., 2011; Codina et al., 2011). By contrast, reorganization occurring for the tactile modality appears considerably more uncertain, both at the behavioral and at the neuroanatomical level (e.g., Auer et al., 2007; Bolognini et al., 2012; Frenzel et al., 2012).

Both these aspects outlined above, then, clearly prevents a straightforward interpretation of the results reported by Karns and colleagues (2012) for what it concerns the properties driving the interaction between reorganized perceptual systems in the deaf population.

A more suitable way to investigate multisensory interactions between vision and touch as a consequence of bilateral deafness it is by testing the competition between these two spared sensory modalities within a spatial task. Indeed, according to the maximum-likelihood estimation model (Ernst & Banks, 2002) vision is the sensory modality, which dominates spatial perception and consequent behavior. I therefore investigated performance of deaf adults and hearing controls in a spatial multisensory interference task, namely, the ‘Cross-modal Congruency Task’ (e.g., Driver & Spence, 1998; Spence, Pavani & Driver, 2000; 2004; see Spence, Pavani, Maravita & Holmes, 2008 for a review). The main idea was that, given that vision seems to be reorganized more than touch as a consequence of bilateral deafness, visual reorganization might unavoidably dominate behaviors in the deaf population. If this is true, it should be particularly evident in a spatial multisensory interference task when irrelevant visual information is presented (**see Chapter 3**).

CHAPTER 2:

Does plasticity triggered by early bilateral deafness exert comparable effects across intact perceptual systems?



Study 1: Response speed advantage for vision does not extend to touch in early deaf adults

2.1.1 Summary

Early deaf adults typically respond faster than hearing controls when performing a speeded simple-detection on visual targets. Whether this robust reaction time advantage can generalise to another intact modality (touch) or it is instead specific to visual processing remained unexplored. We tested 8 early deaf signers and 12 hearing controls in a simple detection task, with visual or tactile targets delivered on the arms and occupying the same locations in external space. Catch trials were included in the experimental paradigm. Results revealed a response time advantage in deaf adults compared to hearing controls, selectively for visual targets. This advantage did not extend to touch. The number of anticipation errors was negligible and comparable in both groups. The present findings strengthen the notion that response speed advantage in deaf people emerges as a consequence of changes specific to visual processing. They also exclude the involvement of sensory-unspecific cognitive mechanisms in this improvement (e.g., increased impulsivity in response releasing, longer lasting sustained attention or higher motivation to perform the task). Finally, they provide initial evidence that the intact sensory modalities can reorganise independently from each other following early auditory deprivation.

2.1.2 Introduction

Despite living in a world without sounds deaf adults typically interact efficiently with their surrounding environment. The behavioural advantages and the changes in brain response that contribute to this adaptive outcome have been the focus of many investigations in the last three decades (for reviews see Bavelier et al. 2006; Pavani & Röder 2012). These studies has primarily examined visual processing in deaf people, but in more recent years also somatosensory processing (e.g., Auer et al. 2007; Bolognini et al. 2012; Frenzel et al. 2012; Heming & Brown 2005; Levänen et al. 1998; Levänen & Hamdorf 2001; Moallem, Reed & Braida, 2010; van Dijk, Kappers & Postma, 2013) and visuo-tactile interactions (Karns et al. 2012) have been considered.

One repeatedly documented behavioural advantage in deaf adults compared to hearing controls is the faster response time measured when the task requires simple detection of visual onsets (for review see Pavani & Bottari 2012). Loke and Song (1991) were the first to describe this behavioural advantage in a group of congenitally deaf adults. Deaf participants were faster (85 ms on average) than hearing controls at detecting asterisks presented briefly at 25 degrees of visual eccentricity. This pioneering study suggested that a similar advantage did not emerge when stimuli were presented closer to central fixation. However, subsequent works have challenged this conclusion by showing response speed advantage in early deaf people also for visual stimuli delivered directly at fixation (Reynolds 1993) or at peri-foveal locations (Bottari et al. 2010; 2011; for a meta-analysis of response speed advantage in deaf people compared to hearing controls as a function of visual target eccentricity see Figure 22.1 in Pavani & Bottari 2012).

It is currently unknown whether the response speed advantage documented for vision also extends to the intact tactile modality. Despite the increasing interest for changes in somatosensory processing following deafness, until now, reaction times to tactile events have never been investigated (e.g., Bolognini et al. 2012; Frenzel et al. 2012; Heming and Brown 2005; Levänen & Hamdorf 2001; Moallem et al. 2010; van Dijk et al. 2013). The most intuitive prediction, however, would be that a similar advantage should emerge for tactile processing as well. This is because response speed advantages in the deaf population have been interpreted as the consequence of *sensory unspecific* changes related to the response phase, and associated with increased impulsivity in response releasing (Parasnis et al. 2003). More generally, a number of sensory unspecific processes are involved in speeded simple detection. These include perceptual decision-making, response preparation and response releasing, in addition to sustained or selective attention abilities and motivation in performing the task.

However, one recent study suggests that response speed advantage in deaf adults might actually reflect *sensory specific* – rather than unspecific – changes, that may primarily involve early processing of the visual stimulus. Using electroencephalography (EEG), Bottari and colleagues (2011) explored the relationship between speeded visual detection and the temporal dynamic of visual processing in the brain of deaf and hearing individuals. They recorded EEG while deaf and hearing participants performed a simple detection task on visual stimuli delivered at peri-foveal or peripheral visual locations, and in response to a warning visual signal that preceded the targets. Differences between the two groups were measured for the C1 component (i.e., a visual evoked potential produced by the striate cortex, with a peak around 80 ms post-stimulus) and for the P1 component (i.e., another early component of visual processing, peaking between 100-130 ms post-stimulus). Most importantly, a significant correlation between the amplitude of the P1 component and the response times advantage emerged selectively for the deaf group. The shorter the average response times to the visual events the ampler the P1, independently of stimulus eccentricity. This led Bottari et al. (2011) to propose that faster response times to visual stimuli in deaf adults reflects early changes in the temporal dynamic of visual processing, and may thus be linked to specific modifications occurring within the visual system.

In the present study, we aimed to further understand the origin of the response speed advantage in deaf adults by introducing two straightforward manipulations. First, we examined whether any advantage in response time for deaf compared to hearing adults emerges equally for vision and for touch. If response speed advantages result from specific changes occurring within visual processing (as proposed by Bottari et al., 2011), no response speed advantage should be found when deaf participants react to tactile targets. By contrast, if response speed advantages reflect sensory unspecific changes related to speeded detection, similar facilitation in response times should emerge regardless of target modality.

The second manipulation we introduced was the presence of catch-trials (i.e., response release when no stimulus is presented) in the design, paired with an analysis of anticipated responses (i.e., response release before any stimulus has been delivered). Surprisingly, all previous studies on simple detection in deaf adults (Bottari et al. 2010, 2011; Chen et al. 2006; Colmenero et al. 2004; Loke and Song 1991; Reynolds 1993) did not include catch trials in the experimental design. If the advantage in reaction times to visual events in the deaf population depends on increased impulsivity in response releasing we should observe a higher proportion of erroneous responses to catch trials and higher proportion of anticipated responses in this population compared to hearing controls.

We tested a group of deaf signers and a group of hearing adults in a simple detection task with visual or tactile stimuli, delivered at central or peripheral locations. To match as closely as possible central and peripheral locations across the two modalities we delivered tactile stimuli on the arms (fingertip or forearm) and aligned central and peripheral visual stimuli with the tactile locations (see Figure 2.1A). For exploratory purposes, we introduced tactile stimuli delivered also in a body region inaccessible to vision, i.e., the back of the neck (see Figure 2.1B). This latter manipulation was conducted only in deaf participants because, due to the characteristic of the available vibrotactile apparatus, it could not be applied in hearing controls without producing mixed tactile and auditory stimulation. The aim of this manipulation was to test whether any reaction time advantage in the tactile modality of deaf adults would be more pronounced in this visually inaccessible area of the body. A growing corpus of evidence suggests that attributes that are shared across sensory modalities may be especially susceptible to reorganisation following sensory deprivation (i.e., in deaf individuals, all those attributes that benefit from auditory convergence; Lomber et al. 2010; Dormal & Collignon 2011). When testing the tactile modality, one way to test this proposal could be by testing inherently multisensory body regions, namely, regions that are sensitive to inputs from different sensory modalities. Because integration of auditory and tactile inputs has been repeatedly documented in the back of the neck in the hearing population (e.g., Farné & Làdavas 2002; Làdavas, Pavani & Farnè, 2001; Tajadura-Jiménez, Kitagawa, Väljamäe, Zampini, Murray & Spence, 2009) this body region may be a good candidate to show reorganisation after auditory deprivation.

2.1.2 Methods

2.1.2.1 Participants

Twelve hearing participants with no experience in sign language (mean age = 28.6 years old, SD = 2.7) and eight early deaf participants non-native signers (mean age = 34.2 years old, SD = 5.5; see Table 2.1 for further information about deaf participants) took part in the experiment. All participants reported to have normal or corrected-to normal vision as well as normal somatosensation and no one reported to suffer from any psychiatric disorder or neurological disease. The Ethical Committee of the University of Trento approved the study.

Deaf	**Age**	**Deafness**			**LIS AoA**
ID	**years**	**Onset**	**Deagree**	**Etiology**	**years**
1	33	2 months	Profound	Otitis	17
2	26	Birth	Profound	Congenital	20
3	31	Birth	Severe	Maternal Rubella	21
4	37	20 days	Profound	Open-heart surgery	Does not use it
5	37	Birth	Profound	Congenital	14
6	29	Birth	Profound	Congenital	8
7	43	Birth	Profound	Congenital	Does not use it
8	38	Birth	Profound	Congenital	7

Table 2.1. Anamnestic information about deaf participants collected through a brief questionnaire they all fill-out prior to the experiment. For the variable 'Degree' of Deafness, 'Profound' means a loss ≥81 dB in the better ear; 'Severe' means a loss ≥61 dB in the better ear. The acronym 'LIS AoA' means Age of Acquisition of Italian Sign Language.

2.1.2.2 Stimuli and Apparatus

Participants sat on a comfortable chair with their chin on a chin-rest, and their hands and forearms resting supine on a table. A wooden cube (7x7x7 cm) placed along the participant's midsaggital plane, at approximately 60 cm from the participant's chest, served as resting position for the index fingers. One green LED positioned on the wooden cube served as visual fixation. Four red LEDs and four bone vibrators (Oticon A; dimensions: 1,5 cm X 2,5 cm) were used to deliver visual and vibrotactile stimuli, respectively. Two pairs of LEDs and bone vibrators were placed on the index fingertips, and two pairs were placed on the forearms. This resulted in four spatially congruent locations for visual and tactile stimulation: (1) right index; (2) left index; (3) right forearm; (4) left forearm (see Figure 2.1A). Note that with this arrangement, retinal eccentricity was perfectly matched for each pair of visual and tactile stimuli. Also, placing the stimuli on the index and forearms allowed testing simple detection in vision and touch for regions of high and low spatial-acuity. Specifically, stimuli at the index fingers were delivered in a region of high spatial acuity for both vision (1° from fixation) and touch (fingertip); similarly, stimuli at the forearms were delivered in a region of low spatial-acuity for both vision (32° from fixation;) and touch (forearm).

An opaque glass, suspended 9 cm above the hands, prevented direct vision of the setup. With this setup, visual stimuli (flashes of lights) were visible as a projection on the opaque glass when the LEDs were switched on, and tactile stimuli were felt but not seen. Vision of the stimulated hands and forearms was prevented throughout. For exploratory purposes, deaf participants were also tested with bone vibrators positioned in the back of the neck, 3 cm behind the ear lobes on either sides of the neck (see Figure 2.1B).

All stimuli were clearly supra-threshold: visual stimuli lasted 60 or 100 ms, whereas tactile stimuli lasted 5 or 25 ms. Hearing participants wore headphones delivering white noise, to prevent any sound related to the operation of the vibro-tactile stimulators. The white-noise volume was adjusted individually. An I/O-box attached to a portable PC was used for stimulus presentation and response registration. The experiment was programmed using MATLAB with Psychtoolbox extensions (Brainard 1997; Pelli 1997).

2.1.2.3 Experimental design and Procedure

At the beginning of each trial, fixation was switched on. After a random interval lasting between 1000 and 1400 ms one stimulus appeared, unpredictably at any of the four possible positions. Participants were instructed to keep central fixation throughout the experiment and to release as fast as possible a foot-pedal positioned under the heel of the right foot every time they detected a stimulus. If no response was given within 2 seconds from the target offset, the next trial started automatically. Inter-trial interval lasted 1500 ms during which fixation remained lit for 1000 ms and then it was switched off for the remaining 500 ms.

The experiment comprised two blocks of 100 trials each. Target modality changed between experimental blocks, in counterbalanced order across participants. In each block, 80% of the trials were stimulation trials (20 stimuli for each of the 4 possible location), whereas the remaining 20% were catch-trials, in which no stimulus was presented. Deaf participants performed also an additional block (50 trials, 10% of catch trials), with tactile stimuli delivered in the back of the neck. All participants received written instructions, paired with Italian or sign language instructions when needed. In addition, before starting the experiment a brief practice (two blocks, one visual and one tactile, 10 trials each) was presented to all the participants to allow familiarisation with the task.

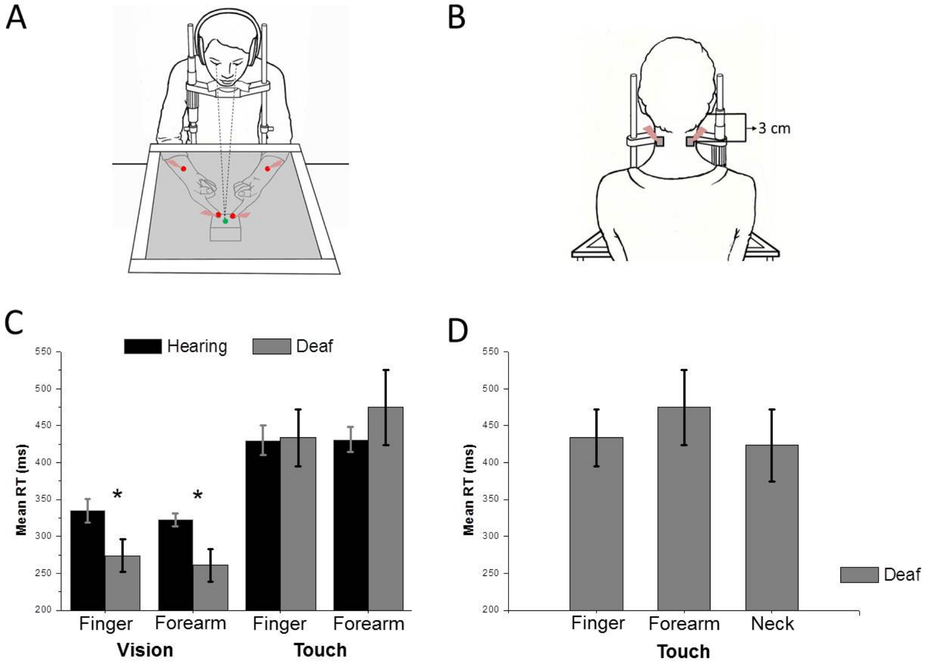


Figure 2.1. **(A)** Experimental setup, participant's posture and location of visual and tactile stimuli, identified by circles or sparkles on the arms, respectively. **(B)** Experimental setup showing tactile stimulus positions in the back of the neck.[1] **(C)** Results (Modality x Group interaction). For visual targets, deaf participants (Mean RTs= 267 ms, SE=22) were significantly faster than hearing controls (Mean RTs= 329 ms, SE=12), regardless of stimulus position. For tactile targets, deaf and hearing participants did not differ between each other (deaf: Mean RTs= 454 ms, SE=44; hearing: Mean RTs= 431 ms, SE= 18). **(D)** Results. Deaf participants showed no difference in RTs across the three tactile positions tested (Finger: Mean RTs=434 ms, SE= 38.7; Forearm: 475 ms, SE= 51.3; Neck: 423 ms, SE= 49).

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[1] For the images of the experimental setup credits to: Paola Rigo and Tommaso Sega

2.1.3 Results

Trials in which reaction times (RTs) were faster than 100 ms or longer than 2000 ms were excluded from the analysis. Importantly, the number of anticipations (i.e., RTs < 100 ms) and false alarms (i.e., responses to catch trials) was negligible and comparable across the two experimental groups (deaf: 0.2%; hearing 0.1%).

Median RTs for each participant were entered into a mixed ANOVA with modality (vision, touch) and target position (peri-foveal/fingertip, peripheral/forearm) as within-participants variables, and group (deaf, hearing) as between-participants variable. This analysis showed a main effect of modality, caused by faster responses to visual compared to tactile stimuli overall ($F(1,18) = 60.9$, $p < 0.0001$, $\eta_p^2 = 0.77$). The interaction between modality and target position also reached significance ($F(1,18) = 5.23$, $p = 0.03$, $\eta_p^2 = 0.23$), showing that both groups were faster when detecting peripheral (298 ms, SE = 12) than peri-foveal visual targets (310 ms, SE = 15) while the opposite was true for tactile targets (fingertip: 432 ms, SE = 19; forearm: 449 ms, SE = 23).

Most importantly, there was a significant interaction between group and modality ($F(1,18) = 5.25$, $p = 0.03$, $\eta_p^2 = 0.23$; see Figure 2.1C). Subsequent t-tests showed that when responding to visual stimuli, deaf participants were significantly faster than hearing controls, regardless of visual targets eccentricity ($t(1,18) = 2.69$, $p = 0.01$). By contrast, when responding to tactile stimuli, there was no difference between groups ($t(1,18) = 0.56$, $p = 0.6$; see Figure 2.1C legend for means and standard errors, as a function of condition and group). No other main effects or interactions reached significance (all other F-values < 2.23).

To test whether a response time advantage in the tactile modality may emerge selectively for region inaccessible to vision, we separately conducted a within group ANOVA, only for the deaf group, with tactile stimulus position as variable (fingertip, forearm, neck). The effect of tactile stimulus position did not reach significance ($F(2,14) = 1.3$, $p = 0.3$), meaning that deaf participants were equally fast in responding to tactile targets, irrespective of their spatial position (see Figure 2.1D legend for means and standard errors).

2.1.4 Discussion

Since the pioneering work by Loke and Song (1991), faster response times to visual events have been repeatedly documented in deaf adults compared to hearing controls (Bottari et al. 2010, 2011; Reynolds 1993; see Pavani & Bottari 2012 for review). However, it remained an open issue to what extent this behavioural advantage could be specific for vision or could be related to more sensory unspecific processes (e.g., increased impulsivity in response releasing, longer lasting sustained attention or higher motivation to perform the task). A critical contribution of sensory unspecific changes predicted an extension of the response speed advantage also to another intact modality (here, touch). The present findings reveal selective response speed advantage for the *visual* modality in deaf adults compared to hearing controls, but no reaction time advantage for tactile events. This dissociation emerged in the context of negligible anticipation errors and false alarms, and despite the fact that tactile and visual targets occupied exactly the same locations in external space.

These findings strengthen the proposal that this response speed advantage in deaf people may reflect early changes in the temporal dynamic of *visual* processing (Bottari et al. 2011), rather than changes occurring in other sensory unspecific mechanisms involved in simple detection. In particular, these findings are not compatible with a role of perceptual decision-making, response preparation, response impulsivity, sustained attention or motivation in the response speed advantage of deaf adults. Response impulsivity in the deaf group should have led to more anticipations and false alarms, which was not the case, as both these aspects of performance were comparable and negligible between the two groups. Furthermore, differences in any of the other aforementioned sensory unspecific mechanisms should have produced response speed advantages for deaf participants in *both* vision and touch.

The visual specificity of this behavioural advantage is in line with other studies documenting changes in early stages of visual processing in the deaf population. Codina and colleagues (2011), showed that deaf participants could detect moving dots, proceeding from the periphery to the central visual field, at more peripheral locations compared to hearing controls (see also Buckley et al. 2010). By combining this behavioural measure with the analysis of the optic nerve structure obtained with Optical Coherence Tomography (OCT), Codina and colleagues (2011) also found that deaf participants (compared to hearing controls) had significantly larger neural rim areas within the head of the optic nerve (a non-invasive indicator of the numbers of retinal gangliar cells). Most strikingly, this measure of retinal reorganisation correlated with the extension of the visual field as measured by the behavioural task, revealing the involvement of very early structures in visual-related changes following deafness.

The present findings also contribute to the emerging literature on somatosensory processing in early deaf adults. Until now, changes in the tactile domain following early auditory deprivation have been investigated without taking into consideration reaction times of participants (Bolognini et al. 2012; Frenzel et al. 2012; Heming and Brown 2005; Karns et al. 2012; Levänen & Hamdorf 2001; Moallem et al. 2010). The absence of tactile response time advantage in our deaf group is compatible with two interpretations. The first possibility is that only some aspects of tactile processing are potentiated in early deaf people. For instance, tactile frequency discrimination could be selectively enhanced by profound deafness (Levänen & Hamdorf 2001), possibly as a consequence of reorganisation occurring within auditory regions (Levänen et al. 1998; Auer et al. 2007; Karns et al. 2012). By contrast performance could remain unchanged – or even become impaired – following early deafness in other tasks such as grating orientation discrimination (Frenzel et al. 2012), vibration detection thresholds (Moallem et al. 2010; Frenzel et al. 2012), tactile spatial discrimination (Bolognini et al. 2012), tactile temporal discrimination (Bolognini et al. 2012; Heming and Brown 2005; Karns et al. 2012; Moallem et al. 2010) and reaction times to tactile targets (the present study). A second possibility is that congenital deafness could be detrimental for proper developing of tactile processing. This account has recently been proposed by Frenzel and colleagues (2012), which documented a significant correlation between tactile and auditory acuity levels in the hearing population. In addition, they have also reported a significant impairment in vibrotactile sensitivity and tactile acuity in congenitally deaf participants and in patients with Usher syndrome with *USH2A* gene mutations compared to hearing controls. This led to the proposal that a common genetic determinant can affect both hearing and touch. This proposal however could be appropriate to explain deficits in tactile processing in profound deafness of genetic origins, whereas it might be less appropriate to account for other forms of deafness.

In conclusion, the present findings suggest that behavioural advantages triggered by auditory deprivation do not necessarily extend across *all* intact sensory modalities. This provides initial evidence that intact sensory modalities can reorganise independently from each other following early bilateral deafness. To the best of our knowledge the only other study that tested the same behavioural ability in both vision and touch was conducted by Heming and Brown (2005). They revealed, however, a sensory unspecific temporal-order judgment deficit in deaf compared to hearing adults. Future research in the deaf population should compare visual and tactile performance in other abilities for which a visual enhancement has been documented (e.g., discrimination of moving stimuli directions; e.g., Bosworth & Dobkins, 2002; Hauthal et al., 2013; Neville and Lawson 1987b), to test whether they are selective to vision or extend also to touch.

Study 2: Discrimination of temporal durations for vision and for touch in early deaf adults

2.2.1 Summary

Accurate temporal processing of sensory events is a crucial ability in daily life. Audition typically contributes to this ability by providing highly reliable perceptual signals, which are also used for calibration of temporal perception in other sensory modalities. Yet, the study of deaf cognition have examined temporal processing to a lesser extent compared to other aspects of perceptual processing, often limiting the investigations to one intact sensory modality at a time. Here, we tested nine early bilateral deaf adults and twelve hearing controls in a duration discrimination task, performed on visual or tactile stimuli. Participants were instructed to perform the task as fast and as accurately as possible. Results showed that deaf adults were significantly faster than hearing controls, irrespective of the stimulus sensory modality. However, this speeded behavior was paired with a systematic detriment in accuracy. In other words, deaf participants showed a clear speed-accuracy trade off (SAT) compared to hearing controls. This prominent SAT behavior could not be explained in terms of increased impulsivity in response releasing in deaf adults compared to hearing controls, because the proportion of anticipation responses was negligible and comparable between groups. Taken together these results provide initial evidence for altered supramodal processing of temporal durations in deaf adults. Furthermore, they add to previous findings in the literature reporting SAT behavior in deaf adults. We discuss the SAT results in terms of recent models of perceptual decision-making.

2.2.2 Introduction

The human capacity for temporal analysis differs between sensory modalities. It has been known for long time that temporal analysis in audition outperforms temporal analysis in vision (Julesz & Hirsh, 1972; Miller & Taylor, 1948). The classic work of Miller and Taylor (1948), for instance, showed that humans detect the presence of interruption in a white noise signal at rates well above 1000 cycles per second, whereas interruptions in a bright light can be detected only below a rate of 60 cycles per second. These precise and reliable temporal signals conveyed by audition are also of great importance for temporal processing of multisensory events, serving for the calibration of temporal analysis in other sensory modalities as well (e.g., Shams, et al., 2000; Mishra, et al., 2007). This key role of audition in temporal perception raises the issue of whether auditory deprivation occurring early in life could alter temporal processing abilities for intact sensory modalities in people with early bilateral deafness.

This hypothesis has been put forward in the second half of the past century (e.g., Blair, 1957; Hanson, 1982; Withrow, 1968), but it was only examined with formal testing in the 80's (Bross and Sauerwein, 1980; Poizner & Tallal, 1987). In particular, Poizner and Tallal (1987) conducted four experiments to test temporal processing abilities in early deaf individuals. One experiment examined flicker fusion thresholds, one experiment explored two-points temporal discrimination thresholds (i.e., the shortest gap required to experience to visual stimuli as separate), one tested temporal order judgment abilities for pairs or triplets of visual targets presented in sequence, and one final experiment measured performance in a serial memory task, in which sequences of three to seven items were presented at 2-Hz rate (i.e. one every 500 ms) and participants were asked to tap out the order of the presented stimuli on the computer keyboard. None of these experiments documented any difference between hearing and deaf participants, leading Poizner and Tallal (1987) to conclude that temporal processing is not altered in deaf individuals.

Since the seminal work by Poizner and Tallal (1987) other studies have explored the issue of visual temporal analysis in people with early deafness through different tasks tapping on different aspects of time perception (Heming & Brown, 2005; Kowalska & Szelag, 2006; Nava, et al., 2008;

see Dye & Bavelier, 2010 for an analysis on the deployment of visual attention in time). The issue of temporal analysis in the tactile modality instead, received much less of attention (Bolognini, et al., 2012; Heming & Brown, 2005). Overall, given the variety of aspects of temporal analyses that have been addressed, rather unsurprisingly, the existing literature investigating this critical aspect of deaf cognition produced contrasting results (see Table 1 for a synthetic description of previous studies and their main outcome). Yet, a direct comparison of the outcomes of the studies that explored temporal analysis for visual or tactile stimuli reveal a potential systematization. Most of the existing results addressing temporal processing for *visual* stimuli showed comparable performance between deaf adults and hearing controls (Bross & Sauerwein, 1980; Nava, et al., 2008; Poizner & Tallal, 1987), whereas existing results investigating temporal processing for *tactile* stimuli suggest an impairment in temporal processing in the deaf population (Bolognini et al., 2012; Heming & Brown, 2005).

Sensory Modality	Task	Authors	Results
V	Flicker Tresholds	Bross & Sauerwein, 1980	D=H
V	Flicker Tresholds	Poizner & Tallal, 1987	D=H
V	Two-points temporal thresholds	Poizner & Tallal, 1987	D=H
V	Temporal Order Judgement	Nava et al., 2008	D=H
V	Temporal Order Judgement	Poizner & Tallal, 1987	D=H
V	Simutaneity Judgement	Heming & Brown, 2005	D<H
V	Duration Judgment	Kowalska & Szelag, 2006	D<H
V	Serial memory task	Poizner & Tallal, 1987	D=H
T	Simutaneity Judgement	Heming & Brown, 2005	D<H
T	Duration Discrimination	Bolognini et al., 2012	D<H
VT	Double-Flash Illusion	Karns et al., 2012	D>H

Table 2.2. Summary of the existing results investigating time perception in deaf adults compared to hearing controls separately for the visual (V), and for the tactile modality (T) as well as for visuo-tactile tasks (VT). 'D' means deaf participants and 'H' means hearing participants.

This suggested asymmetry between vision and touch temporal analysis is particularly surprising given that for the modality appropriateness hypothesis (Welch & Warren, 1980) touch has a higher temporal precision than vision, and therefore it should better substitute the auditory modality for time-related processing as a consequence of auditory deprivation. Instead, existing results suggest that temporal processing of tactile stimuli might be impaired more than the temporal processing of visual stimuli in the deaf population. Two recent works had even suggested a possible neurofunctional mechanism, which might underlie this enhanced tactile deficit (Bolognini et al., 2012; Karns et al., 2012). Karns and colleagues (2012) measured the hemodynamic brain response with fMRI in a group of congenitally deaf adults and hearing controls performing a somatosensory version of the double-flash illusion (see Mishra et al., 2007; Sham et al., 2000 for a double-flash illusion elicited by auditory stimuli). This somatosensory illusion is thought to arise exactly as a consequence of the higher temporal precision of touch over vision and it consists in the phenomenon by which a single flash of light paired with two or more somatosensory stimuli is perceived as multiple flashes of lights (Lange et al., 2011; Violentyev et al., 2005). The task of participants was to detect 'deviant' visual stimuli embedded in a stream of 'standard' visual stimuli while ignoring a concomitant tactile streams also composed by standard and deviant tactile stimulations. Behavioral results showed that only the deaf group was sensitive to the illusion. Moreover, only in the deaf group signal change in the rostrolateral portion of the Helsch's gyrus positively correlated with the strength of the illusion. The more this portion of Heschl's gyrus was activated by somatosensory stimuli, the more deaf participants were sensitive to the double-flash illusion. This result suggests that tactile temporal processing in the deaf population might be mediated by activity in primary auditory cortex and the authors interpreted it as initial evidence in favor of enhanced tactile time perception in deaf adults. Nonetheless, it is not clear to what extent this enhanced auditory activity entails any benefit for actual performance in tactile temporal tasks, especially if one compares this result with the findings of the work by Bolognini and colleagues (2012). These authors tested a group of congenitally deaf adults and a group of hearing controls in two tactile tasks using vibrotactile stimuli: a temporal discrimination task (i.e., discrimination of the duration of tactile stimuli) and a spatial discrimination task (i.e., discrimination of the spatial length of tactile stimuli). In the spatial task performance between groups was comparable, whereas in the temporal task deaf participants performed significantly worse than hearing controls. Moreover, to investigate the neural substrate of this impaired temporal behavior, the authors also performed a TMS experiment stimulating the somatosensory cortex (S1) and the auditory association cortex (STG), while presenting to deaf and hearing participants the same spatial and temporal behavioral tasks. Results showed that STG was involved in both tasks in deaf individuals, with a chronometry comparable to that observed for S1 (STG was involved in both tasks, already 60 ms after stimulus presentation), thus suggesting early involvement of STG in tactile processing. Instead, in hearing controls STG was involved selectively in the temporal task and only at a later stage of processing (compared to S1; 180 ms after stimulus presentation). Intriguingly, when correlating the TMS effect induced by STG stimulation in hearing controls (at 180 ms) with the percentage of errors at baseline in the temporal task, a negative relation emerged. The better participants performed in the temporal task at baseline, the more they were disrupted by TMS. This led the authors to propose that this later involvement of the STG, absent in the deaf group, is fundamental to efficiently integrate tactile and temporal features.

Taken together then, these two studies seem to suggest that early activation of auditory cortices by tactile stimuli, is maladaptive for temporal processing, thus providing a potential mechanism for a modality specific impairment.

However, two notable exceptions in the visual modality challenge the hypothesis of a deficit of temporal processing in deaf adults specific for the tactile modality. The first is a study by Kowalska and Szelag (2006) that reported worse performance of congenitally deaf adolescents, compared to hearing peers, in the ability to judge the duration of visual events lasting several seconds (range 1-6 seconds). Participants were asked to perform a production and a reproduction task, in which they had to stop the presentation of a visual stimulus on a computer screen when they decided it matched the duration in seconds previously indicated on the monitor (production task), or the duration of a previously presented visual stimulus (reproduction task). The second exception is a study by Heming and Brown (2005), in which deaf adults and hearing controls were compared in a simultaneity judgment task. Most interestingly, in this study participants performed exactly the same task on visual or tactile stimuli across different blocks, thus providing the first direct comparison of temporal analysis for the two intact modalities in deaf participants. Results show that regardless of stimulus sensory modality, deaf participants displayed significantly higher temporal thresholds compared to hearing controls, leading Heming and Brown (2005) to link the observed performance to a *supramodal* deficit of temporal processing as a consequence of early auditory deprivation.

In the present study we aimed to investigate further the modality specific vs. supramodal nature of the supposed temporal deficits in deafness, by using the same behavioral task in both vision and touch. Similar to Bolognini et al. (2012), but unlike the only previous study that compared temporal analysis in vision and touch (i.e., Heming & Brown, 2005), we adopted a duration discrimination task, presenting visual and tactile stimuli in separate blocks. Because several previous studies reported faster choice reaction times in deaf compared to hearing adults (e.g., Neville & Lawson, 1987b; Hauthal et al., 2013; see Pavani & Bottari, 2012 for a review), differently from Bolognini and colleagues (2012) we asked participants to perform a speeded discrimination task. Finally, to test whether the precision of temporal abilities in vision could be influenced by the retinal eccentricities of the stimulation, we presented visual stimuli at central or peripheral locations. The rationale for this additional manipulation is linked to the consistent finding that enhanced processing in deaf adults may be particularly pronounced for the periphery of the visual field (Bavelier et al., 2006; Dye et al., 2009). We matched this spatial manipulation of the visual stimuli in the tactile modality in two ways: 1) we delivered touches to the index and forearm, i.e., regions of high and low spatial-acuity; 2) we paired the location of tactile and visual events in external space (see Figure 2.2).

If the ability to correctly perceive the duration of events is impaired supramodally in deaf compared to hearing adults as a consequence of auditory deprivation (as proposed by Heming & Brown, 2005), deaf participants should perform worse than hearing controls regardless of sensory modalities. This deficit should also emerge irrespectively of target position. If instead, the tactile modality is more impaired than the visual modality for what it concerns temporal processing and in particular duration perception (e.g., see Bolognini et al., 2012), differences between deaf adults and hearing controls should emerge only (or more strongly) with tactile compared to visual stimulations.

2.2.2 Methods

2.2.2.1 Participants

Twelve hearing participants with no experience in sign language (mean age = 28.6 years old, SD = 2.7) and nine early deaf participants non-native signers (mean age = 33.1 years old, SD = 6.2; see Table 2.3 for further information about deaf participants) took part in the experiment. All participants reported to have normal or corrected-to normal vision as well as normal somatosensation and no one reported to suffer from any psychiatric disorder or neurological disease. The Ethical Committee of the University of Trento approved the study.

Deaf	**Age**	**Deafness**			**LIS AoA**
ID	**years**	**Onset**	**Deagree**	**Etiology**	**years**
1	33	2 months	Profound	Otitis	17
2	26	Birth	Profound	Congenital	20
3	31	Birth	Severe	Maternal Rubella	21
4	37	20 days	Profound	Open-heart surgery	Does not use it
5	37	Birth	Profound	Congenital	14
6	29	Birth	Profound	Congenital	8
7	43	Birth	Profound	Congenital	Does not use it
8	38	Birth	Profound	Congenital	7
9	24	Birth	Profound	Maternal Rubella	23

Table 2.3 Anamnestic information about deaf participants collected through a brief questionnaire they all fill-out prior to the experiment. For the variable ‘Degree’ of Deafness, ‘Profound’ means a loss ≥81 dB in the better ear; ‘Severe’ means a loss ≥61 dB in the better ear. The acronym ‘LIS AoA’ means Age of Acquisition of Italian Sign Language.

2.2.2.2 Stimuli and Apparatus

Participants sat on a comfortable chair with their chin on a chin-rest, and their hands and forearms resting supine on a table. A wooden cube (7x7x7 cm) placed along the participant’s midsaggital plane, at approximately 60 cm from the participant’s chest, served as resting position for the index fingers. One green LED positioned on the wooden cube served as visual fixation. Four red LEDs and four bone vibrators (Oticon A; dimensions: 1,5 cm X 2,5 cm) were used to deliver visual and vibrotactile stimuli, respectively. Two pairs of LEDs and bone vibrators were placed on the index fingertips, and two pairs were placed on the forearms. This resulted in four spatially congruent locations for visual and tactile stimulation: (1) right index; (2) left index; (3) right forearm; (4) left forearm (see Figure 2.2). Note that with this arrangement, retinal eccentricity was perfectly matched for each pair of visual and tactile stimuli. Also, placing the stimuli on the index and forearms allowed testing simple temporal discrimination abilities in vision and touch for regions of high and low spatial-acuity. Specifically, stimuli at the index fingers were delivered in a region of high spatial acuity for both vision (1° from fixation) and touch (fingertip); similarly, stimuli at the forearms were delivered in a region of low spatial-acuity for both vision (32° from fixation;) and touch (forearm).

An opaque glass, suspended 9 cm above the hands, prevented direct vision of the setup. With this setup, visual stimuli (flashes of lights) were visible as a projection on the opaque glass when the LEDs were switched on, and tactile stimuli were felt but not seen. Direct vision of the stimulated hands and forearms was prevented throughout.

All stimuli were clearly supra-threshold: visual stimuli lasted 60 or 100 ms, whereas tactile stimuli lasted 5 or 25 ms. Hearing participants wore headphones delivering white noise, to prevent any sound related to the operation of the vibro-tactile stimulators. The white-noise volume was adjusted individually. An I/O-box attached to a portable PC was used for stimulus presentation and response registration. The experiment was programmed using MATLAB with Psychtoolbox extensions (Brainard 1997; Pelli 1997).

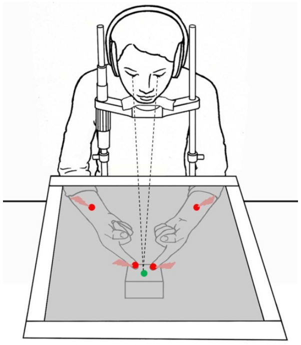

Figure 2.2 Experimental set-up

2.2.2.3 Experimental design and Procedure

At the beginning of each trial, fixation was switched on. After a random interval lasting between 1000 and 1400 ms one stimulus appeared, unpredictably at any of the four possible positions. Participants were instructed to keep central fixation throughout the experiment. The task was to discriminate in each trial whether the stimulus presented was short or long in duration by releasing as fast and as accurate as possible one of the two foot-pedals positioned under the heel and under the tip of the toe of the right foot. For short stimuli participants were asked to release the pedal under the heel and for long stimuli the pedal under the tip of the toe. If no response was given within 2 seconds from the target offset, the next trial started automatically. Inter-trial interval lasted 1500 ms during which fixation remained lit for 1000 ms and then it was switched off for the remaining 500 ms.

The experiment comprised 2 blocks: one visual and one tactile. The tasks in the visual and in the tactile modality were exactly the same the only thing that changed was the sensory modality in which the stimuli were delivered. Each block comprised 96 trials. The order of visual and tactile blocks was counterbalanced across participants.

All participants received written instructions, paired with Italian or sign language instructions when needed. To ensure participants understood the task and were able to disambiguate the two stimuli, before starting to record responses, they all underwent 2 blocks of practice, one for each of the sensory modality tested (32 trials each). In addition, right before starting each block, participants performed another brief practice block (16 trials).

2.2.3 Results

Trials in which reaction times (RTs) were faster than 150 ms or longer than 2000 ms were excluded from the analysis. Importantly, the number of anticipations (i.e., RTs < 150 ms) and missed responses (i.e., RTs > 2000 ms) was negligible and comparable across the two experimental groups for both sensory modalities tested (Anticipations Deaf: vision= 0%; touch= 0%; Anticipations Hearing: vision= 0%; touch= 0%. Misses Deaf: vision= 1%; touch: 4%; Misses Hearing: vision= 1%; touch= 1%).

For each participant and for each sensory modality we calculated median RTs for correct trials, and percentage of correct responses. We entered these values in two separate repeated-measure mixed ANOVAs with sensory modality (vision; touch) and target position (finger; forearm) as within-participants variables and group (hearing; deaf) as between-participants variable. All post-hoc analyses were conducted using the Tuckey test.

The analyses on RTs revealed a significant main effect of sensory modality ($F(1,19) = 80.42$, $p < 0.00001$, $\eta_p^2 = 0.81$), given by overall faster responses to visual ($M = 619.26$ ms, $SE = 26.42$) compared to tactile stimuli ($M = 762.35$ ms, $SE = 30.70$, $p = 0.0002$). Also the main effect of target position reached significance ($F(1,19) = 11.31$, $p = 0.003$, $\eta_p^2 = 0.37$), driven by overall faster responses to stimuli delivered on the fingers ($M = 672.94$ ms, $SE= 27.10$) compared to stimuli delivered on the forearms ($M = 708.67$ ms, $SE = 28.99$, $p = 0.005$). Most importantly, the main effect of group was also significant ($F(1,19) = 5.36$, $p = 0.03$, $\eta_p^2 = 0.22$) caused by overall faster responses in deaf participants ($M = 618.13$ ms, $SE = 41.52$) compared to hearing controls ($M = 745.31$ ms, $SE = 35.96$, $p = 0.03$; see Figure 2.3A). No other factor reached significance (all other F-values < 3.14).

A similar analysis conducted on percent correct also revealed a significant main effect of group ($F(1,19) = 14.04$, $p = 0.001$, $\eta_p^2 = 0.42$). This, however, was caused by overall higher accuracy for hearing controls (M = 80%, SE = 3%) compared to deaf participants (M = 62%, SE = 4%; p = 0.001; see Figure 2.3B). Also the main effect of target position reached significance (F(1,19) = 27.22, p = 0.00005, $\eta_p^2 = 0.59$) caused by overall higher accuracy for target delivered on the fingers (M = 78%, SE = 3%) compared to targets delivered on the forearms (M = 67%, SE = 2%; p = 0.0002), independently of the sensory modalities and groups. No other factor reached significance (all other F-values < 1.02).

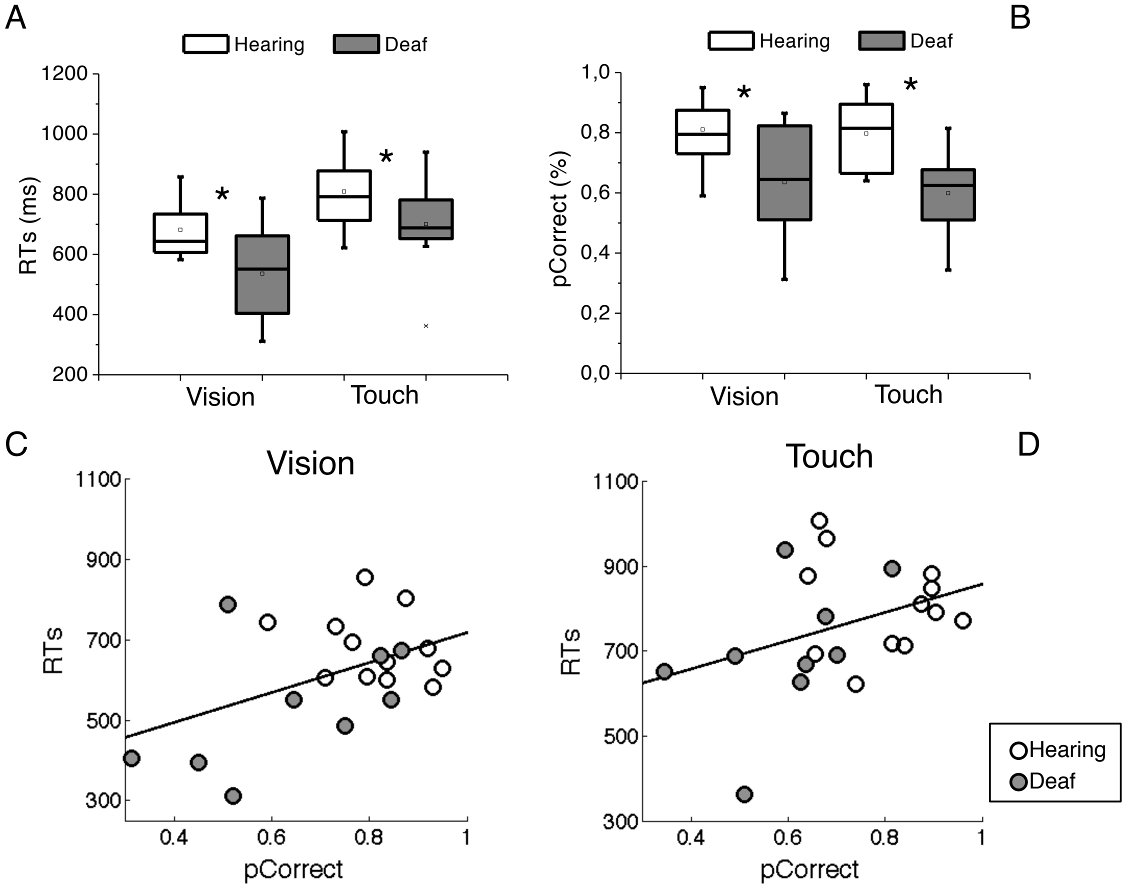

Figure 2.3. Results. **(A)** Reaction times in response to visual and tactile stimuli for deaf and hearing participants. Deaf participants (grey box-plots) resulted faster than hearing controls (white box-plots) for both sensory modalities. **(B)** Accuracy in response to visual and tactile stimuli for deaf and hearing participants. Deaf participants (grey box-plots) resulted less accurate than hearing controls (white box-plots) for both sensory modalities. **(C)** On the x-axes there is the individual accuracy in responding to visual stimuli; on the y-axes there is the individual corresponding reaction time. The speed-accuracy trade-off behavior in the visual modality is evident only for the deaf participants (grey circles). **(D)** On the x-axes there is the individual accuracy in responding to tactile stimuli; on the y-axes there is the individual corresponding reaction time. The speed-accuracy trade-off behavior in the tactile modality is evident only for the deaf participants (grey circles).

These results suggested a speed-accuracy trade-off in the responses of deaf adults rather than a frank impairment in performance (see Figures 2.3C-2.3D). To assess performance in the two groups at the net of speed-accuracy trade-offs we calculated for each participant and for each experimental condition the Inverse Efficiency Score (IES; Akhtar & Enns 1989; Christie & Klein 1995; Kennett, Eimer, Spence & Driver, 2001; Townsend & Ashby ,1983). This index permits relating RTs to accuracy performance by dividing RTs by the corresponding accuracy measure (computed as RT divided by proportion correct). We entered IES as dependent variable in a mixed-repeated measure ANOVA with the same within and between factors of the previous ANOVAs. This analysis revealed a main effect of sensory modality ($F(1,19) = 13.94$, $p = 0.001$, $\eta_p^2 = 0.42$) caused by overall higher IES for stimuli delivered in the tactile modality ($M = 1159.70$ ms, $SE = 82.76$) compared to visual ones ($M = 885.61$ ms, $SE = 57.53$, $p = 0.002$). Also the main effect of target position reached significance ($F(1,19) = 16.26$, $p = 0.0007$, $\eta_p^2 = 0.46$) given by overall higher IES when stimuli were delivered on the forearms ($M = 1141.70$, $SE = 76.83$) compared to when they were delivered on the fingers ($M = 903.69$ ms, $SE = 56.88$, $p = 0.001$; see Figure 2.4). No other effect reached significance (all other F-values < 3.49), in particular the between-group difference was no longer apparent ($p = 0.3$).

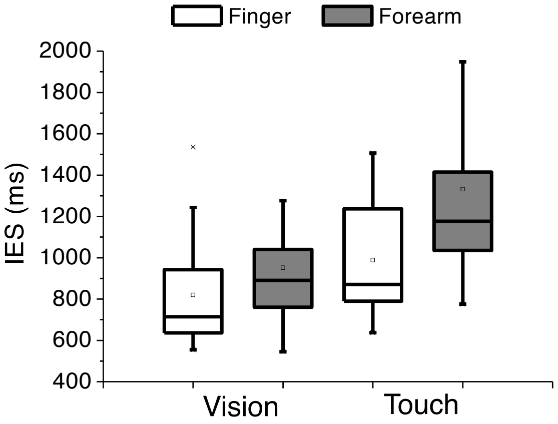

Figure 2.4. IES scores. Higher IES scored were observed for tactile compared to visual stimuli and for stimuli delivered on the forearms (grey box-plots) compared to stimuli delivered on the fingers (grey box-plots). Importantly no effect related to the group factor emerged.

2.4 Discussion

The aim of the present study was to further investigate time perception in deaf adults, a domain of deaf cognition in which contrasting evidence is currently available. In particular, we aimed to explore to what extent any deficit in temporal processing would emerge supramodally (i.e., regardless of the sensory modality of the stimulus on which temporal analysis is performed) or it would instead be selective for temporal analysis in the tactile modality. We compared deaf and hearing adults in a speeded discrimination of temporal durations, with stimuli presented in both the visual and the tactile modality in separate blocks of trials. Our results showed that deaf adults were faster than hearing controls in performing the task for both sensory modalities, but this speed advantage was paired with a significant detriment in accuracy. For both vision and touch, and independently of stimuli positions, deaf participants proved to be less accurate than hearing controls in performing the task. In other words, a clear speed-accuracy tradeoff (henceforth abbreviated with SAT; Chittka, Skorupski & Reine, 2009; Schouten & Bekker, 1967; Wickelgren, 1977) characterized the responses of deaf participants. Indeed, when we related RTs and accuracy measures by calculating Inverse Efficiency Scores, the main effect of group disappeared.

At first glance, these results could suggest that temporal duration processing is not impaired in deaf adults compared to hearing controls, but rather that the observed discrimination difficulty might depend entirely from the speeded behavior implemented by deaf individuals. In other words, one could predict that if deaf participants had been slower in delivering their responses, they would have had comparable performances to hearing controls. This view would suggest increased impulsivity in response releasing in the deaf group compared to hearing controls as a possible explanation for our results (e.g., Parasnis et al., 2003). This explanation, however, do not seem appropriate for the present findings because the number of anticipations was in fact negligible and comparable between groups. Furthermore, the SAT behavior of deaf participants cannot either be explained in terms of increased proportion of omitted responses, which were overall negligible and also comparable between groups. Accordingly, we explored in more details current theoretical models of SAT behaviors in humans, for better framing the pronounced difference between hearing and deaf adults documented by our novel results.

2.4.1 Speed-accuracy trade-offs in deaf participants

The observation of SAT in deaf people compared to hearing controls has been never documented before in temporal tasks, as previous studies did not measure RTs of participants (e.g., Bolognini et al., 2012; Kowalska & Szelag, 2006) or reported a RTs advantage without opposing accuracy profiles (Nava et al., 2008). Furthermore, other studies measuring speeded discrimination abilities for deaf people in non-temporal tasks did not find evidence for speed-accuracy trade-offs. Deaf adults showed comparable performance to hearing controls both in terms of reaction times and accuracy, in a peripheral motion localization task (Hauthal et al., 2013). In addition, two peripheral visual motion direction tasks reported faster reaction times in deaf adults compared to hearing controls at the net of comparable accuracy between the two groups (Neville & Lawson, 1987b; Hauthal et al., 2013).

However, reports of SAT behaviors for deaf adults compared to hearing controls in speeded visual discrimination tasks also exist. For instance, a light SAT in the performance of deaf compared to hearing participants has been reported in a discrimination of directional changes in visual motion (Bosworth & Dobkins, 2002) and in a visual shape-discrimination task (Bottari et al., 2010).

Therefore, useful hints to better interpret the present findings, might come from the arising literature concerning the functional and neural mechanisms underlying speed-accuracy trade-offs (SAT), which during the last years received increased attention (see Bogacz, Wagenmakers, Forstmann & Nieuwenhuis, 2009 for a review). Simple perceptual-decisions (e.g., decide whether stimulus-duration is short or long, as in the present study) have been conceptualized as the outcome of a mechanism of 'accumulation of information', using mathematical models and computational neuroscience approaches (Beck, Ma, Kiani, Hanks, Churchland, Roitman, Shadlen et al., 2008; Furman & Wang, 2008; Wang, 2002). In such models, response initiation occurs when a certain threshold is exceeded. These models postulate that perceptual-decisions involve only brain areas related to decision-making, without any involvement of early sensory areas. Indeed, the neural correlates of information accumulation have been identified in several brain regions (e.g., Heekeren, Marrett & Ungerleider 2008), including the pre-motor cortex (in case of motor response tasks) or the dorsolateral prefrontal cortex (typically associated with higher-order decision-making processes). Instead, no involvement of early sensory areas has been documented (Forstmann, Dutilh, Brown, Neumann, von Cramon, Ridderinkhof & Wagenmakers, 2008; Ivanoff, Branning & Marois 2008; van Veen, Krug & Carter, 2008).

The proposal is that clusters of neurons in the active brain regions are selectively tuned to different perceptual choices (e.g., ‘short’ vs. ‘long’ duration) and operate as accumulators of perceptual evidence (e.g., Beck et al., 2008; Heekeren et al., 2008; Shadlen & Newsome, 2001; Usher & McClelland, 2001). The activation level of these ‘evidence integrator neurons’ is predictive of the participant’s response. In agreement with the notion that these neurons integrate sensory evidence over time, their firing rate gradually increases during the time interval between stimulus presentation and response (Gold & Shadlen, 2001; Heekeren et al., 2008; Schall, 2001). When a critical threshold is reached, response is initiated. Within this framework, mathematical models explain SAT behavior in terms of the distance between the activation at baseline of the ‘evidence integrator neurons’ and the threshold that triggers response initiation (e.g., Brown & Heathcote, 2008; Ratcliff & McKoon, 2008; Vickers, 1970). If the distance between the baseline and the threshold is small (i.e., high baseline activity and/or low response thresholds), responses are fast, but the level of accuracy is low. By contrast, if the distance is large (i.e., low activity at baseline and/or high response thresholds) accuracy is high but responses are slow (Beck et al., 2008; Usher & McClelland, 2001; Wang, 2002). Although these models do not allow disentangling the contribution of baseline changes vs. response-thresholds changes in SAT, several neuroimaging studies have proposed that SAT behavior results from baseline-related changes, whereas response thresholds are fixed (Ivanoff et al., 2008; Mordkoff & Grosjean, 2001; Ratcliff, Cherian & Segraves, 2003; Roitman & Shadlen, 2002).

Within this framework of reference, the clear supramodal SAT behavior in deaf participants compared to hearing controls that we reported for discrimination of temporal durations, might then emphasize a possible critical aspect of deaf behavior which remained largely undetected until now (or simply associated with response impulsivity, which cannot be an explanatory account here as discussed above). In particular, the increased SAT behavior of deaf adults (compared to hearing controls) could be interpreted as enhanced baseline activation of evidence integrator neurons during perceptual-decisions tasks. This, however, opens two possibilities. The first one is that the evidence integrator system in deaf adults compared to hearing adults is altered as a whole. This possibility would predict that *any* perceptual decisions in deaf adults would be impaired. Nonetheless, this option seems quite unlikely, given that comparable discrimination abilities between deaf and hearing adults have been documented in several discrimination tasks such as contrast sensitivity (Finney & Dobkins, 2001), discrimination of luminance changes (Bavelier et al., 2000; 2001) and tactile spatial discrimination (Bolognini et al., 2012). Moreover, deaf adults perform even better than hearing controls in a peripheral localization tasks when a concomitant central identification task was carried-out (Dye et al., 2009). Therefore, the second, more plausible, possibility is that SAT behaviors in deaf adults arise only for those perceptual-decisions for which sensory information arrives already altered to the evidence integrator neurons. In case of temporal duration, this possibility converges with the explanation that Bolognini and colleagues (2012) proposed to explain the impaired tactile duration discrimination they have reported in deaf adults compared to hearing controls. These authors presented to deaf and hearing participants a discrimination of temporal duration of tactile events very similar to the task we used in the present study, except that their task was unspeeded, thus eventual SAT behavior in the deaf population could not be documented. Interestingly, Bolognini and colleagues (2012) based on the results of a TMS experiment (see Introduction for further discussion) proposed that this difficulty in deaf participants might arise from an impaired ability to integrate tactile and temporal information together. Such impairment could indeed explain the altered activity at baseline in the deaf population that is suggested by our SAT results. However, even though plausible, we do not know whether also the SAT behavior we reported for the visual modality subtends to a similarly impaired temporal processing system. As a matter of fact, an alternative possibility would be that the behavioral outcomes of the two sensory systems for temporal analyses in deaf adults are similar, but the impaired mechanisms on which they rely are different. However, the fact that vision and touch were equally impaired in terms of sensory thresholds in a simultaneity judgment task in deaf adults compared to hearing controls (Heming & Brown, 2005) suggest that temporal analyses as a consequence of auditory deprivation might rely on similar impaired mechanisms. Future studies should directly address this issue in the visual modality.

All in all, these results are not completely conclusive for what it concerns the processing of temporal durations across sensory modalities in deaf adults compared to hearing controls. However, taken together with other studies suggesting impaired temporal processing in the deaf population (Bolognini et al., 2012; Heming & Brown, 2005; Kowalska and Szelag, 2006; see Table 2.3), they highlight a possible explanation for deaf impaired behavior, namely, an impairment at the level of evidence accumulators, possibly due to altered sensory information reaching these accumulators, and ultimately leading to the observed SAT behavior compared to hearing controls. Unluckily, the mechanisms underlying perceptual decisions' outcomes have been largely overlooked in the literature on the consequences for behavior of bilateral deafness. However, a more systematic investigation of this topic would be highly informative in order to enrich the understanding of the consequences on behavior of crossmodal changes following early bilateral deafness.

Study 3: The response times advantage of action videogame players generalizes to untrained sensory modalities, untrained features of stimuli and untrained response modes

2.3.1 Summary

Faster reaction times (RTs) to visual stimuli has been reported for avid action videogame players (VGPs) compared to non-gamers (NVGPs) in a wide variety of tasks tapping abilities beyond those trained while playing. Recently, it has been proposed that all AVGPs related behavioral improvements rely on improved probabilistic inference in perceptual-decision making in this population compared to NVGPs (Green, Pouget and Bavelier, 2010). One way to further test this proposal is by testing the generalization properties of the RTs advantage in AVGPs compared to NVGPs in several reactivity tasks, ultimately controlling for eventual violations of the proposed model: generalization to untrained sensory modalities (i.e., touch); generalization to untrained features of stimuli (i.e., temporal duration); generalization to untrained response modes (i.e., responses delivered through foot-pedals). In Experiment 1 we tested 8 AVGPs and 12 NVGPs in a simple detection task and in Experiment 2 we tested 8 AVGPs and 11 NVGPs in two discrimination tasks: duration discrimination task (temporal feature of stimuli) and a spatial, control task, namely, direction of apparent motion (spatial feature of stimuli). In all tasks stimuli were both visual and tactile and we recorded responses through foot pedals. Results show a generalization of RTs improvement to all the tested untrained conditions in AVGPs compared to NVGPs. Our findings represent the strongest evidence of the generalization potentials of this training regimen, further corroborating the proposal of an origin of AVGP-related advantages at the level of perceptual decision-making.

2.3.2 Introduction

The intensive training triggered by avid action video game playing (AVGP) gained an increased level of attention during the last ten years both for plasticity-related research and for rehabilitation practices. This was due to the impressive variety of improvements in behaviors triggered by this type of training regimen (see Bavelier, Green, Pouget, & Schrater, 2012 for a review). Vision is the most trained modality during playing, therefore research on this topic focused predominantly on the visual modality, reporting visual behavioral advantages in AVGPs compared to non-gamers (NVGPs) in many different tasks, such as contrast sensitivity (Li, Polat, Makous, & Bavelier, 2009), crowding acuity (Green & Bavelier, 2007), backward masking (Li, Polat, Scalzo, & Bavelier, 2010), flanker interference task (Bavelier, Achtman, Mani, & Föcker, 2011), useful field of view, enumeration, attentional blink (Green & Bavelier, 2003), multiple-object tracking (Green & Bavelier, 2006), visual short-term memory, mental rotations, executive control (e.g., Boot, Kramer, Simons, Fabiani & Gratton, 2008), task-switching (Green, Sugarman, Medford, Klobusicky, & Bavelier, 2012), even overcoming the physical constraints of the training regimen, such as the dimension of the typically used monitor (Green & Bavelier, 2007). Furthermore, these visual advantages have been shown to arise in naïve people after short training regimens with action videogames, determining the causality of action video game playing in the triggering of these improvements (e.g., Green & Bavelier, 2006; Green & Bavelier, 2007; see for reviews, Achtman, Green, & Bavelier, 2008; Bavelier et al., 2012). Researchers interested in brain plasticity found this generalization very intriguing for unraveling important properties of brain plasticity in the healthy brain. Also the clinical community found these results very promising, given that the biggest limit of rehabilitation techniques is that training-induced learning is often constrained to the particular task adopted, by the context of learning or even by the particular properties of the stimuli used (e.g., Shiu & Pashler, 1992; Fahle, 2005; Xiao, Zhang, Wang, Klein, Levi, & Yu, 2008; Jeter, Dosher, Petrov, & Lu, 2009), ultimately enormously limiting rehabilitation benefits in everyday life. Instead, AVGP related visual improvements seemed to permit the overcoming of this limit, being part of a growing body of evidence showing more generalizable types of learning as an output of complex training regimens (i.e., enriched environmental effects; for a review see, Sale, Berardi, & Maffei, 2009) including for instance, also musical training (Hanna-Pladdy & Gajewski, 2012) and athletic training (Hillman, Erickson, & Kramer, 2008).

Nonetheless, a detailed understanding of the mechanisms underlying these improvements is fundamental in order to better isolate the brain mechanisms still sensitive to plasticity during adulthood, and in order to best embed training with action video games within rehabilitation practices, ultimately individuating those patients that would mostly benefit from the exposure to this type of training regimen.

2.3.2.1 Mechanisms underlying AVGP-related advantages

One of the most robust behavioral visual improvements reported for AVGPs compared to NVGPs is the response speed advantage reported in both simple visual detection and in visual discrimination tasks (Dye, Green & Bavelier, 2009a). In visual simple detection, AVGPs compared to NVGPs resulted faster at detecting abrupt visual events (Castel, Pratt, Chaasten & Scialfa, 2005). This improved response time behavior was repeatedly reported also for more complex tasks, such as visual discrimination tasks, and it has been documented for several discrimination abilities, including spatial cueing (Greenfield, DeWinstanley, Kilpatrick, & Kaye, 1994), direction of motion (Green, Pouget and Bavelier, 2010), Attentional Network Test (ANT; Dye, Green & Bavelier, 2009b), Simon task (Bialystok, 2006), flanker interference (Green & Bavelier, 2003; Bavelier et al., 2011), visual search (Castel et al., 2005). All these studies reported that when compared to NVGPs, AVGPs showed faster responses at the net of comparable accuracy, thus ruling out an explanation in terms of speed-accuracy trade off in the AVGP population (see Dye et al., 2009a).

Given this impressively generalized behavioral outcome, several studies tried to unravel the underlying mechanisms it relies on, as a tool to unravel the level of information processing on which AVGP training regimen acts upon. Indeed, a number of *sensory specific* and *unspecific* processes are involved in reactivity behaviors, thus potentially contributing to the documented RTs advantage. These include specific sensory processes relying on early stages of visual processing as well as a variety of sensory unspecific processes relying on later stages of information processing such as perceptual decision-making, response preparation and response releasing, in addition to sustained or selective attention abilities and general increased motivation in performing the task. Considering the wide variety of tasks in which AVGPs performed better than NVGPs, an involvement of one of these higher-level mechanisms seems quite plausible.

And indeed the first proposal to explain reaction time improvements of AVGPs was related to the response execution phase, namely faster stimulus-response mapping in AVGPs compared to NVGPs (Castel et al., 2005). These authors presented to a group of AVGPs and to a group of NVGPs a task to elicit inhibition of return (IOR). Participants had to respond as fast as possible to the appearance of a target previously cued either congruently or incongruently. The Stimulus Onset Asynchrony (SOA) between the cue and the target varied to capture the time course of IOR. Results showed that AVGPs had overall faster RTs compared to NVGPs but showed the same IOR effect. Participants performed also a visual search task where search difficulty was manipulated. They always had to search for a ‘b’ or a ‘d’ letter embedded among distractor letters. In the easy search condition, all the distractors were the same. In the hard search condition, the distractor letters could have different identities. Results showed faster RTs for AVGPs compared to NVGPs, independently from the search condition. The authors interpreted the results of the comparable IOR effect between the two groups as evidence for unaltered basic mechanisms of visual attention in this population. In addition, the lack of effect in RTs related to search difficulty, suggests a constant, additive increase of response speed, which was unaffected by the difficulty of the task, ultimately suggesting faster stimulus-response mapping in AVGPs compared to NVGPs. However, a meta-analysis on all the studies reporting RTs advantage in AVGPs compared to NVGPs (Dye et al., 2009a) showed that RTs in AVGPs compared to NVGPs increased multiplicatively with the difficulty of tasks and not additively as proposed by Castel and colleagues (2005). This would suggest faster visual processing in AVGPs compared to NVGPs and it would also predict an increase in accuracy in AVGPs once fast stimuli presentation would be tested (Dye et al., 2009a). And indeed subsequent studies showed increased accuracy in AVGPs compared to NVGPs when low-level visual abilities were tested, such as the detection of a moving peripheral dot in a Goldman perimetry task (Buckley, Codina, Bhardwaj, & Pascalis, 2010) or the detection of a gabor-patch presented with different spatial frequencies in one of two possible intervals with fast changing displays (Li et al., 2009). These results then suggested an origin of the AVGPs related advantages at the level of sensory specific processes, namely, at the level of early stages of visual processing.

This latter proposal, though, has been seriously put into question by a more recent work, which ascribed the origin of this RTs improvement to faster perceptual-decision making in AVGPs compared to NVGPs (Green et al., 2010). Participants were tested in a standard coherent dot motion direction task (Palmer, Huk & Shadlen, 2005). By varying the levels of signal-to-noise ratio across trials, the authors could map the full chronometric and psychometric curves of participants' performance. Consistently with the literature, compared to NVGPs, AVGPs gave faster but equally accurate responses, especially for lower levels of visual motion coherence. Furthermore, to determine on which level of information processing this reaction time advantage relies on, the chronometric and psychometric curves were fitted into a Drift Diffusion Model (DDM; Palmer et al., 2005). This model has three free parameters: 1) the rate at which information is accumulated over time, i.e., integration rate; 2) the moment at which a decision is made and the system stops accumulating evidence, i.e., decision bound; 3) an additive amount of time, common to all tasks, reflecting non-decision processes such as motor planning and execution, i.e., non-decision time. Compared to NVGPs, AVGPs chronometric and psychometric curves fit the model with a higher integration rate (i.e., resulting on average 20% faster in accumulating evidence per unit of time compared to NVGPs), as well as lower decision-bound (i.e., AVGPs were faster in reaching a perceptual-decision). Instead, there was no difference between the two groups for what it concerns the third parameter of the model, non-decision time. Moreover, to better characterize their results, the authors fitted also the data in a neural model of decision-making processes (Beck, Ma, Kiani, Hanks, Churchland et al., 2008). This model treats decision-making as a probabilistic inference behavior: in any particular moment, an individual needs to compute a statistical probability aimed at taking the correct decision given the evidence accumulated over time until that particular moment. AVGPs performance was explained by changing one single parameter of this model, namely the strength of the connections between the neural layer providing the evidences available to the participant at that particular moment in time, and the neural layer integrating the evidences over time. This connection resulted enhanced in AVGPs compared to NVGPs. In other words, according to both models AVGPs were faster than NVGPs in accumulating evidence from the environment in order to disambiguate relevant information from noise, thus being able to reach faster than NVGPs a perceptual decision. Importantly, to strengthen their conclusion proposal, Green and colleagues (2010) also tested the generalization of this reaction time advantage to a different sensory modality (i.e., audition). They presented to participants (AVGPs; NVGPs) an auditory analog of the visual motion direction task. Participants were asked to recognize in which of the two ears a sound embedded in different levels of white noise was presented. In this auditory task Green and colleagues (2010) replicated the results obtained in the visual task, both behaviorally and in terms of models fitting. In addition, the authors trained also a group of NVGPs for 50 hours on either action video games or on control video games. Critically for determining the causality of these results, only the group trained with action video games showed a similar behavior to avid AVGPs. Given all these evidences the authors proposed this mechanism as the one underlying all improvements reported in AVGPs behaviors.

2.3.2.2 The present research

Nonetheless, before being able to accept the proposal of increased probabilistic inference in AVGPs compared to NVGPs as a general explanation for AVGPs-related improvements it is fundamental to test in greater detail the generalization properties of AVGPs related advantages. In the present study we focus on RTs, aiming at expanding the understanding of its generalization properties for what it concerns sensory modalities, features of the stimuli and different response-modes tested. The results by Green and colleagues (2010) reporting a generalization of the RTs advantage also to audition do not completely prove the generalization of this advantage across sensory modalities. Indeed, audition even though less trained than vision it is anyhow partly trained in action video games. While playing, vision and audition jointly carry distal information on the upcoming events. In other words, abrupt sounds are often associated with sudden visual events to which players have to promptly respond, thus potentially creating strong associations with motor responses. It could then be that Green and colleagues (2010) found an extension of the RTs advantage also to audition, because also the auditory modality undergoes a training regimen similar to vision. Thus, to really prove the generalization of RTs advantage across sensory modalities in AVGPs, a very poorly trained sensory modality should be tested. We propose it to be touch. Indeed, touch (i.e., vibro-tactile stimulations) is very little involved in action video games. If present, it carries only proximal information, namely, it is used as an occasional feedback signal delivered through the joystick or as a signal of general alert, thus never requiring any active motor response (e.g., a button press).

In addition, by now, RTs advantage in discrimination tasks in AVGPs compared to NVGPs has been reported only for spatial features of stimuli (see for a review Dye et al., 2009a). This is probably due to the fact that the major requirement while playing at action video games is to constantly explore and spatially monitor, a complex visual scene. Nonetheless, if the functional origin of this RTs advantage is indeed linked to faster perceptual-decision making (Green et al., 2010), we should expect the extension of this generalization also to less trained features of stimuli (e.g., discrimination of temporal features of stimuli, as duration).

Finally, the account proposed by Green and colleagues (2010) would suggest that the RTs advantage of AVGPs would hold independently of the response mode used. However, all previous studies mainly tested responses given manually, namely, similarly to how AVGPs delivered responses when playing (i.e., using a joystick; but see Green et al., 2012).

In the present work, we test all the aforementioned critical points by testing a group of AVGPs and a group of NVGPs in a simple detection task and in two discrimination tasks: a duration discrimination task (an ability not directly trained in AVGPs and never tested before in this population) and a direction of apparent motion discrimination task (a spatial task, more similar to previous discrimination tasks in which AVGPs have already been tested). Crucially, all tasks were tested for the tactile modality in addition to the visual modality. Finally, we also registered responses delivered through foot pedals (i.e., a stimulus-response mapping untrained in AVGPs).

If RTs advantage of AVGPs really relies on increased probabilistic inference in perceptual decision-making as proposed by Green and colleagues (2010), we expect a generalization of the advantage across all the conditions tested. The lack of a generalization to any of the aforementioned conditions would argued against an interpretation of AVGPs related advantages in terms of the explanation proposed by Green, Pouget and Bavelier (2010).

2.3.3 Experiment 1

The aim of this first experiment was to test in a simple detection task whether AVGPs simple RTs advantage would generalize across modalities, extending also to the poorly trained tactile modality, and across response modes, extending also to the untrained foot responses. In addition, we also manipulated stimulus positions to test whether it would modulate the RTs improvement observed in AVGPs. To this aim we matched the eccentricities of stimuli across modalities by testing for both sensory modalities stimuli positioned in low-acuity regions and in high-acuity regions. Indeed, the role of stimulus eccentricity has been rarely systematically investigated in AVGPs compared to NVGPs (but see Bavelier et al., 2011).

2.3.3.1 Methods

2.3.3.1.1 Participants

Eight action video game players (AVGPs; mean age = 23.3; SD = 2.3; 1 female) and twelve non-gamers (NVGPs; mean age = 28.6 years old, SD = 2.7; 6 females) took part in the experiment. Before starting the experiment, all participants filled-out a questionnaire on their video games habits in which they were asked to list up to 6 games they played mostly during the last year; to identify the game genre for each of these listed games; to specify how many times per month they would usually play each of the listed games and for how long each session typically lasted; whether or not they would receive any tactile or vibro-tactile stimulation during the game (i.e., through the joystick); the type of console they used.

AVGP and NVGP groups were created on the basis of their responses to this questionnaire: we considered AVGPs only those participants who reported to have played action video games for more than 5 hours per week in the last year (Li et al., 2010; mean number of hours played per week by our AVGP sample = 16.56; see Table 2.4 for weekly hours of action video games played by each participant); the action video games most commonly reported were Unreal Tournament, Call of Duty, Assassin's Creed, Medal of Honor, Gears of war; It should be considered that the AVGP group reported to have experienced in the last year a wider variety of video games genres, including sport and strategy games, even though to a less extent than action video games.

Instead, we recruited as NVGPs participants only those participants reporting to have not played at all to any video games in the last year.

All participants were recruited at the University of Trento and they all had normal or corrected-to normal vision. The Ethical Committee of the University of Trento approved the experiment. Each participant was given written instructions about the task, was asked to sign a consent form and received university credits or a payoff of 7 euros for participating in the study.

ID	Hours per week	Vibrotactile Stimulation
1	17,75	NO
2	5,25	YES
3	25	NO
4	21,75	YES
5	8,5	NO
6	31	YES
7	12	NO
8	11,25	NO

Table 2.4. Relevant information concerning our sample of AVGPs participants, namely the number of hours they played every week at action videogames and whether or not they received vibrotactile stimulation in the majority of the games they reported to play at.

2.3.3.1.2 Stimuli and Apparatus

Participants sat on a chair of adjustable height facing a table, with their hands hidden from view below an opaque glass (see Figure 2.5A). This was done in order to be able to fully isolate touch from vision: visual stimuli were seen as a projection on the opaque glass and tactile stimuli could be only felt but not seen. Participants placed their chin on an adjustable chin rest. Central fixation (i.e., a green LED) was positioned on a wooden cube on which participants were asked to rest their fingers. Visual (red LEDs) and vibro-tactile stimuli (bone vibrators, Oticon A; 1,5 cm X 2,5 cm) were positioned at the same locations in external space, namely on the index fingertips and forearms of both arms (see Figure 2.5A). These positions were chosen because, for both the sensory modalities tested, they represent high spatial-acuity (vision: 1° from fixation; touch: index and middle fingertips; i.e., central fields) and low spatial-acuity regions (vision: 32° from fixation; touch: forearm; i.e., peripheral fields), respectively. Our visual stimuli lasted either 60 or 100 ms and the tactile stimuli lasted either 5 or 25 ms. Throughout the experiment, participants wore headphones delivering white noise. The volume of white noise was carefully adjusted individually for each participant to cover any possible noise delivered by the vibro-tactile stimuli. An Input/Output box attached to a portable PC was used for stimulus presentation and response registration. The whole paradigm was programmed using MATLAB software with the Psychophysics Toolbox extensions (Brainard, 1997; Pelli, 1997).

2.3.3.1.3 Design and procedure

Participants performed a simple detection task, responding as fast as possible to target onset. Across blocks, the target was either visual or tactile. Each trial started with fixation onset. After a random interval lasting between 1000 and 1400 ms one stimulus appeared, unpredictably at any of the four possible positions (i.e., fingertip/center or forearm/periphery of either arms; see Figure 2.5A). Participants were instructed to keep central fixation throughout the experiment and to release as fast as possible a foot-pedal positioned under the heel of the right foot every time they saw (visual detection) or felt (tactile detection) a stimulus. If no response was provided within 2 seconds from the target offset, the next trial started automatically. Inter-trial interval lasted 1500 ms during which the fixation remained lit for 1000 ms and it was switched off for the remaining 500 ms.

The experiment comprised one visual and one tactile block of 100 trials each. Each block included 20% of catch-trials, in which no stimulus was presented.

All participants received written instructions. In addition, before starting the experiment a brief practice (two blocks, one visual, one tactile, 10 trials each) was presented to all the participants to ensure they familiarized with the task. The order of visual and tactile blocks was counterbalanced across participants.

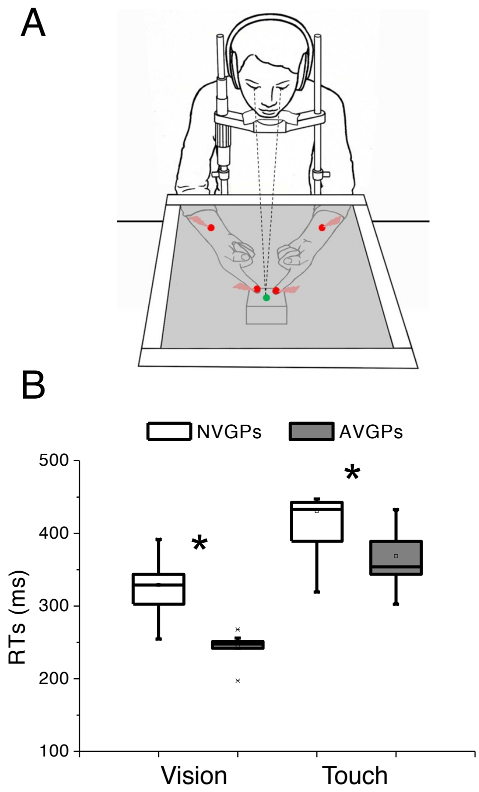

Figure 2.5. (A) Experimental set-up. **(B)** Results: AVGPs (grey box-plots) compared to NVGPs (white box plots) were faster to detect both visual and tactile targets.

2.3.3.2 Results

We excluded from the analyses reaction times (RTs) < 100 ms and RTs > 2000 ms. Importantly the number of anticipations (i.e., RTs < 100 ms) and false alarms (i.e., responses to catch trials) was always negligible and comparable across the two experimental groups (AVGPs: 0.4%; NVGPs: 0.1%).

Median RTs for each participant were entered into a mixed repeated-measure ANOVA with sensory modality (vision; touch) and target position (finger; forearm) as within-participants variables, and group (AVGP; NVGP) as between-participants variable. All post-hoc analyses were conducted using Tukey test. This analysis showed a main effect of sensory modality ($F(1,18) = 131.6$, $p < 0.0001$, $\eta_p^2 = 0.88$), caused by overall faster responses to visual (295 ms; SE=12.01) than to tactile stimuli (405.7 ms; SE=13.9; p=0.0002). Most importantly, also the main effect of group emerged ($F(1,18) = 15.8$, $p = 0.0009$, $\eta_p^2= 0.47$; see Figure 2.5B), showing overall faster responses in AVGPs (306.4 ms; SE=9.5) compared to NVGPs (379.7 ms; SE=13.5; p= 0.001). No other main effects or interactions were significant (all other F-values < 4.4).

As anticipated in the introduction, vibro-tactile stimulation if present in action video games is used as feedback or as a general alerting cue not requiring any active motor response from the player. However, to assure that our results on faster tactile RTs in AVGPs compared to NVGPs did not depend from some sort of training, even indirect, involving the tactile modality, we subdivided the AVGPs sample between AVGPs participants (N=3), which declared to receive tactile stimulation in the majority of the action videogames they reported to play at, and AVGPs participants (N=5), which declared not to receive tactile stimulation in the majority of the action videogames they reported to play at (see Table 2.4). On these data, we performed a t-test for independent groups with mean reaction times to tactile stimuli independently of stimulus position as dependent variable. This test revealed no significant difference between the two groups ($t(6)= 0.237$, $p= 0.8$).

2.3.3.3 Discussion

The present findings demonstrate that RTs advantage in simple detection repeatedly documented in AVGPs compared to NVGPs for visual stimuli extends also to tactile stimuli. This finding represents the strongest evidence of the generalization potentials of AVGP training regimen across sensory modalities, documenting for the first time its extension also to a poorly trained sensory modality (i.e., touch). Significantly, we did not observe any correlation between participants' reaction times in the tactile block and whether or not they declared to receive tactile stimulation while playing, thus excluding training effects related to this sensory modality in the emergence of the tactile RTs advantage reported for AVGPs.

In addition, this improvement occurs for all stimulus positions tested, thus excluding any role of stimulus eccentricity in this advantage, and with a comparable number of anticipation errors and false alarms between groups. Finally, the RTs advantage in AVGPs compared to NVGPs was present even if participants' responses were delivered through a foot pedal, an untrained response mode when playing (see Green et al., 2012, for a similar result reported for vocal responses in a task-switching test).

Taken all together, the present findings strongly corroborate the proposal by Green and colleagues (2010) of a faster rate of evidence accumulation to reach a perceptual decision as the most exhaustive explanation for AVGPs advantages.

2.3.4 Experiment 2

The second aim of the present study was to further investigate to what extent the RTs advantages reported for several visual discrimination tasks (Dye et al., 2009a) generalize also to different, less trained features of stimuli. Indeed, only discrimination abilities to spatial features have been tested so far (Dye et al., 2009a), which are also the most trained features while playing. We therefore tested a group of AVGPs and a group of NVGPs in two discrimination tasks, both in the visual and in the tactile modality, asking participants to deliver their responses through foot-pedals: a direction of apparent motion discrimination task (i.e., manipulating spatial features, in line with previous studies) and a duration discrimination task (i.e., manipulating temporal features of stimuli, never directly tested before, and overall less trained, if trained at all, in AVGPs playing environment). If AVGPs would show improved RTs for both sensory modalities and both tasks, they would both be further evidences in favor of the proposal by Green and colleagues (2010).

2.3.4.1 Methods

2.3.4.1.1 Participants

Eight action video game players (AVGPs; mean age = 23.0; SD = 2.7; 2 females) and eleven non-gamers (NVGPs; mean age = 25.4; SD =3.6; 6 females) took part in the experiment. Before starting the experiment, all participants filled-out the same questionnaire on their video games habits described for Experiment 1. Groups were created on the same basis described in the Participants section of Experiment 1 (mean number of hours played per week by AVGP sample of Experiment 2 = 16.5; see Table 2.5 for weekly hours of action video games played by each participant); the action video games most commonly reported were the same as in Experiment 1. Also in this case the AVGP group reported to have experienced in the last year a wider variety of video games genres, including sport and strategy games, even though to a less extent than action video games.

All participants were recruited at the University of Trento and they all had normal or corrected-to normal vision. The Ethical Committee of the University of Trento approved the experiment. Each participant was given written instructions about the task, was asked to sign a consent form and received university credits or a payoff of 7 euros for participating in the study.

ID	Hours per week	Vibrotactile Stimulation
1	5,25	YES
2	8,5	NO
3	31	YES
4	11,25	NO
5	17,67	--
6	7,75	YES
7	18,68	NO
8	32,5	NO

Table 4.5 Relevant information concerning our sample of AVGPs participants, namely the number of hours they played every week at action videogames and whether or not they received vibrotactile stimulation in the majority of the games they reported to play at.

2.3.4.1.2 Stimuli and Apparatus

The experimental setting was exactly the same as for Experiment 1. In the temporal task, also stimulus nature, stimulus positions and stimulus durations were exactly the same of Experiment 1(see Figure 2.6A), it was just the task of the participants that changed (see section below). In the spatial task, the stimuli were different such that they would generate an apparent motion perception. Visual stimuli were two LEDs lighting up one consecutive to the other and lasting 30 ms each. No Stimulus Onset Asinchrony (SOA) was present between them. Tactile stimuli consisted of two vibro-tactile stimulations lasting 25 ms each with 60 ms SOA between the two. We introduced a 60 ms SOA between the two tactile stimuli because we observed in the pilot study we conducted before running the actual experiment, that participants found extremely difficult to perform the spatial tactile task if the tactile stimuli were really consecutive to each other. We observed that introducing a 60 ms SOA ensured the feasibility of the task still maintaining it difficult enough in order to avoid ceiling effects. It is important to highlight that we felt safe in choosing this SOA because it has been demonstrated, even though only with visual and auditory information, that two stimuli presented with SOAs ranging from approximately 50 to 150 ms are typically reported as occurring simultaneously (e.g., Zampini, Guest, Shore & Spence, 2005). As in the other tasks, visual and tactile stimuli occurred at the exact same positions in external space. Central stimuli were positioned on the index and middle fingertips of both hands; peripheral stimuli were positioned on forearms of both arms, 2cm horizontally separated from each other (see Figure 2.6B).

Everything else was exactly the same as described for Experiment 1.

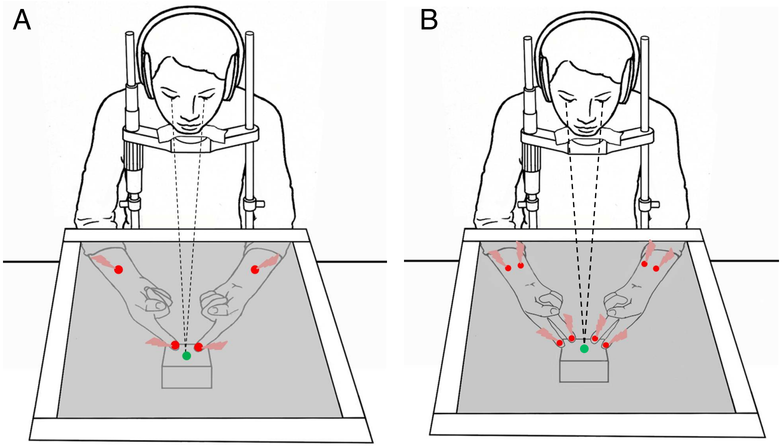

Figure 2.6. **(A)** Experimental setup for the temporal task. **(B)** Experimental setup for the spatial task.[2]

2.3.4.1.3 Design and Procedure

All participants performed both the temporal and the spatial discrimination tasks. Each task was performed both on visual and on tactile stimuli, which occurred in separate blocks. Each trial started with the fixation onset. After a random interval lasting between 1000 and 1400 ms one stimulus appeared unpredictably at any of the four possible positions (i.e., fingers –center- or forearms –periphery- of both arms). Participants had 2 seconds to deliver a response through two foot-pedals positioned under the tip of the toe and under the heel of the right foot. If within this time no response was given, the next trial started automatically. Inter-trial interval lasted 1500 ms during which the fixation was kept on for 1000 ms and then switched off for the remaining 500 ms.

Participants were instructed to keep central fixation throughout the experiment. For both discrimination types, the task in the visual and in the tactile modality was exactly the same the only thing that changed was the sensory modality in which the stimuli were delivered.

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[2] For the images of the experimental setups credits to: Paola Rigo and Tommaso Sega

In the temporal task, participants were asked to perform a duration discrimination task. They were instructed to discriminate in each trial whether the stimulus presented was short or long in duration by releasing as fast and as accurate as possible one of the two foot-pedals. Half of the participants released the pedal under the tip of the toe to report a short stimulus, and the pedal under the heel to report a long stimulus; the remaining participants adopted the opposite stimulus-response mapping.

In the spatial tasks, participants performed a direction of apparent motion discrimination. Specifically, they were asked to discriminate in each trial whether the visual or the tactile stimulus was moving inward or outward with respect to the median of the body. Responses were given by releasing as fast and as accurate as possible one of the two foot-pedals. Also in this task, half of the participants released the pedal under the tip of the toe to report an inward movement and the pedal under the heel to report an outward movement; the remaining participants adopted the opposite stimulus response mapping.

Overall, the experiment comprised 4 blocks: 2 spatial blocks and 2 temporal blocks. Each block comprised 96 trials. Within each task, one block was visual and one was tactile. Before starting to record responses, each participant underwent 4 blocks of practice, 2 spatial and 2 temporal. Within each task, participants were presented with a visual and with a tactile practice block (32 trials each). In addition, right before starting each experimental task, participants performed another brief practice block (16 trials). This was done to ensure they understood the task and they were able to disambiguate the different types of stimuli. Half of the participants did first the spatial, then the temporal discrimination task and the other half did the opposite. Within each task, the order of visual and tactile blocks was counterbalanced across participants.

2.3.4.2 Results

Three NVGP participants were excluded from the analyses. Two participants were excluded for a failure to properly acquire the data. One participant was excluded because RTs and accuracy fell more than 2 standard deviations away from the population mean. We therefore analyzed data from eight NVGPs and eight AVGPs. We conducted separated analyses for the two tasks as well as for the different measures we collected within each task: reaction times to correct trials (RTs) and percentage of correct responses.

2.3.4.2.1 Temporal Discrimination Task

Median response speed values for correct trials (RTs) and percentage of correct responses were entered into 2 separate repeated measure, mixed ANOVAs with sensory modality (vision; touch) and target position (finger; forearm) as within-participants variables and group (AVGPs; NVGPs) as between-participants variable. All post-hoc analyses were conducted using the Tukey test.

For what it concerns response speed, the analyses revealed a main effect of sensory modality ($F(1,14) = 12.54$, $p = 0.003$, $\eta_p^2 = 0.48$) caused by overall faster responses to visual (636 ms, SE=16.9) than to tactile stimuli (729 ms, SE =28.6; p=0.003). Most importantly, we also observed a main effect of group ($F(1,14) = 10.01$, $p = 0.007$, $\eta_p^2 = 0.42$), caused by overall faster responses in the AVGP (621 ms, SE= 27.5) compared to the NVGP group (744 ms, SE= 27.5; p=0.007), regardless of target position and sensory modality (see Figure 2.7A). No other main effects or interactions reached significant (all other F-values < 2.43). As for Experiment 1, we subdivided tha AVGPs sample between participants (N=3), which declared to receive tactile stimulation in the majority of the action videogames they reported to play at, participants (N=4), which declared not to receive tactile stimulation in the majority of the action videogames they reported to play at (see Table 2.5). On these data, we performed a t-test for independent groups with individual mean reaction times to tactile stimuli independently of stimulus eccentricity as dependent variable. This test revealed no significant difference between the two groups ($t(5)= 0.237$, $p= 0.8$).

For what it concerns accuracy, the analyses on the percentage of correct responses revealed only a main effect of target position ($F(1,14)= 9.85$, $p= 0.007$, $\eta_p^2 = 0.41$) given by overall higher accuracy when stimulation was delivered on the fingers (M= 79%, SE= 2%) compared to when it was delivered on the forearms (M= 72%, SE= 2%, p= 0.007). No effect related to the group factor or any other factors reached significance (all other F-values< 1.65).

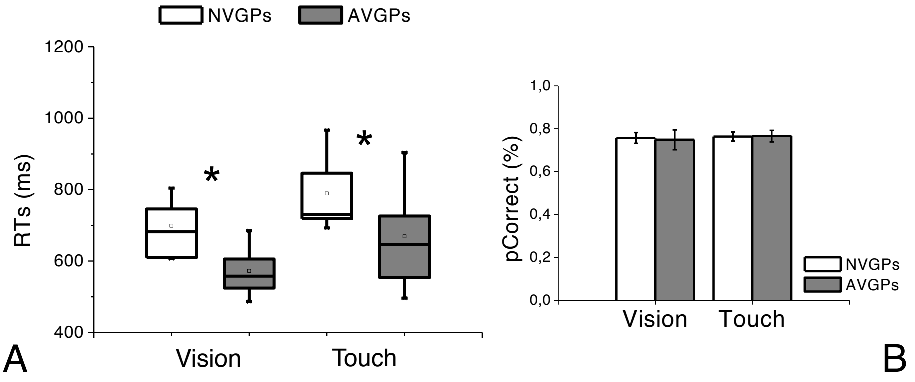


Figure 2.7. Results of the temporal task. **(A)** Reaction times for AVGPs (grey box-plots) and for NVGPs (white box-plots) for targets delivered through vision and through touch. AVGPs resulted overall faster than NVGPs for both sensory modalities. **(B)** Accuracy performance for AVGPs (grey bars) and NVGPs (white bars) for targets delivered through vision and through touch. No difference emerged between the two groups.

2.3.4.2.2 Spatial Discrimination Task

Also in this case, median response speed values to correct trials (RTs) and percentage of correct responses were entered into two separate repeated-measure, mixed ANOVAs with sensory modality (vision; touch) and target position (finger; forearm) as within-participants variables and group (AVGPs; NVGPs) as between-participants variable. All post-hoc analyses were conducted using Tukey test.

Strikingly, for what it concerns response speed, RTs analyses did not reveal any effect related to the group variable. We only observed a main effect of sensory modality (F(1,14) = 12.70, p = 0.003, $\eta_p^2 = 0.48$) due to faster responses for vision (714.52 ms; SE= 40.4) than for touch (874.13 ms; SE= 59.1; p=0.03; see Figure 2.8A), overall. No effect related to the group factor or any other main effects or interactions resulted significant (all other F-values < 3.15).

For what it concerns accuracy, the analyses revealed a main effect of sensory modality (F(1,14)= 12.12, p= 0.004, , $\eta_p^2 = 0.46$) caused by overall higher accuracy for vision (M= 85%, SE= 2%) than for touch (M= 71%, SE= 3%, p= 0.004). Also the two-way interaction between sensory modality and target position reached significance (F(1,14)= 13.24, p= 0.003, $\eta_p^2 = 0.47$). Post-hoc analyses revealed that participants were the most accurate for visual stimuli delivered on the fingers compared to all the other target positions (all ps<0.04). No effect related to the group variable, or any other main effects or interactions reached significance (all other F-values< 1.14).

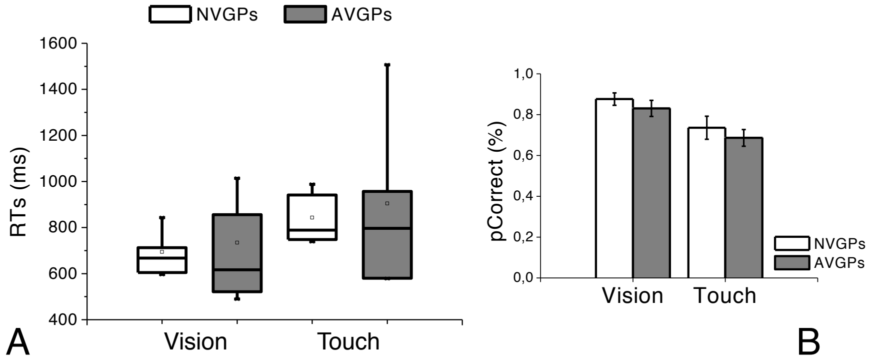


Figure 2.8. Results of the spatial task. **(A)** Reaction times for AVGPs (grey box-plots) and for NVGPs (white box-plots) for targets delivered through vision and through touch. No difference emerged between the two groups. **(B)** Accuracy performance for AVGPs (grey bars) and NVGPs (white bars) for targets delivered through vision and through touch. No difference emerged between the two groups.

2.3.4.3 Discussion

We reported a reaction times advantage in AVGPs compared to NVGPs in the temporal discrimination task where we tested discrimination abilities for stimulus duration, a feature of stimuli not directly trained in videogame playing. Moreover, as observed in Experiment 1, AVGPs reaction time advantage generalizes also to the poorly trained tactile modality and to an untrained response mode (i.e., foot pedal). In line with previous results obtained with AVGPs (e.g., Dye et al., 2009a), we did not observe any difference between the groups in terms of accuracy. These findings are overall in line with the proposal of improved probabilistic inference as a general explanation for AVGPs behavioral improvements compared to NVGPs (Green et al., 2010).

Strikingly, though we did not find any group difference in the apparent motion discrimination task, neither for vision nor touch. AVGPs and NVGPs in this task performed totally comparably not only for what it concerns accuracy, but also in terms of RTs. This result was completely unexpected since AVGPs improvement in reaction times to direction of motion has been previously documented for the visual as well as for the auditory modality (Green, et al., 2010). The difference between our motion task and the one used by Green and colleagues (2010) is that our stimuli were apparent moving stimuli. Some hints to unravel these results might come from a work by Donohue, Woldorff and Mitroff (2010). The authors presented to a group of AVGPs and to a group of NVGPs a simultaneity judgment task and a temporal order judgment task (TOJ) with auditory and visual stimuli. The interesting result for the present work is that in the simultaneity judgment task AVGPs showed better accuracy than NVGPs in judging simultaneous stimuli presentations and they had a point of subjective simultaneity (PSS; i.e., the SOA at which participants were the most likely to judge the auditory and visual stimuli as occurring simultaneously) that did not differ from 0. Furthermore, in the TOJ task, even though not significant, there was a trend for PSS (here the SOA at which participants were the least able to determine which stimulus came first) to be closer to veridical simultaneity in AVGPs compared to NVGPs. These results suggest a narrower window for the perception of simultaneity in AVGPs. Applying these latter results to our apparent motion paradigm, it could be that AVGPs did not perceive the two stimuli as a single moving stimulus in this task, but as two separated stimuli. If this was indeed the case, it is then as we were comparing performances of the two groups in two different tasks. Indeed this possibility is suggested also by the wider variance of RTs responses in AVGPs compared to NVGPs in this task (see Figure 4). To better understand these results, more research is needed to further characterize TOJ and simultaneity judgment's properties in AVGPs especially for short SOAs.

2.3.5 General Discussion

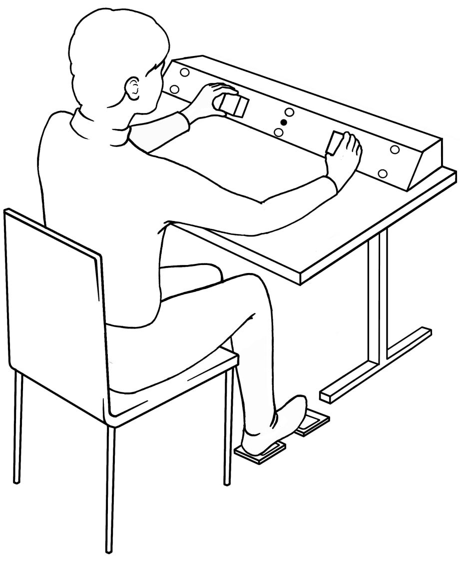
The goal of the present work was to further characterize the properties of the reaction times advantage repeatedly observed in AVGPs compared to NVGPs (Dye et al., 2009a) by testing more deeply its generalization properties. Our final aim was to push to the limits the proposal by Green and colleagues (2010) of improved probabilistic inference in perceptual decision-making as a general mechanism underlying AVGPs advantages, to test to what extent it will hold to several of its consequent predictions. To this aim we tested three crucial situations in which the proposal by Green and colleagues (2010) would predict a generalization of the RTs advantage in AVGPs: 1) generalization to untrained sensory modalities (i.e., touch); 2) generalization to untrained features of stimuli (i.e., temporal features of stimuli); 3) generalization to untrained response modes (i.e., responses delivered through a foot pedal). Our data clearly report a generalization of the AVGPs reaction times advantage to all these manipulations, ultimately corroborating the explanation proposed by Green and colleagues (2010).

We did not test for the causality of our results (i.e., we did not engage a group of NVGPs in a short training with action videogames and subsequently test them in our tasks). This is surely a limit of this study, but the causality of AVGP reaction time advantage has been assessed in several previous studies tapping discrimination abilities (Clark, Lanphear & Riddick, 1987; Green et al., 2010), while here we aimed at further characterizing its properties, given its causality for granted.

Overall, all our findings strengthen the proposal by Green and colleagues (2010) of an origin of AVGPs improvements at the level of perceptual decision-making, and they represent the most widespread evidence of the generalization potentials of AVGPs related advantages. However, the neural mechanisms underlying this impressive transfer of learning remain uncertain. The present findings, though, corroborate the idea that the neural circuits and the brain areas involved in evidence accumulation are not modality specific but instead they seem to be shared across sensory modalities.

CHAPTER 3:

Are the interactions between intact perceptual systems modified as a consequence of bilateral deafness?



Study 1: Multisensory flexibility within a perceptual system reorganized by crossmodal plasticity

3.1 Summary

The widespread intuition that sensory deprivation should enhance processing in the intact modalities has been primarily tested in unisensory contexts. Here we examined whether deafness modifies the interactions between vision and touch, and to what extent enhanced processing of visual stimuli – repeatedly documented in unisensory studies of deafness – dominates behavior also in a multisensory context in which vision is entirely task-irrelevant. Seventeen hearing and fifteen early-deaf adults performed two visuo-tactile tasks. In one task, participants responded to the elevation of a tactile stimulus while ignoring a concurrent visual stimulus (central or peripheral). The distractor was spatially congruent or incongruent with the target. The other task was reversed (i.e., respond to vision, ignore touch). Visuo-tactile interference emerged for all participants, revealing similar multisensory processing in the two groups. However, when touch was the target modality, deaf adults showed increased interference by visual distractors compared to hearing adults. Instead, comparable interference was observed in the two groups in the reversed task, when vision was the target modality. Furthermore, we also observed an effect of task-order: deaf participants showed increased interference in the task with visual distractors particularly when it was the second task they performed (i.e., when vision was initially probed as the target modality), while task-order did not modulate interference strength in the hearing population. Overall, these results reveal some persisting effects of visual dominance in the deaf population, albeit also highlighting a remarkable multisensory flexibility within a perceptual system reorganized by crossmodal plasticity.

3.2 Introduction

Our interactions with the external environment are inherently multisensory. In the last two decades, this notion has re-shaped the field of cognitive neuroscience leading to a wealth of studies addressing the functional and neural basis of multisensory processing (for reviews see Stein, 2012). Parallel to this literature, the field has also witnessed a growing interest for the behavioral and neural reorganizations that result from conditions of unisensory loss, such as blindness or deafness (for reviews see Frasnelli, Collignon, Voss & Lepore, 2011; Merabet & Pascual-Leone, 2010; Pavani & Röder, 2012; Voss & Zatorre, 2013). However, studies on blindness and deafness have typically examined changes occurring within the remaining sensory modalities by studying each sensory function separately. Although this approach proved highly informative, it largely overlooked possible changes in the interactions between reorganized sensory systems, ultimately limiting our understanding of the impact of unisensory loss on perceptual processing (but see Hötting & Röder, 2004; Karns et al., 2012; Van der Lubbe et al., 2010; see Occelli et al., 2013 for a review on blindness). In the present study we examined how two intact sensory modalities (vision and touch) interact with each other following early bilateral deafness.

Research on the consequences of bilateral deafness on brain and behavior, has extensively investigated the reorganization involving the visual modality (for reviews see Bavelier et al., 2006; Pavani & Bottari, 2011). Visual behavioral advantages in deaf compared to hearing adults, include faster reaction times in the detection of abrupt visual stimuli (e.g., Bottari et al., 2010; Loke & Song, 1991; Reynolds, 1993), faster re-orienting of covert spatial attention to the visual periphery (Chen et al., 2006) and improved discrimination abilities for certain visual features such as motion direction (Neville & Lawson, 1987b; Hauthel et al., 2013). In addition, more attentional resources devoted to the periphery of the visual field have been documented in early deaf adults compared to hearing controls (Chen et al., 2010; Proksch & Bavelier, 2002). Importantly, neuroscientific research has started to link these behavioral changes reported in deaf adults, to neuroanatomical modifications occurring within visual processing structures (the retina, Codina et al., 2011; primary and secondary visual cortices, Bottari et al., 2011), as well as in the deafferented auditory regions (in congenitally deaf cats: Lomber et al., 2010; Meredith et al., 2011; Wong et al., 2013). When these recent studies are considered together with other seminal evidence (e.g., Bavelier et al., 2000, 2001; Fine et al., 2005; Finney et al., 2001; Neville & Lawson, 1987b), a clear scenario of reorganized visual processing in deaf people emerges.

A parallel line of investigation has examined the impact of early deafness on tactile processing, albeit considerably less studies have been devoted to this intact sensory modality in comparison to vision. To date, behavioral advantages in tactile processing for deaf adults compared to hearing controls have been documented only for sensitivity to vibrotactile stimuli delivered on the fingers (Levänen and Hamdorf, 2001). Instead, studies addressing other tactile abilities in deaf people have failed to report any behavioral advantage, or even documented deficits compared to the hearing population. For instance, Bolognini and colleagues (2012) found comparable tactile spatial discrimination abilities in deaf and hearing people, and reported a deficit for tactile duration discrimination in deaf adults. Similarly, using a simultaneity judgment task, Heming & Brown (2005) found higher thresholds for tactile stimuli delivered on the fingers in deaf adults compared to hearing controls. In addition, as shown in Chapter 2, Study 1 of the present thesis, I found no response speed advantage in deaf adults compared to hearing controls, when detecting tactile stimuli delivered on the fingers or forearms. Finally, worse performance of deaf adults compared to hearing controls have been also reported in other tasks as grating orientation discrimination (Frenzel et al. 2012) and vibration detection thresholds (Frenzel et al. 2012; but see also Moallem et al. 2010). Studies on the neural correlates of tactile processing in early deafness reported a recruitment of the auditory cortices of deaf adults when perceiving tactile stimuli (e.g., Auer et al., 2007; Karns et al., 2012; Levanen et al., 1998). However, to date it remains unclear to what extent this auditory recruitment may relate to changes in behavioral performance.

Taken together unisensory approaches to the study of crossmodal changes in early bilateral deafness suggest an imbalance in the reorganization occurring in these two intact sensory modalities. Reorganization in vision has been repeatedly documented in both brain and behavior, and the observed behavioral advantages have been linked to neuroanatomical changes starting from the very early stages of visual processing. By contrast, reorganization occurring for the tactile modality appears considerably more uncertain, both at the behavioral and at the neuroanatomical level. In the present study we combined visual and tactile stimulation in the same task and examined to what extent the prominent reorganization occurring for vision might lead to visual dominance behavior when early deaf adults are exposed to a multisensory context.

To this aim we exploited a well-developed multisensory interference paradigm, the 'Cross-modal Congruency Task' (e.g., Driver & Spence, 1998; Spence, Pavani & Driver, 2000; 2004; see Spence, Pavani, Maravita & Holmes, 2008 for a review). In the classic version of this task participants are presented with simultaneous visual and tactile stimuli, delivered on the index finger or thumb of one of the two hands. Participants are instructed to respond to the elevation of the tactile target, ignoring the concomitant visual distractor as much as possible. The distractor is either spatially congruent with respect to the target position (e.g., tactile stimulus up; visual distractor up) or spatially incongruent with respect to the target (e.g., tactile stimulus up; visual distractor down). The cross-modal congruency effect (CCE) is measured as the difference in response times (or errors) between congruent and incongruent trials. Results robustly show that participants are slower (and sometimes less accurate) in incongruent compared to congruent trials and that CCE is maximized when visual and tactile stimuli are close in external space (Spence et al., 2008).

The crossmodal congruency effect has been explained within the theoretical framework of the modality appropriateness hypothesis (e.g., Spence, 2010; Welch & Warren, 1980), for which perception is dominated by the modality that provides the most reliable information for the task at hand. This theory has been modeled using maximum-likelihood estimation (MLE) approach applied to multisensory perception (Ernst & Banks, 2002). Such model suggests that sensory information is *weighted* according to the relative precision of the information conveyed by each sensory modality. The sensory modality that *weights* more in that particular context, will dominate behavior. Within this framework, the visuo-tactile interference phenomenon measured by the CCE, originates by the fact that touch is less precise than vision in conveying spatial information. As a consequence, the incoming visual input *weights* more than the tactile one, resulting in strong interference effects elicited by the task-irrelevant visual modality.

In the present study, we compared performance of bilateral deaf adults and hearing controls in the classic CCE task (i.e., ‘respond to touch/ignore vision’), precisely because the spatial nature of this paradigm is perfectly suited to uncover possible enhanced visual dominance in the deaf population. We predict that if the reorganized visual modality dominates multisensory spatial behavior in early deaf adults even more than already does for hearing individuals, larger CCE should emerge in deaf participants compared to hearing controls. Unlike typical CCE tasks, we did not present visual stimuli in the vicinity of the stimulated hands. Instead, we placed pairs of visual distractors at central or peripheral locations of the display. The rationale for this manipulation is related to the many studies indicating a specific reorganization of the visual periphery in people with bilateral deafness (Bavelier et al., 2000; 2001; Chen et al., 2010; Neville & Lawson, 1987b; Proksch & Bavelier, 2002). Therefore, we predict that visual interference effect in deaf adults might be even more prominent when visual distractors are presented in the periphery of the visual field.

In addition to this classic version of the CCE task, in separate blocks of trials we asked to participants to respond to the elevation of *visual* stimuli, ignoring tactile distractors. Spence and Walton (2004; 2005) have shown that this reversed procedure produce smaller CCE compared to when participants respond to touch and ignore vision, corroborating an interpretation of CCE in terms of the maximum likelihood estimation model: touch as an irrelevant distractor modality interferes less with performance because its incoming spatial information *weights* less than the visual one. By introducing this additional task we aimed to assess if any increased interference effect in the deaf group is specific to the reorganized visual modality, or instead emerges regardless of which sensory modality serves as distractor. If deaf adults are generally more prone to interference effects, larger CCE in deaf compared to hearing participants should emerge regardless of whether the distractor modality is vision (classic CCE) or touch (reversed CCE).

Finally, the use of two complementary interference tasks (i.e., ‘respond to touch/ignore vision’; vs. ‘respond to vision/ignore touch’) allowed us to examine whether visual dominance is modulated by the task-order. In other words, if visual information *weights* more in deaf adults than in hearing controls for conveying spatial information, deaf participants might find it particularly hard to inhibit visual interference when the ‘respond to touch/ignore vision’ task follows the completion of a previous task in which the visual modality was actually task-relevant (i.e., the ‘respond to vision/ignore touch’ task). This result would reveal that visual dominance in deaf adults is sensitive to contextual manipulations. If instead task-order affects equally the interference elicited by both sensory modalities (i.e., the sensory modality initially triggered as target, either vision or touch, is always more interfering once it becomes the distractor modality), it would suggest that any sensory dominance in deaf adults is sensitive to contextual manipulations, and it is not an effect specific for vision. Finally, if instead the task-order proves completely irrelevant, this would constitute strong evidence in favor of mandatory dominance relations between spared sensory modalities in deaf adults.

3.3 Methods

3.3.1 Participants

Thirteen adults with severe or profound bilateral deafness (mean age = 38.7; SD = 7.9) were recruited to participate in the study. Inclusion criteria were: deafness onset before 3 years of age; absence of any neurological complication; hearing loss > 61 dB in the better ear; no cochlear implant). No deaf participant was a native signer. Nonetheless, eleven deaf participants declared to be fluent in Italian Sign Language (LIS), while two deaf participants declared not to know LIS at all (see Table 3.1 for LIS age of acquisitions). Seventeen hearing adults of similar age (mean age = 34.3; SD = 6.5) also took part in the study. None of the hearing participants had experience with sign language.

All participants had normal or corrected-to normal vision. The Ethical Committee of the University of Trento approved the study and all participants signed an informed-consent form. Whenever needed a fluent signer explained consent procedures in Italian Sign Language (LIS). All participants received a payoff of 7 euros for their participation in the research.

Before starting the experiment all deaf participants completed a questionnaire aimed at collecting anamnestic information concerning their deafness characteristics and their linguistic background (see Table 3.1 for selected relevant information acquired through the questionnaire).

Deaf Participants	Age	Deafness Right Ear	Deafness Left Ear	Age of Diagnosis (years)	Mother	Father	Hearing Aid	AoA LIS (years)
1	34	Profound	Profound	3	Hearing	Hearing	No	19
2	43	Severe	Profound	18 months	Hearing	Hearing	1 Ear	17
3	23	Profound	Severe	2	Hearing	Hearing	Both Ears	--
4	47	Severe	Severe	Birth	Hearing	Hearing	1 Ear	30
5	35	Profound	Severe	2	Hearing	Hearing	1 Ear	28
6	45	Profound	Profound	8 months	Hearing	Hearing	1 Ear	8
7	45	Profound	Profound	11,5 months	Hearing	Hearing	Both Ears	4
8	37	Profound	Profound	1	Hearing	Hearing	Both Ears	18
9	43	Profound	Profound	2	Hearing	Hearing	Both Ears	18
10	26	Profound	Profound	2	Hearing	Hearing	Both Ears	--
11	35	Severe	Severe	2	Hearing	Hearing	Both Ears	18
12	42	Profound	Profound	Birth	Hearing	--	Both Ears	13
13	48	Profound	Severe	1,5	Hearing	Hearing	No	17

Table 3.1. Selected information about deaf participants collected through the questionnaire they all fill-out prior to the experiment. For the variables ‘Deafness Right Ear’ and ‘Deafness Left Ear’, ‘Profound’ means a loss ≥81 dB in that ear; ‘Severe’ means a loss ≥61 dB in that ear. The acronym ‘AoA LIS’ means Age of Acquisition of Italian Sign Language.

3.3.2 Experimental Tasks

All participants performed two experimental tasks, during a single experimental session. In one task (respond to touch/ignore vision) they were asked to respond as fast and as accurately as possible to the elevation of a tactile stimulus, delivered on the thumb or index finger of the left or right hand, while ignoring the elevation of a concomitant visual distractor also delivered near the thumb or index finger of one of the two hands. The other task was reversed (respond to vision/ignore touch): participants were asked to respond as fast and as accurately as possible to the elevation of the visual stimulus, while ignoring the elevation of the concomitant tactile distractor. Thus, stimuli and experimental procedures were exactly the same in the two tasks, with the only exception that target modality changed between tasks (touch or vision). Instructions were explained separately for each task, and when needed they were given in LIS by an experimenter fluent in sign language. The order of the two experimental tasks was counterbalanced among participants.

3.3.3 Stimuli and apparatus

The experimental apparatus was modeled on previous works on the crossmodal congruency task (e.g., Spence, Pavani & Driver, 2000). As shown in Figure 3.1, all experimental stimuli were arranged on a parallelepiped wooden structure (90 cm x 11 cm x 30 cm). The fixation point was a green Light Emitting Diode (LED) fixed at the center of the wooden structure (shown as a black circles in Figure 3.1). Six red LEDs served as visual stimuli (distractors in the ‘respond to touch/ignore vision’ task; targets in the ‘respond to vision/ignore touch’ task). Two red LEDs were positioned centrally, vertically aligned with central fixation, and attached 3.5 cm above and below the green LED. The remaining four red LEDs were positioned peripherally: two on the left side and two on the right side of the wooden structure (all red LEDs are shown as empty circles in Figure 3.1). Both peripheral pairs of LEDs were arranged vertically at a distance of 30 cm from the central LEDs. Two parallelepiped polyurethane sponges (7.5 cm x 4.5 cm x 6 cm) were attached to the wooden structure with Velcro hook and served as graspable supports for the tactile stimulators. Each sponge was positioned at mid-distance between the central and peripheral LEDs. Two vibrotactile stimulators (vibrators for Samsung mobile phones, with a flat circle surface of ø 1cm) were positioned on the top and on the bottom surface of each sponge, equidistant (15 cm) with respect to the central LED pair and the ipsilateral peripheral LED pair (see Figure 3.1). All visual and vibrotactile stimuli lasted 200 ms, and were clearly supra-threshold. Two response pedals were attached with Velcro hook on the floor, to allow response collection. Pedals were arranged in order to form an angle of 90° with the knee of the participant. One pedal was positioned under the right foot tip and the other was positioned under the right foot heel of participants.

Vibrators, LEDs and response pedals were all connected to the parallel port of the PC. The experiment was controlled using a custom built program, running under MATLAB with Psychtoolbox extensions (Brainard 1997; Pelli 1997).

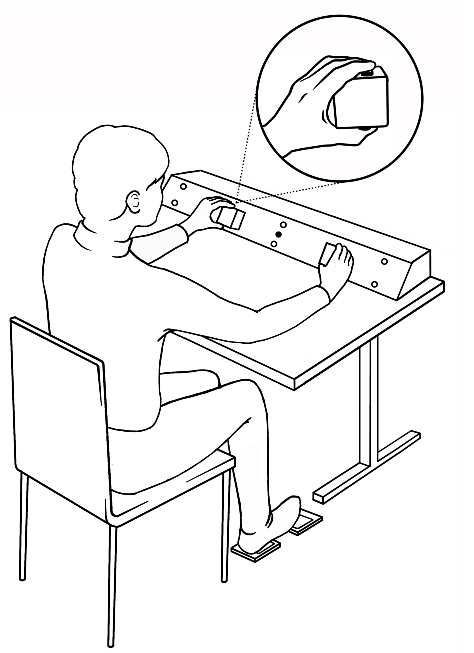


Figure 3.1. Experimental setup. The zoomed image shows the exact position of tactile stimuli.[3]

3.3.4 Experimental Procedure

Participants sat on a chair of adjustable height, in a dimly light room, with their eyes at a distance of approximately 60 cm from the central fixation point. They were asked to hold one parallelepiped polyurethane sponge in each hand and to gently press a pair of vibrotactile stimulators under the index finger and the thumb of each hand, maintaining this position over the whole experiment. In addition they were asked to keep central fixation and to press both response pedals throughout the experiment (see Figure 3.1).

Each trial started with the onset of the fixation LED (1000 ms duration). After a randomized time interval (range between 0 and 400 ms), two simultaneous stimuli, one tactile and one visual, were presented. The task was to determine as fast and as accurately as possible the elevation of the designed target stimulus (either visual or tactile, depending of the experimental task), ignoring the elevation of the distractor (either tactile or visual, depending of the experimental task). Responses were given by releasing one of the two pedals under the right foot. Specifically, participants were instructed to raise their toe to indicate a target stimulus in 'upper' locations (e.g., a tactile event on the index finger; or a visual event in the upper raw of LEDs) and to raise their

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[3] For the image of the experimental setup credits to: Paola Rigo and Tommaso Sega

heel to indicate a target stimulus in ‘lower’ locations (e.g., a tactile event on the thumb; or a visual event in the lower raw of LEDs). After giving the response participants pressed both pedals again to proceed to the next trial. If after 2000 ms no response was given, the next trial started automatically. Inter trial interval was set to 1000 ms, plus a randomized time interval between 0 and 400 ms.

Each task (i.e., ‘attend to touch/ignore vision’ or ‘attend to vision/ignore touch’) comprised two consecutive experimental blocks and started with 12 practice trials. Each block comprised 128 visuo-tactile trials. Regardless of the task, vibrotactile stimuli were delivered with equal probability at the four possible tactile locations (64 stimuli on the right sponge and 64 stimuli on the left sponge). Similarly, visual stimuli were delivered with equal probability at central (64 stimuli) or peripheral locations (32 left peripheral stimuli; 32 right peripheral stimuli). One half of all stimuli (either visual or tactile) were presented in the superior part of the wooden structure, and other half in the lower part. Finally, half of the visuo-tactile pairs were spatially congruent (e.g., tactile stimulus up, visual stimulus up) and half were spatially incongruent (e.g., tactile stimulus up, visual stimulus down). After each block participants were invited to take a break. In addition, they were allowed to pause the experiment in any moment, simply by releasing both pedals. The whole experimental session lasted approximately 40 minutes.

3.4 Results

For each participant we computed the median RTs for correct trials and the percentage of errors, as a function of experimental task and experimental conditions. For the analyses on reaction times (RTs), we excluded one hearing participant and two deaf participants due to too excessive mistakes (more than 50% of errors in at least two experimental conditions). Consequently, analyses on RTs were conducted on sixteen hearing participants and eleven deaf participants. Instead, we included all participants in the analyses on percentage of errors.

3.4.1 Respond to touch/ignore vision task

3.4.1.1 RTs

Median RTs for correct trials in each of the experimental conditions were entered into a mixed repeated-measure ANOVA with visual distractor position (Central; Peripheral on the Same Side as the tactile target; Peripheral on the Different Side with respect to the tactile target) and visuo-tactile spatial congruency (Congruent; Incongruent) as within-group factors, and group (Hearing; Deaf) as between-group factor. Post-hoc analyses were conducted using Newman-Keuls test. The rationale for analyzing separately peripheral visual distractors on the same vs. different side with respect to tactile targets is the well-documented modulation of visuo-tactile interference in the CCE task as a function of the distance between visual and tactile stimuli in external space (e.g., Spence et al., 2008).

This analysis revealed the expected main effect of visuo-tactile spatial congruency ($F(1, 25) = 54.82$, $p < 0.00001$, $\eta_p^2 = 0.69$) caused by overall faster responses to congruent ($M = 675.60$ ms, $SE = 26.68$) compared to incongruent trials in all participants ($M = 741.84$ ms, $SE = 25.78$; CCE = 66.24 ms; $p < 0.0001$). This main effect was better explained by the two-way significant interaction between visuo-tactile spatial congruency and visual distractor positions ($F(2,50) = 9.48$, $p = 0.0003$, $\eta_p^2 = 0.27$). As expected, central visual distractors provoked the largest interference in performance, particularly when compared to visual distractors positioned on the opposite side of space of the tactile targets, which provoked the smallest interference effect (all p-values < 0.04; see Table 2 for mean and SE; see Figure 3.2). No other main effect or interactions reached significance (all F-values < 2.40), in particular there was no interaction or main effect involving the group variable.

3.4.1.2 Percentage of errors

Percentage of errors for each participant and each experimental condition were entered into a similar mixed repeated-measure ANOVA. This analyses revealed only the expected main effect of visuo-tactile spatial congruency (F(1,28) = 8.47, p = 0.007, η_p^2 = 0.23) caused by overall more mistakes for incongruent (M = 10%, SE = 2%) compared to congruent trials (M = 5%, SE = 1%, p = 0.007). No effects related to the group variable or any other main effect or interaction reached significance (all F-values < 0.06).

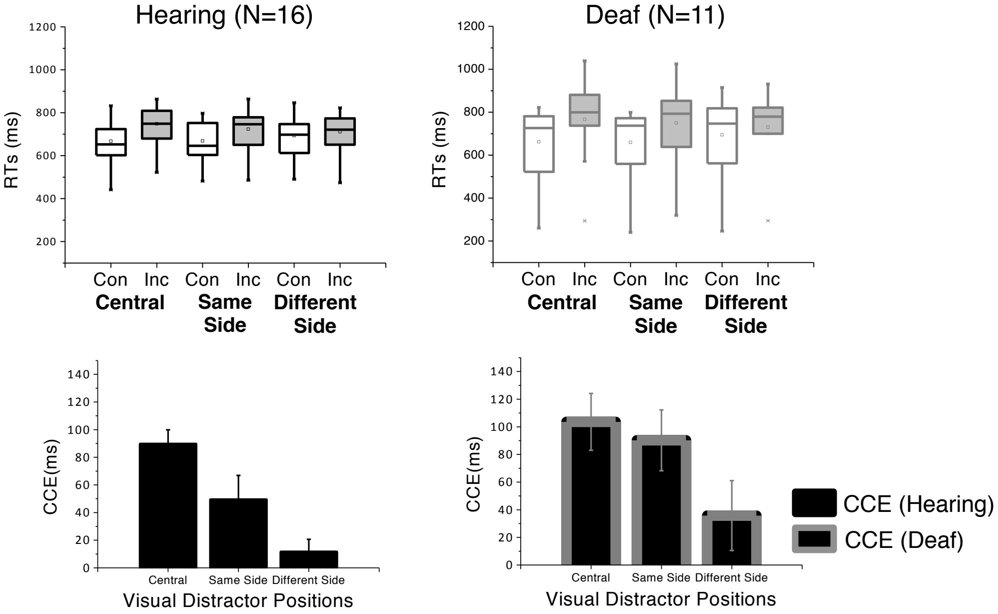


Figure 3.2. Results Respond to Touch/Ignore Vision. **Left top panel:** Reaction times of hearing participants for congruent (Con) and incongruent (Inc) trials, separately for each possible visual distractor position (Central; Same Side; Different Side). **Left bottom panel:** Cross-modal congruency effect (CCE) for visual distractor positions (i.e., CCE= RTs to congruent trials-RTs to incongruent trials). **Right top panel:** Reaction times of deaf participants for congruent (Con) and incongruent (Inc) trials, separately for each possible visual distractor position (Central; Same Side; Different Side). **Right bottom panel:** Cross-modal congruency effect (CCE) for visual distractor positions (i.e., CCE= RTs to congruent trials-RTs to incongruent trials). No difference emerged between the two groups.

3.4.1.3 Task-order effect

As described in the Methods section, half of the participants performed the ‘respond to touch/ignore vision’ task as the 1st task in the session, whereas the other half started the session using vision as the target modality (i.e., performed the ‘respond to touch/ignore vision’ task as the 2nd task in the session). To investigate whether task-order influenced performance differently in deaf and hearing participants, we entered CCE values (i.e., the difference in RTs between incongruent and congruent trials) calculated for each participant and each experimental condition into a mixed repeated-measure ANOVA with visual distractor positions (Central; Peripheral Same

Side; Peripheral Different Side) as within-participant factor, plus group (Deaf; Hearing) and task-order (Touch 1st; Touch 2nd) as between-participant factors.

This analysis replicated the main effect of visual distractor position (F(2,46) = 12.98, p = 0.00003, $\eta_p^2 = 0.36$) caused by a significant difference among the three visual distractor positions, with overall larger CCE for central visual distractors and overall smaller CCE for different side peripheral visual distractors (see mean and SE reported in Table 3.2; all p-values < 0.05). Most importantly, the analysis revealed a main effect of group (F(1,23) = 5.59, p = 0.03, $\eta_p^2 = 0.19$), a main effect of task-order (F(1,23) = 14.02, p = 0.001, $\eta_p^2 = 0.38$), and a significant two-way interaction between group and task-order (F(1,23) = 14.93, p = 0.0008, $\eta_p^2 = 0.39$). Post-hoc analyses revealed that the CCE elicited by visual distractors in deaf participants was significantly larger compared to hearing participants (p = 0.0007; see Figure 3.3A), when vision had just been treated as the target modality in a preceding 'respond to vision/ignore touch' task (i.e., Touch 2nd) compared to when participants started the session with the instruction that visual stimuli were entirely task irrelevant (Touch 1st). No other interactions were significant (all F-values < 0.52).

A similar mixed repeated-measure ANOVA using the CCE obtained for percent of errors for each participant as dependent variable revealed no significant main effect or interaction effect (all F-values < 3.20).

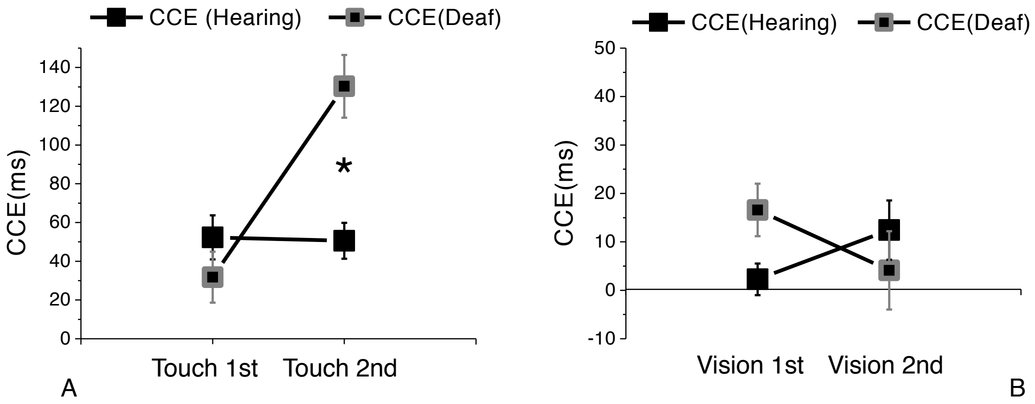


Figure 3.3. Task-order effects. **(A)** Respond to Touch/Ignore Vision. Deaf participants (gray) and hearing controls (black) did not differ in overall CCE when the task with tactile targets was the first task they performed (Touch 1st; Deaf: CCE= 49.61 ms, SE= 10.96; Hearing: CCE= 51.17, SE= 12.43). Instead, deaf showed a larger CCE compared to hearing controls when they first performed the task with visual targets and as the second task the one with tactile targets (Touch 2nd; Deaf: CCE= 130.29, SE= 14.71; Hearing: CCE= 31.73, SE= 13.42). **(B)** Respond to Vision/Ignore Touch. For this task there was no difference between groups related to the task-order.

	Visual stimulus position											
	Central				Peripheral Same Side				Peripheral Different Side			
	RT (ms)	SE	Errors (%)	SE	RT (ms)	SE	Errors (%)	SE	RT (ms)	SE	Errors (%)	SE
Respond to touch (ignore vision)												
Hearing												
Congruent	667,46	(25)	3%	(0,01)	668,46	(23)	3%	(0,01)	693,3	(23)	4%	(0,01)
Incongruent	748,18	(22)	11%	(0,04)	723,66	(26)	8%	(0,03)	711,4	(23)	6%	(0,02)
CCE	**89,8**	**(10)**	**8%**	**(0,03)**	**49,5**	**(17)**	**5%**	**(0,03)**	**11,6**	**(9)**	**1%**	**(0,02)**
Deaf												
Congruent	662,56	(52)	6%	(0,02)	659,86	(51)	8%	(0,03)	694,4	(58)	7%	(0,02)
Incongruent	766,16	(58)	13%	(0,05)	750,08	(57)	13%	(0,03)	730,2	(54)	11%	(0,05)
CCE	**103,6**	**(21)**	**7%**	**(0,04)**	**90,2**	**(22)**	**4%**	**(0,03)**	**35,8**	**(25)**	**4%**	**(0,05)**
Respond to vision (ignore touch)												
Hearing												
Congruent	470,34	(19)	1%	(0,004)	514,81	(23)	3%	(0,01)	532,7	(21)	4%	(0,01)
Incongruent	471,68	(21)	2%	(0,00)	536,43	(27)	4%	(0,01)	529,9	(20)	5%	(0,02)
CCE	**1,35**	**(6)**	**1%**	**(0,01)**	**21,6**	**(10)**	**1%**	**(0,02)**	**-2,8**	**(7)**	**0%**	**(0,02)**
Deaf												
Congruent	486,82	(41)	2%	(0,01)	518,31	(41)	4%	(0,01)	522,3	(40)	2%	(0,01)
Incongruent	487,32	(34)	3%	(0,01)	533,54	(43)	5%	(0,01)	535,9	(46)	5%	(0,01)
CCE	**0,49**	**(9)**	**2%**	**(0,01)**	**15,2**	**(11)**	**1%**	**(0,02)**	**13,6**	**(11)**	**2%**	**(0,02)**

Table 3.2. Reaction times (RTs) with standard errors (SE) for congruent and incongruent trials and percentage of errors with standard errors (SE) for congruent and incongruent trials as well as the resulting Cross-modal Congruency effect (CCE), which is the difference between RTs (or percentage of errors) to incongruent and congruent trials. These measures are reported for deaf and hearing participants depending on visual stimulus positions (i.e., Central; Same Side; Different Side) separately for each experimental task (Respond to touch/Ignore vision; Respond to vision/Ignore touch).

3.4.2 Respond to vision/ignore touch task

3.4.2.1 RTs

Median RTs for correct trials in each of the experimental conditions were entered into a mixed repeated-measure ANOVA with visual target positions (Central; Peripheral on the Same Side as the tactile distractor; Peripheral on the Different Side with respect to the tactile distractor) and visuo-tactile spatial congruency (Congruent; Incongruent) as within-participants factors, and group (Hearing; Deaf) as between-participants factor. Post-hoc analyses were conducted using Newman-Keuls test.

This analysis revealed the expected main effect of visuo-tactile spatial congruency ($F(1,25) = 7.75$, $p = 0.01$, $\eta_p^2 = 0.24$) given by overall faster responses to congruent ($M = 507.55$ ms, $SE = 20.66$) compared to incongruent trials ($M = 515.80$ ms, $SE = 21.32$; CCE = 8.25 ms; $p = 0.01$; see Figure 3.4). The main effect of visual target position also reached significance ($F(2,50) = 38.91$, $p < 0.00001$, $\eta_p^2 = 0.61$) caused by overall faster responses to central visual targets ($M = 479.04$, $SE = 19.60$) compared to the other two peripheral visual target positions (Same Side:

M = 525.77, SE = 22.62; Different Side: M = 530.21, SE = 21.50; all p-values < 0.0001; see Figure 3.4). No effects related to the group variable or any other main effect or interactions reached significance (all F-values < 1.76).

3.4.2.2 Percentage of errors

Percentage of errors for each participant and each experimental condition were entered into the same mixed repeated-measure ANOVA. In this case, when needed, Greenhouse-Geisser correction for non-sphericity was used. This analyses revealed a main effect of visual target position (F(1.55, 56) = 4.11, p = 0.22, , $\eta_p^2 = 0.13$) due to overall less mistakes when visual targets were central (M = 2%, SE = 0.004%) compared to when they were at peripheral locations (Same Side: M = 4%, SE = 1%; Different Side: M = 4%, SE = 1%; all p-values < 0.02). The main effect of visuo-tactile spatial congruency was only marginally significant (F(1,28) = 4.14, p = 0.052, $\eta_p^2 = 0.13$). No other main effect or interaction reached significance (all F-values < 1.21).

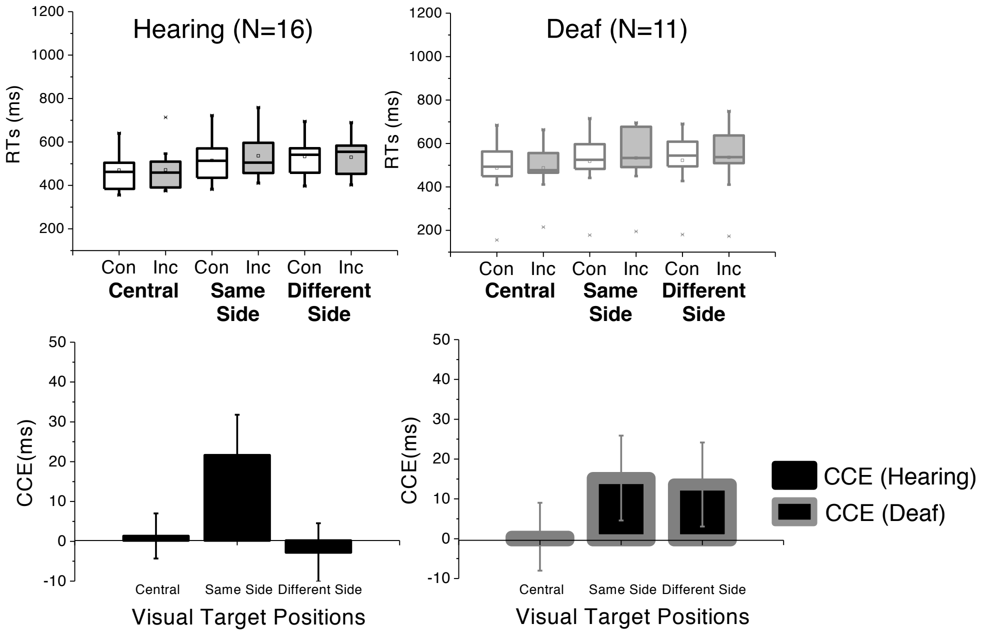


Figure 3.4 Results Respond to Vision/Ignore Touch. **Left top panel:** Reaction times of hearing participants for congruent (Con) and incongruent (Inc) trials, separately for each possible visual target position (Central; Same Side; Different Side). **Left bottom panel:** Cross-modal congruency effect (CCE) for tactile distractors depending on visual target positions (i.e., CCE= RTs to congruent trials-RTs to incongruent trials). **Right top panel:** Reaction times of deaf participants for congruent (Con) and incongruent (Inc) trials, separately for each possible visual target position (Central; Same Side; Different Side). **Right bottom panel:** Cross-modal congruency effect (CCE) for tactile distractors depending on visual target positions (i.e., CCE= RTs to congruent trials-RTs to incongruent trials). No difference emerged between the two groups.

3.4.2.3 Task-order effect

For comparison with results obtained in the 'respond to touch/ignore vision' task (described above), we computed CCE values for each participant separately for each visual target position and entered these values into a mixed repeated-measure ANOVA with visual target positions (Central; Peripheral Same Side; Peripheral Different Side) as within-participant factor, plus group (Deaf; Hearing) and task-order (Vision 1st; Vision 2nd) as between participant factors. This analysis did not result in any significant main effects or interactions (see Figure 3.3B; all F-values < 3.88).

A similar mixed repeated-measure ANOVA using the CCE obtained for percentage of errors for each participant as dependent variable revealed only a main effect of task-order ($F(1,26) = 5.08$, $p = 0.03$, $\eta_p^2 = 0.16$). This was caused by more mistakes when the task with visual targets and tactile distractors was the second task to be performed ($p = 0.04$). This effect, however, was not modulated by the group variable. No other main effect or interactions reached significance (all F-values < 1.24).

3.5 Discussion

In the present study we used multisensory interference as a tool to investigate multisensory interactions between vision and touch in early bilateral deafness. The literature investigating the effects of bilateral deafness on brain and behavior for unisensory functions suggests a disparity between vision and touch, such that vision seems to undergo a wider and also more behaviorally evident reorganization compared to touch. The ultimate aim of the present study was to unravel possible dominance properties of vision over touch by directly investigating to what extent documented visual advantages unavoidably dominate behaviors of deaf adults. In order to maximize possible visual dominance effects in the deaf population, we took advantage of CCE, which is a multisensory interference spatial task. Indeed according to the modality appropriateness hypothesis (e.g., Spence, 2010) and the maximum-likelihood estimation model (Ernst & Banks, 2002), vision is the dominant modality when it comes to spatial processing.

Contrary to a prediction of pervasive visual dominance in deaf adults, the results of the present study reveal that CCE in both experimental tasks (‘respond to touch/ignore vision’ and ‘respond to vision/ignore touch’) was comparable between deaf adults and hearing controls, independently of visual stimulus eccentricities. These novel results show a remarkable flexibility of the reorganized visual system of deaf people, which is particularly impressive if one thinks to the early stages of visual processing for which differences between deaf and hearing individuals have been documented (e.g., retinal level: Codina et al., 2011; primary and secondary visual cortices: Bottari et al., 2011). Nonetheless, for efficient everyday interactions with the external multisensory world, the ability to inhibit visual dominance when disruptive for the task it is highly adaptive, because it permits to deaf individuals to not be impaired in their performance compared to hearing controls.

However, our findings still reveal some aspects of visual dominance in the deaf population, albeit context-dependent. As a matter of fact, when deaf adults were initially presented with the task in which vision was the target modality (i.e., respond to vision, ignore touch), they showed, compared to hearing controls, larger CCE in the following task, in which vision became the distractor modality (i.e., respond to touch/ ignore vision). On the contrary, this task-order effect was not present for the tactile modality (i.e., when touch was initially probed as the target modality and then it became the distractor modality). These latter findings then, suggest that when the reorganized visual system is initially activated as the to-be-attended sensory modality, deaf participants find it particularly hard to inhibit its dominance over the tactile modality if they are subsequently required to ignore spatial visual information.

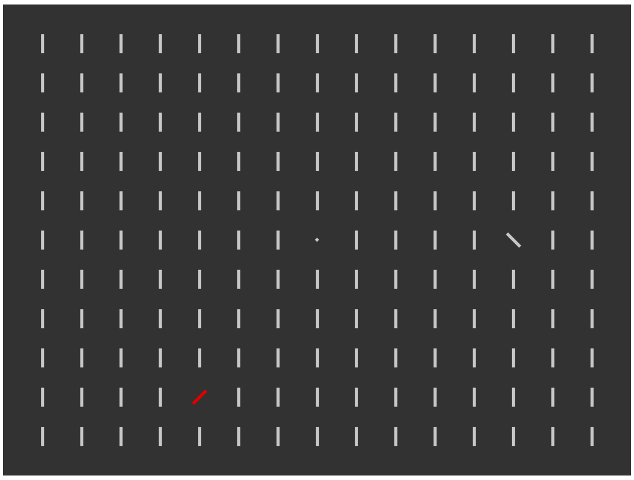
Importantly, there is one other recent study, which investigated visuo-tactile interactions following bilateral deafness albeit focusing on temporal processing, rather than spatial processing as here (Karns et al., 2012). Karns and colleagues (2012) recorded fMRI activity in a group of deaf adults and hearing controls while participants were presented with a somatosensory double-flash illusion, a phenomenon that is experienced when a single flash of light paired with two or more somatosensory stimuli, is perceived as multiple flashes of lights (e.g., Lange et al., 2011; Violentyev et al., 2005; see Shams et al., 2000; Mishra et al., 2007 for a double-flash illusion elicited by auditory stimuli). The task of the participants was to detect rare visual target events (20% of trials) consisting of two consecutive shorter stimuli compared to the repeatedly presented visual stimuli (80% of trials), while ignoring a concomitant tactile streams of events also composed of repetitive and rare stimulations. The idea is that given that this task taps on temporal precision, and touch has higher temporal precision than vision, for the maximum likelihood estimation model, tactile information would *weight* more than visual information, thus leading to the wrong detection of tactile rare and to-be-ignored events as targets, instead of detecting only the correct visual targets. Furthermore, as a control task, Karns and colleagues (2012) presented also the opposite condition to participants (i.e., detect rare tactile events, while ignoring the concomitant visual stream), in which, given the lower temporal precision of the visual modality, no illusion was predicted. Results showed that only the deaf group was susceptible to the somatosensory double-flash illusion. Indeed, only deaf participants incorrectly responded to deviant tactile stimulations, in the condition in which they were instead required to respond only to visual deviant stimulations and to ignore the concomitant tactile stream. Instead, as predicted, in the control condition in which participants had to attend to touch and ignore vision, both groups did not perceive the illusion. Moreover the strength of the somatosensory double-flash illusion in deaf participants positively correlated with the activation of the rostrolateral portion of the Heschl's gyrus. The authors concluded that these results suggest enhanced reliance on the tactile modality for temporal precision in deaf adults compared to hearing controls. Nonetheless, this proposal seems not to be confirmed by behavioral studies tapping on tactile temporal abilities, which reported impaired performance in the deaf population (Bolognini et al., 2012; Heming & Brown, 2005).

The different multisensory interference behaviors reported in the present study and in the study by Karns and colleagues (2012) might suggest that multisensory perception reorganizes differently depending on the set of abilities investigated. Indeed, both these results strengthen a growing corpus of evidence suggesting that as a consequence of early bilateral deafness, spatial abilities reorganized adaptively (at least in the visual modality, the documented brain reorganization entails benefit for actual behaviors; see Bottari et al., 2011; Codina et al., 2011), whereas temporal abilities might reorganize maladaptively (especially for the tactile modality, the documented brain reorganization might be disruptive for performance; e.g., Bolognini et al., 2012). Moreover, the results of the work by Karns and colleagues (2012) suggest that the context-dependent flexibility that we reported for visual dominance in deaf adults might be specific to the reorganized visual system, not extending to the tactile modality. We thus propose that this flexibility might depend from reinforced top-down modulatory feedback connections between frontal and visual regions in the deaf population compared to hearing controls. However, Karns and colleagues (2012) did not test for task-order effects in their work therefore the non-specificity of those context-dependent mechanisms cannot be totally excluded. A more systematic evaluation of multisensory interference tasks tapping different spatial and temporal abilities in deaf adults compared to hearing controls would certainly help in further unraveling these issues.

In addition, also the nature of the stimuli used should be further investigated. Indeed, faster reaction times to abrupt and static visual events in deaf adults compared to hearing controls have been linked to changes occurring in primary and secondary visual cortices (Bottari et al., 2011), while better detection of peripheral moving stimuli, for instance, have been linked to changes at the retinal level in the deaf population compared to hearing controls (Codina et al., 2011). It would be then very informative to test whether changing the nature of stimuli (e.g., static vs. moving) would alter the spatial dominance relations between vision and touch in the deaf population, ultimately further investigating the nature of the mechanisms underlying multisensory spatial interference effects.

CHAPTER 4:

Is the temporal dynamic of the interplay between automatic vs. voluntary components of visual attention modified by bilateral deafness?



Study 1: The impact of saliency on overt visual selection in early-deaf adults

4.1.1 Summary

Following bilateral deafness, visual attention extensively reorganizes to overcome the lack of audition. Results from covert attention studies suggest that plastic changes may prioritize saliency-driven attention capture in the deaf population. However, deaf individuals also need to maintain goal-directed behaviors. We investigated the time-course of overt visual selection in deaf adults, to assess when in time deaf individuals implement efficient goal-driven behaviors over saliency-driven search. Twenty early-deaf adults and twenty hearing controls performed an oculomotor additional singleton paradigm. For deaf participants language proficiency in sign language was assessed. Participants made a speeded saccadic eye movement to a unique orientation singleton. The target was presented among homogenous non-targets and one additional orientation singleton that was more, equally or less salient than the target. Results showed that in both groups fast initiated saccades were saliency-driven whereas later initiated saccades were more goal-driven. However, deaf participants resulted overall slower than hearing controls at initiating saccades and they were also less captured by saliency early in time. Importantly, a multinomial model applied to the data revealed comparable underlying mechanisms between the two groups. Finally, the delayed oculomotor behavior of deaf adults was not explained by any linguistic measure we have collected. These results then highlight the intriguing perspective that deafness-related effects might also involve subtle, very simple modifications (i.e., delayed saccadic latencies), which in turn influence the outcome of behaviors without modifying the underlying mechanisms. Notably, the present findings show that plastic changes as a consequence of bilateral deafness not always prioritize saliency-driven attention capture.

4.1.2 Introduction

Bilateral deaf adults are immersed in a silent world that they primarily explore through vision. In this atypical sensory condition, visual processing alone fulfills the two fundamental functions of attentional selection: (1) the automatic orientation to unexpected and salient visual events in the external environment (i.e., stimulus-driven selection), and (2) the ability to steer visual behaviors in a voluntary goal-driven manner to complete intentional tasks or actions. The majority of the studies focusing on visual attention properties in the deaf population have documented a reorganization occurring in both these fundamental attentional components, albeit typically examined separately from one another (see Dye & Bavelier, 2010; Pavani & Röder, 2012 for reviews). Recent works in the hearing population demonstrated the crucial role of time for disambiguating the relative contributions to performance of stimulus-driven and goal-driven processes (see see van Zoest et al., 2010 for review). These studies investigated the temporal dynamics of the interplay between these two mechanisms of visual selection by manipulating the relative saliency of stimuli presented in search displays, while registering participants' eye-movements. Results showed that fast initiated eye-movements following scene onset predominantly reveal automatic attentional capture to salient stimuli, independently of whether or not these salient elements are relevant for the task. Instead, it takes time for voluntary, intentional strategies to be efficiently implemented in behaviors (e.g., Donk & van Zoest, 2008; van Zoest et al., 2004; van Zoest & Donk, 2005; 2008). The aim of this study is to characterize the temporal dynamics of the interplay between these two components of visual selection in the deaf population, ultimately and innovatively aiming at investigating to what extent auditory deprivation influence their interaction. In addition, this type of paradigm also allows us to expand the understanding of *overt* attentional mechanisms in the deaf population, which until now has received very little consideration beyond research on sign language processing (e.g., Agrafiotis, Canagarajah, Bull, Kyle, Seers, & Dye, 2006; Bélanger, Slattery, Mayberry, & Rayner, 2012; Letourneau & Mitchell, 2011; Emorrey et al., 2009; Muir & Richardson, 2005; Watanabe et al., 2011; but see Bottari, Valsecchi & Pavani, 2011).

The majority of the studies that examined visual attention and visual selection in the deaf population have focused on covert attention mechanisms (see Bavelier et al., 2006 for review). Among those, research on the effects of stimulus-saliency in deaf adults has extensively investigated spatial orienting to abrupt visual onsets in this population (see Pavani & Bottari, 2012 for reviews), suggesting faster and more efficient automatic orienting in the deaf population, particularly for the periphery of the visual field. For instance, these works demonstrated that deaf adults are faster in responding to abrupt visual events compared to hearing controls (e.g., Bottari et al., 2010; 2011; Loke & Song, 1991). Moreover, several studies reported that deaf adults are also faster than hearing controls in reorienting visual attention to the peripheral portion of the visual field in response to abrupt onsets of static (Chen et al., 2006; Colmenero et al., 2004) as well as of moving visual stimuli (Bosworth & Dobkins, 2002). Given that abrupt onsets represent a salient stimulus-feature, these results might be interpreted as evidence for enhanced attentional resources in the deaf population devoted to the detection of saliency information in the surrounding environment, particularly in the visual periphery. A related finding corroborating and extending this idea comes from distractor compatibility tasks conducted in deaf adults compared to hearing controls (e.g., Chen et al., 2010; Proksch & Bavelier, 2002). These studies have demonstrated that deaf adults are more influenced than hearing participants by peripheral visual distractors incompatible in shape with a concurrent visual target (Bavelier et al., 2000; 2001; Chen et al., 2010; Proksch & Bavelier, 2002). This result has typically been explained as evidence for increased attentional resources devoted to peripheral visual field in the deaf population (Lavie, 1995; Lavie & Cox, 1997; Maylor & Lavie, 1998; Rees, Frith, & Lavie, 1997). However, it may also be interpreted as evidence suggesting increased attentional capture by salient information (i.e., the visual distractor) presented in the visual periphery in deaf adults compared to hearing controls.

A parallel line of work in the last decade has examined voluntary deployment of attention in visual selection processes in the deaf population. This research has also mainly tapped into covert attention mechanisms and focused primarily on the center of the visual field (e.g., Parasnis et al., 2003; Dye & Bavelier, 2010; Stivalet, Moreno, Richard, Barraud, & Raphel, 1998; but see Bottari, Turatto, Bonfioli, Abbadessa, Selmi, Beltrame & Pavani, 2008 for converging results with visual peripheral stimuli) or on the ability to divide visual attention between central and peripheral vision (Dye et al., 2009). For instance, Parasnis and colleagues (2003) tested a group of deaf adults and a group of hearing controls in a vigilance task on central stimuli (Test of variable attention, T.O.V.A.). This test provides a measure of both, the maintenance of focused attention over time and the impulsivity related to the response. Parasnis and colleagues (2003) reported reduced perceptual sensitivity in the attentional focus task as well as increased response-impulsivity in deaf participants compared to hearing controls. These results can be interpreted as evidence for a difficulty in the deaf population in implementing efficient voluntary strategies to select only the visual information relevant for the task. Thus, this finding suggests a reorganization in the visual selection components of deaf adults, which prioritizes stimulus-driven selection mechanisms. However, more recent studies on covert focused attention in deaf people did not reveal differences in performance with respect to hearing peers, when stimuli were presented in the center of the visual field (Dye & Bavelier, 2010). Dye and Bavelier (2010) presented to participants a central Rapid Serial Visual Presentation task (RSVP) and found comparable abilities between deaf and hearing participants in implementing and efficiently maintaining voluntary central visual behaviors. Likewise, Bottari et al. (2008) came to a similar conclusion by examining search efficiency in a change blindness task for perifoveal as well as for peripheral stimuli in deaf and hearing adults, again suggesting that voluntary attention deployment was not affected by early auditory deprivation.

Finally and most importantly in relation to the present work, there is one recent study that provides a first attempt to characterize the relative contribution of stimulus-driven and voluntary control in overt visual selection processes. Bottari, Valsecchi and Pavani (2011) compared deaf signers and hearing participants in a pro- and anti-saccade task. When making a pro-saccade participants are asked to make a direct eye-movement (saccade) to a target-stimulus appearing in the visual scene, whereas in an anti-saccade, the saccade has to be directed in the opposite direction with respect to the delivered visual stimulus. In the work by Bottari and colleagues (2011), participants were instructed in each trial whether they would have to produce a pro-saccade or an anti-saccade. Results showed more mistakes in the anti-saccade trials and faster eye-movements in repeated pro-saccade trials in deaf participants compared to hearing controls. Bottari and colleagues (2011) interpreted these findings as initial evidence for a prominent role of overt attention-capture mechanisms in the deaf population. In other words, this work suggested a dominance of stimulus-driven automatic eye-movements over voluntarily controlled eye movements.

Taken together, there is evidence in the aforementioned studies to suggest that visual selection in deaf adults may prioritize stimulus-driven exploration of the external environment over maintenance of goal-directed visual behaviors. The present study innovatively aims to characterize the temporal dynamic of the interplay between these two components of attentional selection to test whether or not this suggested prioritization of stimulus-driven exploration of the external environment does indeed reveal it-self when the developing over time of these two processes is taken into account. To this aim, we tested deaf adults and hearing controls in a visual target selection task, while registering participants' eye-movements. Previous studies on overt target selection conducted in the hearing population showed that saccadic latencies (i.e., the time between the appearance of the display and the initiation of a saccade) provide direct insight on the impact on performance of saliency-driven information over time. Specifically, as anticipated above, they provide a way to define *when* in time voluntary strategies are able to dominate visual selection behaviors (e.g., van Zoest et al., 2004; van Zoest & Donk, 2005; 2008; van Zoest et al., 2010). For instance, van Zoest and Donk (2005) instructed participants to search for a target (a tilted line) that was embedded in a homogeneous set of non-targets (i.e., vertical lines). In the search display one additional distractor was always presented (a line tilted in the opposite direction to the target). The saliency of target and distractor was manipulated in the color dimension: in one third of trials the *target* was colored and it was the most salient stimulus in the display; in one third of trials the *distractor* was colored and it was the most salient stimulus in the display; and in the remaining third of trials neither the target or the distractor were colored (no unique color). van Zoest and Donk

(2005) found that early initiated saccades were strongly driven by stimulus-saliency, such that they were directed to the most salient element in the display (i.e., the colored singleton), independently of whether it was the target or the distractor. Instead, later initiated saccades, starting about 250 ms following display appearance, could escape saliency automatic capture and could be directed in line with the task instruction, thus suggesting a goal-driven guidance (see also Donk & van Zoest, 2008; van Zoest & Donk, 2008).

Exploiting this experimental design, and based on the existing literature suggesting that deaf observers might be more prone to the automatic stimulus-driven influences from the external environment (see for instance Bottari et al., 2011), we predict that salient information should have greater impact on performance in deaf adults than in hearing controls. In other words, we should observe stronger saliency capture in the deaf group, possibly paired with overall faster saccadic latencies in deaf compared to hearing adults.

However, since the temporal interplay between stimulus-driven and goal-driven processes was never directly investigated before in the deaf population compared to hearing controls, based on our experimental design two other outcomes are possible: one alternative possibility is that precisely because deaf observers have to rely primarily on vision when exploring the environment, they might become more efficient in the deployment of voluntary overt selection strategies compared to hearing controls with the adaptive aim of avoiding continuous and potentially disruptive attentional capture by salient events in the scene. If this is the case, we should expect a decrease in the impact of stimulus-saliency, such that deaf compared to hearing observers would be less captured by saliency. This behavioral response might also be paired with overall slower saccadic latencies in deaf compared to hearing participants. A second alternative possibility is that the interplay between these two overt selection mechanisms does not change between deaf adults and hearing controls. In this case we should expect comparable temporal dynamics of saccadic latencies between the two groups.

4.1.3 Experiment

4.1.3.1 Methods

4.1.3.1.1 Participants

Twenty early bilateral deaf adults (hearing loss > 61 dB in the better ear; mean age = 28 years old; SD = 5; 11 females) were recruited by the ISTC-CNR personnel to participate in this research and were tested in ISTC-CNR laboratories. Twenty hearing controls (mean age = 22.9 years old; SD = 1.9; 11 females), which were students of the University of Trento, also took part in the study. All participants had normal or corrected-to normal vision. All participants signed an informed-consent form to participate in the study, which was approved by the Ethical Committee of the University of Trento. All received a payoff of 7 euros for their participation. Whenever needed a fluent signer explained consent procedures in Italian Sign Language (LIS).

Before starting the experiment all deaf participants completed a questionnaire aimed at collecting anamnestic information concerning their deafness characteristics and their linguistic background (see Table 4.1 for selected relevant information acquired through the questionnaire). In addition, deaf participants performed the Raven's Progressive Matrices test, to exclude from the experiment eventual participants with a Raven's score below pathological cut-off. Importantly, no deaf participant was excluded from the study based on this criterion (see Table 4.1 for Raven's Progressive Matrices scores).

Deaf Participants	Age	Degree of Deafness: Right ear	Degree of Deafness: Left ear	Age of Diagnosis (Years)	Mother:	Father:	Hearing Aid Usage	Raven's Progressive Matrices Scores
1	24	Severe	Severe	1	Hearing	Hearing	2 ears	-
2	43	Profound	Profound	2	Hearing	Hearing	No	128
3	23	Severe	Severe	Birth	Deaf	Deaf	No	110
4	27	Profound	Severe	Birth	Deaf	Deaf	1 ear	128
5	22	Severe	Severe	3	Deaf	Deaf	2 ears	120
6	23	Profound	Profound	Birth	Deaf	Deaf	No	120
7	34	Severe	Severe	2	Hearing	Hearing	2 ears	112
8	25	Profound	Profound	Birth	Deaf	Deaf	No	108
9	32	Severe	Severe	2	Hearing	Hearing	2 ears	127
10	29	Profound	Profound	2	Hearing	Hearing	2 ears	125
11	26	Profound	Profound	5/6 months	Hearing	Hearing	2 ears	127
12	32	Profound	Profound	Birth	Hearing	Hearing	No	110
13	24	Profound	Profound	6/8 months	Hearing	Hearing	2 ears	106
14	33	Profound	Profound	Birth	Hearing	Hearing	1 ear	118
15	25	Severe	Profound	3	Hearing	Hearing	2 ear	110
16	29	Profound	Severe	Birth	Deaf	Deaf	No	108
17	27	Profound	Profound	2	Hearing	Hearing	1 ear	127
18	25	Profound	Profound	3	Hearing	Hearing	2 ear	127
19	29	Profound	Profound	1	Hearing	Hearing	3 ear	128

Table 4.1. Selected anamnestic information about deaf participants (as collected through the questionnaire completed at the beginning of the experiment) and scores in the Raven's Progressive Matrices (all above pathological cut-off, which was an inclusion criteria for the study). For the variable 'Degree of Deafness', 'Profound' means a loss ≥81 dB in that ear, 'Severe' means a loss ≥61 dB in that ear. The questionnaire was developed by the ISTC-CNR personnel.

4.1.3.1.1.1 Assessment of sign language competence

Several studies have suggested that sign language can have specific influences on eye movement control (e.g., Bélanger et al., 2012; Emmorey et al., 2009; Watanabe et al., 2011). For example, during a sign comprehension task, face exploration's patterns were shown to differ between deaf native signers and hearing participants who were beginners in sign language (e.g., Emmorey et al., 2009). Hearing participants spent more time looking to the signing hands, whereas deaf native signers tended to keep their eyes more stable, looking predominantly at the eye-area of the signer. This different oculomotor behavior might impact on both overtly and covertly attention distribution and therefore we carefully controlled sign language experience in our participants.

However, it is still unknown whether the non-linguistic visual changes documented in deaf signers, such as, for instance, those documented in the work by Emmorey and colleagues (2009), depend from the early acquisition of a sign language (i.e., before the age of three; e.g., Mayberry & Lock, 2003) or they are the result of the massive visual training exerted by sign language, thus being linked more with sign language proficiency than with its age of acquisition.

To be able to disentangle this issue and test whether or not sign language exerts an effect on overt visual selection performance in deaf adults, we conducted a systematic assessment of deaf participants' linguistic proficiency in Italian Sign Language (LIS) through a series of linguistic tests developed ad-hoc by the ISTC-CNR group (see Participants section for description). This linguistic assessment was carried-out in a separate and dedicated experimental session. LIS assessment was conducted by a deaf native signer, with all instructions also provided in LIS. All deaf participants were presented with comprehension and sentence repetition tasks. In the comprehension task, deaf participants watched a five minutes video of a story in LIS, followed by 12 written forced-choice questions regarding the signed story they just saw. In the sentence repetition task, deaf participants were presented with fifteen sentences in LIS, of increasing length and difficulty. Sentences were delivered through a video, one at a time, and repeated if necessary. Deaf participants were instructed to repeat in signs exactly the same sentence. The entire task was registered by a video camera. It is important to highlight that these LIS tests are part of a larger battery developed by the ISTC-CNR group to assess the level of bilingualism in our deaf population. To this aim the battery also included tests aiming at assessing proficiency in Italian, which paired the LIS tasks. Specific results of this comprehensive linguistic assessment will be described in full details in future reports. In the present work LIS scores (see Table 4.2) were only used for correlational analyses with the performance of deaf participants in the overt visual selection paradigm.

Deaf Participants	AoA of LIS (Years)	LIS Comprehension	LIS Sentence Repetition
1	22	-	-
2	17	0,14	-0,53
3	Native	0,14	0,02
4	Native	0,14	-0,53
5	7	0,14	-0,71
6	Native	1,18	0,75
7	18	0,14	0,38
8	Native	1,69	1,29
9	6	-0,37	0,57
10	20	0,14	-1,25
11	26	-1,92	-0,53
12	2	-0,89	0,75
13	-	-1,92	-2,71
14	15	-1,41	0,38
15	20	0,14	0,02
16	Native	0,66	1,29
17	18	0,14	0,93
18	21	1,18	-0,71
19	24	0,66	0,57

Table 4.2. Age of acquisition of Italian Sign Language (AoA of LIS) and z-scores of deaf participants in the LIS tests. These values were used in correlation analyses with the individual mean saccadic latencies.

4.1.3.1.2 Experimental set-up

A Dell PC controlled the timing of the events and generated the stimuli. Eye movements were recorded through an Eyelink tracker (EyeLink 1000 Desktop Remote, SR Research) with 1000 Hz temporal resolution and 0.05° spatial resolution. The system uses an infrared video-based tracking technology to compute the pupil center and pupil size of both eyes. The monitor used to display stimuli was a 19-inch SVGA color monitor, with 1024 x 768 pixels resolution and a 75 Hz refresh rate. All subjects were tested in a dimly lit room with their head resting on a chinrest. The monitor was located at eye level, 60 cm from the chinrest.

In each trial, the display comprised 165 segments, arranged in a 15 x 11 matrix and covering a raster width of 30.7° x 25° of visual angle. Embedded in the display were one target and one distractor, each defined in the orientation dimension. Across the whole experiment, the target was tilted in a pre-specified direction (e.g., 45° to the right), whereas the distractor was tilted in the opposite direction with respect to the target (e.g., 45° to the left). All remaining segments were vertically oriented (non-targets). While vertical non-targets were always white, stimulus saliency of target and distractor was manipulated through color between experimental trials. In one third of trials, the target was colored red and the distractor was white (target-colored singleton), thus making the target the most salient singleton in the display. In another third of trials, the distractor was colored green and the target was white (distractor-colored singleton), thus making the distractor singleton the most salient stimulus in the display. In the remaining third of trials both target and distractor were white (no-color singleton), thus there was no unique color singleton in the display and no saliency manipulation. Targets and distractors could appear at six different locations. These six potential locations were placed at the vertex of an imaginary hexagon in such a way that, embedded in the matrix of non-targets, targets and distractors were always presented at equal eccentricity from fixation (12.4° of visual angle). When a target and a distractor were presented, the angular distance between the two elements was always 120° (see Figure 4.1). Segments had an approximate height of 0.9° of visual angle, an approximate width of 0.3° visual angle and were displayed on a dark gray background. Each stimulus matrix lasted for 1500 ms and was preceded by a fixation point presented for 1000 ms.

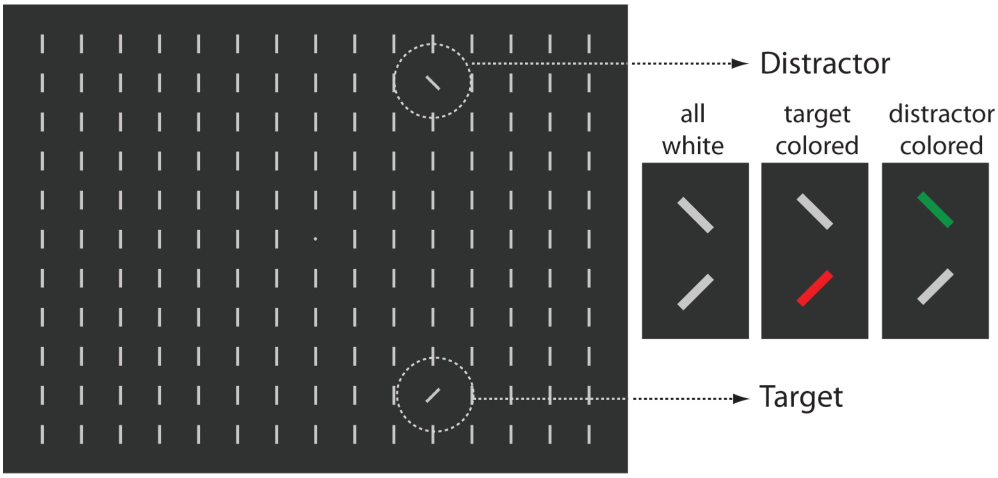


Figure 4.1. An example of a stimulus-display. Target and distractor were either both white, the target was colored red or the distractor was colored green.

4.1.3.1.3 Procedure and experimental design

Before the experiment participants were informed that they were about to take part in a visual search task. They were shown an example of the visual display (with no-colored singleton) printed on an A4 paper, and were instructed as to which tilted line was the target. Participants were instructed to maintain fixation until the search display appeared and then to move their eyes as fast as possible to the target, ignoring the distractor. They were also told that sometimes the target or the distractor would have been colored, however it was emphasized that this information would not be informative and therefore they were instructed to ignore color information. All participants received written instructions. Further instruction, when needed, were given in Italian or in LIS, depending on participants' preferences.

Each participant performed 24 practice trials, followed by 432 experimental trials divided into 16 blocks of 27 trials each. At the end of each block participants saw on the screen the average mean latency of their initial saccades and were free to take a break. The three conditions manipulating target and distractor saliency (no-colored singleton, target-colored singleton, distractor-colored singleton) were randomly intermixed within each block of trials. Target and distractor orientations (i.e., right-tilted target with a left-tilted distractor and vice versa) were counterbalanced among participants. Prior to the recording and every 4 blocks, participants viewed a calibration display consisting of nine points in a square array, which had to be fixated sequentially (standard calibration procedure of the Eye Link system).

4.1.3.2 Results

We included in the analyses only trials in which initial saccades ended 6° of visual angle around either the target or the distractor and excluded all trials in which initial saccade latencies were below 80 ms (anticipation errors; Hearing: 1% of trials; Deaf: 1% of trials) or above 600 ms (Hearing: 4 % of trials; Deaf: 6% of trials); trials that started when the eyes of the participants were more than 2.5° of visual angle away from fixation (Hearing: 4%; Deaf: 6%) as well as trials were the initial saccade missed either the location of the target or of the distractor (Hearing: 7%; Deaf: 9%). Direct between group t-tests revealed no significant differences between deaf and hearing participants for any of these criteria for excluding trials. Based on the cleaned data, one deaf participant and one hearing participant were discarded from further analyses because of too many excluded trials (i.e., more than one third of all trials). Thus subsequent analyses were conducted on nineteen hearing participants and nineteen deaf participants.

4.1.3.2.1 Temporal dynamics analyses

In order to address our main experimental question, namely, describing the temporal dynamics of selection performance in the deaf population, we subdivided the overall distribution of the initial saccade latencies of each participant among the three saliency-conditions and then we divided the latency distribution of each condition in quintiles. For each quintile of the latency distribution we calculated the proportion of correct saccades to the target. Then we averaged together the saccadic latencies as well as the proportion of correct saccades to the target of every participant in each quintile (for a similar procedure see: van Zoest et al., 2004; van Zoest & Donk, 2005; 2008).

4.1.3.2.1.1 Saccadic latency

On data organized this way, we conducted a mixed, repeated-measures ANOVA on mean saccadic latencies with saliency condition (colored-target; colored-distractor; no-colored singleton) and quintile (1-5) as within factors, and group (Hearing; Deaf) as between factor. When needed, we used Greenhouse-Geisser correction for non-sphericity. All post-hoc analyses have been conducted using the Newman-Keuls test. This analysis revealed a significant main effect of group ($F(1,36) = 7.64$, $p = 0.009$, $\eta_p^2 = 0.17$) caused by overall slower saccadic latencies in the deaf group ($M = 344.79$ ms; $SE = 17.53$) compared to the hearing group ($M = 276.24$ ms; $SE = 17.53$, $p = 0.009$; see Figure 4.2). Also, a significant main effect of quintile emerged ($F(1.5,53.1) = 224.69$, $p < 0.000001$, $\eta_p^2 = 0.86$) due to the expected significant increased in saccadic latencies across quintiles (all p-values < 0.00002). Finally, we observed a significant main effect of saliency condition ($F(1.7,61.1) = 6.81$, $p = 0.003$, $\eta_p^2 = 0.16$) due to overall slower saccadic latencies in the no-color saliency condition ($M = 315.32$ ms; $SE = 12.36$) compared to the other two conditions (colored-target: M = 309.57 ms; SE = 12.36; colored-distractor: M = 306.64 ms; SE = 12.39; all p-values < 0.02). No other factor was significant (all other F-values < 2.56).

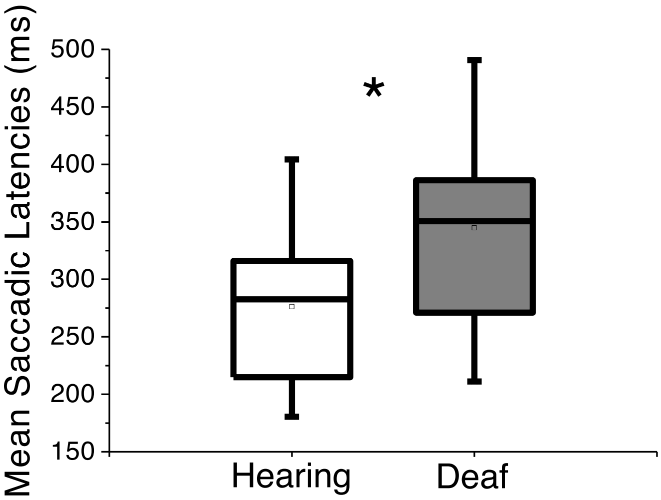


Figure4.2. Overall mean saccadic latencies of hearing participants (white box-plot) and deaf participants (gray box-plot). Deaf adults resulted significantly slower than hearing controls at initiating their saccades.

4.1.3.2.1.2 Proportion to the target

We also conducted a similar mixed, repeated-measures ANOVA using the percentage of correct saccades to the target as dependent variable. This analysis revealed significant main effects of saliency condition (F(2,72) = 5.26, p = 0.023, $\eta_p^2 = 0.13$) and of quintiles (F(4,144) = 23.60, $p < 0.00001$, $\eta_p^2 = 0.40$), which were subsidiary to the expected significant two-way interaction between saliency condition and quintiles (F(8,288) = 20.10, $p < 0.00001$, $\eta_p^2 = 0.36$). Most importantly, also the three-way interaction among group, saliency condition and quintiles reached significance (F(8,288) = 4.02, p = 0.004, $\eta_p^2 = 0.10$; see Figure 4.3). Post-hoc analyses revealed that in quintile 1, deaf participants were significantly more accurate in the colored-distractor trials (M = 41%, SE = 5%) compared to hearing controls (M = 27%, SE = 5%; p = 0.03). In addition, accuracy patterns differed within each of the two groups. Hearing participants in quintile 1 and 2 were the most accurate in colored-target trials (quintile 1: M = 81%, SE = 4%; quintile 2: M = 67%, SE = 5%) and the least accurate in colored-distractor trials (quintile 1: M = 27%, SE = 5%; quintile 2: M = 41%, SE = 6%; all p-values < 0.00004); in quintile 5 they were the most accurate in colored-distractor trials (M = 81%, SE = 4%) and the least accurate in colored-target trials (M = 64%, SE = 4%; p = 0.02). Deaf participants instead, differed in accuracy only in quintile 1 in which they were the most accurate in colored-target trials (M = 69%, SE = 4%) and the least accurate in colored-distractor trials (M = 41%, SE= 5%; p=0.00005). No other factor was significant (all other F-values < 0.98).

4.1.3.3 Discussion

Unexpectedly, when the crucial factor of time was taken into account for describing the temporal dynamic of the interplay between stimulus-driven and goal-driven selection processes in deaf adults compared to hearing controls, a clear difference between the two groups emerged, albeit opposite to our initial predictions. In particular when we took into account saccadic latencies, results indicated that deaf adults were overall slower at initiating their saccades compared to hearing controls. Moreover, when we analyzed the crucial measure of accuracy performance, results indicated that in the first quintile deaf participants were less captured by the irrelevant salient distractors compared to hearing controls.

These results, then, seem to suggest that contrary to our expectations deaf adults might prioritize goal-driven exploration of the external environment over stimulus-driven selection.

Given the repeatedly documented crucial role of saccadic latencies to the relative contribution of saliency-driven and goal-driven components to oculomotor behavior (e.g., van Zoest et al., 2004; van Zoest & Donk, 2005; 2008; van Zoest et al., 2010), one possibility to account for these results is that the differences we reported for the time-course of accuracy performance between deaf adults and hearing controls might be biased by the slow-down in response latency that we observed. In other words, deaf participants appeared less susceptible to saliency capture because they were able to slow-down their saccades to a larger extent than hearing controls. Note that this interpretation highlight a beautifully simple mechanism to achieve control, namely delayed saccadic latencies.

However, we cannot exclude based on these analyses that these results arise also as a consequence of different underlying stimulus-driven and goal-driven processes between deaf adults and hearing controls. With the aim of unraveling this issue, we developed a model allowing us to separately estimate the contribution of these two components on overt selection behavior of both deaf and hearing participants, while taking into account the individual response latencies (see for a similar approach: Dombrowe, Donk, Wright, Olivers & Humphreys, 2012).

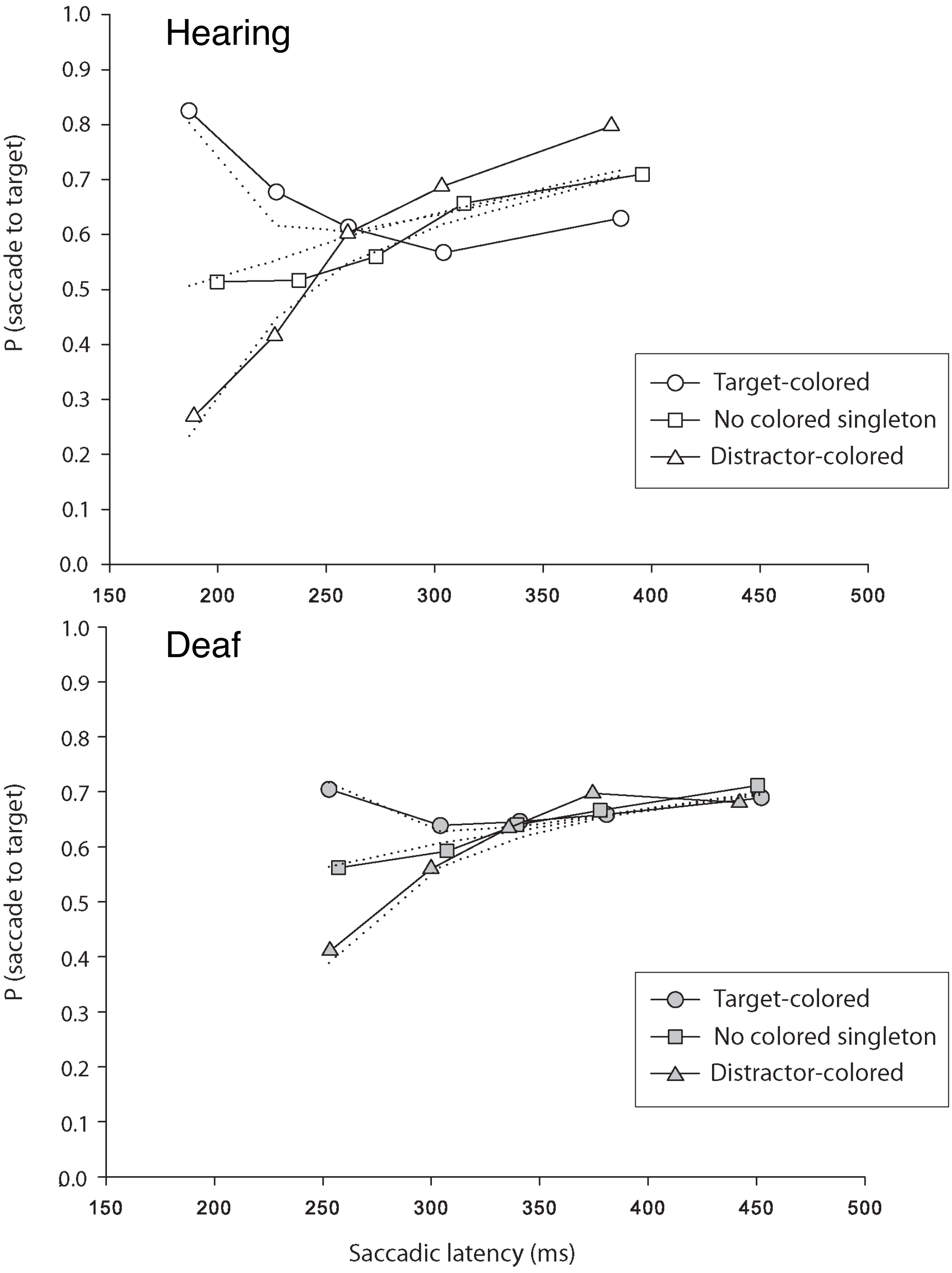


Figure 4.3. The proportion of saccades correctly directed to the target as a function of saccade latency. There were 3 saliency conditions: target-colored; no-colored singleton; distractor-colored. **Top panel:** Speed-accuracy function for hearing participants together with the fit of the model (dashed lines). **Bottom panel:** Speed-accuracy function for deaf participants together with the fit of the model (dashed lines).

4.1.4 Data modeling

The model we adopted is based on two main assumptions. The first assumption is that the binary decision to move the eyes towards either a target or a distractor (in an otherwise homogeneous visual field) is driven by the presence of two concurrent biases: a goal-driven bias favoring the selection of the target over the distractor, and a saliency-driven bias favoring the selection of the more salient singleton over the less salient one. The second assumption is that the contribution of goal-driven processes increases with time whereas the contribution of saliency-driven processes decreases with time (e.g., Jonides, 1981; Muller & Findlay, 1988; Nakayama & Mackeben, 1989; Weichselgartner & Sperling, 1987).

4.1.4.1 Methods: Model parameters

Within the model, the probability that the visual system is subjected to a goal-driven bias is assumed to be a function that gradually increases over time since the presentation of a display, and it equals $G(t)$, which is given by:

(1) $G(t) = 1 - e^{-r_G(t - t_{0G})}$ for $t > t_{0G}$; $G(t) = 0$ for $t \leq t_{0G}$

with t representing the time since the presentation of a display, r_G indicating the rate of the function, and t_{0G} representing the moment in time since the presentation of the display at which the function starts to increase. The function ranges between 0 and 1 with 0 indicating that the system is not subjected to any goal-driven bias and 1 indicating the presence of a full bias towards the target. When two simultaneously presented singletons differ in relative salience (with one being more distinct from its direct surrounding than the other), selection behavior may also be affected by a saliency-driven bias. The probability that the system is biased towards the most salient element in a display on the basis of stimulus-driven processes is assumed to be a decreasing function of time since the presentation of a display and it equals $S(t)$, which is given by:

(2) $S(t) = e^{-r_S(t - t_{0S})}$ for $t > t_{0S}$; $S(t) = 1$ for $t \leq t_{0S}$

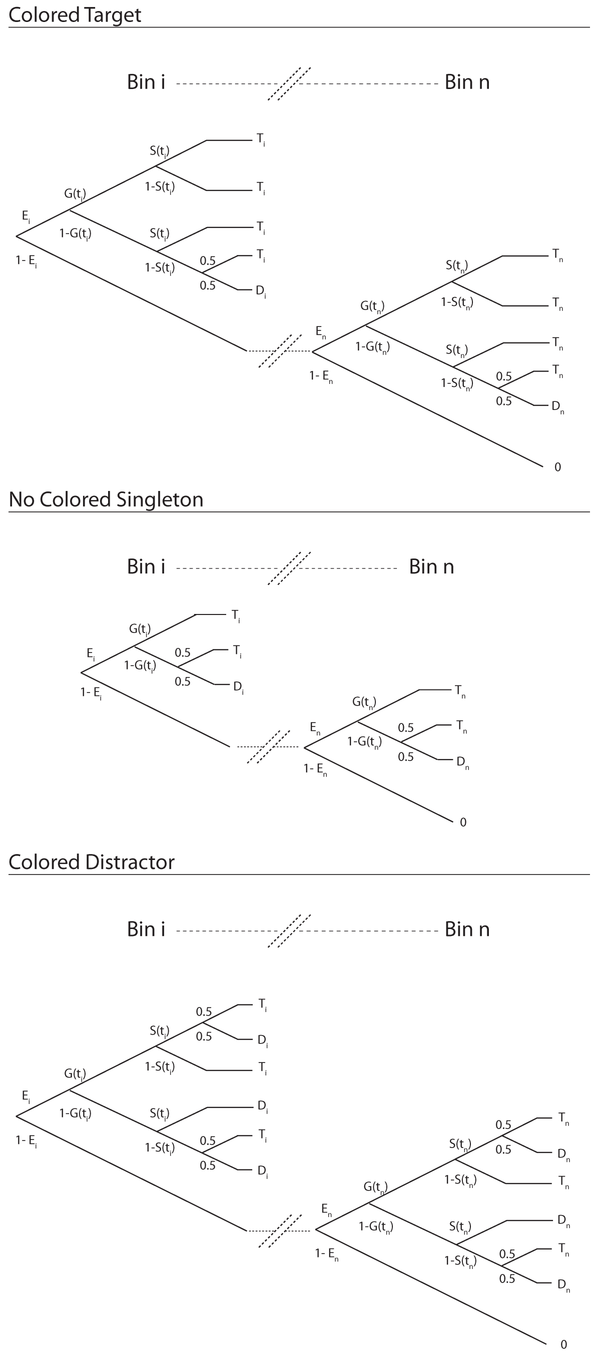
with t representing the time since the presentation of a display, r_S reflecting the rate of the function, and t_{0S} indicating the moment in time since the presentation of the display at which the function starts to decrease. The function ranges from 1 to 0, with 1 indicating that the system's bias towards the most salient element is maximal and 0 indicating that the system's bias is minimal.

Within the model it is assumed that the time-course of oculomotor selection is a function of *G(t)* and *S(t)*. Even though, these functions cannot be directly observed, it is possible to estimate the parameters of these functions (i.e., r_G, t_{0G}, r_S, and t_{0S}) separately per condition (colored-target, colored-distractor, no-colored singleton) and participant on the basis of the individual saccadic latencies and response frequencies obtained as a function of quintile, using the tree diagrams presented in Figure 4.4 (Batchelder & Riefer, 1999).

In particular, the tree models presented in Figure 4.4 outline how the probability of making a saccade (yes: E_i; no: 1-E_i), the probability of a goal-driven bias (*G(t)*) and the probability of a stimulus-driven bias (*S(t)*) lead to specific responses (either an eye movement towards the target or an eye movement towards the distractor) in the five quintiles (bins) of the saccadic latency distributions, separately for each of the three different conditions. Consider, for instance, the tree corresponding to the Colored-Distractor Condition (Figure 4.4). The probability that an eye movement is made during the first Bin (E_1) equals 0.2. If an eye movement is made, an observer may or may not have a goal-driven bias towards the target and may or may not have a saliency-driven bias towards the distractor. If an observer does not have a goal-driven bias towards the target in the first bin (i.e., 1-$G(t_1)$), but does have a saliency-driven bias towards the distractor in the first bin (i.e., $S(t_1)$), the resulting response in Bin *1* will be an eye movement towards the most salient singleton, the distractor. Similarly, if an observer neither has a goal-driven bias nor a salience-driven bias, the resulting eye-movement will be equally likely to be directed towards the target and the distractor, with 0.5 probability.

The overall probability on a particular response in a particular Bin *i* equals the sum of the paths leading to that response in Bin *i*. For instance, the probability to correctly saccade towards the target in the first bin $p(T_1)$ of the Colored-Distractor Condition is given by:

$$p(T_1) = (E_1*G(t_1)*S(t_1)*0.5) + (E_1*G(t_1)*(1-S(t_1)))+(E_1*(1-G(t_1))*(1-S(t_1))*0.5)$$



Colored Target

No Colored Singleton

Colored Distractor

Figure 4.4. Tree diagrams depicting how $G(t_i)$ and $S(t_i)$ determine the occurrence of the different responses separately per condition. $G(t_i)$ corresponds to the probability that the system is biased towards the target at time t_i which equals the average saccadic latency of the corresponding Bin i of the response latency distribution; $S(t_i)$ corresponds to the probability that the system is biased towards the most salient singleton at time t_i which equals the average saccadic latency of the corresponding Bin i of the response latency distribution; E_i corresponds to the probability that an eye movement is made in Bin i;[4] T_i represents an eye movement towards the target in Bin i; D_i represents an eye movement towards the distractor in Bin i.

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[4] By definition E_i equals .2 for the first bin, .25 for the second bin, .33 for the third bin, .50 for the fourth bin, and 1 for the final (fifth) bin

4.1.4.2 Results: Model fitting

On the basis of the tree models presented in Figure 4.4 and the observed numbers of target saccades and distractor saccades in the different quintiles of the saccadic latency distributions, we estimated *G(t)* and *S(t)* separately per condition and participant. For each participant, there were 3 conditions (Colored-Target, No-colored Singleton, and Colored-Distractor), 5 quintiles (1 to 5), and 2 possible response categories (Target saccade and Distractor saccade), resulting in 3 x 5 x 2 = 30 cells in each individual data matrix. The tree models corresponding to the three conditions (Colored-Target, No-colored Singleton, and Colored-Distractor) were fitted to these individual data sets consisting of the frequencies of responses observed in the 30 cells of the data matrix with their concomitant saccadic latencies, corresponding to the average saccadic latencies per quintile in each condition.

Two models were fitted to the data: an unconstrained and a contrained one. In the unconstrained model fits, r_G, t_{0G}, r_S, and t_{0S} were separately estimated for each condition, resulting in 10 free parameters per participant, i.e., r_G, t_{0G}, r_S, and t_{0S} in the Colored-Target condition, r_G and t_{0G} in the No-Colored Singleton condition, and r_S, and t_{0S} r_G, t_{0G}, r_S in the Colored-Distractor condition. In the constrained model fits, r_G, t_{0G}, r_S, and t_{0S} were assumed to be equal across conditions (i.e., r_G and t_{0G} in the Colored-Target condition = r_G and t_{0G} in the No-Colored Singleton condition = r_G and t_{0G} in the Colored-Distractor condition, and r_S and t_{0S} in the Colored-Target condition = r_S and t_{0S} in the Colored-Distractor condition) resulting in 4 free parameters per participant.

We used Maximum Likelihood Estimation (MLE), with the constraint that all parameter values were larger than 0. The maximum likelihood estimates are those parameter that maximize ln(*L*) which is given by:

$$(3)\quad \ln(L) = \sum_j f_j * \ln(p_j)$$

with f_j referring to the observed response frequency in cell *j* of the data matrix and p_j to the probability of the response according to the model. ln(*L*) was maximized using the Solver function in Excel.

To compare the goodness of fit of the constrained relative to the unconstrained model, we used the Bayesian Information Criterion (BIC) statistic (Schwarz, 1978), which is given by $-2\ \ln(L) + v\ \ln(N)$, in which v equals the number of free parameters and N equals the number of valid trials. The best model is the model associated with the smallest BIC value. Table 4.3 depicts the BIC values obtained for the alternative models, with smallest BIC values underlined. The results depicted in Table 4.3 show that the constrained model results in the best fit for all except one participant (see also Figure 4.5).

Hearing Participants	Total Trials	BIC Unconstrained Model	BIC Constrained Model	**Deaf Participants**	Total Trials	BIC Unconstrained Model	BIC Constrained Model
1	385	1772,53	1736,03	1	403	1881,39	1866,26
2	412	1797,28	1847,33	2	343	1579,61	1543,83
3	425	1891,67	1874,81	3	423	1907,79	1875,75
4	425	1993,54	1973,23	4	155	682,86	663,62
5	362	1683,30	1647,90	5	382	1724,40	1703,99
6	400	1818,05	1802,33	6	407	1894,19	1861,31
7	401	1853,00	1826,58	7	420	1951,05	1909,85
8	391	1773,52	1745,38	8	332	1401,91	1367,44
9	401	1801,96	1781,81	9	367	1716,13	1665,13
10	382	1769,84	1743,74	10	365	1633,25	1605,69
11	419	1850,74	1821,40	11	395	1854,36	1818,49
12	394	1791,44	1744,68	12	370	1734,51	1702,95
13	368	1546,21	1519,07	13	339	1445,37	1428,07
14	389	1815,34	1785,13	14	399	1627,61	1593,79
15	298	1287,89	1257,57	15	378	1731,22	1706,10
16	392	1779,82	1744,28	16	344	1582,48	1555,74
17	403	1794,21	1772,78	17	406	1832,79	1808,15
18	412	1905,57	1870,18	18	366	1706,01	1672,55
19	395	1640,94	1616,06	19	298	1406,55	1372,39

Table 4.3. Individual BIC values for the unconstrained model and the constrained model fits together with the number of valid trials (underlined values correspond to the smallest values).

Subsequent analyses on the individually estimated parameters derived from the constrained model fits showed that the groups did not differ in r_G ($t(36) = 1{,}17$, $p > 0.05$), t_{0G} ($t(36) < 1$), r_S ($t(36) < 1$), and t_{0S} ($t(36) < 1$). To dissociate the relative contributions of saliency-driven and goal-driven processes to selection we also calculated the areas under the estimated curves, separately for the S(t) and G(t) curves, within the interval between 0 and 500 ms. The size of the areas under the estimated curves was also comparable between groups: area under S(t) (t(36) < 1), area under G(t) (t(36) = 1.32, p > 0.05).[5]

Figure 4.3 shows the observed proportions correct, separately per condition and bin of the saccadic latency distributions, together with the proportions as predicted on the basis of the best fitting constrained models on the averaged data patterns obtained in each group. The constrained model shows a very good fit of the data (see Figure 4.5), which is also evident from the values of $\chi^{2,}$ which equals to 4.43 for the hearing group and 0.34 for the deaf group (critical value of χ^2 = 25.00 with df = 15 and α = 0.05).

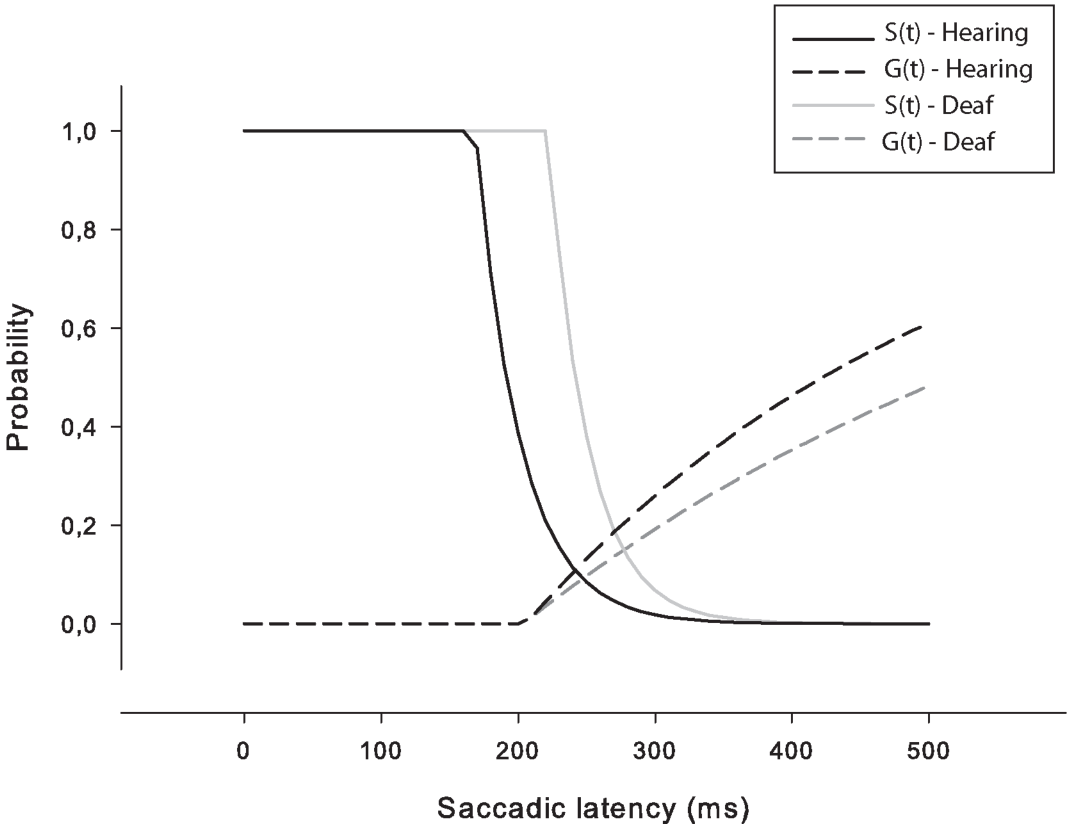

Figure 4.5. Best fitting S(t) and G(t) functions for hearing participants (black) and for deaf participants (gray).

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[5] The same analyses were also conducted on the individually estimated parameters derived from the unconstrained model fits. Neither these analyses resulted in any significant difference between groups nor in any significant interaction involving the group variable.

4.1.4.3 Discussion of modeling results

First of all, the present findings corroborate previous results suggesting that visual selection is guided by two dissociable components: a fast rising and slowly decaying stimulus-driven process and a gradually increasing goal-driven process (e.g., Dombrowe et al., 2012; Jonides, 1981; Muller & Findlay, 1988; Nakayama & Mackeben, 1989; Weichselgartner & Sperling, 1987). Furthermore, the results of the model fitting on our dataset clearly show that the temporal development of the underlying goal-driven and stimulus-driven processes are entirely comparable between deaf adults and hearing controls.

This latter result then, supports an interpretation of the different oculomotor behaviors we reported between deaf and hearing participants as dependent from the modification of a remarkably simple – yet highly efficient – behavior, namely, the slow-down of saccadic latencies. In other words, deaf adults and hearing controls share exactly the same temporal interplay between stimulus-driven and goal-driven selection processes. However, deaf adults were able to slow-down their saccadic latencies, and this slow-down permitted them to enter the search function at a later step compared to hearing controls.

4.1.5 Further analyses

4.1.5.1 What could explain the slower saccadic latencies of deaf participants?

To further investigate the origin of the overall slow-down of saccadic latencies we observed in deaf participants, we conducted a series of Analyses of Covariance (ANCOVAs) with the mean saccadic latencies of each deaf participant as dependent variable, and either the age of acquisition of LIS, the score obtained in LIS comprehension test, or the score obtained in LIS sentence repetition test as covariates (see Table 4.2). However, none of these covariates predicted saccadic latencies of deaf participants (all F-values< 1.62).

In addition, we also conducted an ANCOVA on the same dependent variable with scores obtained in the Raven test as a covariate (see Table 4.1). Also this covariate did not reliably predict saccadic latencies of deaf participants ($p= 0.12$).

Finally, we wanted to exclude a role of age at the moment of testing as a covariate to predict the saccadic latencies outcome. Therefore we conducted an ANCOVA with the mean saccadic latencies of all participants as dependent variable, age at the moment of testing as covariate, and group (Deaf; Hearing) as between-group factor. This analysis revealed only a slightly significant main effect of group ($F(1,35)= 3.76$, $p= 0.06$, $\eta_p^2= 0.10$). Instead, the effect of age as covariate was not significant ($p= 0.56$).

4.1.5.2 Disengaging attention from distractor

Finally, we wanted to assess whether deaf participants were quicker than hearing controls at disengaging attention from the distractor when the eyes were first incorrectly directed to this element (see for instance Chen et al., 2006; Colmenero et al., 2004 for results on covert attention mechanisms suggesting faster re-direction of peripheral visual attention in deaf adults compared to hearing controls). To this aim we conducted a mixed, repeated-measures ANOVA on the fixation-duration of the first saccade on the distractor, when the second saccade was correctly directed to the target, with saliency condition (colored-target; colored-distractor; no-colored singleton) as within factor and group as between factor (Hearing; Deaf). This analysis revealed no significant main effect or interactions (all F-values < 1.93).

4.1.6 General Discussion

In the present study we tested a group of deaf adults and a group of hearing controls in an overt target-selection task with the innovative aim of characterizing the temporal dynamic of the interplay between stimulus-driven and goal-driven processes in the deaf population, ultimately aiming at investigating to what extent auditory deprivation influences their interaction. Indeed, previous studies using the same task in the hearing population have robustly shown that early initiated saccades are predominantly driven by stimulus-saliency whereas later initiated saccades are primarily goal-directed (van Zoest et al., 2004; van Zoest & Donk, 2005; 2008).

The analyses on oculomotor behaviors of deaf adults and hearing controls when the crucial factor of time was taken into account are in overall agreement with these previous findings. Crucially, however, two important differences emerged between the two groups. First, deaf adults proved overall slower than hearing controls at initiating their first saccadic responses; second, the fastest saccades of deaf participants were captured by saliency to a lesser extent compared to the fastest saccades of hearing controls. To directly investigate whether the latter finding reflected a different temporal interplay between the underlying saliency-driven and goal-driven mechanisms in the two populations, we fitted our data with a multinomial model (see Dombrowe et al., 2012 for a similar approach). This model estimates the individual functions describing saliency-driven and goal-driven response biases based on response frequencies and saccadic latencies in each quintile for each of the three saliency manipulations (i.e., colored-target; colored-distractor; no-colored singleton), separately for each group. In particular our aim was to disambiguate whether or not the decreased saliency capture we reported for the fastest saccades of deaf participants was explained by the presence of a lower stimulus-driven bias in deaf compared to hearing adults. The model clearly showed that this was not the case and revealed, instead, that the temporal dynamic of the interplay between stimulus-driven and goal-driven processes was comparable between the two populations. These results strongly suggest that the reduced saliency capture in deaf participants was the result of the delayed oculomotor behavior observed in this population, rather than the consequence of reorganized search mechanisms. In other words, the fact that deaf people postponed their responses to a larger extent than hearing controls, led to an oculomotor behavior less driven by saliency information. This is most remarkable if one considers that the task was a speeded one. This result then implies that although deaf participants proved faster than hearing peers in a number of behavioural tasks (e.g., simple detection: Bottari et al., 2010; Loke & Song, 1991; discrimination of visual motion direction: Neville & Lawson, 1987b; Hauthal et al., 2013; visual temporal order judgment: Nava et al., 2008) and even fell into speed accuracy trade-offs (see **Chapter 2, Study 2** of the present thesis), faster response release is not an unavoidable behavior in the deaf population. Indeed these results suggest that deaf adults are perfectly capable of refraining their responses under the circumstances in which such a behavior could entail benefits for performance. Importantly, we also showed that this slow-down of saccadic latencies in the deaf population was not explained by any of the linguistic measures we collected or by any other measures we had available (i.e., Raven Progressive Matrices scores; age of participants).

However, these results leave open two possible interpretations: the first one is that this deleyed oculomotor behavior of deaf participants compared to hearing controls is the result of a motivational strategy deaf adults adopt to perform well in the task. A second possibility is that this delayed oculomotor behavior is the result of an adaptive outcome of deafness-related plasticity aiming at avoiding potentially disruptive capture by salient stimuli in the environment. Even though we cannot disambiguate these two possible accounts in the present study, we believe that the main point highlighted by the present findings is the evident parsimonious nature of the behavioral changes we are reporting. Deaf adults were able to differ in their performance compared to hearing controls by modifying a very simple feature of oculomotor behavior, namely by delaying saccadic latencies. This simple modification proved to be already sufficient to enter the search function at a later step in which the stimulus-driven response bias was already decreasing, ultimately allowing to be less captured by irrelevant salient stimuli in the display compared to hearing controls. Furthermore, the present findings on deaf oculomotor behaviors strongly argue in favor of the idea that deaf adults are indeed able to control their eye-movements. Consequently the present results also rule-out an explanation in terms of a prioritization of stimulus-driven over goal-driven mechanisms of attention selection as a consequence of early auditory deprivation.

4.1.6.1 Disengaging attention from distractors

One further interesting aspect of the present findings emerged from the analysis on the time needed to disengage attention from distractor locations. Indeed, previous studies suggested faster re-direction of covert peripheral visual attention in deaf adults compared to hearing controls (Chen et al., 2006; Colmenero et al., 2004). Instead, in the present work, we found no difference between the two groups for what it concerns the time needed to disengage overt visual attention from the wrong distractor position to the correct target position. Future studies should further investigate this issue with the aim of investigating whether or not the properties underlying the reorganization of overt attention might differ from those underlying reorganization of covert attention mechanisms following early bilateral deafness.

Another difference between the present overt attention study and the covert attention studies suggesting a faster re-orienting of peripheral visual attention in the deaf population compared to hearing controls (Chen et al., 2006; Colmenero et al., 2004) is in the aspect of selection that is addressed. Whereas those covert attention studies focused on spatial orienting of attention, in the present study we are focusing on feature-based selection. In other words, while in spatial-orienting tasks participants search for a stimulus knowing where in space it should appear, in feature-based selection tasks participants search for a stimulus knowing which particular visual property it should have (e.g., right/left-tilted singleton as in the present study). Therefore the absence of any evidence suggesting faster re-orienting of peripheral visual attention in our deaf sample compared to hearing controls might also highlight differences in the reorganization properties underlying these two different aspects of visual selection. Indeed, research on deafness has predominantly focused on investigating the properties of spatial attention (e.g., Bottari, Valsecchi & Pavani, 2011; Chen et al., 2006; 2010; Neville & Lawson, 1987; Proksch & Bavelier, 2002; see for a review Bavelier et al., 2006) whereas properties of feature-based attention as a consequence of auditory deprivation received much less consideration (but see for instance Stivalet et al., 1998). Future studies should also focus on further define the properties underlying this important aspect of visual attention in the deaf population.

4.1.6.2 Manipulating saliency through color information

Lastly, another open-aspect of the present findings that could have influenced both the results regarding the interplay between stimulus-driven and goal-driven processes as well as the results obtained for the disengaging of attention from distractor locations in the deaf population, it concerns the nature of the saliency manipulation we adopted. In the present study we chose to manipulate saliency through color information. However, no reorganization has been ever reported in deaf adults when irrelevant color stimuli were presented, leading to the proposal that only visual functions and visual properties processed by the dorsal visual stream are sensitive to reorganization as a consequence of early bilateral deafness (Armstrong et al., 2002; Bavelier & Neville, 2002).

To further address this critical issue, future research should investigate also whether or not this same pattern of results holds true when saliency is manipulated through dorsal-stream stimuli for which behavioral advantages have been robustly demonstrated in deaf individuals (e.g., abrupt onsets; moving stimuli).

Study 2: Increased saliency capture in action videogame players: Evidence form eye-movements

4.2.1 Summary

Action videogame players (AVGPs) have been shown to outperform non-gamers (NVGPs) in covert visual attention tasks. These advantages have been attributed to improved top-down control in this population. The time-course of visual selection, which permits to highlight when top-down strategies start to control performance has rarely been investigated in AVGPs. Here, we addressed specifically this issue through an oculomotor additional singleton paradigm. Participants were instructed to make a saccadic eye movement to a unique orientation singleton. The target was presented among homogenous nontargets and one additional orientation singleton that was more, equally or less salient than the target. The results showed a similar pattern of performance for both AVGPs and NVGPs where fast initiated saccades were saliency-driven whereas later initiated saccades were more goal-driven. However, AVGPs were overall less accurate than NVGPs and showed greater saliency capture for short-latency responses. Additional analyses showed that these differences in performance were explained primarily by the faster saccadic latencies in AVGPs and suggested that the underlying mechanisms ultimately driving selection in the two groups are similar.

Taken together, the present findings show that in both AVGPs and NVGPs alike, the implementation of top-down control in visual selection takes time to come about. This argues against the idea of a general enhancement of top-down control in AVGPs.

4.2.2 Introduction

Action video games are a form of entertainment with the potential to trigger astonishing plastic changes in our brain and behavior (for a review see Bavelier et al., 2012). In the last decade a growing body of data showed that action video game players (AVGPs) outperform non-gamers (NVGPs) in a wide variety of visual attention abilities, such as selective attention (Hubert-Wallander, Green, Sugarman & Bavelier, 2011), sustained attention and divided attention (Green & Bavelier, 2003; 2006); in skills that go well beyond the abilities that were trained within the game environment. Moreover, the same advantages have been observed in naïve subjects who were trained for a short period of time with action videogames, demonstrating a direct causal role of action video game playing in these improvements in visual attention (Green & Bavelier, 2003; 2006). Until now, the most shared explanation for this superior performance is that AVGPs show enhanced top-down control compared to NVGPs. This is generally expressed through a more efficient suppression of irrelevant information in AVGPs relative to NVGPs (Bavelier, Achtman, Mani & Focker, 2011; Mishra, Zinni, Bavelier, & Hillyard, 2011; Hubert-Wallander et al., 2011; Green, Sugarman, Medford, Klobusicky & Bavlier, 2012). However, specifically how and when in time this enhanced top-down control is established during performance has not been investigated (van Zoest et al., 2010 for a review). Evidence from overt visual selection paradigms suggests that top-down strategies generally take time to be implemented, such that early in time visual selection is driven by stimulus-salience and only later in time by top-down strategies (Donk & van Zoest, 2008; van Zoest et al.,2004; van Zoest & Donk, 2005; 2008). The aim of the present study was to investigate the time-course of overt visual selection in AVGPs compared to NVGPs and, more specifically, to examine possible differences in the temporal dynamics of bottom-up and top-town contributions to performance in the two populations. Notably, the results on AVGPs would also permit to further contribute to the debate within the visual selection literature on the properties and constraints concerning top-down control acquisition.

The majority of results on the effects of intensive action videogame playing on performance have been collected in covert orienting tasks measuring manual responses and involving restricted eye-movements. When eye-movements were permitted, they were not recorded. These works consistently reported that AVGPs-related improvements involve top-down (endogenous) mechanisms of attention (Green & Bavelier, 2003; Castel, Pratt & Drummond, 2005; West, Stevens, Pun & Pratt, 2008; Hubert-Wallender, Green & Bavlier, 2010). Moreover, when bottom-up (exogenous) contributions were tested, results showed that the exogenous processing between AVGPs and NVGPs was comparable (Castel et al., 2005; Dye, Green & Bavelier, 2009; Hubert-Wallander et al., 2011; but see West et al., 2008). Importantly, the lack of exogenous-related changes in AVGPs has been corroborated also by studies that have directly compared the role of these two attentional mechanisms within the same paradigm (Chisholm, Hickey, Theeuwes & Kingstone, 2010; Chisholm & Kingston, 2012; West, Al-Aidroos & Pratt, 2013). Chisholm and colleagues (2010) using an attentional capture paradigm, asked AVGPs and NVGPs to search for a unique target shape presented among a number of homogenous non-targets and to respond to the orientation of the line inside the target element, while maintaining fixation. In half of the trials one of the non-targets was a unique colored singleton. Participants were told to ignore any color information and to concentrate only on the orientation of the line inside the target element. Response times revealed that AVGPs resulted in overall faster responding than NVGPs. Moreover, AVGPs were also less affected in their search rate by the presence of the colored distractor. It was concluded that video game players have enhanced top-down attentional control, which, in turn, can modulate the negative effects on performance due to bottom-up attentional capture.

Two recent studies have investigated this same issue through overt visual selection (thus recording eye-movements and not manual responses) confirming the results coming from covert attention studies. This has led to the conclusion that overt and covert attentional mechanisms are modified in a similar way by training in AVGPs (Chisholm & Kingstone, 2012; West et al., 2013). Chisholm and Kingstone (2012) presented to AVGPs and NVGPs an oculomotor version of the attentional capture task. In each trial six circles appeared arranged in a hexagonal display. Only one of these circles randomly changed color and the task of the participants was to make an eye-movement (saccade) as fast and as accurate as possible toward the unique color singleton. In half of the trials, concurrent to the color change, an additional circle in the same color of the distractors was added to the display. Results showed that AVGPs were faster than NVGPs at searching and finding the target in the trials when the distractor with the same target onset was present. However, AVGPs and NVGPs showed comparable initial saccade latencies as well as comparable fixation-durations on the distractor, when they made an incorrect saccade toward this location instead of a correct saccade toward the location of the target. Nonetheless, less overall saccades toward distractors were found in AVGPs compared to NVGPs. The authors conclude that the enhanced top-down control in AVGPs is the result of more efficient suppression of task-irrelevant information and that this reflects a general principle of human cognition such that the top-down modulation of capture can be realized before selection is determined (e.g., Folk, Remington & Johnston, 1992; Bacon & Egeth, 1994).

West and colleagues (2013) instead, through a saccadic trajectory deviation task took into account also the role of time in saccades latencies, thus directly investigating the interplay between bottom-up and top-town contributions to performance in AVGPs. In this task the dynamics between bottom-up and top-down mechanisms was inferred from the trajectories of saccadic eye-movements. Performance in this paradigm typically shows that early initiated saccades tend to curve toward the distractor, thus being captured by irrelevant information, while later initiated saccades tend do curve away from the distractor. The latter oculomotor behavior is considered a consequence of the inhibition of the irrelevant distractor and an index of top-down control acquisition (McSorely, Haggard & Walker, 2006; Walker, McSorley & Haggard, 2006). West and colleagues (2013) showed that saccade trajectories of early initiated saccades were equally affected by distractors in the two groups, whereas the curvature of later initiated saccades differed between AVGPs and NVGPs. Indeed when AVGPs initiated later their saccades, they were better able than NVGPs to ignore distractors (i.e., less saccades were directed incorrectly to the distractor) but this was true only for the second part of the experiment. These findings, then, clearly demonstrate the benefit of tracing the time-course of control acquisition. At the same time, the results also suggest that the training benefit in AVGP as measured via overt saccadic responses is not substantially different from the benefits measured in performance via covert manual responses. It should be highlighted though, that saccade trajectory deviations reflect very subtle variation in saccade programming. In these paradigms, the eye movements are ultimately goal-driven as the saccades always end up at the target location. In the present study, we aim at tracing the time-course of bottom-up and of top-down control strategies in AVGPs in a visual selection task that typically reveals dramatic errors in course of oculomotor programming. This task provides direct insight in the impact on performance of bottom-up information (i.e., stimulus-saliency) over time and provides a way to see when in time top-down strategies control overt selection. The approach proposed is similar to previous works by van Zoest & Donk (2005; 2008) who used a search task in which participants searched for a target while competing powerful -but irrelevant for the task-salient information was presented (van Zoest & Donk, 2005). For example, van Zoest and Donk (2005) presented to participants a search display always composed of a target and a distractor (i.e., two tilted lines) embedded in a homogeneous set of non-targets (i.e., vertical lines). The saliency of target and distractor was manipulated in the color dimension: in one third of trials the target was colored and it was the most salient stimulus in the display; in one third of trials the distractor was colored and it was the most salient stimulus in the display; and in the remaining third of trials neither the target or the distractor were colored (no unique color). Van Zoest and Donk found that early in time eye-movements were strongly driven by stimulus-saliency. Saccades were directed to the most salient element, independently of the task instructions. Later in time saccades were no longer affected by irrelevant salience but were directed in line with the task instructions. This study suggested that it takes about 250 ms before goal-driven strategies are available to guide selection (see also, van Zoest, Donk & Theeuwes, 2004; van Zoest & Donk, 2008).

In the present study a group of action videogame players were tested in this oculomotor additional singleton paradigm to investigate how and when in time top-down control is implemented in this population. If, as suggested by Chisholm and Kingstone (2012), top-down enhancement concerns a general principle that guides selection in AVGPs, we expect to see top-down modulations early and late during selection. In particular, the general ability to implement enhanced top-down control would result in a better suppression of the irrelevant salient information thus reducing or nearly eliminating, the impact of stimulus-salience early during processing. In addition, this same ability might also permit to achieve more efficient top-down control later during processing.

If, instead, top-down control needs time to come about also in AVGPs, namely, if it is time-dependent, as West and colleagues (2013) have proposed, we expect to see initially no modulation of top-down control. The impact of stimulus-salience would be similar in both AVGPs and NVGPs, resulting, nonetheless, in relatively more control later during processing in AVGPs.

4.2.3 Methods

4.2.3.1 Participants

Twenty-four action-videogame players (AVGPs; mean age= 21.4; SD = 2.9) and 17 non-gamers (NVGPs; mean age = 21.5; SD = 1.5) took part to the experiment. Before starting the experiment, all participants completed a questionnaire on their video games habits in which they were asked a) to list up to 6 games they played mostly during the last year; b) to identify the game genre for each of these listed games; c) to specify how many times per month they would usually play each of the listed games and d) for how long each session typically lasted; e) the console they used.

AVGP and NVGP groups were created on the basis of their responses to this questionnaire: we considered AVGPs only those participants who reported to have played action video games for more than 5 hours per week in the last year (Li, Polat, Scalzo & Bavelier, 2010; mean number of hours played per week by our AVGP sample = 19.5); we considered NVGPs those participants who reported to have never played very little, if not at all, to any video games in the last year. We also note that the AVGP group reported to have experienced a wider variety of video games genres, including sport and strategy games in the last year.

All participants were recruited at the University of Trento and they all had normal or corrected-to normal vision. The Ethical Committee of the University of Trento approved the experiment. Each participant was given written instructions about the task, was informed of the general purpose of the study, was asked to sign a consent form and received credits or a payoff of 7 euros for participating in the study.

4.2.3.2 Apparatus

A Dell PC controlled the timing of the events and generated the stimuli. Eye movements were recorded through an Eyelink tracker (EyeLink 1000 Desktop Remote, SR Research) with 1000 Hz temporal resolution and 0.05° spatial resolution. The system uses an infrared video-based tracking technology to compute the pupil center and pupil size of both eyes. The display was a 19-inch SVGA color monitor, with 1024 x 768 pixels resolution and a 75 Hz refresh rate. All subjects were tested in a dimly lit room with their heads resting on a chinrest. The monitor was located at eye level, 60 cm from the chinrest.

4.2.3.3 Stimuli

Participants performed a visual search task in which they were instructed to make a speeded saccade as fast as possible to a target. The target was defined in the orientation dimension (e.g., a line oriented 45° to the right). Displays consisted of one target, a series of vertical oriented non-targets, and one distractor tilted in the opposite direction of the target (e.g., a line oriented 45° to the left). Saliency was manipulated through color. The vertical non-targets were always white. In one-third of trials the target was colored red, and the distractor was white (target-colored singleton), thus making the target the most salient singleton in the display. In another third of trials the distractor was colored green and the target was white (distractor-colored singleton), thus making the distractor singleton the most salient stimulus in the display. In the remaining third of trials both target and distractor were white (no-color singleton), thus there was no unique color singleton in the display. Elements were presented on a dark gray background, arranged in a 15 x 11 square matrix with a raster width of 30.7° x 25° of visual angle. Targets and distractors could appear at six different locations. These six potential locations were placed at the vertex of an imaginary hexagon in such a way that, embedded in the matrix of non-targets, targets and distractors were always presented at equal eccentricity from fixation (12.4° of visual angle). When a target and a distractor were presented, the angular distance between the two elements was always 120° (see Figure 4.6). Elements had an approximate height of 0.9° of visual angle and approximate width of 0.3° visual angle.

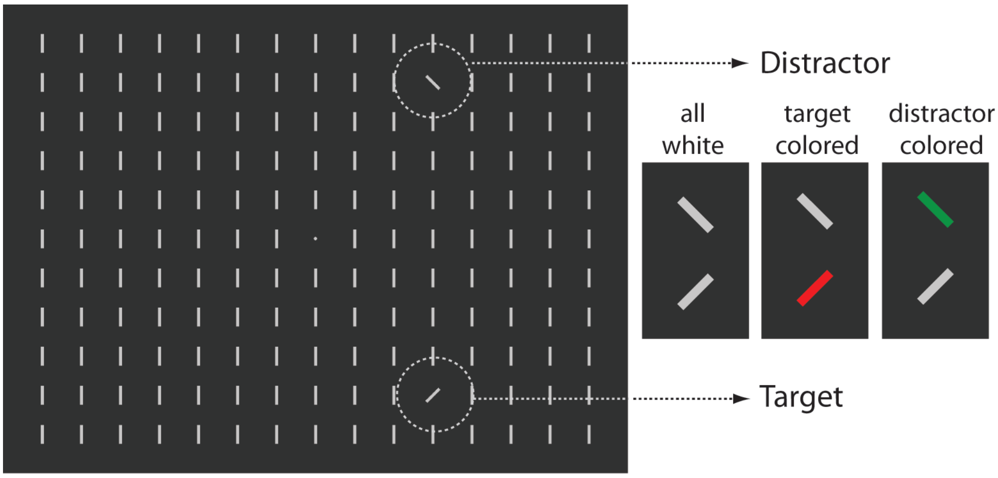

Figure 4.6. An example of a stimulus-display. Target and distractor were either both white, the target was colored red or the distractor was colored green.

4.2.3.4 Design and procedure

Each participant performed 24 practice trials, followed by 432 experimental trials. The three conditions manipulating target and distractor saliency (no-colored singleton, target-colored singleton, distractor-colored singleton) were mixed. Target and distractor orientations (i.e., right-tilted target with a left-tilted distractor and vice versa) were counterbalanced among participants. To start a trial participants pressed the space bar, then the fixation point was presented for 1000 ms followed by the stimulus matrix for 1500 ms. Participants were instructed to maintain fixation until the search display appeared and then to make a speeded saccade to the target as fast as possible, ignoring the distractor. They were also told that sometimes the target or the distractor would have been colored but that this information would not be informative and therefore they were instructed to ignore color information. All participants received written instructions. Feedback on initial saccades mean latencies was provided every 27 trials. The experiment was divided in 16 blocks. Participants were free to take a break between experimental blocks. Prior to the recording and every 4 blocks, participants viewed a calibration display consisting of nine points in a square array, fixated sequentially.

4.2.4 Results

Four participants initially recruited as potential AVGPs were then excluded from the sample (i.e., from both the AVGP and NVGP groups) because played at action video games, but less than our criterion for inclusion. Two AVGPs have been discarded due to problems during data acquisition; one AVGP and one NVGP were discarded because of too many excluded trials (i.e., more than one third of all trials); one AVGP has been discarded because his mean initial saccade latencies (350.6 ms) fell more than 2 standard deviations above the AVGP group mean (M= 234.8 ms). Following these exclusions, all analyses were conducted on sixteen NVGPs and sixteen AVGPs. In our remaining samples, we excluded all trials in which initial saccade latencies were below 80 ms (anticipation errors; NVGPs: 1% of trials; AVGPs: 1% of trials) or above 600 ms (NVGPs: 3 % of trials; AVGPs: 1% of trials); trials that started when the eyes of the participants were more than 2.5° of visual angle away from fixation (NVGPs: 4%; AVGPs: 3%) as well as trials were the initial saccade missed either the location of the target or of the distractor (NVGPs: 13%; AVGPs: 14%). We analyzed only those trials in which initial saccades ended 3.5° of visual angle around either the target or the distractor.

4.2.4.1 Saccadic latency

In order to look at the temporal dynamics of selection performance (van Zoest et al., 2004; van Zoest & Donk, 2005; 2008), we divided in quintiles the distribution of the initial saccade latencies of each participant. For each quintile of the latency distribution we calculated the proportion of correct saccades to the target. Then we averaged together the saccadic latencies as well as the proportion of correct saccades to the target of all participants in each quintile.

On data organized this way, we conducted a mixed, repeated-measures ANOVA on mean saccadic latencies, with saliency condition (colored-target; colored-distractor; no-colored singleton) and quintile (1-5) as within factors and group (NVGPs; AVGPs) as between factor. All post-hoc analyses have been conducted using the Newman-Keuls test. First of all, this analysis revealed a trivial significant main effect of quintile (F(4,120)=319.15, p<0.000001, η_p^2=0.91) due to the expected significant increased in saccadic latencies across quintiles (all ps<0.0001). We also observed a significant main effect of saliency condition (F(2,60)=16.63, p=0.000002, η_p^2=0.36) due to overall slower saccade latencies in the no-colored singleton condition (mean= 262.16 ms, SE=7.92) compared to the other saliency conditions (colored-target: mean= 253.65 ms, SE=8.13; colored-distractor: mean= 253.97 ms, SE=7.64, p<0.00013). Most importantly, we found a significant main effect of group (F(1,30)=13.7, p=0.0009, η_p^2= 0.31) due to overall faster initial saccade latencies in AVGPs (mean= 227.56 ms, SE=11.1) than in NVGPs (mean= 285.6 ms, SE=11.1, p=0.001). This main effect was better explained through the significant two-way interaction between quintile and group (F(4, 120)=11.09, p<0.000001, η_p^2= 0.27). Post-hoc analyses revealed that AVGPs were significantly faster than NVGPs only in the last three quintiles (see Figure 4.7; quintile 3: AVGPs: mean= 212.93 ms, SE=12.18; NVGPs: mean= 272.12 ms, SE=12.18, p=0.006; quintile 4: AVGPs: mean= 240.45 ms, SE=13.78; NVGPs: mean= 317.41 ms; SE=13.78, p=0.0004; quintile 5: AVGPs: mean= 314.94 ms, SE=15.39; NVGPs: mean= 400.87 ms; SE=15.39, p=0.0001). No other main effects or interactions resulted significant (all Fs<2.51).

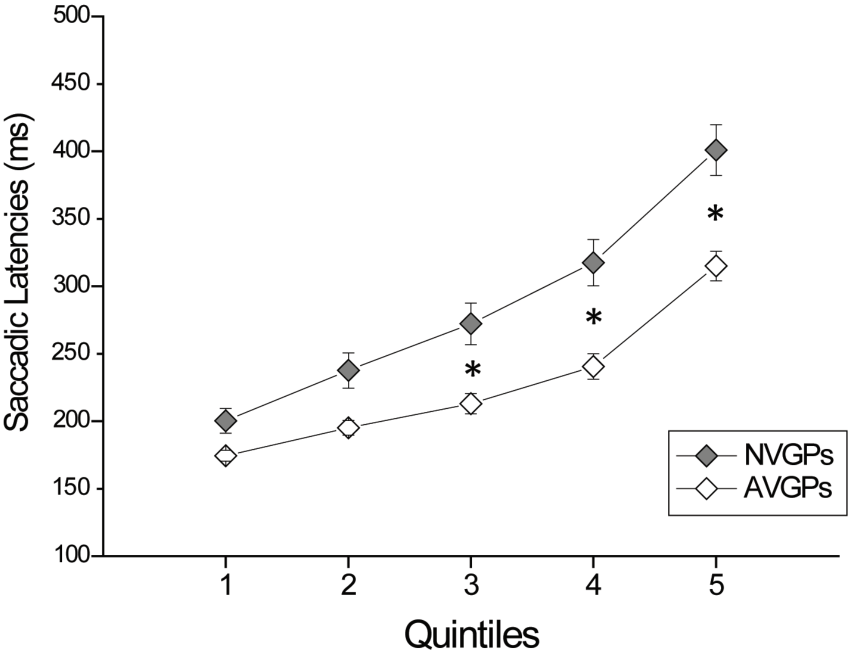

Figure 4.7. Two-way significant interaction between quintiles and group. AVGPs (i.e., opened diamonds) are overall faster than NVGPs (i.e., filled diamonds) but this difference resulted significant only for the last three quintiles (all ps<0.006).

4.2.4.2 Proportion to the target

To examine the crucial aspect of overt-selection as a function of time, we conducted similar ANOVA on mean proportion of initial saccades correctly directed to the target, again with saliency condition (colored-target; colored-distractor; no-colored singleton) and quintile (1-5) as within factors and group as between factor (NVGPs; AVGPs). All post-hoc analyses have been conducted using the Newman-Keuls test. This analysis as expected, revealed a main effect of quintiles ($F(4,120)=13.35$, $p<0.000001$, $\eta_p^2= 0.31$) due to increased proportion of correct initial saccades across quintiles, namely, as saccade latencies increased, with the last quintile being the most accurate of all (mean=65%, SE= 2%; all ps<0.009). Importantly, also the two-way interaction between saliency condition and quintile was significant ($F(8,240)=35.97$, $p<0.000001$, $\eta_p^2= 0.54$). Post-hoc analyses revealed that for quintiles 1 and 2 all participants were most accurate when the target was colored (quintile 1: mean= 79%, SE=3%; quintile 2: mean= 67%, SE=4%) compared to the other two saliency conditions (all ps< 0.006) and the least accurate when the distractor was colored compared to the other two saliency conditions (quintile 1: mean= 29%, SE= 3%; quintile 2: mean=39%, SE= 4%; all ps< 0.0007). Instead, for longer saccadic latency (i.e., quintiles 4 and 5) participants were the most accurate for the colored-distractor condition (quintile 4: mean= 69%, SE= 3%; quintile 5: mean= 76%, SE=2%) compared to the other two conditions (all ps<0.04) and the least accurate for the colored-target condition compared to the other two conditions (quintile 4: mean= 49%, SE= 3%; quintile 5: mean= 54%, SE=4%; all ps<0.03). More interestingly, we again found a main effect of group (F(1,30)=7.06, p=0.01, η_p^2= 0.19), due to overall less accurate performance in AVGPs (mean=54%, SE= 2%) compared to NVGPs (mean= 61%, SE= 2%; p=0.01). This effect was qualified by the three-way significant interaction between quintile, condition and group (F(8,240)=3.68, p=0.0004, η_p^2= 0.11). Subsidiary to this triple interaction, we also obtained significant two-way interactions between quintile and group (F(4,120)=4.37, p=0.002, η_p^2= 0.13) and between saliency condition and group (F(2,60)=4.21, p=0.02, η_p^2= 0.12).

The three-way interaction is illustrated in Figure 4.8. In quintile 2, AVGPs were more accurate than NVGPs when the target was colored (AVGPs: mean=77%, SE= 5%; NVGPs: mean= 56%, SE= 5%; p=0.01) but less accurate than NVGPs when the distractor was colored (AVGPs: mean= 29%, SE=6%; NVGPs: mean=49%, SE=6%; p=0.008). Moreover, AVGPs resulted also less accurate than NVGPs in quintile 4 (AVGPs: mean= 52%, SE=3%; NVGPs: mean=65%, SE=3%; p=0.01) and 5 (AVGPs: mean= 60%, SE=3%; NVGPs: mean=71%, SE=3%; p=0.004), and this was true especially for the colored-distractor condition (AVGPs: mean= 46%, SE=4%; NVGPs: mean=62%, SE=4%; all ps<0.01). No other main effect or interactions resulted significant (F=2.3).

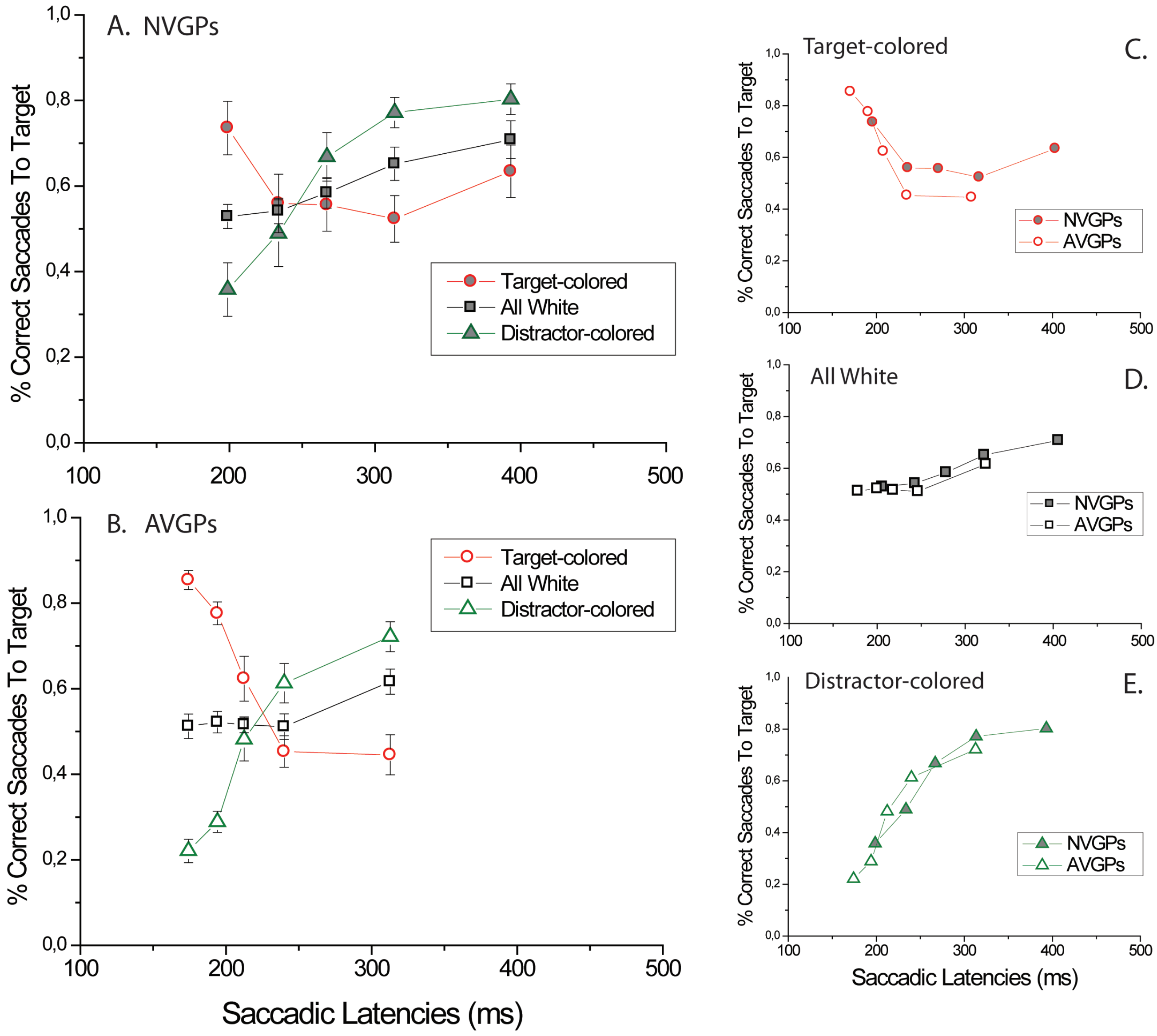

Figure 4.8. The proportion of saccades correctly directed to the target as a function of saccade latency. There were 3 saliency conditions: target red (target-colored); target and distractor white (all white); distractor green (distractor-colored). **A.** Speed-accuracy function for NVGPs **B.** Speed-accuracy function for AVGPs **C.** Comparison between NVGPs (filled circles) and AVGPs (opened circles) in their speed-accuracy functions for the target colored condition. **D.** Comparison between NVGPs (filled squares) and AVGPs (opened squares) in their speed-accuracy functions for the all white condition. **E.** Comparison between NVGPs (filled triangles) and AVGPs (opened triangles) in their speed-accuracy functions for the distractor colored condition.

In order to quantify the amount of saliency capture in visual selection processes in the two groups, we calculated for each participant the difference in proportion of correct initial saccades to the target between the target-colored condition and the distractor-colored condition for each quintile. We then normalized the saliency capture values obtaining a set of data with a range between 1 and -1. Positive values mean that a participant in a certain quintile made more saccades toward the salient stimulus independently of whether it was the target or the distractor, thus saccades were driven by saliency. Negative values, instead, mean that a participant in a certain quintile made more saccades away from the salient stimulus independently of whether it was the target or the distractor, thus saccades were driven by saliency inhibition. Values around 0 mean either that the participant is switching between the two visual selection criteria or that he/she achieved a top-down control specifically on the target identification, not influenced by saliency information. We inserted this set of data in a mixed repeated-measures ANOVA with quintile (1-5) as within factor and group (AVGPs; NVGPs) as between factor. Post-hoc analyses were conducted with Newman-Keuls test.

First of all, this analysis revealed the expected main effect of quintile ($F(4,120)=40.37$, $p<0.00001$, $\eta_p^2=0.57$) due to a decrease of saliency capture across quintiles going from the highest positive value in the first quintile (mean=0.48, SE=0.06) to the highest negative value in quintile 4 (mean=-0.19, SE=0.05) and quintile 5 (mean=-0.2, SE=0.04; all ps<0.003). Most importantly we also observed a significant main effect of group ($F(1,30)=4.24$, $p=0.05$, $\eta_p^2=0.12$) due to overall more saliency capture in AVGPs (mean=0.16, SE=0.06) compared to NVGPs (mean=-0.007, SE=0.05, p=0.05) better explained through the significant two-way interaction between quintile and group ($F(4,120)=4.18$, $p=0.003$, $\eta_p^2= 0.12$). Post-hoc analyses revealed that AVGPs differed from NVGPs especially in the saliency effect observed in the second quintile. While in this quintile AVGPs were still strongly captured by saliency (mean=0.46, SE=0.1), NVGPs were already changing visual selection criterion (mean=0.08, SE=0.1; p=0.008; see Figure 4.9).

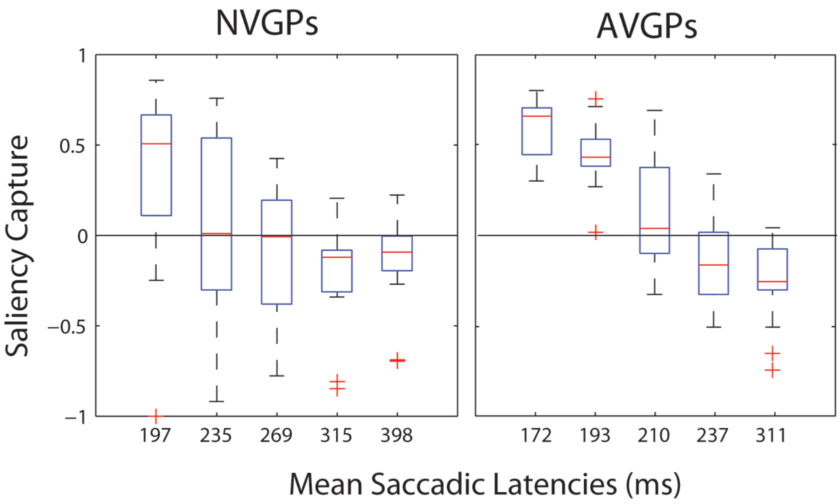

Figure 4.9. Amount of saliency capture as a function of time (quintiles) for NVGP and AVGP. Positive values mean that participants selected the most salient element independently of whether it was the target or distractor. Negative values mean that participants are inhibiting saliency information. AVGPs showed a significant greater amount of saliency capture for the second quintile compared to NVGPs (p=0.008)

4.2.4.3 Analysis of Covariance (ANCOVA)

Looking directly at the differences between groups in the Figures 4C-D-E, results revealed that the performance functions of AVGPs and NVGPs are strongly overlapping. This suggests that the differences between groups in proportion to the target may be primarily driven by differences in saccade latency. To test the potential contribution of saccade latency in accuracy performance, mean saccadic latencies of each participant were included as a regressor in two separate covariate analyses (ANCOVA) with accuracy as dependent measure or with saliency capture as dependent measure.

The ANCOVA with proportion of correct saccades to the target as dependent variable, quintile and saliency conditions as within factors, group as between factor and mean saccadic latencies as covariate did not show any significant effect or interaction involving the group variable (all Fs< 0.9). Instead, all the interactions involving the group factor that we have observed in the ANOVA on the same data (i.e., without mean saccadic latencies as a covariate; see Paragraph 3.2), now involved only the covariate in the ANCOVA. We observed a main effect of the covariate saccade latency ($F(1,29)=21.4$, $p<0.00001$, $\eta_p^2=0.42$); a significant two-way interactions between saliency conditions and the covariate saccade latency (F(2,58)=14.2, p<0.00001, η_p^2=0.33) and between quintile and the covariate saccade latency (F(4,116)=2.6, p=0.04, η_p^2=0.08) and a significant three-way interaction between saliency conditions, quintile and the covariate saccade latency (F(8,232)=6.9, p<0.00001, η_p^2=0.19).

Extending this ANCOVA approach to saliency capture (with quintile as within factor, group as between factor and mean saccadic latencies as covariate) confirmed this result. No significant effect or interaction involving the group variable emerged, instead we observed a main effect of the covariate saccade latency (F(1,29)=14.9, p=0.001, η_p^2=0.34) and a two-way significant interaction between quintile and the covariate saccade latency (F(4,116)=9.4, p<0.00001, η_p^2=0.25).

4.2.4.4 Disengaging attention from distractor

Finally, we wanted to assess whether AVGPs were quicker than NVGPs at disengaging attention from the distractor when the eyes were first incorrectly directed to this element. To this aim we conducted a mixed, repeated-measures ANOVA on the fixation-duration of the first saccade on the distractor, when the second saccade was correctly directed to the target, with saliency condition (colored-target; colored-distractor; no-colored singleton) as within factor and group as between factor (NVGPs; AVGPs). All post-hoc analyses have been conducted using the Newman-Keuls test. This analysis revealed a main effect of saliency condition (F(2,60)=4.61, p=0.01, η_p^2= 0.13) due to shorter fixation-duration when the distractor was colored (mean= 168.2 ms, SE=7.95) compared to the other two conditions (colored target: mean= 186.88 ms, SE= 8.56; no color singleton: mean= 183.42 ms, SE= 7.48; all ps<0.02). There was also a marginally significant two-way interaction between saliency condition and group (F(2,60)=3.05, p=0.055, η_p^2= 0.1), due to the fact that fixation-duration across saliency conditions did not differ in NVGPs (colored-target: mean= 183.25 ms, SE= 12.1; no-colored singleton: mean=179.92, SE=10.57; colored-distractor: mean= 178.62 ms, SE= 11.25), whereas AVGPs had the shortest fixation-durations for the distractor-colored condition (colored-target: mean= 190.5 ms, SE= 12.1; no-colored singleton: mean=186.91, SE=10.57; colored-distractor: mean= 157.78 ms, SE= 11.25; all ps<0.02; see Figure 4.10). No other effect was significant (F=0.02).

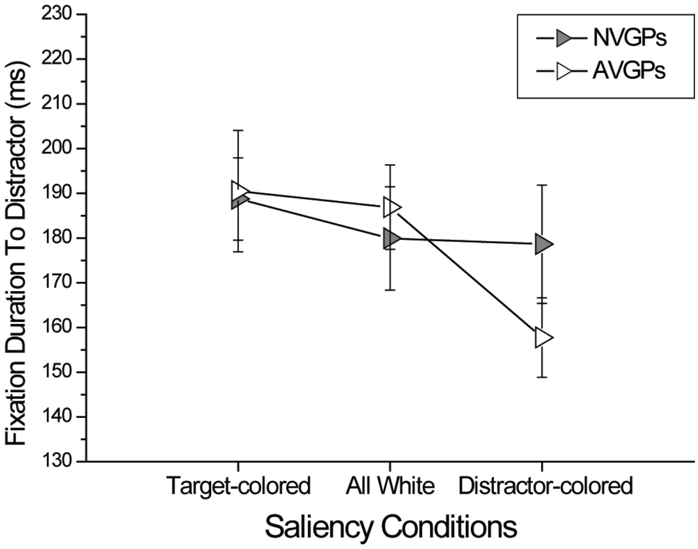

Figure 4.10. Fixation duration (ms) on the distractor for incorrect saccades for the 3 saliency conditions. In NVGPs (filled triangles) fixation duration on the distractor was not different for 3 saliency conditions. In AVGPs (opened triangles), fixation duration was shorter in the distractor-colored condition compared to the other 2 saliency conditions (p<0.02).

4.2.5 Discussion

The purpose of the present study was to investigate when and how top-down control is established in AVGPs. In order to address this question, we compared the time-course of bottom-up and top-down contributions in overt visual selection in AVGPs compared to NVGPs.

Our results replicated previous findings showing the interplay between bottom-up and top-down contributions to overt visual selection processes over time (van Zoest, Donk & Theeuwes, 2004; van Zoest & Donk, 2005; 2008). In the present study this interplay is mainly expressed by the significant two-way interaction between saliency condition and quintiles that we observed for proportion of correct initial saccades to the target independently from the group variable. Fast initial saccades were saliency-driven, meaning that the majority of these saccades were directed toward the most salient singleton in the display, independently of whether it was the target or the distractor. This resulted in overall high accuracy in the colored-target condition and low accuracy in the colored-distractor condition. Instead, slower initial saccades (i.e., with latencies longer than 250 ms) were more controlled and tended to go toward the target stimulus also in the trials where the distractor was the most salient singleton in the display.

While the overall pattern of performance was similar between AVGP and NVGP groups, we additionally observed substantial differences between the two populations. AVGPs had overall shorter initial saccade latencies compared to NVGPs, an effect that was driven mainly by later initiated saccades (i.e., in the last three quintiles only). In addition, AVGPs were also overall less accurate than NVGPs and this was true not only for later initiated saccades, but also for early saccades. Moreover, the analysis on the amount of saliency capture confirmed and clarified this pattern of results showing the biggest difference between the two groups early in time, in the second quintile, with AVGPs being more captured by saliency than NVGPs.

Previous works that has investigated the effects of irrelevant information on performance based on covert reaction times measures (Bavelier et al., 2011; Mishra et al., 2011) typically reported increased response speed together with enhanced accuracy in AVGPs compared to NVGPs. These studies were taken as evidence for enhanced top-down control due to a better ability to suppress irrelevant information in AVGPs. Our novel findings based on saccadic programming (i.e., initial saccadic latencies and saccadic selection) are only partly in line with previous work. In the present study, AVGPs were indeed faster than NVGPs at initiating their saccades but AVGPs also found it harder to ignore irrelevant salient information. In our study, they never achieved higher level of accuracy nor were they able to implement more efficient top-down strategies compared to non-gamers.

Nonetheless, the present results, in line with previous findings using the same paradigm (van Zoest & Donk, 2005; 2008), clearly point out that saccadic latencies is directly related to the relative impact of saliency capture and it strongly influences accuracy performance: the faster participants are at initiating saccades the more they are driven by saliency in their selection processing, and the slower participants are at initiating saccades the more efficient they are at implementing correct top-down strategies. Through analyses of covariance (ANCOVA) we directly tested the hypothesis that the increased sensitivity to stimulus-salience in AVGPs may have been the direct outcome of the shorter saccade latencies in this population. In other words we tested whether differences between groups were primarily the result of quantitative changes in processing speed, or reflect qualitative differences in the underlying mechanisms. From the ANCOVA it emerged that the differences we observed between AVGPs and NVGPs in terms of accuracy and in terms of saliency capture disappeared once taking into account mean saccadic latencies as a covariate in the analyses. These findings showed that the pattern of behavior observed in AVGPs ultimately was very similar to NVGPs, the only difference being that the former group acted much more quickly than the NVGPs. This suggests that the underlying processing between the two groups in the end may be very similar. These results are in line with previous studies on covert exogenous attention in AVGPs that have reported faster responses but comparable underlying processes over time compared to NVGPs (Castel et al., 2005; Hubert-Wallander et al., 2011). Interestingly, even though AVGPs were faster at initiating saccades compared to NVGPs, they also tended to be faster at disengaging attention and to redirect the eyes to the correct target, following incorrect saccades to the salient distractor. This latter result differs from Chisholm and Kingstone (2012), who did not report any reliable differences between AVGPs and NVGPs in terms of speed of disengaging attention from distractors in an oculomotor version of an attentional capture task (see the Introduction for more details). Nonetheless the authors reported faster search rate to find the target in AVGPs for the distractor present trials. Differently from our study though, Chisholm and Kingstone did not inform participants about the presence of distractors during the experiment and this lack of information may have subsequently influenced the fixation duration on this element. Moreover, the salience of the irrelevant distractor depended on it being presented as an abrupt onset. Once presented in the display, including potentially when the participant's saccade was directed at this location, this element was essentially no different than the other surrounding non-targets. Instead, in the present paradigm the salient distractor was a unique singleton, which stood out for the total duration of the trial. Therefore, the different result might stem from this difference in the stimuli properties: disengaging attention from a 'neutral' identical to non-target stimulus may have been easy for all participants, instead disengaging attention from a stimulus that is also unique in the display (as was the case in present study) may have proved more effective in revealing differences between groups. Previous works (Bavelier et al., 2011; Mishra et al., 2011) has indeed shown that differences between AVGPs and NVGPs are harder to detect in an easy task compared to a more difficult task.

Another critical difference from previous studies in AVGP is the fact that the present study looked at the time-course of performance. Evidence suggests that responses triggered earlier in time reveal vastly different outcome than responses later in time (e.g., Godijn & Theeuwes, 2002; Ludwig & Gilchrist, 2002; van Zoest et al., 2004; 2010). This dynamic aspect of performance has rarely been addressed explicitly in experimental research investigating difference between AVGPs and NVGPs (however, see Hubert-Wallander et. al. 2011). To our knowledge, there is only one other study on overt attention (West et al., 2013), which directly investigated the interplay between bottom-up and top-down contributions to performance in AVGPs over time. This study reported comparable bottom-up selection early in time between AVGPs and NVGPs but better top-down control in AVGPs for later initiated saccades, which nonetheless was observed only in the last part of the experiment. West and colleagues (2013) used a saccade trajectory deviation task where participants had to look as fast as possible to a target ignoring a concomitant distractor (see the Introduction for further details). In this task the target locations were pre-specified as were the locations of the irrelevant distractors. Target selection was therefore relatively straightforward; competition between target and distractor was limited and very few saccades went incorrectly to the distractor. As previously stated, evidence suggests that differences between AVGPs and NVGPs at least in covert attention studies, are stronger in attentional demanding tasks (Mishra et al., 2011; Bavelier et al., 2011). Perhaps, it is the case that when target selection is relatively undemanding as in West and colleagues' study (2013) AVGPs can learn to better inhibit irrelevant distracting information over time. Instead, when the task of localizing the target is more difficult and competition is considerable, AVGPs find it harder to refrain to move their eyes, thus making emerge more clearly differences between the training outcomes related to covert and overt attentional mechanisms.

In any case, the results of West and colleagues (2013) together with the present findings clearly show the benefit of investigating the time-course of performance in order to better characterize how top-down control is established. A time-course-approach may benefit studies that investigate covert attentional selection and this is something that may prove insightful in the future to better characterize training effects within the two attentional mechanisms as a consequence of intensive action videogame playing.

Taken together, our results show substantial differences between AVGPs and NVGPs in overt visual selection, which seem to be driven mainly by their faster oculomotor behavior compared to NVGPs. Importantly, our findings clearly show that AVGPs found it more difficult than NVGPs to 'inhibit' their saccades, exhibiting a more impulsive oculomotor behavior, which negatively affected their performance. This overall more impulsive behavior that we are documenting might seems at odd with other literature on the effects of action videogame training regimens on performance, which consistently reported an increased ability to suppress irrelevant information in this population expressed through enhanced reactivity and accuracy (Bavelier et al., 2011; Mishra et al., 2011; Hubert- Wallander et al., 2011; Green et al., 2012). An important further difference between the present study and these other studies is that only manual responses were collected in the latter. Indeed while playing at action videogames the requirements to the eyes and to the hands are very different: the eyes need to efficiently and rapidly monitor the visual scene, while the hands need to respond only when necessary. Thus our results may differ from previous findings because of the different behavior we are tapping and the different training this behavior received through playing. Indeed, the work of Chisholm and colleagues (2010) allows insight in this contrast. They used a covert version of an attentional capture task that was in many ways similar to the paradigm used in the present work. In this task they collected only manual responses (see the Introduction for more details), and found enhanced reactivity and a better performance in trials where a distractor was present in AVGPs compared to NVGPs. In other words, when AVGPs are required to give manual responses in a task similar to our oculomotor paradigm, they did show an enhanced ability to suppress irrelevant information. Taken together, this may suggest for the first time that different abilities (i.e., react to events through eyes vs. react to events through hands) may be differently modified by training. Once again, more studies are definitely needed to better describe to what extent modifications in overt attention mechanisms in AVGPs are different from the influences on covert attention.

Finally, the present findings contribute to the literature on visual selection per se showing that time is essential in the acquisition of top-down control: if participants are quick at initiating saccades, they are unlikely to have acquired top-down control and they will tend to be captured by stimulus saliency. Evidence for control was only found for longer response latencies. Overall, the results of the present study argue against the idea of a general enhancement of top-down control in AVGPs. Like NVGPs, AVGPs clearly required time to establish control in saccadic selection. Even though AVGPs were faster to respond, there was no evidence for the acquisition of more efficient top-down control earlier in time in this group. If anything, faster responses lead to more capture by stimulus-salience.

CHAPTER 5:

How is covert attention deployed in deaf adults when powerful social-cues are used?

Study 1: Deaf and hearing early signers can resist the gaze cueing effect

5.1 Summary

The present study investigated social attention in deaf adults using the gaze-cue paradigm. As an adaptive outcome to overcome the lack of audition within social contexts, we expected deaf adults to show larger gaze-cueing effect (GCE) compared to hearing controls. In Experiment 1, 22 early deaf adults and 23 hearing controls performed a peripheral shape discrimination task, while ignoring an uninformative central gaze-cue. We confirmed GCE in hearing controls, but contrary to our predictions we found no GCE in response times of deaf participants – particularly for early signers. In Experiment 2, we further explored the role of early sign-language exposure by testing a group of hearing native signers in the same task. No GCE emerged for this hearing group. These findings suggest that early acquisition of sign language can limit attentional capture by irrelevant gaze-shifts. Implications for automatic processing of gaze-cues and attentional changes in the deaf population are discussed.

5.2 Introduction

Profound bilateral deafness is an invisible handicap. This informal description reflects the ability of deaf people to interact with the environment very efficiently, despite the lack of auditory input. Research in the last twenty years has revealed that this acquired skill involves reorganization of the mechanisms underlying visual attention, inducing changes particularly in the peripheral visual field (Bavelier et al., 2001; Chen et al., 2010; 2006; Proksch & Bavelier, 2002; for reviews see Pavani & Bottari, 2011). However, to what extent these attention-related changes generalize to social contexts remains largely unexplored. To investigate this issue, in the present work we examined attentional deployment in response to eye-gaze direction of others (see Lachat, Conty, Hugueville & Gearge, 2012 for review) in early deaf adults with severe or profound bilateral deafness and in hearing controls.

In gaze-cueing paradigms participants are typically presented with a central face, whose gaze is directed to the right or to the left in each trial (e.g., Driver, Davis, Ricciardelli, Kidd, Maxwell & Baron-Cohen, 1999; Friesen & Kingstone, 1998; 2003; Friesen, Ristic & Kingston, 2004; Khurana, Habibi, Po & Wright, 2009; Quadflieg, Mason & Macrae, 2004; Tipples, 2005). The task is to discriminate a peripheral target, appearing either on the same side indicated by eye-gaze (cued location) or on the opposite side (uncued location). Results have robustly shown that participants respond much faster when gaze-direction validly cues target location, compared to when the gaze-direction is invalid with respect to target location (gaze-cueing effect; GCE). Crucially, GCE is also observed when gaze-direction is entirely unpredictive of the position of the upcoming target (e.g., Friesen & Kingston, 1998; Tipples, 2005), or even when it is counterpredictive with respect to target location (e.g., Driver et al., 1999; Friesen et al., 2004; Galfano, Dalmaso, Marzoli, Pavan, Coricelli & Castelli, 2012). This led to the proposal that attentional orienting exerted by these social cues is automatic (see Frischen, Bayliss & Tipper, 2007 for a review).

In the deaf population, given the reduced or absent auditory input, gaze-direction might represent the preferential way to direct attention on the same object and location attended by the social partner. Furthermore, in deaf people gaze-direction might convey important information about the surrounding visual environment, while their primary orienting modality (vision) is absorbed by social interactions. For instance, deaf people may follow gaze-shifts of their social partner as an alerting cue for events occurring in the surrounding space. We therefore predicted greater sensitivity to this type of social cues (i.e., larger GCE) in deaf participants compared to hearing controls.

In addition, eye-movement research has documented a predominant exploration of the eye-area of the face in deaf native signers compared to hearing controls, when performing comprehension tasks on signed narratives (Emmorey, Thompson & Colvin, 2009) or when evaluating static faces for their emotional valence (Watanabe, Matsuda, Nishioka & Namatame, 2011). Therefore, we hypothesized that life-long sign language experience might further modulate the magnitude of the GCE in the deaf population. Specifically, we predicted that deaf participants with earlier acquisition of sign language (Mayberry & Lock, 2003) and higher signing proficiency should be more sensitive to gaze-shifts as a cue for orienting their spatial attention.

5.3 Experiment 1

5.3.1 Methods

5.3.1.1 Participants

Twenty-two early bilateral deaf adults (hearing loss ≥ 70 dB in the better ear; mean age = 28 years old; SD = 5) were recruited by the ISTC-CNR personnel to participate in this research and were tested in ISTC-CNR laboratories. Twenty-three hearing controls (mean age = 24 years old; SD = 3.4) also took part in the study. All participants had normal or corrected-to normal vision. The Ethical Committee of the University of Trento approved the study and all participants signed an informed-consent form and received a payoff of 7 euros for their participation. Whenever needed a fluent signer explained consent procedures and experimental instructions in LIS.

All deaf participants completed a questionnaire aimed at collecting anamnestic information concerning their deafness and linguistic background. Furthermore, they completed a set of linguistic tests aimed at assessing linguistic proficiency at the moment of testing in Italian Sign Language (LIS) and in spoken and written Italian (see Supplementary Material). These tests were developed by the ISTC-CNR personnel and will be described in full details in future reports. A hearing experimenter conducted Italian assessment, while a deaf native signer conducted LIS assessment.

5.3.1.2 Stimuli and procedure

Figure 5.1 shows the stimuli used in the study as well as the trial sequence. The trial sequence included one of two types of pre-cue face stimuli (eyes-open; eyes-closed), to control for possible performance differences between deaf and hearing participants attributable to visual motion processing (e.g., Bavelier et al., 2001; Codina, Pascalis, Mody, Toomey, Rose, Gummer & Buckley, 2011; Neville & Lawson, 1987). The sequence in which the eyes-open pre-cue preceded the gaze-cue produced strong visual motion. Instead, the sequence with the eyes-closed pre-cue did not. Crucially, gaze-cue direction was never predictive of target location. On half of trials the target appeared on the side indicated by gaze (cued trials), while in the remaining half the target appeared on the opposite side (uncued trials). Two Stimulus Onset Asynchronies (SOA; 250 ms; 750 ms) between gaze-cue and target appearance were used to detect any changes in the properties of GCE over time.

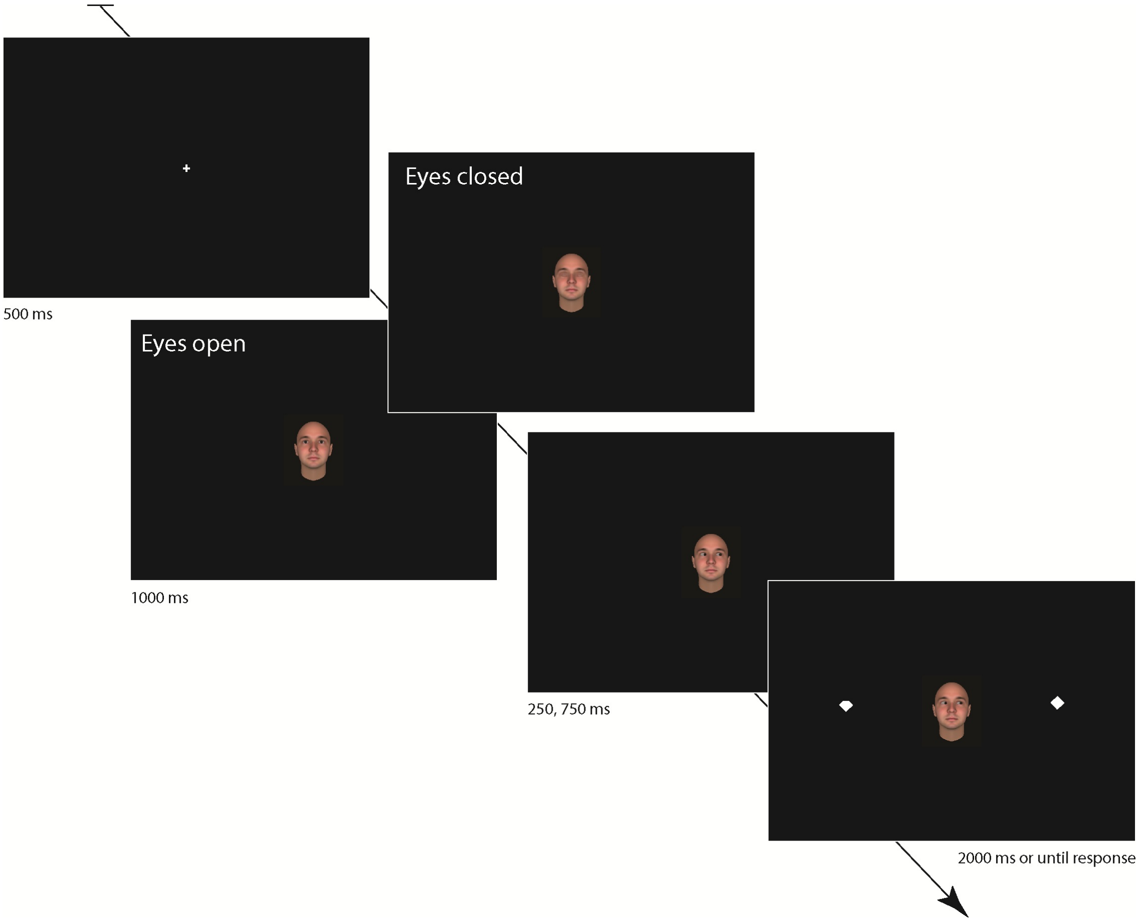

Figure 5.1. Trial sequence and stimuli. Participants sat at a distance of approximately 60 cm from the center of a computer monitor (34x27 cm; resolution 1024x768; refresh rate 60 Hz). Each trial began with central fixation (500 ms). A pre-cue stimulus lasting 1000 ms (a face with eyes-open gazing straight ahead or a face with the eyes-closed) always preceded the face with shifted gaze (cue-stimulus). After 250 ms or 750 ms (SOA), the target stimulus appeared (2000 ms or until response). In this example an uncued trial is shown: the gaze is directed to the right, whereas the target (cut diamond) appears on the left.

Participants were instructed to fixate the central face, to ignore gaze-cues because uninformative, and to indicate as fast and as accurately as possible whether the target diamond missed the top or the bottom part, independently of the side of the screen in which the target appeared. Responses were given by pressing the up/down arrow keys on the computer keyboard. The experiment comprised 16 practice trials and 320 experimental trials divided in 16 blocks. At the end of each block participants received feedback on the average reaction time (RTs) and on the percentage of correct responses.

5.3.2 Results

Two hearing participants and two deaf participants were excluded from the analyses due to too many mistakes or too slow mean RTs compared to the other participants of their group. All analyses were thus conducted on 21 hearing controls and 20 deaf participants. Correct RTs within ± 3 standard deviations from the overall group mean were calculated for each participant and for each experimental condition and inserted into a mixed, repeated measure ANOVA with Pre-cue Type (eyes-closed; eyes-open), SOA (250 ms; 750 ms), Validity (cued; uncued) as within-participants variables, and Group (hearing; deaf) as between-participants variable. GCE was calculated as the difference in RTs (or accuracy) between uncued and cued trials. All post-hoc analyses were conducted using the Newman-Keuls test.

This analysis revealed the main effect of SOA, caused by faster RTs in the 750 ms SOA trials compared to the 250 ms SOA trials ($F(1,39) = 55.03$ $p < 0.00001$, $\eta_p^2 = 0.58$), and the main effect of Validity ($F(1,39) = 10.60$ $p = 0.002$, $\eta_p^2 = 0.21$). More importantly, a significant interaction between Validity and Group emerged ($F(1,39) = 5.09$, $p = 0.03$, $\eta_p^2 = 0.12$; see Figure 5.2A). Hearing participants were significantly faster for cued (M = 671 ms; SE = 20) compared to uncued trials (M = 693 ms; SE = 21; $p=0.0005$; GCE= 22 ms). By contrast, no significant difference between cued (M = 698 ms; SE = 20) and uncued trials (M = 702 ms; SE = 22; $p = 0.5$; GCE = 4 ms) emerged for deaf participants.

A similar analysis on percentage of errors as dependent variable did not reveal any effect related to the group variable (all F-values < 1.38). Only the main effect of Validity ($F(1,39) = 7.39$, $p = 0.009$, $\eta_p^2 = 0.16$; GCE= 3%) and the main effect of Pre-cue Type reached significance ($F(1,39) = 4.48$, $p = 0.04$, $\eta_p^2 = 0.1$).

To examine the role of sign language experience in modulating GCE in deaf participants, Pearson's correlations were conducted between GCE and performance in each of the sign-language tests, at each level of SOA. None of these correlations reached significance. However, there was a significant correlation between self-reported AoA of LIS and the magnitude of GCE for the 250 ms SOA ($r(20) = 0.595$, $p = 0.006$). Deaf participants who reported to have acquired LIS later in life showed greater GCE compared to deaf participants who acquired LIS early in life (see Figure 5.2B, left panel). No significant correlation between AoA of LIS and gaze-cue effect was observed for the 750 ms SOA (r(20)=0.009, p=0.97; Figure 5.2B, right panel).

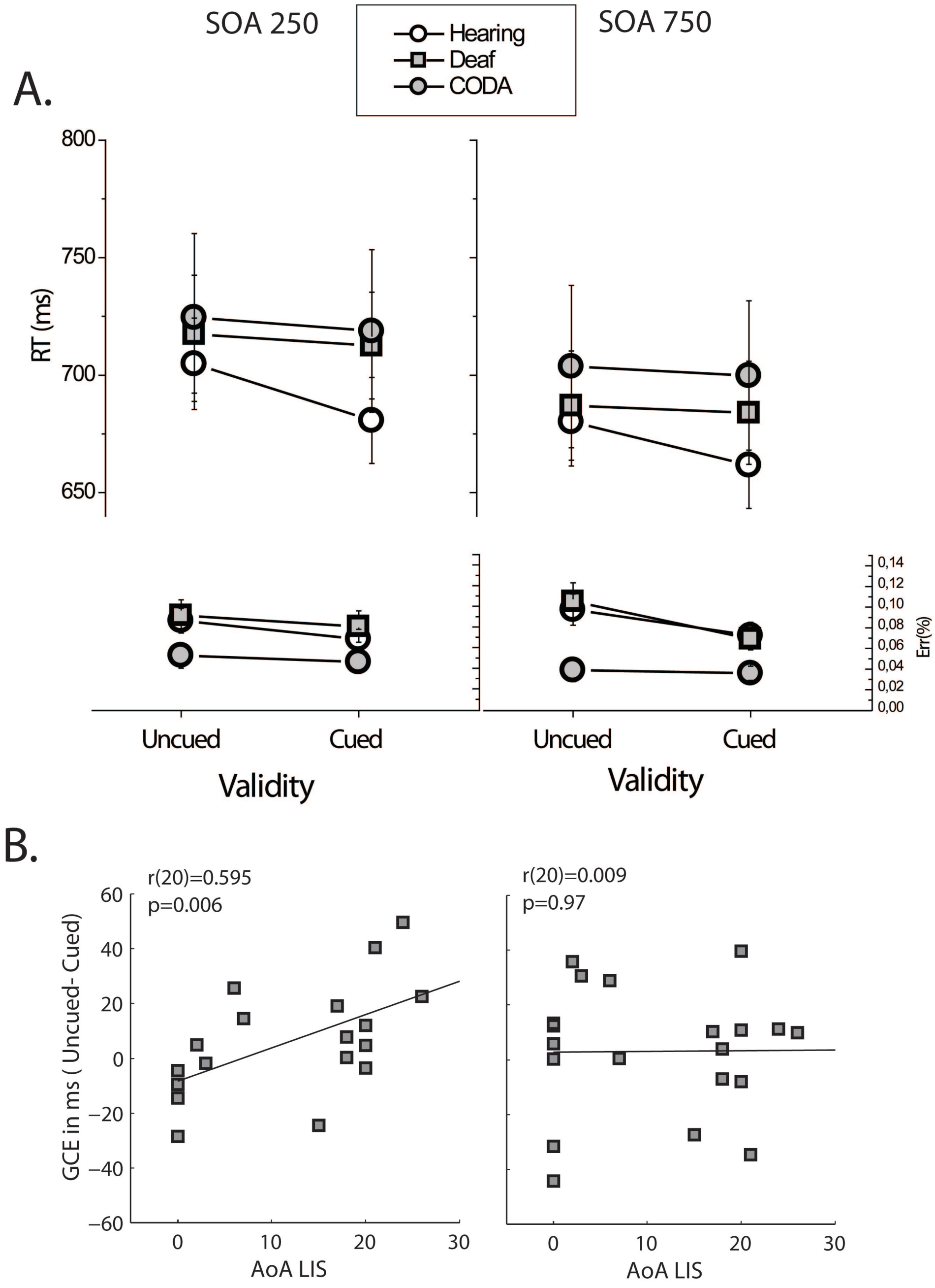

Figure 5.2. Results. **(A)** Mean reaction times (top) and percentage of errors (bottom) for uncued and cued trials, as a function of experimental group and SOA. **(B)** Correlations between AoA of sign language and gaze cueing effect (GCE) in deaf participants for the two SOAs.

5.4 Experiment 2

To test more directly the hypothesis that the absence of GCE in the deaf group reflects early acquisition of LIS rather than auditory deprivation, in Experiment 2 we tested a group of hearing native signers using the same paradigm of Experiment 1. If early acquisition of sign language is the determinant factor in modulating GCE, a reduced or abolished GCE should emerge also in hearing native signers.

5.4.1 Methods

5.4.1.1 Participants, stimuli and procedure

Eight hearing native signers, which were Children of Deaf Adults (CODAs), were recruited by the ISTC-CNR personnel to take part in Experiment 2 (mean age=28.2; SD=5.3) and tested in the ISTC-CNR laboratories. All participants reported to have normal or corrected-to normal vision, they signed an informed-consent form and received a payoff of 7 euros for their participation in the study. All experimental details were identical to Experiment 1.

5.4.2 Results

We compared performance of this additional control group with the deaf adults and hearing controls tested in Experiment 1 by entering all RTs into a mixed repeated measure ANOVA with Validity (cued; uncued) as within-participants variable and Group (hearing; deaf; CODA) as between-participants variable. Results revealed a significant interaction between Validity and Group ($F(2,46)=3.32$, $p=0.04$, $\eta_p^2=0.13$). Hearing controls were significantly faster for cued compared to uncued trials (GCE= 22 ms; $p=0.002$). By contrast, both deaf adults and CODAs showed comparable RTs to cued and uncued trials (GCE= 4 ms, $p=0.5$; GCE= 5 ms, $p=0.4$, respectively; see Figure 5.2A). A similar analysis on percentage of errors revealed no effect related to the group variable (all Fs < 2.21). The main effect of Validity reached significance due to more mistakes in uncued compared to cued trials overall ($F(2,46)=7.26$, $p=0.01$, $\eta_p^2=0.14$).

5.5 General Discussion

The aim of the present study was to investigate social attention in deaf adults using the gaze-cueing paradigm. Contrary to our initial predictions, we observed the well-known advantage in response times when responding to validly cued targets only in hearing controls. In contrast, this gaze-cue facilitation did not emerge in deaf adults. Correlation analyses revealed that the magnitude of GCE was modulated by AoA of LIS, at least when the time between gaze-cue and target was short. Instead, none of the other measures of linguistic proficiency in deaf participants correlated with GCE. To further examine the relation between GCE and early sign-language exposure, we tested a group of hearing native signers and revealed also for this hearing population no influence of gaze-cues on RTs. These two pieces of evidence suggest that the absence of GCE in our study might depend upon early acquisition of sign language, rather than deafness per se.

GCE has been documented using a wide variety of experimental manipulations (see Lachat et al., 2012, Table 1) and it is currently conceived as an automatic and unavoidable effect (see Galfano et al., 2012 for review). For instance, GCE emerges even when gaze-cue stimuli are processed outside conscious awareness (Sato, Okada & Toichi, 2007), when the gaze-shift is conflicting with other cue stimuli in the scene (Kuhn & Kingston, 2009), or when a concomitant secondary task has to be carried out (Law, Langton and Logie, 2011). Furthermore, GCE has been reported also in autistic individuals, with deficits in the domain of social cognition (Swettenham, Condie, Campbell, Milne & Coleman, 2003). In the context of this consistent literature, our main finding that deaf or hearing early signers do not show GCE in RTs is particularly striking. This is even more surprising considering the enhanced tendency to look at the eye-area documented in deaf proficient signers (Emmorey et al., 2009; Watanabe et al., 2011).

In sign languages, however, the eye-area carries linguistic information in addition to attention-orienting ones (for discussion see Emmorey, 2002). In particular, eye-gaze shifts serve to indicate role shifting among characters during narrations (e.g., Pizzuto, 2007). For instance, a signer telling a story about two friends would move always the eyes in one direction to refer to one of the two characters, and in the other direction to refer to the other one. In this context, orienting spatial attention toward the direction of gaze could be detrimental for efficient linguistic interaction, because no relevant information will appear at the gaze-cued location. Thus, one first explanation for our findings is that early exposure to this special linguistic training could promote the consolidation of voluntary strategies, to prevent spatial attention-orienting triggered by gaze shifts (see Vecera & Rizzo, 2006, for a previous proposal of a predominant role of voluntary strategies in GCE). This explanation challenges the notion of strong automaticity of GCE, supported by many empirical studies (see Galfano et al., 2012). An alternative account is that in early and native signers gaze-direction acquires a primarily linguistic valence, rather than exclusively a social or visuo-spatial one. Eye-gaze might remain an automatically processed stimulus, but for linguistic rather than just attention-orienting purposes. The fact that in our deaf sample the correlation between the magnitude of GCE and AoA of LIS reached significance only for the shorter SOA can be considered as preliminary evidence toward this interpretation.

In conclusion, the current results demonstrate that the gaze-cue spatial orienting effect can be resisted in deaf and hearing early signers. Further research should help clarifying the role of sign language experience in modulating GCE. For instance, it would be interesting to expand the current paradigm to a context in which gaze-shifts are more directly relevant for linguistic communication (unlike here), or to contexts in which non-social and non-linguistic cues are used (e.g., arrow cues instead of gaze-shifts). Notwithstanding these future directions, our findings open the intriguing possibility that even the automaticity of a potent social cue (gaze-shift) can be resisted, when the same type of cue is processed automatically for different purposes (e.g., linguistic). Furthermore, they reveal that attentional deployment in deaf adults may obey to different mechanisms when processing stimuli with a social and communicative valence, rather than non-social ones (e.g., Chen et al., 2006; 2010; Parasnis & Samar, 1985). These findings point to a more determinant role of sign language when the former type of cues is adopted.

Study 1: Supplementary Material

5.2.1 Supplementary Methods

5.2.1.1 Participants

Table 5.1

Deaf Participants	Age	Degree of Deafness: Right ear	Degree of Deafness: Left ear	Age of Diagnosis (Years)	Mother:	Father:	Hearing Aid Usage	Raven's Progressive Matrices Scores
1	43	Severe	Severe	1	Hearing	Hearing	No	123
2	34	Severe	Severe	Birth	Hearing	Hearing	1 ear	118
3	23	Severe	Severe	Birth	Deaf	Deaf	No	120
4	27	Profound	Profound	Birth	Deaf	Deaf	No	110
5	22	Severe	Severe	Birth	Hearing	Hearing	No	110
6	23	Severe	Severe	3	Hearing	Hearing	2 ears	127
7	22	Severe	Severe	Birth	Deaf	Deaf	No	108
8	29	Severe	Severe	1	Hearing	Hearing	2 ears	128
9	25	Profound	Profound	3	Deaf	Deaf	2 ears	120
10	29	Profound	Profound	1	Deaf	Deaf	2 ears	110
11	34	Profound	Profound	1	Hearing	Hearing	2 ears	125
12	32	Severe	Profound	Birth	Deaf	Deaf	1 ear	128
13	25	Profound	Severe	3	Hearing	Hearing	1 ear	110
14	27	Severe	Severe	2	Hearing	Hearing	2 ears	125
15	27	Profound	Profound	2	Hearing	Hearing	2 ears	112
16	24	Severe	Severe	6/8 months	Hearing	Hearing	2 ears	106
17	26	Severe	Severe	5/6 months	Hearing	Hearing	2 ears	127
18	32	Severe	Severe	2	Hearing	Hearing	No	128
19	33	Profound	Profound	2	Hearing	Hearing	2 ears	127
20	27	Severe	Severe	3 months	Hearing	Hearing	2 ears	114
21	28	Severe	Severe	2	Hearing	Hearing	1 ear	127
22	25	Severe	Profound	Birth	Deaf	Deaf	No	108

Table 5.1: Selected anamnestic information about deaf participants (as collected through the questionnaire completed at the beginning of the experiment) and scores in the Raven's Progressive Matrices (all above pathological cut-off, which was an inclusion criteria for the study). For the variable 'Degree of Deafness', 'Profound' means a loss ≥81 dB in that ear, 'Severe' means a loss ≥61 dB in that ear. The questionnaire was developed by the ISTC-CNR personnel.

5.2.1.2 Linguistic measures

All deaf participants were assessed for their linguistic proficiency at the moment of testing, in spoken and written Italian and in Italian Sign Language (LIS). To collect an exhaustive and comprehensive assessment of both languages we used comprehension, production and repetition tasks in Italian and comprehension and production tasks in LIS. The Italian comprehension test was a standardized test (see below). All the other tests were developed by the ISTC-CNR personnel.

5.2.1.2.1 Italian Assessment

Comprehension test

To assess comprehension abilities in deaf participants we used a standardized test for written Italian used for students starting the 8th grade (MT test; Cornoldi & Colpo, 1995). Deaf participants read a text in Italian and answered 12 forced-choice questions regarding the text.

Production test

Deaf participants watched a 2 minutes cartoon twice. They were then asked to report to the experimenter what they have seen using spoken Italian. Subsequently, they were asked to summarize in a written text the plot of the cartoon. The entire test was registered through a video-camera.

Repetition test

Deaf participants were presented with 10 sentences in spoken Italian, of increasing length and difficulty. The experimenter said the sentence once (and repeated it if necessary) and deaf participants were instructed to repeat exactly the same sentence. The entire test was registered with a video-camera.

5.2.1.2.2 LIS Assessment

Comprehension test

Deaf participants watched a 5 minutes video of a story in LIS. Then participants had to answer to 12 forced-choice questions regarding the signed story they just saw.

Repetition test

Deaf participants were presented with 15 sentences in LIS, of increasing length and difficulty. The sentences were presented through a video, one at a time, and repeated if necessary. Deaf participants were instructed to repeat in signs exactly the same sentence. The entire test was registered with a video-camera.

Table 5.2

Deaf Participants	AoA of LIS (Years)	Production: Italian	Sentence Repetition: Italian	Comprehension: Italian	Comprehension: LIS	Sentence Repetition: LIS
1	3	-1,70	-1,64	-1,85	-1,33	0,59
2	15	-0,53	-0,28	-1,85	-1,33	0,42
3	Native	-1,11	-1,19	-0,03	1,29	0,77
4	Native	0,04	0,17	-0,76	0,24	0,06
5	2	-0,07	-0,28	-0,03	-0,81	0,77
6	21	0,44	1,08	0,70	1,29	-0,66
7	Native	1,43	-1,19	1,42	1,81	1,31
8	24	0,08	1,08	0,70	0,76	0,59
9	7	1,03	-1,64	0,33	0,24	-0,66
10	8	-	-	-0,39	0,24	-
11	20	0,11	0,17	0,33	-1,33	-1,20
12	Native	0,25	0,63	0,70	0,24	-0,48
13	20	-0,39	1,08	0,33	0,24	0,06
14	20	-0,06	0,63	-1,12	0,24	-1,20
15	18	-1,08	-0,28	-0,39	0,24	0,42
16	-	2,19	1,08	1,42	-1,85	-2,63
17	26	0,92	1,08	1,42	-1,85	-0,48
18	17	0,70	0,17	1,79	0,24	-0,48
19	6	-1,99	-1,64	-0,39	-0,28	0,59
20	Native	0,13	1,08	-0,03	-0,28	-1,20
21	18	0,82	0,63	-0,03	0,24	0,95
22	Native	-0,22	-0,74	-0,03	0,76	1,31

Table 5.2: Age of acquisition of Italian Sign Language (AoA of LIS) and z-scores of deaf participants in the LIS tests. These values were used in correlation analyses with the gaze cueing effect (GCE).

CHAPTER 6:

General Discussion

6.1 General Overview

The overall aim of the present thesis was to contribute to a deeper understanding of deafness-related plasticity in humans. To this aim I have addressed some critical aspects of the reorganization exerted by early auditory deprivation on behavior that remained largely overlooked by the existing literature. In particular, I focused on four main aspects: (i) the behavioral reorganization that occurs within the tactile modality of deaf adults; (ii) the possible modifications of the interactions between two intact sensory systems (i.e., vision and touch) as a consequence of auditory deprivation; (iii) the finer-grained definition of which mechanisms of visual attention are modified by bilateral deafness; (iv) the further investigation of the role of extensive visual training in driving the behavioral improvements reported in the deaf population compared to hearing controls (i.e., sign-language effects; action videogame players).

I will first summarize the results of all the studies reported in the previous chapters and then I will discuss them in a more general framework highlighting what they reveal in relations to the critical aspects I briefly recapitulated above.

6.1.1 Reaction to the environmental stimuli

Faster response times to visual events have been repeatedly documented in deaf adults compared to hearing controls (Bottari et al. 2010, 2011; Loke & Song, 1991; Reynolds 1993; see Pavani and Bottari 2012 for review). However, it remained an open issue to what extent this behavioral advantage could be specific for vision or could be related to more sensory unspecific processes (i.e., perceptual decision-making, response preparation, response impulsivity, sustained attention or motivation). Critical contribution of sensory unspecific changes predicted an extension of the response speed advantage also to other intact sensory modalities.

To further investigate the nature of this behavioral improvement and test directly to what extent behavioral effects of auditory deprivation are comparable across intact sensory modalities, I tested whether or not this visual reaction time advantage extended also to the intact tactile modality in the deaf population, using a simple detection task (**see Chapter 2, Study 1**).

Our findings revealed selective response speed advantage for the visual modality in deaf adults compared to hearing controls, which did not extend to tactile events. Overall, these findings strengthen the proposal that the repeatedly documented response speed advantage in deaf people may reflect early changes in the temporal dynamic of visual processing (Bottari et al. 2011), rather than changes occurring in other sensory unspecific mechanisms involved in simple detection. Furthermore, the present findings suggest that behavioral advantages triggered by auditory deprivation do not necessarily extend across all intact sensory modalities, ultimately suggesting that intact sensory systems reorganize independently from each other. Finally, these findings also highlight the relevance of the approach we adopted, namely, using the same task to test the same function across intact sensory modalities (see Heming & Brown, 2005 for a similar approach), as a valid tool to compare the effects of plasticity exerted by unisensory deprivations in the remaining perceptual systems (**see Chapter 2, Study 1**).

6.1.1.1 Detection of visual and tactile stimuli in hearing AVGPs

I presented the same simple detection task also to a group of hearing action videogame players (AVGPs) comparing their performance to a group of hearing non-gamers (NVGPs; **see Chapter 2, Study 3**). The rationale for running this study in AVGPs was the consideration that this hearing population undergoes a visual training for many aspects similar to the visual training deaf individuals constantly experience while interacting with the external world, without experiencing any sensory deprivation. Therefore, testing hearing AVGPs in the same task used for deaf adults also permits to indirectly investigate to what extent the plasticity exerts by avid action videogame playing acts upon the same mechanisms recruited by plastic changes related to bilateral deafness. Interestingly, reaction time improvement in response to abrupt visual events is also one of the most solid findings reported in hearing AVGPs compared to NVGPs (e.g., Castel et al., 2005; see Dye et al. 2009a for a review). However, it was still unknown whether this reaction time advantage would extend also to the tactile modality, which constitutes the sensory modality receiving the least training in the gaming environment.

Differently from what I reported for the deaf population, our findings demonstrated that in hearing AVGPs compared to NVGPs, the reaction time advantage for visual stimuli extended also to tactile stimuli. These findings represent strong evidence of the generalization potentials of AVGP training regimen across sensory modalities, documenting for the first time its extension also to a poorly trained sensory modality (i.e., touch). Furthermore, they strengthen the explanation proposed by Green and colleagues (2012) of AVGPs-related advantages in terms of a faster rate of evidence accumulation to reach a perceptual-decision compared to NVGPs (**see Chapter 2, Study 3**).

6.1.2 Localizing, discriminating and recognizing environmental stimuli

Several studies in the tactile modality reported impaired performance in deaf adults compared to hearing controls for time-related abilities (Bolognini et al., 2012; Heming & Brown, 2005). Instead, results obtained on the visual modality for the same domain of deaf cognition, produced more contrasting results (e.g., Heming & Brown, 2005; Kowalska & Szelag, 2006; Nava et al., 2008; Poizner & Tallal, 1987). These findings are particularly relevant because they highlight the possibility that abilities typically ascribed to the auditory system, such as time perception (Julesz & Hirsh, 1972; Miller & Taylor, 1948), could not developed adequately in the deaf population, suggesting the possibility that indeed some aspects of deafness-related plasticity fall within the perceptual deficiency hypothesis rather than within the compensatory hypothesis.

To further investigate this intriguing aspect of deaf cognition, I presented deaf adults and hearing controls with a duration discrimination task, in which stimuli were presented both in the visual and in the tactile modality (**see Chapter 2, Study 2**). My aim was to investigate whether the impairment of temporal processing was indeed more pronounced for touch compared to vision as the existing literature seemed to suggest, or whether it was instead supramodal, namely, equally affecting both sensory modalities.

Our findings show a clear supramodal speed-accuracy trade off in deaf adults compared to hearing controls. Regardless of whether the task was performed on vision or touch, deaf participants resulted faster than hearing controls, yet being also less accurate. We discussed this result in terms of recent mathematical models and computational neuroscience approaches for describing perceptual decision-making processes, which have conceptualized simple perceptual-decisions (e.g., decide whether stimulus-duration is short or long, as in this case) as the outcome of a mechanism of 'accumulation of information' (e.g., Beck et al., 2008; Furman & Wang, 2008; Ho et al., 2012; Wang, 2002; see Bogacz et al., 2009 for a review). The proposal is that clusters of neurons in decision-making related brain regions are selectively tuned to different perceptual choices (e.g., 'short' vs. 'long' duration) and operate as accumulators of perceptual evidence (e.g., Beck et al., 2008; Heekeren et al., 2008; Shadlen & Newsome, 2001; Usher & McClelland, 2001). In agreement with the notion that these neurons integrate sensory evidence over time, their firing rate gradually increases during the time interval between stimulus presentation and response (Gold & Shadlen, 2001; Heekeren et al., 2008; Schall, 2001). Therefore, the activation level of these 'evidence integrator neurons' is predictive of the participant's response. When a critical threshold is reached, response is initiated. Within this framework, speed-accuracy trade-off (SAT) behaviors have been generally described as arising either as the result of altered activity of the evidence integrator neurons at baseline or as the result of reduced response thresholds (e.g., Brown & Heathcote, 2008; Ratcliff & McKoon, 2008; Vickers, 1970). Importantly, results from several neuroimaging studies have suggested that SAT behavior results from baseline-related changes, as they reported fixed response thresholds (Ivanoff et al., 2008; Mordkoff & Grosjean, 2001; Ratcliff et al., 2003; Roitman & Shadlen, 2002).

We then proposed that the increased SAT behavior we observe in deaf adults (compared to hearing controls) might reflect enhanced baseline activity of the evidence integrator neurons. However, given previous evidence of non-SAT behavior in the deaf population for other types of perceptual-decisions (e.g., Bavelier et al., 2000; 2001; Bolognini et al., 2012; Dye et al., 2009; Finney & Dobkins, 2001; Hauthal et al., 2013) we excluded it as a general mechanism underlying all perceptual-decision making in the deaf population. Instead, we propose that the SAT behavior we reported in deaf adults might depend from altered sensory information that reaches the evidence integrator system already impaired, in turn eventually determining enhanced baseline activity of the integrator neurons (see Bolognini et al., 2012 for a proposal on the altered sensory mechanisms underlying temporal tactile impairment; **see Chapter 2, Study 2**).

6.1.2.1 Discrimination of duration of visual and tactile events in hearing AVGPs

I also tested a group of hearing action videogame players (AVGPs) and a group of non-gamers (NVGPs) in the same task I used for deaf adults (**see Chapter 2, Study 3**). The aim of this study was again to provide indirect evidence on whether or not AVGPs related plasticity acts upon the same mechanisms of deafness-related plasticity. Interestingly, as in the deaf population, plasticity effects in AVGPs compared to NVGPs involving spatial processing have been much more investigated than plasticity effects related to temporal processing of stimuli (see Bavelier et al., 2012 for a review). This is probably due to the fact that in action video games temporal features are trained to a lesser extent, as these games predominantly require allocating attention to spatial features of visual stimuli rather than to temporal features.

Again differently from the results obtained in the deaf population, AVGPs resulted supramodally faster than NVGPs at discriminating the duration of events, at the net of equal accuracy between the two groups. These results extend the evidence documenting the impressive generalization potentials of AVGP training regimen to untrained stimulus features (i.e., temporal features) in addition to untrained sensory modalities (i.e., touch). Moreover, they further corroborate the explanation proposed by Green and colleagues (2012), of AVGPs-related advantages in terms of a faster rate of evidence accumulation to reach a perceptual-decision compared to NVGPs (**see Chapter 2, Study 3**).

6.1.3 Control and orientation of visual attention in space

Recent studies carried-out in the hearing population have highlighted the crucial role of time for successfully disambiguating the relative contributions to performance of the two fundamental mechanisms of attention selection, namely, stimulus-driven and goal-driven selection (see van Zoest et al., 2010 for a review). By manipulating the relative saliency of stimuli presented in search displays during overt target-selection tasks, these studies revealed that early initiated responses are predominantly guided by stimulus-driven selection, whereas it takes time for voluntarily directed behaviors to control performance (e.g., van Zoest et al., 2004; van Zoest & Donk, 2005; 2008).

With the innovative aim of characterizing the temporal dynamic of the interplay between these two attentional components in the deaf population, ultimately aiming at investigating to what extent auditory deprivation influences their interaction, I tested a group of deaf adults and a group of hearing controls in a version of the overt target-selection task repeatedly used in the hearing population (e.g., van Zoest et al., 2004; van Zoest & Donk, 2005; 2008; **see Chapter 4, Study 1**). In this study I also carefully controlled for linguistic abilities of deaf participants. In collaboration with the ISTC-CNR in Rome we developed a set of linguistic tests for assessing the proficiency of deaf participants both in Italian and in Italian Sign Language (LIS). In this particular study I focused only on the results obtained in the tests assessing LIS proficiency and I correlated them with the performance to the overt target-selection task (**see Chapter 4, Study 1** for the description of the tests). My aim was to carefully investigate to what extent performances of deaf participants could be explained by linguistic proficiency.

Results showed that deaf adults were overall slower than hearing controls at initiating their saccades as well as initially less captured by irrelevant salient information. However, a multinomial model applied to the data documented comparable underlying stimulus-driven and goal-driven processes between the two populations. Therefore these results strongly suggest that the different oculomotor behavior we documented for deaf adults and hearing controls is a consequence of the slow-down in saccadic latencies we observed in the deaf population rather than a consequence of modified underlying mechanisms. In other words, deaf people were able to postpone their responses to a larger extent than hearing controls, consequently limiting their initial capture by salient information. Importantly, we also showed that this slow-down of saccadic latencies in the deaf population was not explained by any of the linguistic measures we collected. Taken together, what we consider the most relevant aspect of these results is the evident parsimonious nature of the plastic changes we reported. Indeed, deaf adults were able to differ in their performance compared to hearing controls by modifying a very simple feature of oculomotor behavior, namely by delaying saccadic latencies. This simple modification proved to be already sufficient to enter the search function at a later step in which the stimulus-driven response bias was already decreasing, ultimately allowing deaf participants to be less captured by irrelevant salient stimuli in the display compared to hearing controls (**see Chapter 4, Study 1**).

6.1.3.1 Overt target-selection in hearing AVGPs

Following a similar logic to the one presented for the previous studies, I used this same overt target-selection task to characterize the temporal dynamic of automatic vs. voluntary components of attention as a consequence of intensive action videogame playing (**see Chapter 4, Study 2**). My aim was to test to what extent intensive visual training that is not paired with a sensory deprivation exerted the same type of reorganization on visual attention mechanisms as intensive visual training as a consequence of auditory deprivation.

Once again differently from results obtained with the deaf population, the results of this study revealed overall faster initial saccades in hearing AVGPs compared to NVGPs paired with overall less accurate responses in AVGPs, especially for early initiated responses. Additional analyses showed that these differences in performance were explained primarily by the faster saccadic latencies reported in AVGPs and they suggested that the underlying mechanisms ultimately driving selection in the two groups are similar (**see Chapter 4, Study 2**).

6.1.4 Visual attention to social cues

The majority of studies addressing the reorganization occurring within visual attention as a consequence of early bilateral deafness focused on covert attention mechanisms (see Dye & Bavelier, 2010; Bavelier et al., 2006 for reviews). One aspect that remained unexplored in this extensive literature, it is the deployment of covert visual attention when social cues are into play. To specifically address this issue, I tested covert attentional orienting properties when complex, social cues were presented in deaf adults compared to hearing controls. In particular, I used a gaze-cue paradigm (e.g., Driver et al., 1999; Friesen & Kingstone, 1998; 2003; Friesen et al., 2004; Khurana et al., 2009; Quadflieg et al., 2004; Tipples, 2005) in which participants were required to ignore the direction of gaze of a central face, while performing a peripheral shape discrimination task (**see Chapter 5**). To control for possible effects due to linguistic proficiency, also in this study we administered to deaf participants the same set of linguistic tests used in the overt target-selection task (see **Chapter 5, Additional Materials**), which I then correlated with the performance of deaf participants to the gaze-cue task.

Contrary to our predictions and differently from hearing controls, deaf adults did not show the typical facilitatory effect on their reaction times when a valid gaze-cue was presented. Interestingly, among all the linguistic measures we collected, only the age of acquisition of Italian Sign Language (LIS) correlated with the performance of deaf participants. The earlier deaf participants acquired LIS, the less they were sensitive to the gaze-cue effect. In a control experiment, I also tested a group of hearing native signers (CODAs: Children Of Deaf Adults), which also did not show any gaze-cue effect (**see Chapter 5**).

Taken together, these findings challenge the widespread notion of gaze-cues as automatic and unavoidable cues to orient attention in space (see for instance Galfano et al., 2012). Interestingly, in sign language gaze-directions are used to convey linguistic rather than social or attentional information. In particular, they are used in narrations to indicate role shifting among characters (e.g., Pizzuto, 2007). We thus proposed that this absence of gaze-cue effect we observe in deaf early signers and hearing native signers have two possible explanations. The first one is that early exposure to sign language might elicit the development of voluntary strategy to prevent automatic spatial-orienting to gaze directions, which otherwise, might be disruptive for efficient communication. Alternatively, it could also be that in early signers gaze-shifts are still processed automatically, but they acquired a linguistic rather than a social valence (**see Chapter 5**).

Overall, this work suggests that attentional deployment in deaf adults may obey to different mechanisms when processing stimuli with a social and communicative valence, rather than non-social ones (e.g., Chen et al., 2006; Colmenero et al., 2004; Parasnis & Samar, 1985) and it also suggests a more determinant role of sign language when the former type of cues is adopted.

6.1.5 Interaction among intact sensory modalities

An important limit of the literature on the effects of unisensory deprivations on behavior concerns the fact that typically it has investigated changes in cognitive functions examining one remaining sensory modality at a time. Although, this approach clearly proved highly informative, it largely overlooked possible changes in the interactions between reorganized sensory systems, ultimately limiting our understanding of the impact of unisensory loss on perceptual processing (but see for blindness: Hötting & Röder, 2004; Van der Lubbe et al. 2010; see Occelli et al., 2013 for a review; for deafness: Karns et al., 2012). Moreover, unisensory approaches to the study of crossmodal changes in early bilateral deafness suggest an imbalance in the reorganization occurring in vision and touch. As already mentioned, reorganization in vision has been repeatedly documented in both brain and behavior, and some of the observed behavioral advantages have been linked to neuroanatomical changes starting from the very early stages of visual processing (Bottari et al., 2011; Codina et al., 2011). By contrast, reorganization occurring for the tactile modality appears considerably more uncertain, both at the behavioral and at the neuroanatomical level (e.g., Auer et al., 2007; Bolognini et al., 2012; Frenzel et al., 2012). These results ultimately suggest that reorganization in vision might always dominate behaviors of deaf adults.

To test this hypothesis I compared deaf and hearing adults in a multisensory, spatial interference task namely, the ‘Cross-modal Congruency task’ (CCE; e.g., Spence, Pavani & Driver, 2000; 2004; see Spence, Pavani, Maravita & Holmes, 2008 for a review; **see Chapter 3**). We chose this task because its spatial nature could have maximized the possibility of showing visual dominance effects in the deaf population. Indeed, according to the maximum-likelihood estimation model (Ernst & Banks, 2002) vision is the sensory modality that dominates spatial perception and consequent behavior. We hypothesized that this visual spatial dominance could have been stronger in the deaf population compared to hearing controls. We thus presented to deaf and hearing participants the classic CCE task in which participants are required to respond to the elevation of the tactile target while ignoring a concomitant visual distractor, which could be either congruent or incongruent with the elevation of the target. In addition, we asked our participants to perform also the reciprocal of this task, namely, respond to vision and ignore touch (**see Chapter 3**).

Contrary to a prediction of pervasive visual dominance in deaf adults, results revealed that CCE in both experimental tasks (‘respond to touch/ignore vision’ and ‘respond to vision/ignore touch’) was comparable between the two groups. These novel results show a remarkable flexibility of the reorganized visual system of deaf people, which is particularly impressive if one thinks to the early stages of visual processing for which differences between deaf and hearing individuals have been documented (e.g., retinal level: Codina et al., 2011; primary and secondary visual cortices: Bottari et al., 2011).

However, our findings still reveal some aspects of visual dominance in the deaf population, albeit context-dependent. When deaf adults were initially presented with the task in which vision was the target modality (i.e., respond to vision, ignore touch), they showed, compared to hearing controls, larger CCE in the following task, in which vision became the distractor modality (i.e., respond to touch/ ignore vision). On the contrary, this task-order effect was not present for the tactile modality (i.e., when touch was initially probed as the target modality and then it became the distractor modality). These latter findings then, suggest that when the reorganized visual system is initially activated as the to-be-attended sensory modality, deaf participants find it particularly hard to inhibit its dominance over the tactile modality if they are subsequently required to ignore spatial visual information (**see Chapter 3**).

6.2 General conclusions

All the findings summarized in the previous sections confirm the notion of the multifaceted nature of deafness-related plasticity (see for instance Bavelier et al., 2006; Pavani & Röder, 2012) by contributing to further extend our understanding of its effects on behavior.

To provide a more general framework for interpreting these results, in the following sections I will try to address the main points and related critical issues that emerged from the set of studies I just described.

6.2.1 Plasticity in the tactile modality of deaf adults

The further investigation of behavioral changes involving the tactile modality as a consequence of early bilateral deafness represents a crucial aspect for understanding plasticity effects triggered by auditory deprivation. Indeed, the existing literature produced fewer and contrasting results when this sensory modality has been investigated, as opposed to much more consistent findings obtained in the visual modality. In particular, behavioral advantages in tactile processing for deaf adults compared to hearing controls had been documented only for sensitivity to vibrotactile stimuli delivered on the fingers (Levänen & Hamdorf, 2001). Instead, studies addressing other tactile abilities in deaf people have failed to report any behavioral advantage (e.g., Bolognini et al., 2012; Moallem et al., 2010), or even documented deficits compared to the hearing population (Bolognini et al., 2012; Frenzel et al., 2012; Heming & Brown, 2005). Furthermore, there is a growing corpus of evidence that is now suggesting that in deaf adults the deafferented auditory regions, and in particular the primary auditory cortex, are heavily recruited by the somatosensory modality (Auer et al., 2007; Karns et al., 2012; Levänen et al, 1998), possibly due to its functional similarity and also to its structural proximity to the auditory cortices. However, it is not clear to what extent this recruitment follows the functional organization of hearing auditory cortices, as for instance it has been documented for tactile and auditory recruitment of the blind visual cortices (e.g., Bedny et al., 2010; Collignon et al., 2011; Stilla et al., 2008). Moreover, it is still uncertain also whether this recruitment entails any benefits for actual performance (e.g., Bolognini et al. 2012; Karns et al., 2012). Indeed, there is some evidence suggesting that crossmodal recruitment of auditory regions by the somatosensory modality might lead to impaired behaviors in the deaf population (Bolognini et al., 2012). Importantly, these findings point to the possibility that some aspects of crossmodal recruitment might be maladaptive, producing, in turn, behaviors falling within the predictions of the perceptual deficiency hypothesis.

The approach I used to further test reorganization occurring in the tactile modality of deaf adults was a comparative approach between the effects on behaviors exerted by the same task in both the visual and in the tactile modality (see Heming & Brown, 2005 for a similar approach). This approach proved to be very informative, highlighting though, a complicated pattern of results.

In particular, exploiting this approach, I tested whether one of the most robust finding reported for the visual modality in deaf adults, namely reaction time to visual events, extended also to the tactile modality. Results confirmed the visual advantage, which however did not extend to the tactile modality in deaf adults compared to hearing controls (**see Chapter 2, Study 1**). Importantly, we observed comparable performance between the two groups of participants for detecting tactile events, ultimately excluding an interpretation of this result in terms of the perceptual deficiency hypothesis, which would have predicted impaired tactile performance in the deaf population.

Instead, when testing vision and touch in a duration discrimination task, I observed a supramodal-impaired behavior in deaf adults compared to hearing controls (**see Chapter 2, Study 2**). This result suggests that there are some aspects of deaf-related performance that indeed fall within the perceptual deficiency hypothesis, but they seem to involve supramodally a set of abilities (i.e., temporal abilities generally ascribed to the auditory system such as the discrimination of subtle differences in the duration of events), rather than involving selectively the tactile modality.

Overall, then these results suggest that the plasticity exerted by deafness in the tactile modality is highly dependent by the function tested. Future studies should investigate whether there are also functions that are supramodally improved in early deaf adults. I propose that one potential good candidate for testing this hypothesis it is the discrimination of motion direction, which has been repeatedly reported as improved for the visual modality of deaf adults compared to hearing controls (e.g., Neville & Lawson, 1987; Hauthal et a., 2013), involving also deaf auditory cortices (e.g., Finney et al., 2001; Fine et al., 2005).

Finally, these results highlight the critical role of time-related abilities as a key set of abilities to be studied in order to shed light on the principles underlying cross-modal recruitment of auditory cortices as a consequence of early bilateral deafness.

6.2.2 Interaction among intact sensory modalities

Given the suggested disparity in the reorganization occurring in vision and touch as a consequence of bilateral deafness, and moreover, given the early level of visual processing for which differences between deaf and hearing participants have been identified (i.e., the retinal level: Codina et al., 2011; primary and secondary visual cortices: Bottari et al., 2011), I wanted to test the hypothesis that vision would always and unavoidably dominate behavior in deaf adults compared to hearing controls (**see Chapter 3**). However, when testing multisensory interference in a spatial task, namely, Cross-modal Congruency task (CCE), I found comparable interference effects in deaf adults and hearing controls. These novel results show a remarkable flexibility of the reorganized visual system of deaf people, which is indeed highly adaptive for achieving efficient everyday interactions with the external multisensory world. Actually, inhibiting visual dominance when disruptive for the task, it permits to deaf individuals to not be impaired in their performance compared to hearing controls. However, also some aspects of visual dominance emerged, albeit context-dependent (**see Chapter 3**).

Importantly for interpreting multisensory interactions in the deaf population, there is one other recent study that investigated visuo-tactile interactions following bilateral deafness, yet focusing on temporal processing, rather than on spatial processing as here (Karns et al., 2012). This study showed enhanced interference of tactile irrelevant stimuli in deaf adults compared to hearing adults, which was paired with increased activation of the rostrolateral region of the Heschl's gyrus. Even though the authors interpreted this result as preliminary evidence in favor of enhanced tactile temporal processes in the deaf population, there is also some evidence suggesting that this auditory activation might be disruptive for actual performance (Bolognini et al., 2012; see **Chapter 2, Study 2** for further discussion).

The different multisensory interference behaviors reported in my work on CCE (**see Chapter 3**) and in the work by Karns and colleagues (2012) might suggest that multisensory perception reorganizes differently depending on the set of abilities investigated. Moreover, the comparison between the results of these two studies suggests that spatial and temporal abilities reorganize differently as a consequence of early auditory deprivation, not only at the unisensory level (as documented above), but also at the multisensory level.

6.2.3 Mechanisms of visual attention modified by bilateral deafness

An extensive literature has been dedicated to the investigation of the mechanisms of visual attention that reorganize as a consequence of early auditory deprivation (see Dye & Bavelier, 2010; Bavelier et al. 2006 for reviews). This literature mainly focused on identifying which aspects of stimulus-driven or goal-driven attentional processes were modified by bilateral deafness, using covert attention tasks.

Within this context, I aimed at characterizing whether the temporal dynamic of the interplay between these two components of attentional selection differed between deaf adults and hearing controls by exploiting a task, namely, overt target-selection, which proved to be effective for providing this information when used in the hearing population (see van Zoest et al., 2010 for a review). By adopting this overt-attention task, I also aimed at further characterizing oculomotor behavior in the deaf population, which until now received little consideration (**see Chapter 4, Study 1**). Results showed that deaf adults were overall slower at initiating their saccades compared to hearing controls as well as initially less captured by irrelevant salient information. However, the underlying stimulus-driven and goal-driven processes resulted comparable between the two populations. Importantly, the delayed oculomotor behavior of deaf adults was not explained by any linguistic measure we have collected (see next section for further discussion). These results then strongly suggest that it was *simply* the slow-down of saccadic responses that we observed in the deaf population to cause their decreased saliency capture by irrelevant salient stimuli (**see Chapter 4, Study 1**). Thus, these results highlight the intriguing perspective that deafness-related effects might also involve subtle, very simple modifications, which in turn influence the outcome of behaviors without modifying the underlying mechanisms. Indeed, these modifications carry the advantage of being very versatile, namely, prone to adapt them-selves to potentially every specific context and every specific request coming from the external environment. In other words, this result once again suggests the flexibility of the reorganized visual system of deaf adults and its property of being subjected to context-dependent plasticity effects (see previous section on the interaction across reorganized sensory systems).

In line with this flexibility account, these findings also suggest that bilateral deafness does not always prioritize the stimulus-driven exploration of the external environment, as suggested by several previous studies (e.g., Bottari, Valsecchi & Pavani, 2011; Chen et al., 2006; Proksch & Bavelier, 2002). Indeed, another novel and intriguing finding that emerges from my work on overt orienting is that deaf adults appear to be able to exert enhanced control on their oculomotor behavior compared to hearing participants.

Finally, the other aspect of attention I have investigated concerned the orienting of covert attention when social-cues (i.e., gaze-cues) were presented (**see Chapter 5**). In this work, I reported an absence of the typical gaze-cue effect for orienting attention in space in the deaf population, which appeared to be modulated by early age of acquisition of a sign language. Importantly the same pattern of results was observed also when a group of hearing native signers was tested in the same task (see next section for further discussion of these results; **see Chapter 5**).

Overall, at a fast glimpse, these results might seem to further corroborate the context-dependent nature of the visual changes related to bilateral deafness. Indeed, in sign languages gaze-shifts convey linguistic rather than social or attentional-orienting meanings (e.g., Pizzuto, 2007). Consequently, our results might be interpreted as evidence documenting the influence of the particular context in which deaf participants mostly experienced this type of stimulation (i.e., linguistic contexts; social contexts) on the way they preferentially and automatically process gaze-shifts. However, in our paradigm the gaze-shifts did not convey any linguistic information. This result then might also highlight some constraints to the flexibility of visual-related behavioral changes as a consequence of bilateral deafness. Future studies are therefore particularly needed to test for instance in further detail whether or not this lack of orienting-effect would extend to other types of stimuli (i.e., not gaze-related stimuli) or whether or not this lack of orienting-effect would extend to actual linguistic contexts.

6.2.4 Role of visual training in driving deafness-related behavioral improvements

To address as systematically as possible the role of extensive visual training in behavioral improvements documented in deaf adults compared to hearing controls, I identified two types of training, which could dramatically influence deaf people behaviors. The visual training linked to the intensive use of a sign language to communicate, and the visual training due to the everyday experience with a mainly visual world. In an attempt to isolate the first training aspect, I collected when possible, quantitative data on the linguistic proficiency of deaf participants, which I then correlated with actual performances to the tasks I used. In an attempt to isolate the second training aspect, I tested when possible, also a group of hearing action videogame players (AVGPs) in exactly the same tasks I used for deaf adults. Hearing AVGPs undergo an intensive visual training for many aspects similar to the one required to deaf adults to orient them-selves in the external environment, without being sensory deprived. In the last ten years many works showed impressive improvements in visual tasks in this population compared to non-gamers (see Bavelier et al., 2012 for a review). Finally, investigating plasticity effects in hearing AVGPs also permit to directly compare (i) plasticity effects exerted in a sensory deprived brain with those exerted in a non-sensory deprived brain and (ii) plasticity effects developed since infancy with those developed only during adulthood.

6.2.4.1 Effects of sign language on deaf adults behavior

Until now, several studies demonstrated the importance of an early acquisition of a sign language (i.e., before the age of three) in order to develop an efficient linguistic system (e.g., Mayberry & Lock, 2003), which also recruits the same brain regions of the hearing linguistic system (e.g., Mayberry et al., 2011; see for a review MacSweeney et al., 2008). However, it was still unknown whether the same early acquisition constraints also applied to the non-linguistic visual changes documented in deaf signers (e.g., Emmorey et al., 2009; Watanabe et al., 2011). For instance, Emmorey and colleagues (2009) showed different face exploration's patterns in deaf native signers compared to hearing participants who were beginners in sign language, during a sign comprehension task. Hearing participants spent more time looking to the signing hands, whereas deaf native signers tended to keep their eyes more stable, looking predominantly at the eye-area of the signer (see also Watanabe et al., 2011 for converging results obtained during an evaluation of emotion task). Indeed these visual, non-linguistic modifications could also be the result of the massive visual training exerted by sign language, thus being linked more with sign language proficiency than with the age of acquisition of a sign language.

To be able to disentangle this issue we developed, in collaboration with the ISTC-CNR in Rome, a set of linguistic tests aiming at systematically assessing the linguistic proficiency of deaf participants both in Italian and in Italian Sign Language (LIS) and we administered it to as many deaf participants as possible (see **Chapter 4, Study 1; Chapter 5** for a description of the tests). Afterwards, I correlated the results of these linguistic tests with the performance of deaf participants in the overt-target selection task (**Chapter 4, Study 1**) and in the gaze-cue task (**Chapter 5**).

As anticipated above, we found no correlation between the performance in the overt-target selection task and the scores obtained in the linguistic tests (**see Chapter 4, Study 1**). Instead we found a significant modulation of the gaze-cue effect by the age of acquisition of LIS. All the other linguistic measures did not correlate with the performance to the gaze-cue task (**see Chapter 5**).

The fact that we do not find any sign-language modulation in the overt-target selection task, it corroborates the notion that lower-order abilities or the processing of simple stimuli, are not influenced by sign language and that instead, observed differences in behavior should be attributed to deafness per se (for similar conclusions see Bavelier et al., 2001; Fine et al., 2005; Neville & Lawson, 1987c; Proksch & Bavelier, 2002). Instead, higher-order, more complex abilities, or more complex stimuli, as directing-attention to social or linguistic-cues, seem to depend more on sign language than on deafness per se (see also for instance, Boutla, Supalla, Newport & Bavelier, 2004; Geraci, Gozzi, Papagno & Cecchetto, 2008 for results on short-term memory).

Furthermore, these results extend the crucial role of early sign-language acquisition not only to the development of an efficient linguistic system (e.g., Mayberry & Lock, 2003) but also to the development of the non-linguistic modifications related to sign language, highlighting the importance of respecting the constraints of sensitive periods also to develop these ‘secondary effects’ of sign language acquisition.

6.2.4.2 Effects of training induced by action videogames

The rationale for testing hearing action videogame players (AVGPs) in the same tasks used for the deaf population was the consideration that while playing, hearing AVGPs undergo a similar training to the one required to deaf people for efficiently interacting with the external environment, without being sensory deprived. Therefore we thought they would make a good control group to exclude training-effects as an explanation for behavioral differences reported in the deaf population in perceptual tasks.

Interestingly, our results clearly suggest that besides the similar visual training these two populations undertake, the two forms of plasticity that are elicited, act upon different underlying mechanisms. Indeed, when I tested deaf adults and hearing AVGPs in the same tasks, the two populations showed different behavioral modifications. In particular, while in deaf adults the reaction time advantage in simple detection was selective for the visual modality not extending to touch, AVGPs compared to non-gamers (NVGPs) showed a supramodal reaction time advantage involving both vision and touch (**see Chapter 2, Study 3**). Furthermore, while deaf adults compared to hearing controls showed a clear supramodal speed-accuracy trade off when tested in a discrimination of durations of visual and tactile events, AVGPs compared to NVGPs showed faster responses to both visual and tactile stimuli at the net of comparable accuracy performance between the two groups (**see Chapter 2, Study 3**).

Overall, all these results obtained with AVGPs corroborate the proposal by Green and colleagues (2010) for which all the perceptual advantages documented in AVGPs compared to NVGPs are ascribable to faster perceptual-decision making in this population. In particular, Green and colleagues fitted the behavioral data obtained by AVGPs and NVGPs in a standard coherent dot motion direction task (Palmer, Huk & Shadlen, 2005), into two models of perceptual-decision-making (Beck et al., 2008; Palmer et al., 2005). According to both models AVGPs resulted faster than NVGPs in accumulating evidence from the environment in order to disambiguate relevant information from noise, ultimately being able to reach faster than NVGPs a perceptual decision (see **Chapter 2, Study 3** for a more detailed description of this work).

Instead, our results obtained with deaf adults in the same tasks corroborate the notion that all the perceptual advantages documented for deaf adults compared to hearing controls are ascribable to changes occurring at the sensory level (e.g., Bolognini et al., 2012; Bottari et al., 2011), rather than at higher levels of information processing.

Finally, deaf adults and hearing AVGPs also differed in the performance to the overt target-selection task. Indeed while deaf adults compared to hearing controls resulted overall slower at initiating their saccades, consequently being also less captured by irrelevant salient information early in time, AVGPs compared to NVGPs resulted overall faster at initiating their saccades, consequently being overall more captured by irrelevant salient information, especially for early-initiated saccades (**see Chapter 4, Study 2**). Similar to deaf adults, subsequent analyses suggested that the underlying mechanisms subserving stimulus-driven and goal-driven processes did not differ between AVGPs and NVGPs. These latter findings could highlight a possible limit of the speeded behavior repeatedly reported in AVGPs compared to NVGPs (see Dye et al., 2009a for a review), as their faster oculomotor behavior was detrimental for the actual performance to the task. However, we cannot conclusively comment on these findings as we are now developing a multinomial model similar to the one we used for deaf adults (**see Chapter 4, Study 1**), which we want to apply also to the data of AVGPs and NVGPs obtained in the overt target-selection task. Indeed, results of this model will permit us to better investigate whether or not AVGPs and NVGPs differ for what it concerns the developing over time of the stimulus-driven and goal-driven functions.

Overall, however, these sets of results strongly suggest that the plasticity exerted by early bilateral deafness and the plasticity exerted by avid action videogame playing substantially differ for what it concerns the mechanisms these two forms of plasticity recruit. In other words, these results strongly suggest that beside being exposed to a similar visual training, plasticity effects exerted in a sensory deprived brain (early bilateral deafness) differ from those exerted in a non-sensory deprived brain (AVGPs) as well as that plasticity effects developed since infancy (early bilateral deafness) differ from those developed only during adulthood (AVGPs).

6.3 Concluding remarks

Deafness-related plasticity exerts a wide variety of effects on behavior. As clearly documented throughout this thesis, plastic effects as a consequence of early bilateral deafness extend selectively to certain functions but not to others ultimately producing some aspects of modified behaviors falling within the compensatory hypothesis and some other aspects falling within the perceptual deficiency hypothesis. Importantly, these data also provide initial evidence that vision and touch might to a certain extent, reorganize independently from one another as a consequence of early bilateral deafness and that also the way they interact with each other shows some modified aspects. Notably, the majority of the behavioral modifications I documented in this thesis were not modulated by training-related abilities, thus being ascribable only to deafness-related plastic changes.

Overall, what amazed me the most of this set of results is the remarkable flexibility of which are capable the reorganized sensory systems, and in particular the reorganized visual system of deaf adults, which I believe clearly emerged from my findings. This flexibility is particularly intriguing given that the deaf participants that I have tested were either congenitally deaf adults or anyway they had acquired bilateral deafness early in life (i.e., before the age of three).

Future studies should investigate whether the same flexibility in plastic effects on behavior is present also in conditions of bilateral deafness acquired later in life. In addition, it would be interesting to investigate the development of this flexibility across the lifespan. In other words, it would be relevant to assess whether this flexibility emerges gradually during the life of deaf people or instead it is an intrinsic property of deafness-related plasticity (i.e., once plastic effects appear in the behaviors of deaf children, they are already as flexible as they appear to be in deaf adults).

Importantly, this research direction has the potential to inform education and rehabilitation protocols and orient policy-making experts for designing dedicated interfaces for deaf children and adults or dedicated work or school environments aiming at maximizing their efficiency in the interaction with the external environment.

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