Processing resources and interplay among sensory modalities: an EEG investigation

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The primary aim of the present thesis was to investigate how the human brain handles and distributes limited processing resources among different sensory modalities. Two main hypothesis have been conventionally proposed: (1) common processing resources shared among sensory modalities (supra-modal attentional system) or (2) independent processing resources for each sensory modality. By means of four EEG experiments, we tested whether putative competitive interactions between sensory modalities – regardless of attentional influences – are present in early sensory areas. We observed no competitive interactions between sensory modalities, supporting independent processing resources in early sensory areas. Consequently, we tested the influence of top-down attention on a cross-modal dual task. We found evidence for shared attentional resources between visual and tactile modalities. Taken together, our results point toward a hybrid model of inter-modal attention. Attentional processing resources seem to be controlled by a supra-modal attentional system, however, in early sensory areas, the absence of competitive interactions strongly reduces interferences between sensory modalities, thus providing a strong processing resource independence.

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1. General introduction

Despite our naive impression that we can process the bigger part of the information that we receive in a given amount of time and space, we are actually able to deeply process a rather small fraction of information at a time.

Our capacity to process stimuli is, indeed, highly limited (Broadbent, 1952), but at the same time very efficient; such a capacity implies that the human brain has developed throughout its evolution effective ways to circumvent such constraints. Beyond a remarkable ability to predict and recognize patterns, the most essential way the human brain “knows” to optimize processing resources is *selective attention*.

Although, according to William James (1890) everyone intuitively knows what attention is, currently a comprehensive definition of attention is still missing. Attention has been generally seen as a sort filter mechanism that the brain adopts to select behaviourally relevant information to the detriment of irrelevant one and/or to highlight specific relevant information. Although, for theoretical reasons and empirical convenience, research has mainly focused on uni-sensory attentional processing, it is quite arduous to find in our environment exclusively “uni-sensory” stimuli.

Indeed, in order to have unified and coherent representation of the outside world, the majority of stimuli require to integrate information relative to different sensory modalities. However, despite the fact that several sensory modalities are simultaneously present, we often need to select a specific sensory modality and ignore other ones to optimize our perception. Imagine to be in a crowded public place: you are desperately trying to have a conversation with a friend, people around talk out loud, bump into you; nevertheless you try to focus on the voice of your interlocutor. Given the limited amount of information processing, how can the human brain handle such a constant flow of competing information? A further and more fundamental question arises: is there any competition between different sensory modalities or is it just a characteristic specific to single modalities?

The aim of the present work is to test whether basic competitive interactions in primary sensory areas, traditionally observed within a single modality (Desimone & Duncan,1995), can be observed across sensory modalities. Consequently, we aim to investigate whether there is a supra-modal attentional control mechanism or whether there are distinct independent control mechanisms for each sensory modality.

In order to pursue our investigation, we considered two main sensory modalities, namely vision and touch, although in one experiment we employed also the auditory modality. In the following chapter, I will give a short overview regarding the current knowledge about visual and tactile attention and the interplay between sensory modalities and attention.

1.1 Selective attention

Even though attention cannot be strictly considered as a unitary process – given the diverse types of attention and processes that this concept comprises – in this paragraph I will give a short overview of the common characteristics of visual and tactile attention.

As introduced in the previous section, limited processing resources make attention intrinsically a selective process. Imagine, for instance, to observe a cluttered scene, your brain is unable to process simultaneously each element that composes it. Single elements or a specific subgroup of elements need to be selected among others in order to receive a further neural processing and thus gain behavioural advantage in terms of faster reaction times, lower thresholds and higher accuracy (Pestilli & Carrasco, 2005; Posner, Snyder, &

Davidson, 1980).

In order to accomplish that, attention can be voluntarily directed towards a behaviourally relevant stimulus or involuntarily redrawn by a sudden unexpected event. Hence, selective attention has been traditionally subdivided into two main kinds of processes: *bottom-up* and *top-down*.

Bottom-up processes pertain the so called *exogenous attention:* it refers to that kind of attention *involuntarily* captured by a sudden appearance or change of a stimulus – independent of the sensory modality – as a function of the potential behavioural relevancy and saliency of the stimulus.

Top-down processes instead concern *endogenous attention:* it refers to that kind of attention *voluntarily* addressed towards a relevant stimulus.

Although there is a continuous interplay between them (see for review: Corbetta & Shulman, 2002), for theoretical and empirical reasons these two processes have been mostly studied separately. It is not yet clear whether these processes are entirely or partly independent and consist of two separate neural systems. Several studies support the view that the respective underlying physiological circuits might overlap, although the two types of processes might still maintain a certain degree of independence. Numerous visual imaging studies reported several common neo-cortical areas – occipital, parietal and frontal regions (Corbetta & Shulman, 2002; Hopfinger, Buonocore, & Mangun, 2000; Kastner, Pinsk, De Weerd, Desimone, & Ungerleider, 1999) – active during both processes, therefore suggesting at least a partial coincidence between the two processes. However, while re-entrant feedbacks – from parietal and frontal cortices to primary sensory areas – seem to play a crucial role in endogenous attention, the same cortical areas are not necessarily involved in exogenous attention. While initially, endogenous attention was thought to be confined to neo-cortical structures, recent studies have shown the involvement of sub-cortical structures, such as the superior colliculus, during deployment of endogenous attention. A recent study conducted in non-human primates (Busse, Katzner, & Treue, 2008) shows a faster time course in exogenous attention as compared to the time course relative to endogenous attention. This difference clearly supports the view of two independent systems, although strictly related.

1.2 Visual attention

A further distinction usually made in visual attention research is between *overt* and *covert attention.* The former term indicates the case in which a person's sight is *directed* towards the attended stimulus, while the latter term, on the contrary, indicates a situation in which a person's sight is *not directed* towards that specific stimulus, but attention is “covertly” directed to the relevant stimulus. Thus overt attention is inherently a serial process, while covert attention can be directed in parallel to different locations (e.g. Müller, Malinowski, Gruber, & Hillyard, 2003). Covert and overt attention are naturally linked to *spatial attention.* Among the features necessary to select information from the environment, space is certainly the most studied one. In 1980, Michael Posner conceived an experimental paradigm that allowed to investigate how the probability of predicting a stimulus location could effect the response to a peripheral stimulus. Posner presented a central cue that predicted in 80% of the cases the valid location (left or right portion of a screen) of a stimulus and consequently in 20% of the cases the invalid location. A neutral cue, instead, did not provide any prediction serving as baseline. As expected, reaction times (RT) were slower in the valid condition as compared to the neutral condition, while RT were slower in the invalid condition when compared to the neutral condition. Since then, spatial attention has been extensively investigated by means of different methods (Electroencephalogram:

Hillyard, Vogel, & Luck, 1998 functional magnetic resonance imaging: Corbetta & Shulman, 2002) in order to understand the nature and the role of different pathways involved in endogenous and exogenous spatial attention (see previous section).

In order to select information from the environment, the human brain does not rely exclusively on spatial information, but also on different types of stimulus features, such as colour, orientation, spatial frequency, movement etc. For instance, if you are looking for a friend wearing a red t-shirt in a crowded square, you naturally tend to rely on the colour feature to individuate each potential candidate red t-shirt.

The relevant colour guides your selection and the items that present the same feature receive further processing and a behavioural benefit as compared to items with different colours. This type of attention, known as *feature based attention* (Treue & Martínez Trujillo, 1999), has been extensively studied both in monkeys (Treue & Martínez Trujillo, 1999) and humans (Andersen & Müller, 2010; M M Müller et al., 2006). As formalised by the *feature similarity gain model* (Treue & Martínez Trujillo, 1999), the neural response relative to a selected feature is boosted across the entire visual field and importantly distinct features can be processed in parallel (Andersen & Müller, 2010).

A further manner the human brain adopts to choose relevant information is by selecting an *object*. According to object based attention, information selection does not have to be necessarily only based on spatial information or features, but can be done by selecting a whole object (Duncan, 1984). In accordance to this view, several studies (e.g. Blaser, Pylyshyn, & Holcombe, 2000; O'Craven, Downing, & Kanwisher, 1999) showed that when attention is directed to a part of an object, the rest of the object is equally processed.

1.2.1 Neural correlates of visual attention

In a seminal study conducted in non human primates, Moran and Desimone (1985) investigated the influence of visual attention on two stimuli – one *effective* and one *non-effective* stimulus – placed inside a specific neuron's receptive field (RF, in V4 or inferior temporal cortex). The overall neuron's response was modulated depending on which of the two stimuli was attended. When the effective stimulus was attended, the recorded neuron exhibited the strongest response, on the contrary, when the non-effective stimulus had to be attended the overall response was reduced regardless of the presence of the effective stimulus inside the RF. This result suggested that attention works as a filter shaping a neuron's response according to the attended stimulus. The authors described this process as if the receptive field was contracted around the attended stimulus in order to filter out the irrelevant stimulus.

This whole process has later found a valuable framework in the *biased competition hypothesis*. Put forward by Duncan and Desimone (1995), *biased competition* rests on two main assumptions: (1) *competition* for processing resources among multiple stimuli and (2) selective attention as a means to “defeat” competition (*attentional bias*).

(1) When two or more stimuli are placed within a neuron's RF, given the limited processing resources available, these stimuli compete with each other in order to gain a neural representation. Thus they elicit a response that is a linear combination of the neuron's response relative to each stimulus when singularly presented (J H Reynolds, Chelazzi, & Desimone, 1999a). Specifically, two or more stimuli exhibit a mutual suppression that is directly dependent on the single stimuli characteristics.

(2) In order to release stimuli from mutual suppression, selective attention has to come

> into play. When attention is directed towards one of the competing stimuli the neuron's response changes according to the response of the attended stimulus when presented alone. Importantly, competition can be biased both by top-down and bottom-up processes (Beck & Kastner, 2005).

Kastner and colleagues (1998), by means of functional magnetic resonance (fMRI), extended the biased competition account to the human brain, replicating results previously obtained in single cell studies. The authors presented four peripheral items – able to elicit an optimal neuronal responses in the occipital area V4 – either singularly or simultaneously, while attention was maintained on an independent discrimination task. As predicted by the model, the simultaneous presentation produced a blood oxygen-level-dependent (BOLD) signal that was lower than the responses produced by each single items when presented singularly.

Notably, mutual suppression effects were stronger within area V4 – where receptive fields are bigger and can “contain” more items – as compared to the effect obtained in V1 and V2, where receptive fields are smaller. Additionally, in line with the latter observation, when the distance between stimuli was increased, the mutual suppression was reduced, proving that competition was taking place inside the receptive fields.

A series of following studies (Kastner & Ungerleider, 2001), showed that by voluntarily moving the attentional focus towards one of the items, suppressive interactions were released. Furthermore, Beck and Kastner (2005) showed that suppressive interactions could be as well released by bottom-up processes. Presenting four Gabor patches with equal orientation, the authors were able to show the typical competition effects, however, changing the orientation of one Gabor patch, and thus promoting a pop-up effect, suppressive interactions were released by stimulus-driven attention.

Although biased competition provided a valuable account for multiple stimuli processing, it did not provide any explanation regarding the specific mechanisms that guide neural modulations of selective attention.

Two general types of attentional mechanisms have been observed: a *contrast gain* and a *response gain*. The contrast gain control mechanism decreases the minimum contrast needed by a neuron to respond to a stimulus (John H Reynolds & Chelazzi, 2004). In terms of a psychophysics curve (see Figure 1), it can be observed in a shift of the curve to the left side of the contrast axes (Pestilli, Ling, & Carrasco, 2009) indicating the need of less contrast to obtain a correct response.

The response gain control mechanism (see Figure 1) is instead characterized by an increase in firing rate as a function of stimulus contrast. At neuronal response level, this mechanism is translated into a fixed multiplicative neuronal response (Martínez-Trujillo & Treue, 2002). Psychophysically, the psychometric curve moves upwards exhibiting a response increase, but leaving the contrast threshold virtually unchanged. Additionally, it has been found that the neuronal response can be a combination of response and contrast gain (John H Reynolds & Desimone, 2003).

A recent computational model – *the normalization model of attention* – proposed by Reynolds and Heeger (2009), see also, Carandini & Heeger, 2012) tried to reconcile such apparently conflicting findings. The model considers two fundamental factors: the *stimulus size* and the *attention field* (the attentional spreading). Manipulating these factors the model is able to account for a variety of attentional modulations. For instance, a small stimulus and a large attention field should result in a contrast gain response, while a large stimulus combined with a small attention field should give rise to a response gain (see Figure 1). A crucial characteristic of the model is the divisive normalization that simulates the suppressive interactions across neurons. The model comprises three major components: (1) the *stimulus drive:* a virtual condition where neurons characterized by their own spatial and feature stimulus preferences are not affected neither by attention nor by suppression. (2) the *attentional drive:* simulates the gain that attention provides to neurons. Once the stimulus drive is multiplied by the attentional field, the *suppressive drive* comes into play as a divisive normalisation (each neuron is divided by the sum of the activity of the pool of neurons involved). Divisive normalisation seems to be a recurrent computation in different processing stages and species (Carandini & Heeger, 2012). Recently, Hermann and colleagues (Herrmann, Montaser-Kouhsari, Carrasco, & Heeger, 2010) successfully tested the model's assumptions in a psychophysical study investigating both endogenous and exogenous attention.

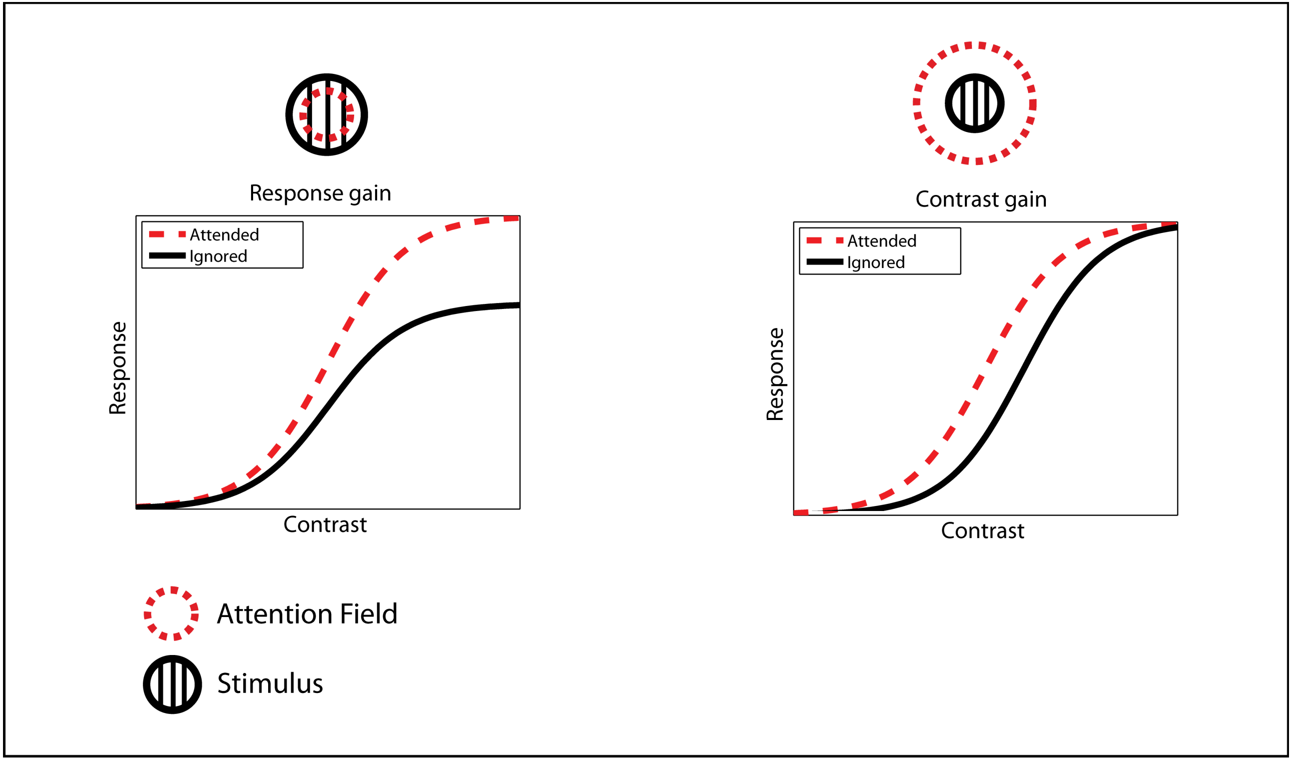

Figure 1: Psychophysical functions according to the normalization model of attention

Figure 1 Representation of a psychophysical function according to the normalization model of attention. On the left, the combination of a big stimulus and a small attention field promotes a Response Gain, translated in an upwards shift of the psychophysics curve (dashed red line). On the right, the combination of small stimulus with a big attention field induces a Contrast Gain, resulting in a shift of the attended curve (dashed red line) on the contrast axis.

1.3 Tactile attention

In comparison to visual attention, much less is known about the underlying neural processes of tactile attention. Initially, tactile studies mostly adapted prototypical visual and auditory paradigms to tactile settings in order to investigate endogenous and exogenous spatial attention. Most of these studies (e.g. Sathian & Burton, 1991; Spence & McGlone, 2001) were able to show that attention can facilitate tactile processing of cued body locations as compared to uncued body locations, thus replicating earlier visual and auditory results.

Additionally, spatial tactile attention has been also shown to modulate early (P50, N80) and mid-latency (P100, N140) ERP components (Desmedt & Robertson, 1977; Martin Eimer & Forster, 2003; Schubert et al., 2008) as well as steady-state evoked potential amplitudes (C.-M. Giabbiconi, Trujillo-Barreto, Gruber, & Müller, 2007; Nangini, Ross, Tam, & Graham, 2006) relative to cued tactile locations. In order to select information within the tactile modality, as in the visual modality, we do not rely only on spatial cues, but also on other features (H Burton & Sinclair, 2000; Sathian & Burton, 1991) such as frequency, texture, intensity etc. Klatzky and colleagues (1989) conducted a tactile search task based on different features and observed distinct attentional influences on the reaction time slop depending on the relevant feature. For instance, features related to surface properties did show a small effect on the RTs slope, while search for other features as bar orientation resulted in the steepest RTs slope and features with three dimensional contours exhibited intermediate RTs. More recently, Forster and Eimer (2004), by means of ERPs, investigated the relation between spatial and feature based attention. The authors observed that spatial and feature related components (space and intensity: N140, frequency: P100) were modulated in parallel, and, strikingly, feature related components were modulated regardless of the cued location, thus suggesting a potential independence of the type of modulations.

Tactile selective attention has been shown to have some effects on sub-cortical structures such as ventral-posterior area of the thalamus (VP, see Bushnell, Duncan, Dubner, & He, 1984), but primarily on primary (S1, comprising areas: 3a, 3b, 1 and 2) and secondary (S2) somatosensory cortices (for review see Johansen-Berg & Lloyd, 2000). Given the direct connections from VP to S1 and from S1 to S2, selective attention was thought to affect S1 and S2 serially. However, the relation between these areas is still not completely understood. As emphasised by Chapman and colleagues (2005), S2 exhibits more frequent and more robust attentional modulations as compared to S1 modulations (Harold Burton, Sinclair, & McLaren, 2008; Hsiao, O'Shaughnessy, & Johnson, 1993; Meftah, Bourgeon, & Chapman, 2009; Mima, Nagamine, Nakamura, & Shibasaki, 1998). Johansen-Berg et al. (2000) argued that S1 lack of modulation might be related to the type of control task adopted. Control tasks generally did not consist of tactile tasks, but involved passive, non-demanding tasks such as relaxing, reading or watching videos, thus they did not provide a reliable comparison, as different levels of arousal were likely elicited by the two tasks. For this reason Schubert and colleagues (2008) conducted a combined EEG/fMRI experiment where both each condition – attend either left or right hand – involved a spatial tactile task. The authors were able to find that early (P50) and later (190 ms) ERP modulations correlated with S1 BOLD response.

However, a recent fMRI study by Burton and colleagues (2008) used a demanding backwards counting task as control task and did not observe any S1 modulation.

The aforementioned mixed results suggest that although the type of control task and the task demand can play a crucial role on the S1 attentional modulation, different factors must be involved. Chapman and colleagues (2005) proposed that S1 and S2 might constitute two independent tactile attentional control systems. The authors – recording from S1 and S2 cells in macaque monkeys – observed *no response gain in S1*, while *S2 cells exhibited multiplicative responses*, thus the different types of modulation were considered as an indication for two independent systems in the two somatosensory cortices.

In line with this dichotomy between S1 and S2, in a recent visual-tactile study, Meftah and colleagues (2009) measured the activity relative to the pre-target period. The authors observed that after the visual cue presentation – indicating which modality had to be attended – both S1 and S2 neurons were modulated, but crucially only S2 neurons exhibited a further attentional modulation. Attention appeared indeed to provide an additive effect to the presentation target period with respect to the activity registered during the pre-target period.

Beyond the debate concerning the attentional modulations of specific somatosensory areas, a positron emission tomography (PET) study conducted by Drevets and colleagues (1995) revealed an interesting filtering mechanism. Together with the usual blood flow increase expected in S1 and S2, the authors observed a blood flow decrease in somatosensory areas related to unattended body parts. Thus Drevets suggested a mechanism by which *“signal enhancement may rely on generalized suppression of background activity”* thus facilitating the processing of relevant body locations.

1.4 Selecting a specific sense among others: inter-modal attention

Traditionally, attention research has been mostly kept within a uni-modal context, falling into a reductionistic approach and confining single sensory modalities to rigid categories.

Despite such an approach, the human brain must constantly handle information coming from different sensory sources. Frequently, this information needs to be merged in order to perceive a unified representation of the outside world (multisensory integration, see Talsma, Senkowski, Soto-Faraco, & Woldorff, 2010). In many other circumstances, information coming from a specific sensory source needs to be selected to the detriment of other sensory information.

Such process, known as *inter-modal attention,* has been generally investigated by presenting simultaneously two or more sensory modalities and cueing the participant's attention towards one sensory modality while ignoring the others. This experimental manipulation usually led to increased accuracy and lower reaction times relative to the behaviourally relevant sensory modality as compared to the irrelevant ones (Spence, Nicholls, & Driver, 2001a; Turatto, Benso, Galfano, & Umiltà, 2002).

In line with behavioural results, ERPs and gamma band studies (M Eimer & Schröger, 1998; Karns & Knight, 2009; Talsma, Kok, Slagter, & Cipriani, 2008) showed that besides the established behavioural advantages, inter-modal attention modulates ERP components, ongoing gamma oscillations and steady state potentials (Keitel, Schröger, Saupe, & Müller, 2011a; Saupe, Widmann, Bendixen, Müller, & Schröger, 2009) relative to the relevant modality. Crucially, several ERP (M Eimer & Schröger, 1998; Martin Eimer & Forster, 2003) and fMRI studies (Busse, Roberts, Crist, Weissman, & Woldorff, 2005; Macaluso, Frith, & Driver, 2000) observed that, besides the common neural processing reserved to the attended modality, unattended sensory modalities received significant neural processing as well even though at a lower degree. Such *cross-modal links,* as these modulations have been termed, suggested that inter-modal attention can spread (Busse et al., 2005) to unattended sensory modalities and locations. Importantly, the latter results implies that although the human brain seems able to selectively attend to a specific modality, attention appears to be controlled by a unique system independent of each sensory modality. However, other studies (Wickens, 2008) suggested alternative models, although generally two are the main hypothesis proposed to explain how attention operates across sensory modalities. (1) A supra-modal or a-modal control system that – regardless of the senses involved – monitors the stimuli selection and regulates processing resources between sensory modalities; (2) independent control systems, specific for each single modality (Wickens, 2008). Further hybrid models combine a supra-modal control system – placed in higher cortical areas – with either partially or totally independent early sensory areas or independent but yet linked control systems (Driver & Spence, 1998). In line with a supra-modal view of inter-modal attention, a recent influential work in non-human primates (Lakatos et al., 2009) revealed an appealing mechanism which seems to play a crucial role in the way a supra-modal system might lead the attentional selection as well as the multisensory integration process. Lakatos and colleagues (2009) presented visual stimuli alternating auditory stimuli with pseudo-random inter stimulus intervals and trained monkeys to direct the attention towards one or the other sensory modality. The authors observed that inter-modal attention, besides modulating the attended modality, crucially resets the phase of the ongoing oscillation in the primary sensory cortex of the unattended modality (e.g. when attending vision, the phase relative to the auditory signal was reset according to the visual oscillation). Notably, this mechanism has been recently shown in human subjects by means of behavioural and EEG measurements (Fiebelkorn et al., 2011; Romei, Gross, & Thut, 2012).

1.5 Vision and touch, different or same processing resources?

In the last few decades, a number of studies has investigated whether different modalities share common attentional resources or whether each modality rely on its own independent resources. Despite the number of studies, this topic is still under debate.

Previous studies included a huge variety of methodologies and tasks which makes arduous to reconcile the different outcomes. Generally, the main approach adopted consisted of creating the conditions to induce competitive interactions between modalities, usually by means of a dual task, dividing attention between different sensory modalities. Hence, physiological and/or behavioural indices were used to assess whether there was any difference between uni-modal and bi-modal presentations.

As argued by Bonnel and Hafter (1998), depending on the type of task employed, a *dual task* paradigm might be misleading. Attentional processing limits across modalities seem indeed to be strictly dependent on the nature of the task adopted. Two kind of tasks have been normally chosen: a detection task that consists of determining the presence or not of a stimulus (e.g. detecting a near threshold stimulus in a specific modality), a discrimination task consists instead of distinguishing a specific relevant change in a stimulus between different irrelevant changes (e.g. finding a specific letter in a stream of different letters).

In an audio-visual experiment the authors manipulated systematically task types, showing that a detection task requires significantly less attentional deployment than a discrimination task. Thus, the two kinds of tasks might naturally lead to two completely different outcomes and conclusions. A detection task might erroneously lead to conclude that each different modality has its own independent processing resources, while a discrimination task might suggest common attentional resources between modalities. In other words, we might mistake effort or cognitive load (Lavie, 2005) for the actual amount of processing resources.

Although it seems a plausible explanation, this dichotomy between discrimination and detection tasks does not account for the various discrepancies observed in the literature. An exemplary case regarding such a variety of outcomes concerns two behavioural studies conducted by Duncan (1997a) and Jolicoeur (1999). Although both authors adopted a very similar attentional blink paradigm to investigate cross-modal processing resources, they found opposite results. Namely, Duncan did not observe any interference between the two sensory modalities, while Jolicoeur reported a cross-modal attentional blink effect.

As discussed by Jolicoeur, there are a few differences between the two experiments that might account for such result discrepancies: a time presentation interval between items (250 ms for Duncan's study and 100 ms for Jolicoeur's) and the type of response. Duncan adopted a delayed response and Jolicoeur a speeded response. The response type has been repeatedly indicated as one of the possible behavioural causes of discrepant results in cross-modal paradigms (Spence, Nicholls, & Driver, 2001).

In a recent fMRI study, Johnson and Zatorre (Jennifer Adrienne Johnson & Zatorre, 2006) asked participants to either divide attention between vision and audition or to focus on a single modality. They observed reduced BOLD response within sensory areas during the divided attention condition as compared with the single modality condition. Notably, the authors, in line with other fMRI studies (Loose, Kaufmann, Auer, & Lange, 2003), observed the involvement of higher processing areas, such as pre-frontal cortex exclusively during the divided attention condition.

Hence, Johnson and Zatorre suggested that suppressive effects observed in sensory areas might have been the result of re-entrant feedbacks from higher processing areas recruited to balance the processing resources between early sensory cortices. On the contrary, recent behavioural and imaging studies (Alais, Morrone, & Burr, 2006; Arrighi, Lunardi, & Burr, 2011a; Keitel, Maess, Schröger, & Müller, 2013) have found no evidence for common resources between modalities. The authors proposed that such effects might exclusively reflect the involvement of each specific primary sensory cortices where less interferences among modalities might be expected.

1.6 Multisensory interactions, finding a common ground

In this section, I will briefly summarise the conditions favourable to promote multisensory interactions and the most relevant brain areas involved in such interactions that will be necessary for future discussions. In the last two decades, multisensory research has primarily focused on multisensory integration.

Multisensory integration is the process by which the brain merges different sensory information (e.g. visual, tactile, auditory, taste etc.) in order to create a coherent representation of a percept. To successfully merge information coming from different sensory modalities, a few specific conditions seem to be necessary. A fundamental condition is the spatial-temporal co-occurrence of two or more sets of sensory information; in other words: stimuli in different sensory modalities need to occur in the same space and/or time to be more likely to be integrated. Although the brain can dynamically adapt to time and/or space discrepancies between two sources of information (Ernst & Bülthoff, 2004), integration is usually stronger when space and time have spatial-temporal congruency. Recently, time coincidence has been considered more crucial for integrative processes (see Charles Spence, 2013), however this topic is beyond the aim of the present work.

Although space and time coincidence is a crucial feature, different sensory modalities have intrinsically different time and space resolutions: for instance, space information is better provided by vision or touch, while time is better expressed in audition. These characteristics are summarized in the *"modality appropriateness hypothesis"* (Welch & Warren, 1980) which claims that depending on the task and context – in order to obtain an optimal integration – the brain relies primarily on the most appropriate modality to solve a specific task. Such hypothesis has been extensively tested by Ernst and colleagues (2002), who by means of Bayesian inference have shown how the brain, according to known priors, weights different sensory channels in order to optimize multisensory integration.

A further fundamental principle that regulates integration is the so called *principle of inverse effectiveness*. First described by Stein and Meredith (1993), this principle affirms that it is more likely to obtain multisensory integration when different sensory information is presented with a low intensity. Inverse effectiveness has been extensively shown in superior colliculus neurons of cats and monkeys and recently in human EEG (Senkowski, Saint-Amour, Höfle, & Foxe, 2011).

Multisensory interactions take place in numerous brain areas, in the following sub-sections I will briefly summarise some of the most relevant areas.

Multisensory interaction in sub-cortical structures: multisensory interactions have been shown to occur quite early during the sensory processing (~50 ms, Giard & Peronnet, 1999) most likely as a consequence of sub-cortical activations. Numerous studies have shown that multisensory interactions already take place in sub-cortical structures such as superior colliculus (SC, a structure that controls the overt orienting of the oculomotor system), and thalamus (Cappe, Morel, Barone, & Rouiller, 2009).

Such interactions have been primarily observed in cats, non humans primates (Barry E

Stein & Stanford, 2008) and only recently in humans (Maravita, Bolognini, Bricolo, Marzi, & Savazzi, 2008). Maravita and colleagues (2008) considered that while blue stimuli are mainly detected by S-cones which do not project directly to the SC, red stimuli have an effect on SC. Presenting red and blue stimuli coupled with sounds, the authors observed faster reaction times when the red stimulus was displayed together with the sound as compared to the blue stimulus, supporting the hypothesis that SC might play a crucial role in multisensory integration.

Less research has been generally devoted to the role of the thalamus in multisensory interactions. Cappe and colleagues (Cappe et al., 2009) proposed four potential mechanisms – based on an anatomical tracing study in monkeys – by which the thalamus might be involved in multisensory interactions. Specifically, the authors described (1) thalamo-cortical connections, (2) non-specific neurons that relay multisensory information originally merged in the thalamus, (3) cortical sensory areas that receive information from thalamic areas devoted to specific modalities and (4) cortical areas that might have cross-modal connections via cortico-thalamo-cortical loops.

Recently, Lakatos and colleagues (2009) suggested a thalamo-cortical pathway as the most likely pathway to convey competitive interactions between sensory modalities in primary sensory cortices.

Multisensory interaction in primary sensory areas: primary sensory cortices have been traditionally thought to be uniquely devoted to the processing of a specific sensory modality. Only recently such a rigid modular view has been challenged by a number of studies showing multisensory interactions in human and non human primary sensory cortices (see Driver & Noesselt, 2008; Ghazanfar & Schroeder, 2006, for review).

Multisensory interplay in early and even in primary sensory areas can take place in different manners: via lateral connections between primary sensory areas (e.g. Cappe & Barone, 2005; Falchier, Clavagnier, Barone, & Kennedy, 2002; Iurilli et al., 2012), via re-entrant feedback from higher order multisensory regions (e.g. Macaluso et al., 2000) or by feed-forward connections from sub-cortical structures (e.g. Cappe et al., 2009).

Recently an fMRI study (Liang, Mouraux, Hu, & Iannetti, 2013) extended further in the concept of multisensory primary cortices. By means of a multivariate pattern analysis, the authors showed that an isolated stimulus of one sensory modality can elicit a specific recognizable pattern in an other sensory cortex. In the same line, another recent study in non-human primates (Lemus, Hernández, Luna, Zainos, & Romo, 2010), measured whether neurons in auditory cortex could encode the frequency characteristics of a tactile stimulus and vice-versa. The authors were merely able to show that somatosensory neurons responded to auditory stimuli, but were incapable to encode the specific characteristic of the auditory stimuli.

As Lakatos and colleagues (2007) claimed: *“neuronal activity in auditory cortex is not related to either somatosensory or visual perceptual experiences”* and it *“is likely that appropriately timed somatosensory and visual inputs to the auditory cortex help us to hear better”.* Paraphrasing Lakatos's claim, even though primary sensory cortices are modulated by non-specific sensory modalities, such areas remain devoted to their own specific modalities and the multisensory interactions have uniquely the role to improve perception, to help a sensory modality A to perceive better a stimulus in sensory modality B.

Multisensory interaction in higher cortical areas: parietal cortex has been always considered an “associative” area in which multisensory inputs converge. Posterior parietal cortex (PPC) is indeed known to be involved in the transformation of coordinates linked to different sensory modalities. Several region of the PPC play significant and distinct roles in multisensory interactions: the ventral intraparietal sulcus (VIP and the human homologue hVIP), for instance, is engaged in processing stimuli in the proximity of the face (Sereno & Huang, 2006), anterior intraparietal suclus (hAIP/AIP) implicated in visuo-motor functions such as grasping and superior temporal sulcus (STS) mainly involved in audio-visual speech perception.

*Suppressive interactions across sensory modalities: a*lthough multisensory interactions mostly refer to integrative processes, a few studies reported suppressive interactions between concurrent sensory modalities in the superior colliculus of cats (Kadunce, Vaughan, Wallace, Benedek, & Stein, 1997; Meredith & Stein, 1986). According to previous models of SC (Meredith & Stein, 1986), in order to induce suppressive interactions, Kadunce and colleagues presented a visual stimulus inside a SC neuron's receptive field and a second stimulus in a different modality – either auditory or tactile – within a so called suppressive region outside the neuron's receptive field. The responses relative to 69 % of neurons were significantly reduced by within-modality suppression while only 20 % of neurons exhibited a reduction due to cross-modal suppression. The authors suggested that such a discrepancy might be ascribed on the one hand to a modality specific pathway that project to SC – related to the within modality suppression – on the other hand, the cross-modal suppression reflects an inhibitory circuit intrinsic to SC.

A more recent study (Iurilli et al., 2012) reported suppressive interactions in mouse primary visual cortex induced by the presentation of a sudden auditory stimulus. Suppressive interactions changed as a function of sound intensity; with higher intensity more suppression was observed.

1.7 More on the notion of processing resources

The concept of processing resources, although broadly used in cognitive neuroscience and cognitive science, is still lacking a precise definition. Generally, processing resources or processing capacities – the two terms will be used interchangeably throughout this thesis – have been intended as a *limit; a*s an undefined amount of sensory information that the human brain can *simultaneously* process and hold in memory in absence of any significant processing decrement.

From a strictly physiological viewpoint, brain processing resources can be seen as the overall amount of energy available in the brain (Attwell & Laughlin, 2001). Lennie (2003) established that neuron's single spike is highly energy consuming, thus the number of simultaneously active neurons needs to be limited and the amount of energy resources available need to be flexibly allocated among cortical regions according to task demand (Lennie, 2003). Hence, the energy consumption related to task demand or any other neural activity can be seen as an index of the amount of energy that the neocortex can concurrently use (Lennie, 2003). Obviously, the real issue is to establish the exact amount of energy relative to a cognitive task and more importantly to establish which "variable" needs to be manipulated in order to change the amount of resource consumption.

Recently, Franconeri and colleagues (2013) sought to provide a more precise definition and to individuate a "locus" for limited resources in attention and working memory tasks. The authors rediscovered the classic concept of *map:* a map is a two-dimensional anatomical space characterized by *"a coherent spatial organization where the preferred stimuli of a neuron change smoothly from one location to the adjacent one"*. Representation maps can be found at different level of processing, from the perceptual level (e.g. retinotopic maps in V1) to action plans and notably maps can have shared coordinates, such as spatial representations from visual and auditory stimuli in the superior colliculus. The processing capacity within a map is defined by the spatial arrangement of stimuli, namely while stimuli close to each other exert a mutual suppression, conversely distant stimuli exert lower or no effects on each other, thus making the capacity of a map to flexibly vary as a function of space. Such a definition clearly recalls the first assumption of the biased competition hypothesis previously introduced.

As, indeed, Desimone and Duncan (1995) themselves stated: *"receptive fields can be viewed as a critical visual processing resource, for which objects in the visual field must compete". S*uch a statement restricts the concept to a more precise anatomical definition which can find a solid empirical and theoretical support within the biased competition account. Although biased competition referred specifically to the visual modality, a number of studies has reported the presence of suppressive interactions already in superior culliculi (SC) neurons of cats and monkeys (Meredith & Stein, 1986).

As mentioned in section 1.5, parietal cortex has been repeatedly indicated associative area, thus this area seems to provide the common supra-modal space, a 'real cortical estate' – to paraphrase Franconeri and colleagues (2013) – necessary to promote competitive interactions and therefore putative resource constraints.

1.8 Outline of the experiments

As mentioned in section 1.7, competition between stimuli can be seen as synonymous of limited processing resources or, more specifically, as a consequence of limited resources (Franconeri et al., 2013; Kastner et al., 1999). Following this assumption, we aimed to investigate:

(1) whether basic competitive interactions between different sensory modalities – in

absence of attentional biases – might emerge in primary sensory areas, and consequently

(2) whether manipulating endogenous attention, we can observe evidence in favour of a supra-modal attentional control system or in favour of modality specific attentional control systems.

To this end, we conducted four EEG experiments by using frequency-tagging technique as main method of investigation.

First experiment: the first experiment aimed to test whether previous findings obtained in audio-visual inter-modal attention (Keitel, Schröger, Saupe, & Müller, 2011; Saupe, Schröger, Andersen, & Müller, 2009) by means of SSEPs (see chapter 2) could be replicated using a visual-tactile experimental setting. Specifically, this experiment aimed to investigate whether inter-modal attention could dynamically modulate SSEP amplitudes and phase. Therefore, we simply asked participants to focus, on trial by trial basis, either on vision or on touch. Hence, we used changes in SSEP amplitudes and phase as measures of inter-modal attention modulations.

Second experiment: as already mentioned, competition can be considered as an index of limited resources. Thus, in the second experiment, we aimed to test whether the competition hypothesis might extend to a cross-modal situation. To this end, employing SSEPs, we tested whether competitive interactions previously observed in single sensory modalities could occur also between sensory modalities in primary sensory cortices. The presence of competitive interactions would naturally point towards limited processing resources for the two modalities. On the contrary, the absence of competitive interactions might suggest distinct processing resources, at least relative to primary sensory cortices.

Third experiment: the third experiment was primarily designed in order to extend findings of Experiment 2 to different sensory modalities combination, namely auditory and tactile modalities.

Fourth experiment: in the previous two experiments any attentional bias was avoided, hence we focused exclusively on putative interactions independent of attentional influences. Thus in the last experiment we aimed to investigate whether manipulating endogenous attention we could observe data in line with a supra-modal attentional control system or in line with distinct attentional system for each modality. To this end, we combined a classical dual task with the frequency-tagging approach. We were thus able to compare changes in SSEP amplitudes relative to both modalities in a single and dual task.

2. General experimental methods

2.1 Steady-state evoked potentials (SSEPs)

The main approach employed in the present thesis are steady-state evoked potentials (Regan, 1989). This method consists of a specific type of evoked response recorded from the human scalp by means of the electroencephalogram (EEG). This particular response is elicited by presenting a stimulus, regardless of the sensory modality (Ross, Miyazaki, & Fujioka, 2012; Tobimatsu, Zhang, & Kato, 1999), at a predefined temporal frequency for a variable duration, usually several seconds. The elicited response is a quasi-sinusoidal signal characterized by the same frequency as the stimulus frequency (fundamental frequency) and higher order harmonics (integer multiples of the fundamental frequency). The underlying mechanisms of SSEPs are not yet completely understood, however two main hypotheses have been suggested. The first one claims that SSEPs are the result of the neural entrainment driven by the stimulation train (e.g. Herrmann, 2001), while the second hypothesis suggests that SSEPs are merely the outcome of a temporal superimposition of transient evoked potentials (e.g. Capilla, Pazo-Alvarez, Darriba, Campo, & Gross, 2011). SSEPs sources have been consistently localized within primary sensory cortices of the respective sensory modalities (C.M. Giabbiconi et al., 2007; Nangini et al., 2006; Pastor, Valencia, Artieda, Alegre, & Masdeu, 2007; Ross et al., 2012). Notably, it has been found that different sensory modalities show the strongest signal within specific frequency ranges: 4-20 Hz for vision, 18-30 Hz for touch and around 40 Hz for audition; however the cause of such phenomenon is not yet clear.

2.1.1 Advantages of employing SSEPs

Among numerous advantages that SSEPs offer over different experimental approaches, two crucial characteristics make SSEPs a suitable means for the specific purposes of this work: (1) selective attention modulates SSEPs and (2) SSEPs can be used to frequency-tag concurrent stimuli.

SSEP amplitudes and phase can be indeed modulated by selective attention regardless of the sensory modality (C.M. Giabbiconi et al., 2007; M M Müller et al., 1998a; Ross & Pantev, 2004). This characteristic allows to investigate different types of attention such as spatial attention (Muller et al. 1998), feature based attention (Andersen & Müller, 2010; M M Müller et al., 2006) as well as inter-modal attention (Keitel et al., 2011a; Saupe, Widmann, et al., 2009; Talsma, Doty, Strowd, & Woldorff, 2006b).

Additionally, by assigning a specific frequency to different stimuli, it is possible to frequency code multiple stimuli simultaneously and, thus, to obtain a distinct SSEP response for each stimulus. This method, known as frequency-tagging method, originally employed by Regan (1989), permits to track and distinguish the EEG signal relative to each single stimulus. The frequency tagging method allows to trace multiple stimuli for several seconds, thus allowing the analysis of the time course of the stimulus processing. Moreover, if compared to other EEG methods, such as ERPs, SSEP assures a better signal to noise ratio, thus generally requiring less trials to obtain a reliable signal.

2.1.2 A bit of mathematics behind the SSEPs analysis

Any signal can be mathematically considered as a summation of simple sine and cosine waves of different frequencies (Fourier series). Hence, a complex signal, such as the human EEG signal, can be decomposed into basic waveforms (sinusoids or co-sinusoids) by means of various mathematical methods. One of the most popular methods is the

Discrete Fourier Transform (DFT). The DFT is a mathematical procedure – the discrete analogous of the continuous Fourier transform – that allows to transform a discrete time-domain signal into its respective *frequency* information and consequently to estimate *amplitude* and *phase* of each frequency component.

$$X(m) = \sum x(n) \, [\cos(2\pi nm / N) - i \sin(2\pi nm / N)] \qquad (1)$$

Where $X(m)$ is the mth DFT output component (e.g. X(1), X(2), X(3), etc.), m is the index of the DFT output in the frequency domain, $x(n)$ is the sequence of input samples, n is the time-domain index of the input samples i is $\sqrt{-1}$ and N is the number of samples of the input sequence.

Although the DFT is the most straightforward procedure adopted to determine the frequency content of a time-domain signal, it is not a very efficient computational technique. A faster and more efficient method is provided by the Fast Fourier Transform (FFT) algorithm, a widely used method to perform the DFT. In the present work we used FFT to transform the EEG signal from time-domain to frequency-domain.

The amplitude information of each frequency can be consequently represented in a typical spectrogram that shows peaks amplitude relative to the frequencies that are present in the EEG signal. Changes in amplitudes are used as dependent variables to asses attentional modulations on SSEP frequency components. The frequency spectrum is usually calculated either by means of the absolute value of the FFT coefficients or by means of the Pythagorean equation:

$$Magnitude = |X(m)| = \sqrt{} \, X_{real}(m)^2 + X_{imag}(m)^2 \qquad (2)$$

Where X_{real} and X_{imag} constitute the real part and the imaginary part of the FFT coefficients. As well as for peaks, phase can be influenced by attentional manipulation and thus SSEP phase can be adopted as a further index of attentional deployment.

Phase estimation: phase estimation is a non time-locked measure, therefore the phase extraction is performed on each single trial. As for the amplitude estimation, numerous methods such as, DFT, Hilbert transform or various wavelet analysis can be applied to obtain instantaneous phase and the time course of the phase. In the present work, instantaneous phase will be estimated uniquely by means of DFT. Once complex coefficients are obtained for each trial, phase is calculated by the inverse tangent of the ratio between the imaginary (I) and real (*R*) part of the complex values:

$$\Phi = \tan^{-1} (X_{imag}(m) / X_{real}(m)) \tag{3}$$

In this work we were interested in calculating the so called Phase Locking Factor (PLF) as an index of phase coherence across trials. PLF was calculated according to the following equation:

$$PLF = | 1 / n \sum e^{i(\varphi_{kf} 2\pi)} | \tag{4}$$

Where *n* is the number of trials, *e* indicate the Euler number, *f* indicates the frequency of interest and *φ* indicates the phase.

2.2 Experimental methods

2.2.1 Participants

In all the experiments, participants – within an age range of 19-36 – were generally recruited from the student population of the University of Leipzig. Participants had normal or corrected to normal vision; none of them reported a history of neurological diseases. All procedures were in accordance with the Declaration of Helsinki, and approved by the local ethics committee. Prior to the experiment, participants gave informed written consent. They received course credits or monetary compensation of 6 € per hour.

2.2.2 Materials

Participants were comfortably seated in an acoustically dampened and electromagnetically shielded chamber in front of a 19” cathode ray tube (CRT) screen (distance 80 cm) and a resolution of 800 x 600 pixels (width x height). The monitor's refresh rate was set at 60 Hz in experiments 1 and 4 and at 120 Hz for experiments 2 and 3.

Vibro-tactile device: tactile stimulation was produced and presented by means of an electromagnetic stimulator (Dancer Design, St. Helens, UK) constituted by a light metallic cylinder (see Figure 2.1, diameter: 18 mm, height: 12 mm) with a plastic plate at the upper part of the cylinder. In the centre of the plate a hole allowed a tiny – electromagnetically driven – rod to move up and down at different rates and deliver the stimulation to the fingers skin. The plate was directly fixed on the finger's first phalanx via a sticker to assure a continuous contact with the skin throughout the experiment.

Hands were concealed in order to avoid any visual influence on tactile stimulus processing. To cover the noise produced by stimulators, white noise (intensity = ~72 dB sound pressure level) was played through headphones for the entire block duration. White noise was used in all the experiment except for experiment 3 given that auditory stimuli were employed.

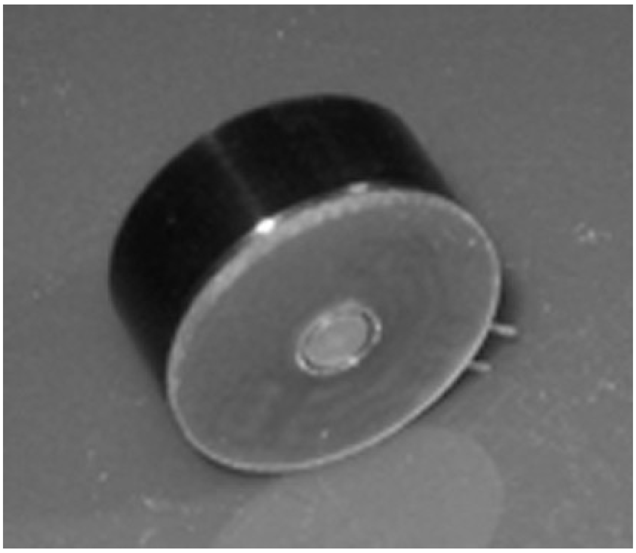

Figure 2: Electromagnetic stimulator

Figure 2.1 Electromagnetic stimulator used in the experiments

Tactile stimulus: in each individual experiment tactile stimulus consisted of an amplitude modulated (AM) waveform obtained as a product of a carrier signal and an amplitude modulation sinusoid that varied between 0-1 (Snyder, 1992). The AM waveform can be expressed by the following equation:

$$AM(t) = (A/2)\,[1 + \sin(2\pi f_m t)]\,\sin(2\pi f_c t) \qquad (5)$$

where A is the maximum peak to peak displacement, 1 is the modulator factor and f_m and f_c are the modulation and carrier frequency ($f_c >> f_m$), respectively.

Visual, tactile and auditory stimuli used in all the experiments have been created by means of custom routines written in Matlab (The Mathworks, Natick, MA) and Cogent Graphics developed by John Romaya at the LON at the Wellcome Department of Imaging Neuroscience.

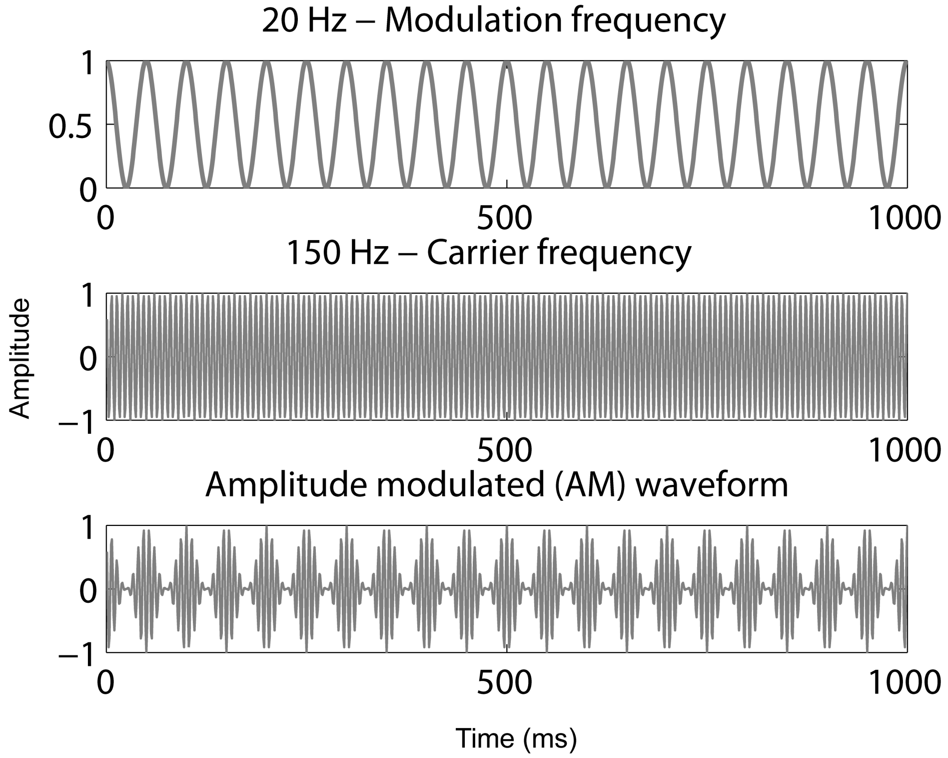

Figure 3: Amplitude modulated waveform

Figure 2.2 Amplitude modulated waveform. The sinusoid (20 Hz) on the top represents a typical modulation sinusoid, while the sinusoid (157 Hz) in the middle represents the carrier wave. The waveform on the bottom represents the amplitude modulated wave.

2.3 EEG recording and analysis

2.3.1 EEG recording equipment

Brain electrical activity was recorded from 64 Ag/AgCl scalp electrodes and amplified by a Biosemi ActiveTwo amplifier (Biosemi, Amsterdam, Netherlands) set to a sampling rate of 256 Hz. Electrodes were mounted in a nylon cap according to the 10-20 international system. Vertical eye movements and blinks were monitored by a bipolar montage located above and below the right eye. Lateral eye movements were monitored by a bipolar outer canthus montage.

2.3.2 EEG pre-processing

The following pre-processing procedure was generally used in each experiment, if any change was made within the process, it will be specified in the appropriate section of each experiment. Data processing was entirely performed by using EEGlab toolbox (Delorme & Makeig, 2004) combined with custom routines written in Matlab (The Mathworks, Natick, MA).

Once extracted from continuous data, epochs containing targets or distracters were discarded in order to avoid any signal contamination due to ERPs related to targets/distracters and corresponding motor responses in case of button presses.

Trials with blinks or eye movements exceeding a specific threshold, that will be specified in each experiment EEG pre-processing Section, were automatically rejected. A modified version of '*statistical control of artefacts in dense array EEG/MEG studies*' (Junghöfer, Elbert, Tucker, & Rockstroh, 2000) procedure was applied to identify and correct further artifacts. This procedure replaced artifact-contaminated channels with spherical-spline interpolations based on data from artifact-free channels. Epochs with more than 12 contaminated channels were excluded from further analysis. Artifact-free data were consequently re-referenced to average reference. Subsequently, data were averaged across epochs for each participant and experimental condition, separately. Data relative to each subject were then detrended (removal of mean and linear trends) and then transformed from time-domain to frequency domain by means of FFTs. Prior to statistical analysis, data relative to the frequency of interest were then normalised according to the following expression:

$$Norm = X(f,c)\ 1/N\ (\sum(X(f,c))) \tag{6}$$

Where f is the specific frequency of interest and c the specific condition, N is the total number of conditions. This normalisation procedure assures that possible differences between subjects' amplitudes are levelled out, thus avoiding biased results.

2.3.3 Statistical analysis

Statistical analysis were performed by means of repeated measures analysis of variance (ANOVA) or two taled paired t-tests. A p value of 0.05 was used as statistical threshold. If necessary Greenhouse Geisser correction was applied. When post-hoc tests were required, multiple comparisons were controlled by means of Bonferroni-Dunn test in experiment 2 and 3, only in experiment 4 a less conservative method – False Discovery Rate (FDR) – was applied in order to control the proportion of false positives among significant post-hoc comparisons (Benjamini & Hochberg, 1995).

3 Experiment 1

3.1 Introduction

Despite the advantages provided by the frequency-tagging method, up to date, inter-modal attention effects on visual and tactile processing have been found and described almost exclusively in ERP paradigms (Martin Eimer, van Velzen, & Driver, 2002; Karns & Knight, 2009; Zhang et al., 2007). In the present study, we aimed to extend latter findings by employing SSEPs in a visuo-tactile experimental setting. In contrast to ERP paradigms, our approach allowed us to present visual and tactile stimuli simultaneously over extended periods of time while still being able to track the processing of each individual stimulus. Therefore, we were able to test whether sustained inter-modal attention influenced ongoing concurrent visual and tactile processing beyond transient effects as reflected in ERPs and evoked GBRs. Attentional influences were assessed by means of visual and tactile SSEP amplitude as well as phase coherence. Moreover, we compared inter-modal attention effects on fundamental responses and corresponding second harmonics as the functional relationship between the two responses is still debated (Y. J. Kim, Grabowecky, Paller, Muthu, & Suzuki, 2007). Both SSEP components have been shown in a few cases to modulate differently under the influence of inter-modal attention; Saupe et al. (2009), for instance, observed a systematic modulation in the second harmonic of the visual SSEP amplitudes, only.

Here, we presented concurrent visual and tactile stimuli, frequency-tagged at 7.5 Hz and 20 Hz, respectively. Participants were cued, on a trial-by-trial basis, to attend to the visual or the tactile stimulus while performing a task in the relevant modality. We hypothesised that SSEP amplitudes and phase coherences of the fundamental frequencies and the second harmonics were greater when the driving stimulus was attended as compared to when it was unattended.

We found that attention modulated visual SSEP amplitudes of the fundamental frequency (7.5 Hz), while the second harmonic (15 Hz) was not modulated. The opposite scenario was observed in tactile SSEPs, where the 20 Hz SSEP component did not show a consistent attentional modulation, while the second harmonic (40 Hz) was modulated systematically. We further observed modulations of phase synchrony for visual SSEPs, exclusively. Therefore, as expected, inter-modal attention generally modulated visual as well as tactile processing in our experiment. However, our results also point towards differences of how inter-modal attentional influences are conveyed in both modalities.

3.2 Methods

3.2.1 Participants

Sixteen right-handed participants (range of age: 19-36, 10 women) took part in the experiment. Due to the absence of a visual 7.5 Hz SSEP above noise level, one participant was excluded from further analysis.

3.2.2 Procedure and stimuli

Participants were comfortably seated in an acoustically dampened and electromagnetically shielded chamber in front of a 19” cathode ray tube (CRT) screen at a distance of 80 cm, set to a refresh rate of 60 Hz. Participant's right hand was positioned on a table in front and aligned with the sagittal midline of the participant's body. A small electromagnetic stimulator (Dancer Design, St. Helen) was attached to the first phalanx of the index finger to deliver vibratory stimulation (see tactile stimulus section). The stimulated hand was concealed in order to avoid any visual influence on tactile stimulus processing. The left hand served as the responding hand and was placed on a keyboard. In order to mask the stimulator sound, white noise (intensity = 72 dB sound pressure level) was played through headphones for the entire block duration.

Visual stimulus. A rapid serial visual presentation (RSVP) of grey Gabor patches (diameter = ~6.5°, spatial frequency = ~1.2 per visual angle, Figure 3.1), with varying orientations, was centrally displayed on a grey background (~36.40 cd/m^2). A red dot (0.15°) superimposed on the RSVP centre served as fixation point. The rate of the RSVP was set to 8 cycles per second (= 7.5 Hz), each cycle of which consisted of 8 frames (= 133 ms). Gabor patches were shown during the first four frames of a cycle to produce a 50/50 on/off luminance flicker.

With each presentation cycle, Gabor patch orientation changed by a fixed step of 3° of visual angle in clockwise or anti-clockwise direction following a random walk rule. The starting orientation was randomly chosen from a set of 60 different orientations (0°-180° in steps of 3° of visual angle). Occasionally, a target, consisting of a larger step (15°) occurred and participants were instructed to give accurate speeded responses by a button press upon detection.

Tactile stimulus. The tactile stimulus stream consisted of a 20 Hz amplitude-modulated (AM) wave delivered to the right index finger with a maximum force of ~0.19 N. The AM wave was obtained as the product of a 157 Hz carrier frequency and 20 Hz sine (Figure 3.1). Participants were asked to detect short (100 ms) unpredictable decreases of the carrier frequency to 80 Hz; these targets were inserted within the carrier sinusoid before the latter was modulated by the 20 Hz sinusoid. As for the visual task, participants were instructed to give accurate speeded responses by button press.

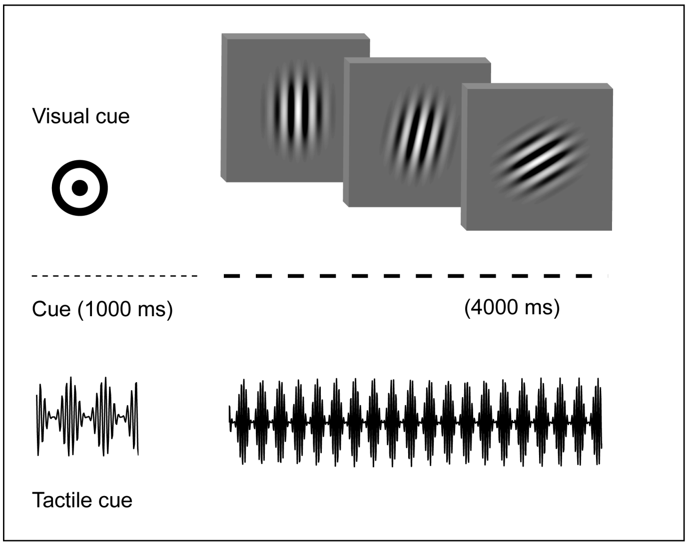

Figure 4: Schematic illustration of a typical trial

Figure 3.1 Schematic illustration of a typical trial. Trials started with the presentation of a visual or tactile cue. Subsequently, concurrent visual and tactile stimulus streams were presented.

Each trial started with the simultaneous presentation of a central red fixation point (0.15°) and a visual or tactile cue. The visual cue consisted of a white circle (diameter = 1°, width = 0.1°, duration = 1000 ms) surrounding the fixation point. The tactile cue consisted of a short (100 ms) salient vibration with the same magnitude as the stimulus stream (see tactile stimulus section). When the tactile cue was presented, the circle was absent and vice versa. After cue presentation, participants were instructed to maintain attention to the cued modality for 4000 ms, during which they were engaged in a detection task (see below for tasks description). Participants were instructed to keep their gaze on the fixation point regardless of the condition. At the end of each trial a white “X” (1000 ms) was presented to allow participants to blink. After each block, participants received feedback upon their performance (percentage of hit rates and false alarms).

The experiment was subdivided into 8 blocks. Each block consisted of 40 trials (20 trials per condition). Within blocks, trials of the two experimental conditions “attend vision” and “attend touch” were presented in randomised order. Prior to EEG recording, each participant practised visual and tactile tasks for at least 2 blocks.

In both visual and tactile stimulus streams, targets were present in 50% of the trials, within a time interval of 500 – 3200 ms after stimulus onset. Trials contained up to 2 targets (15 targets per block and condition). Prior the experiment, during the training session, the number of targets per block was increased from 15 to 24 in each stimulus stream to assess the initial performance of participants more reliably and accelerate training effects.

3.3 Data Analysis

3.3.1 Behavioural data analysis

Responses to targets were considered as correct when the button press occurred within a time interval of 200 – 800 ms after target onset. Responses to targets that occurred in the unattended modality were considered as false alarms. The sensitivity index, d-prime (d'), was computed in order to estimate accuracy within each modality. D' values were then subjected to a two-tailed paired t-test to test for differences in performance between visual and tactile tasks. Reaction times were not compared between visual and tactile conditions as differences were to be expected due to dissimilarities in visual and tactile target presentation (e.g. target durations; see above).

3.3.2 EEG analysis

Epochs of 4000 ms, starting with the onset of stimulus streams, were extracted from continuous data. We discarded epochs containing targets or distractors in order to avoid signal contaminations due to ERPs related to targets/distractors and corresponding motor responses in case of button presses.

On average, 10% of trials per participant and condition were contaminated with artifacts and had to be excluded. Artifact-free data were re-referenced to average reference. Subsequently, data were averaged across epochs for each participant and experimental condition, separately.

Fourier transforms of detrended averaged data from 500 to 4000 ms after stimulus onset at each sensor yielded spectral representations of EEG time series. SSEP amplitudes were quantified as the absolute value of the complex Fourier coefficients at the stimulation frequencies 7.5 Hz and 20 Hz as well as for corresponding second harmonics, 15 Hz and 40 Hz, respectively. The first 500 ms of each epoch were excluded from analyses to reduce influences of ERPs to stimulus onset on spectral analyses.

For each frequency, SSEP amplitudes were averaged across electrode sites showing maximum amplitude in scalp topographies collapsed across all participants and all experimental conditions. Electrode sites showing maximum SSEP amplitudes were grouped in modality-specific clusters. The visual cluster for 7.5 Hz and 15 Hz was identified at occipital sites (I1, 1z, I2, Oz, O1, O2, POz, PO3, PO4, PO7, PO8, P6), the tactile cluster for 20 Hz and 40 Hz, encompassed fronto-central sites contra-lateral to the stimulated hand (F1, F3, Fz, FC1, FC3, FCz). (see Fig. 3.2 for the specific choice of electrodes). Subsequently, we divided the obtained absolute amplitudes by the individual mean across conditions for each participant and frequency. This normalisation procedure removed inter-individual variance in absolute SSEP amplitude while retaining the net inter-modal attention effect.

Differences in normalised amplitudes between experimental conditions were tested by a two-tailed paired t-test for each frequency.

To test the functional relationship between fundamental frequency and second harmonic, we performed a Pearson correlation between SSEP amplitude modulations of fundamental frequencies and second harmonics in each modality. Individual amplitude modulations were obtained by subtracting normalized amplitudes of conditions in which the corresponding sense was unattended from normalized amplitudes of conditions in which the same sense was attended for each participant, separately.

To further investigate whether inter-modal attention effects were of similar magnitude in both sensory modalities and influenced amplitudes of both SSEP components similarly, we performed a repeated measures analyses of variances (ANOVA) with factors of *sensory modality* (vision vs. touch) and *SSEP component* (fundamental frequency vs. second harmonic) on individual amplitude modulations (attended minus unattended, see above).

In addition to SSEP amplitude, we analysed SSEP phase to test for differences in phase synchrony between experimental conditions. We calculated the phase locking factor (PLF, Tallon-Baudry, Bertrand, Delpuech, & Permier, 1997) for each frequency, condition and participant, separately. To this end, SSEP phase was extracted from each electrode by means of Fourier transforms of detrended single trial data within 500 to 4000 ms after stimulus onset.

PLFs were computed from phase values averaged across clustered electrodes by means of the circular statistics toolbox for Matlab (Berens, 2009) and subjected to two-tailed paired t-tests.

A general alpha criterion of $p < 0.05$ was used for all statistical comparisons performed in our study. Cohen's D (indicated with D) was used to estimate effect sizes in conducted paired comparisons. For the ANOVA, effect sizes are reported as η^2.

3.4 Results

3.4.1 Behavioural results

Participants performed equally well in visual and tactile tasks (mean visual d' = 2.8, SEM = 0.26, mean tactile d' = 2.5, SEM = 0.31). No significant difference was observed between d' values (t(14) = 1.8, p = 0.1, D = 0.24).

3.4.2 SSEP results

Visual 7.5 Hz SSEP amplitudes exhibited significantly higher amplitudes for the *attend vision* compared to the *attend touch* condition (t(14) = 2.9, p < 0.05, D = 0.23), i.e. when vision had to be ignored (Fig. 3.2A). The visual second harmonic (15 Hz) showed no significant amplitude differences between the two experimental conditions (t(14) = 0.4, p = 0.6, D = 0.02). As Figure 3.2C illustrates, 4 out of 15 participants showed higher amplitudes in the attend touch conditions as compared to attend vision condition. With regard to the tactile modality, 20 Hz amplitudes did not exhibit any significant difference (t(14) = -1.33, p = 0.2, D = 0.13) between *attend touch* and *attend vision* conditions. As illustrated in Fig. 3.2C, a closer inspection of individual attention effects showed that 5 out of 15 participants exhibited lower amplitudes when touch was attended compared to when touch was unattended.

The second harmonic signal showed significantly greater amplitudes (Fig. 3.2A) in the *attend touch* compared to the *attend vision* condition (t(14) = 3.4, p < 0.005, D = 0.4). The pattern observed across the single participants' spectra in the 20 Hz signal was not visible in the 40 Hz SSEPs (see Fig. 3.2A).

No significant correlation was observed between fundamental frequency and second harmonic in both modalities (20 Hz and 40 Hz, r = -0.26, p = 0.35; 7.5 Hz and 15 Hz, r = -0.34, p = 0.2).

An ANOVA revealed that attentional effects on SSEP amplitude neither varied systematically between vision and touch (main effect *sensory modality*: F(1,14) = 0.03, p = 0.9, $\eta^2 < 0.01$) nor between fundamental and second harmonic SSEP components (main effect *SSEP component*: F(1,14) = 0.06, p = 0.8, $\eta^2 < 0.01$). However, specific combinations of *sensory modality* and *SSEP component* gave rise to differences in attentional effects (interaction: F(1,14) = 6.39, p = 0.02, $\eta^2 = 0.14$).

PLF analysis revealed higher phase locking when participants attended the visual stimulus as compared with when it was unattended for both, 7.5 Hz (t(14) = 4.9, p < 0.001, D = 1) and 15 Hz (t(14) = 2.7, p < 0.05, D = 0.5). On the contrary, no difference in PLF between conditions was observed in the 20 Hz tactile SSEP (t(14) = -0.9, p = 0.36, D = 0.1) as well as in 40 Hz SSEP (t(14) = -1.9, p = 0.08, D = 0.3).

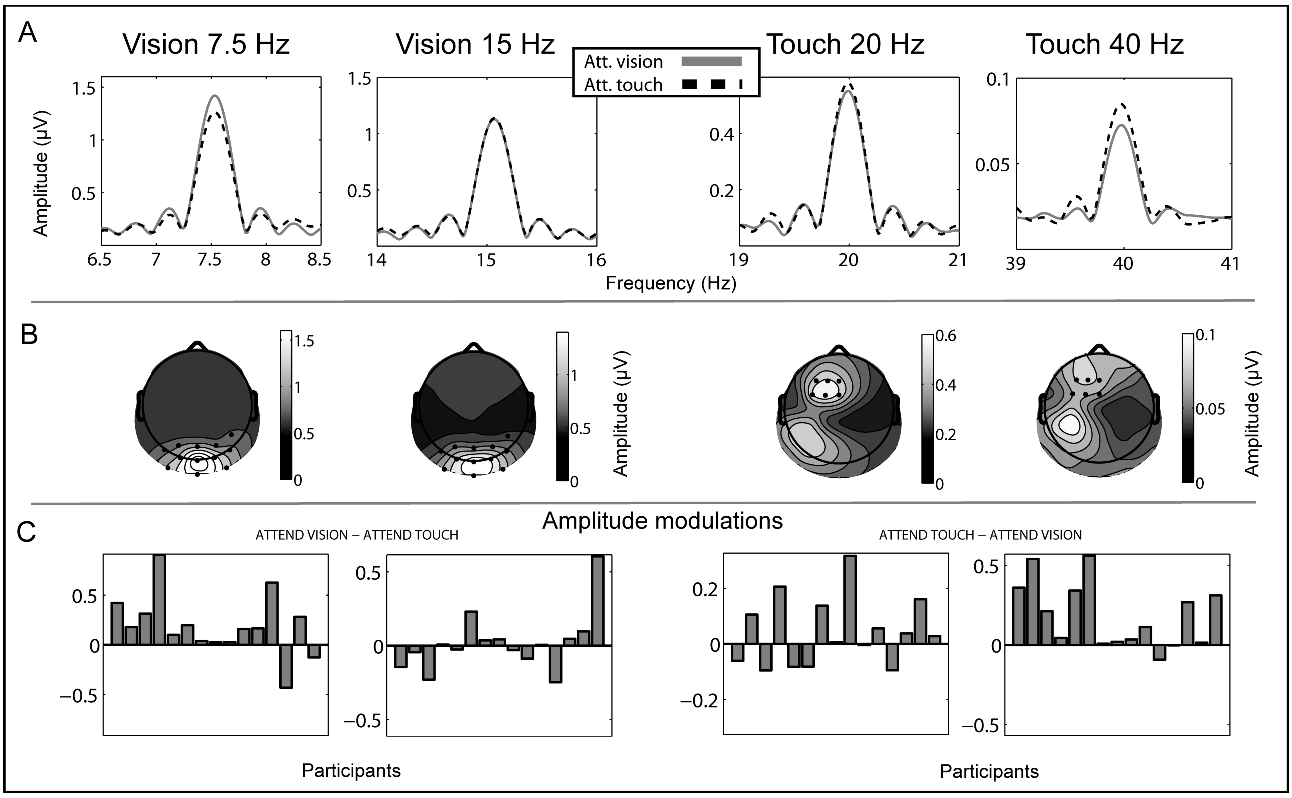

Figure 5: EEG results

Figure 3.2 EEG results. (A) Grand average visual and tactile SSEP amplitude spectra centred on fundamental frequency and second harmonic responses, respectively. Solid grey lines indicate amplitudes during attention-to-vision conditions. Dotted black lines indicate attention to touch. (B) Grand average scalp topographies representing mean amplitudes across the two conditions for each frequency component. Heavy dots indicate electrode clusters chosen to extract visual and tactile amplitudes (visual cluster: I1, 1z, I2, Oz, O1, O2, POz, PO3, PO4, PO7, PO8, P6, tactile cluster: F1, F3, Fz, FC1, FC3, FCz). (C) SSEP amplitude modulations (attended minus unattended) of individual participants relative to each frequency components (amplitude modulations were obtained by subtracting the unattended from attend condition for each frequency component).

3.5 Discussion

In the present study, we investigated effects of sustained inter-modal attention on early visual and tactile processing by means of SSEPs. To this end, we frequency-tagged visual and tactile stimuli to index the allocation of attention to each sensory modality. Participants were cued on a trial-by-trial basis to either attend to the visual or the tactile stimulus. Thus, we were able to test whether – regardless of the sensory modality – SSEP amplitude and phase synchrony were modulated by attention during continuous simultaneous stimulation of both modalities.

While the amplitude of the visual SSEP at the fundamental frequency (7.5 Hz) resulted in systematic inter-modal attention effects as in previous studies (Keitel et al., 2011a; Saupe, Widmann, et al., 2009), amplitudes of the visual second harmonic response (15 Hz) remained unaffected. Phase coherence of both responses, however, was greater when vision was attended. Regarding tactile SSEP amplitudes, in contrast to vision, only the second harmonic response (40 Hz) indicated influences of inter-modal attention on tactile processing. Neither the fundamental nor the second harmonic response showed differences in phase coherence.

Our results show that inter-modal attention dynamically modulates SSEP amplitudes in both visual and tactile modalities, thus extending previous findings in audio-visual SSEP studies (Keitel et al., 2011a; Saupe, Widmann, et al., 2009). Moreover, we demonstrate once more that inter-modal attention can be considered as a general mechanism common to different combinations of sensory modalities (Martin Eimer et al., 2002; Karns & Knight, 2009).

Interestingly, we observed a clear dichotomy between fundamental frequency and second harmonic amplitude modulations in both visual and tactile modalities indicating that attention affected the two SSEP components independently. The absence of any correlation between amplitude modulations supports the notion that fundamental frequencies and second harmonics might, at least partially, arise from distinct neural populations (Y.-J. Kim, Grabowecky, Paller, & Suzuki, 2011; Langdon, Boonstra, & Breakspear, 2011).

In line with our findings, recent studies reported a clear dissociation between attentional modulations of fundamental frequency and second harmonic of visual SSEPs (Y.-J. Kim et al., 2011; Saupe, Widmann, et al., 2009) as well as distinct sources of the two SSEP components (Pastor et al., 2007). A tactile SSEP study (Langdon et al., 2011), investigating a broad range of stimulation frequencies (from 16 Hz to 30 Hz in steps of 2 Hz), provides further support by showing a consistent phase decoupling between fundamental frequency and second harmonic, which argues against a simple harmonic relation of both SSEP components.

To date, it has yet to be determined under which circumstances attention influences one or the other frequency component in vision and touch. The possibility remains that the dichotomy reported here is not a consequence of inter-modal attentional influences on visual and tactile processing per se. It might rather reflect participants focusing on stimulus aspects that were coded in different frequency components for each modality in order to perform the task (Benucci, Frazor, & Carandini, 2007): in the visual modality, participants attended to stimulus orientation, which alternated at the stimulus presentation rate (i.e. the fundamental frequency), thus, making it the likely candidate of attentional influences (see Saupe, Widmann, et al., 2009 for a reversed case). In the tactile modality, the task-relevant decrease in carrier frequency was independent of the 20-Hz amplitude modulation of the tactile stream. Carrier frequency might have been encoded by neuronal populations that contributed to second harmonic responses of tactile SSEPs.

Regarding SSEP phase synchrony, we found attentional modulations, i.e. significantly greater phase locking when Gabor patches were attended, for the visual but *not* for the tactile SSEP. Notably, for the tactile modality we observed relatively high phase locking (~0.8) for the 20-Hz SSEP in both conditions. Obviously, attention had no effect on phase, hence, challenging whether the ideas and findings of (Kashiwase, Matsumiya, Kuriki, & Shioiri, 2012; Y. J. Kim et al., 2007) that phase synchronisation is the crucial factor of attentional modulation of visual SSEPs also apply to the tactile modality. On the other hand, one might also argue that the absence of phase modulation led to the absence of amplitude modulation. Given that phase estimation is highly dependent on the signal-to-noise ratio in single trials, one can hardly avoid that this discussion results in an “egg-hen” problem. Discrepancies observed between amplitude and phase modulations (in the 15 Hz and 40 Hz signals) might therefore be attributed to differences in amplitude and phase derivation from EEG time series. Note that for phase analysis, in contrast to SSEP amplitudes, we averaged single epoch Fourier transforms making phase estimates more likely to be influenced by non phase-locked electrophysiological brain activity.

Taken together, our results corroborate previous findings regarding audio-visual inter-modal attention and extend them to the tactile modality. We further demonstrate that the frequency-tagging approach holds viable in visuo-tactile multi-stimulus situations. Closer investigations of SSEP amplitude and phase modulations as well as a comparison of amplitude modulations of fundamental frequency and second harmonic SSEP components, however, revealed slight differences of how inter-modal attention modulated visual and tactile processing.

4. Experiment 2 and 3

4.1 Introduction

In section 1.5, we have briefly seen that the predominant paradigm used to investigate processing resources among sensory modalities consisted mainly of comparing behavioural and/or physiological indexes relative to divided attention across different modalities with indexes relative to attention to a single modality. Although, such approach provided fundamental suggestions on this topic, one of the main challenges concerns the difficulty to design stimuli and tasks which involve comparable attentional deployment for both modalities. Hence, in the following two experiments we tried to address this issue from a different prospective, that is we tested basic competitive interactions between sensory modalities regardless of attentional influences.

According to Franconeri and colleagues (2013, see section 1.7), competitive interactions between stimuli should take place within a common anatomical map, where two stimuli can compete for processing resources. Although Franconeri referred primarily to single modalities this view can be extended to different senses. As proposed by Talsma and colleagues (Iurilli et al., 2012; Talsma et al., 2010), different sensory modalities might compete for processing resources already in early sensory areas. Moving from the previous hypothesis and in line with bias competition assumptions (see section 1.4 for further details) we reasoned that if competitive interactions between different sensory modalities occurred in absence of attentional modulations, such results would suggest limited resources between sensory modalities already in early sensory areas.

To this end, we conducted two experiments, all employing similar paradigms, yet, each featuring a unique combination of stimuli from two sensory modalities: visual and tactile stimuli in Experiment 2 and tactile and auditory stimuli in Experiment 3. In each experiment we frequency-tagged continuous sensory stimulus streams (’reference stimuli’). Frequency-tagged stimuli elicited oscillatory brain responses, phase-locked to stimulation that indexed the ongoing sensory processing in corresponding sensory modalities. These so-called steady-state responses (SSEPs; Regan, 1989) have been shown to decrease in amplitude when a competing stimulus was presented in the same sensory modality (vision, Fuchs, Andersen, Gruber, & Müller, 2008; Keitel, Andersen, & Müller, 2010) audition, Kawase et al., 2012; Ross et al., 2012 touch, Severens, Farquhar, Desain, Duysens, & Gielen, 2010). During the presentation of respective reference stimuli, we therefore introduced transient frequency-tagged ‘competitors’, i.e. stimuli of the same and/or different sensory modality, to induce competition. We compared amplitude changes of reference-driven SSEPs between competitor-absent and competitor-present periods. In all three experiments, participants were engaged in a visual discrimination task designed to withdraw their attention from critical stimulation in order to control for a biased competition. More specifically, participants had to count brief contractions of the central foveally presented fixation cross while ignoring elongations. Critical visual reference and competitor stimuli were presented to unattended perifoveal regions of the visual field (see Methods section of Experiment 1 for details on visual stimulation).

We hypothesized that, if, on the one hand, stimuli of different sensory modalities entered a cross-modal competition we would observe effects of suppression. SSEP amplitudes during the competitor-present period would be lower than during the competitor-absent period. On the other hand, if no suppression occurred, SSEP amplitudes would remain constant. Additionally, in line with previous studies on intra-modal competition, we expected reduced SSEP amplitudes during competitor-present periods to indicate suppression between stimuli within senses.

Generally, we found that suppression only occurred between stimuli of the same sensory modality but not between stimuli of different sensory modalities. Therefore, while well in line with biased competition governing processing within senses, our results challenge the notion of a biased competition for common processing capacities between senses.

4.2 General Methods of Experiments 2 and 3

4.2.1 Participants

Participants gave informed written consent prior to experiments. None reported a history of neurological diseases or injury. The experiments were conducted in accordance with the Declaration of Helsinki and the guidelines of the ethics committee of the University of Leipzig.

4.2.2 Stimuli

In each of the two experiments stimuli from two sensory modalities were presented. Experiment 2 employed visual and tactile stimuli. Experiment 3 featured the presentation of auditory and tactile stimuli. Detailed descriptions of stimuli are given below (see respective Methods sections).

4.2.3 Experimental procedure and task

Participants were seated comfortably in an acoustically dampened and electromagnetically shielded chamber in front of a 19" cathode ray tube (CRT) screen. The screen was set to a refresh rate of 120 frames per second and a resolution of 800 x 600 pixels (width x height). A white fixation cross (0.64° of visual angle in width and height) was presented in the center of the screen at a viewing distance of 80 cm. Participants were instructed to fixate the cross and to perform a demanding task, namely to discriminate between brief changes in length of one of the two bars of the fixation cross. Length increased or decreased by 20, 40 or 60%. These changes lasted 8 frames (67 ms) and occurred up to three times in every trial with a minimum interval of 600 ms between subsequent onsets. Participants had to count contractions in either one of the beams (= targets). Corresponding elongations had to be ignored (= distracters). Responses were given after each trial by pressing one of four buttons indicating zero, one, two or three counted targets. Response button layout was reassigned randomly for each trial to control for effects of motor preparation during trials.

As index and middle fingers were occupied by the vibro-tactile stimulators, participants used both thumbs to respond. To this end, they placed both hands on a flat keyboard with palms facing down. The keys [S], [X], [:] (= colon) and [Ö] (= O with dieresis) of the standard German keyboard layout served as response alternatives that were assigned to the four different possible target counts (0, 1, 2, 3).

Both experiments formed full-factorial designs with two factors: In each trial, the reference stimulus was presented in one of two sensory modalities (factor *reference modality*). Additionally, a competitor was presented either in the same sensory modality as the reference stimulus, in the second sensory modality or competitors from both sensory modalities were presented in combination (factor *competitor modality*). In each experiment, we presented 420 trials divided into 6 blocks of 70 trials each with trials of all six conditions intermingled randomly (see descriptions of individual experiments for respective conditions). Blocks were started by a button press and lasted ~5 min each. Prior to the experiment, participants performed a short training session of at least one block (duration ~5 min as in the experiment). After each training and experimental block, they received feedback about their average correct-response rate.

Each trial began with the presentation of the fixation cross for 800 ms followed by the onset of the reference stimulus, which was presented for 3,000 ms (see Fig. 4.1). Competitor presentation started with a randomly chosen lag of 200 or 400 ms after reference stimulus onset. Both stimuli were presented simultaneously for a randomly chosen interval of 1,200, 1,400 or 1,600 ms. After competitor offset, the reference stimulus was presented alone until the end of each trial.

Task-relevant changes of the fixation cross occurred during the presentation of reference and competitor stimuli only. At the end of each trial, the fixation cross was replaced by a graphical scheme of the current button layout for 1,700 ms prompting participants for a response (see Fig. 4.1 for a trial schematic). Additionally, participants were instructed to blink during the response-prompt period to minimize eye movements during trials. If participants did not press a button the target count in respective trials was considered incorrect. Any button press started the next trial immediately.

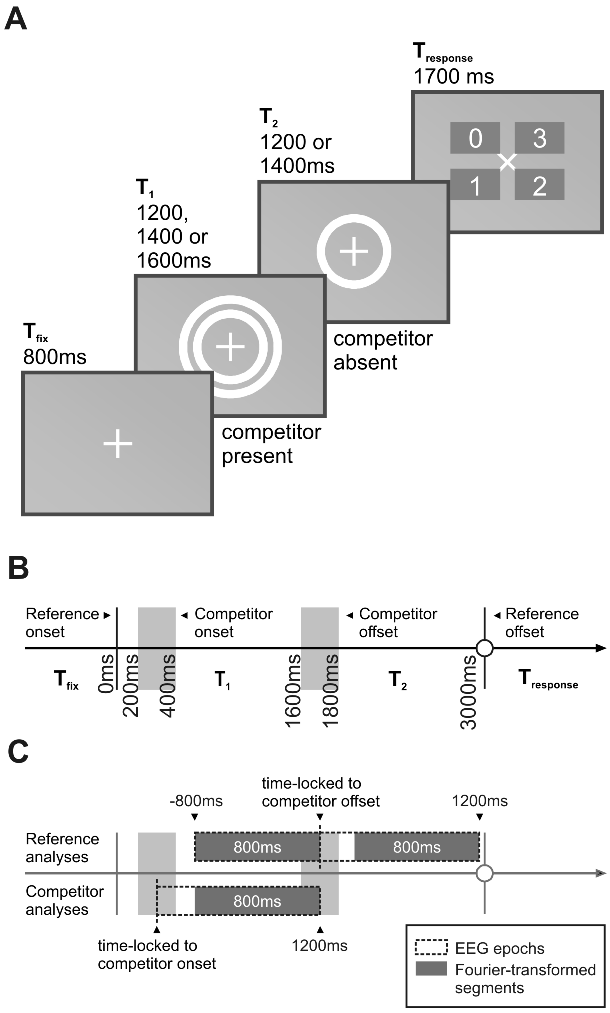

Figure 6: Schematics of the experimental paradigm

Figure 4.1 Schematics of the experimental paradigm. (A) Example displays from a trial with a visual reference stimulus and a visual competitor illustrate the four phases of each trial: fixation period (T_{fix}), reference stimulus presentation during competitor-present (T_1) and competitor-absent (T_2) periods, response-prompt ($T_{response}$). (B) Timeline corresponding to A. Grey shaded areas signify the jitter in competitor on- and offsets. (C) Timeline adapted from B. Dashed boxes represent epochs extracted from raw EEG for the purpose of reference SSEP (upper half) and competitor SSEP analyses (lower half). Dark grey boxes depict epoch segments used for SSEP quantification by means of Fourier transforms (see Methods sections on SSEP analyses for further details).

4.3 Data analysis

4.3.1 Behavioural data analysis

Only responses that exactly matched the number of targets in a trial were considered correct. Total correct responses for each experimental condition were entered into a two-way repeated measures ANOVA with factors: *reference modality* and *competitor modality* (see above).

4.3.2 EEG analysis

For EEG recordings details see section 2.5.1. From continuous recordings we extracted two different sets of epochs (for details see following sections). The first set served to analyse changes in *reference* SSEP amplitude from competitor-present to competitor-absent periods within trials. The second set allowed an investigation of *competitor* SSEPs.

Reference SSEPs

For the analyses of SSEPs driven by reference stimuli, we extracted epochs of 2,000 ms that started 800 ms before competitor *offsets* (in the following referred to as epochs of the 'reference set'). Individual trials were rejected automatically when contaminated with blinks or eye movements that exceeded a threshold of 20 µV.

Competitor SSEPs

Competitor SSEPs could not be analyzed in the reference set as variable competitor presentation durations (1,200, 1,400 or 1,600 ms) did not allow for an integer number of cycles of respective competitor tagging frequencies in all cases. As a consequence, tagging frequency phase at competitor offset varied across trials. Averaging epochs time-locked to competitor offset – as performed for reference SSEPs analyses – would thus have averaged out competitor SSEP waveforms of different phases. To avoid this problem, we extracted a second set of epochs of 1,200 ms starting with competitor *onset*, which served to examine competitor-driven SSEPs (in the following referred to as epochs of the 'competitor set').

Reference SSEPs

Reference SSEPs at each electrode were quantified by a Fourier transform of data from two 800-ms time windows within averaged artifact-free epochs of the reference set. The first time window started 800 ms before competitor offset and, hence, yielded reference SSEPs during competitor presentation (*competitor-present* time window). The second time window started 400 ms after competitor offset and yielded reference SSEPs in the absence of competitors (*competitor-absent* time window). Both time windows were chosen in order to reduce the influence of ERPs to stimulus on- or offset on spectral analyses. SSEP amplitudes were calculated as the absolute value of the complex Fourier coefficients at the respective driving frequencies.

Note that we employed two different reference stimuli in each experiment, one of which was presented in three of the six conditions while the other reference stimulus was presented in the remaining conditions. Therefore, reference SSEPs were only quantified from data of conditions that included the presentation of the corresponding driving stimulus.

For subsequent statistical analyses, reference SSEP amplitudes were averaged over electrodes sites showing maximum amplitude in scalp topographical voltage distributions (see respective results sections for the specific choice of electrodes for each frequency).

These processing steps yielded SSEP amplitudes for each reference SSEP frequency in both time windows. As we were interested in the modulation of absolute reference SSEPs amplitude in the presence of a competitor, we computed a sensory suppression index (SSI; modified after Kastner et al., 2001) for each condition according to:

$$SSI = (A_{TW1} - A_{TW2}) / (A_{TW1} + A_{TW2}) \quad (1)$$

where A_{TW1} and A_{TW2} denote absolute reference SSEP amplitudes from the first competitor-present and the second competitor-absent time window. The SSI expresses SSEP amplitude changes between time windows: negative SSI values indicate suppression, whereas positive values indicate facilitated processing in the presence of a competing stimulus. SSI values were subjected to a two-way repeated measures analysis of variances (ANOVA) with factors of *reference modality* and *competitor modality* (see above). For each condition, specific planned comparisons tested whether respective SSI values differed significantly from zero.

Competitor SSEPs

Additionally, we analysed the amplitudes of the two competitor-driven SSEPs in each experiment to cross-validate putative multisensory stimulus interactions as inferred from reference SSEP results. Note that each competitor was only presented in four out of six experimental conditions. Therefore, below-described analyses were only applied to data from conditions with respective competitors.

Competitor SSEP amplitudes were calculated from Fourier transforms of 800-ms time windows starting 400 ms after competitor onset within artifact-free epochs of the competitor set (see above) and collapsed across electrode sites exhibiting maximum amplitude in scalp topographical voltage distributions.

First, we tested whether competitor SSEP amplitudes varied with the modality of the reference stimulus (same vs. other modality) by means of paired t-tests for each SSEP frequency, separately. Prior to testing, SSEP amplitudes were divided by the individual mean amplitude across conditions to control for differences in absolute amplitude between participants. Thus normalized amplitudes were further collapsed across conditions in which a given competitor was presented alone and in combination with another competitor. Second, we compared the magnitude of reference-modality effects between the two competitor modalities and the two modes of competitor presentation (presented alone vs. combined competitors). To this end, we subtracted SSEP amplitudes of conditions in which the reference stimulus was presented in the same sensory modality as the competitor from SSEP amplitudes in conditions in which the reference stimulus was presented in the other sensory modality. Differences were divided by the sum of amplitudes from the same conditions. These normalized differences were subjected to a two-way repeated-measures ANOVA with factors of *competitor modality* and *competitor presentation mode*.

4.4 Methods experiment 2

4.4.1 Subjects

Data from fifteen participants (age: 19 - 32 years, 10 women, one left-handed) were recorded and entered analyses. All participants reported normal or corrected-to-normal vision.

4.4.2 Stimuli and procedure

Experiment 2 investigated interactions between visual and tactile stimuli.

Visual stimulation consisted of two concentric black (RGB: [0 0 0]) rings that surrounded the fixation cross in front of a grey background (RGB: [128 128 128], luminance = 41 cd/m^2). The inner ring (inner diameter = 1.9°, width = 2°) flickered at 15 Hz to elicit the reference visual SSEPs. The outer ring (inner diameter = 4.7°, width = 2°) flickered at 24 Hz to elicit the competitor visual SSEPs. For both visual stimuli, luminance over time was physically identical given a 50/50 flicker on/off ratio regardless of stimulation frequency.

Vibro-tactile stimuli were generated by four small electromagnetic stimulators (Dancer Design). Two stimulators - carrying the reference stimulus vibration - were attached to the index fingers of both hands. The other two stimulators – carrying the competitor stimulus vibration – were attached to the middle fingers of both hands. The reference stimulus consisted of an amplitude-modulated wave obtained by multiplying a carrier sine wave (150 Hz) with a modulating sine wave of 20 Hz. The competitor AM wave was obtained by multiplying a carrier sine wave (150 Hz) with a modulating sine wave of 28 Hz. Both stimuli were amplitude-modulated with a depth of 100%. The maximum intensity of all four stimulators was kept stable at 0.2 N. During the experiment, both hands were concealed to avoid visual influences on tactile stimulus processing.

4.5 Results

4.5.1 Behavioural Data

Neither the *reference modality* (F(1,14) = 0.17, p = 0.69) nor the *competitor modality* (F(2,28) = 1.09, p = 0.35) influenced performance in the fixation cross task (see Tab. 4.1). Task performance was further independent of a specific combination of *reference* and *competitor modality* (interaction: F(2,28) = 0.76, p = 0.48).

Table 4.1 Correct responses for each condition averaged across participants in Experiment 2 (maximum correct responses = 70).

Table 1: Correct responses - experiment 2

Reference Competitor		Vision *S*	 *D*	 *C*	Touch *S*	 *D*	 *C*
Correct responses	*M*	62.3	61.7	61.7	62.4	61.9	60.9
	SEM	1.2	1.3	1.5	1.0	1.7	1.4

Competitor sensory modality: S = same as reference, D = different from reference, C = combined presentation; M = mean, SEM = standard error of the mean.

4.5.2 SSEP data

Due to artefacts, we rejected a total average of 6% of reference-set epochs and 3% of competitor-set epochs from SSEPs analyses (see General Methods for details on artefact detection).

Reference SSEPs

15 Hz visual SSEP amplitudes averaged across conditions with a visual reference stimulus were maximal at a cluster of five occipital electrode sites (Oz, O1, O2, POz, Iz; see Fig. 4.2A). 20 Hz tactile SSEP amplitudes averaged across conditions with a tactile reference stimulus amplitudes were maximal at a cluster of six frontocentral electrode sites (Fz, FCz, F1, F2, FC1, FC2; see Fig. 4.2A). Averaged data across electrodes of each cluster were used in statistical analyses.

Grand average spectra from each electrode cluster during competitor presentation show distinct peaks that correspond to the visual flicker and tactile flutter frequencies of respective driving reference stimuli (Fig. 4.2B). Presenting a competitor in the same modality as the reference stimulus resulted in smaller SSR amplitudes.

We calculated the sensory suppression index (SSI) that expressed reference SSEP amplitude modulation between competitor-present and competitor-absent periods (see Fig. 4.2C and D). A two-way repeated measures ANOVA of SSIs revealed that reference SSEP amplitude modulation did not depend on the modality of the reference stimulus (main effect *reference modality*: $F(1,14) = 1.50$, $p = 0.24$). However, SSEP modulation varied systematically with the modality of the competitor (main effect *competitor modality*: $F(2,28) = 33.02$, $p < 10^{-6}$, $\varepsilon_{GG} = 0.81$, $\eta^2 = 0.37$). Competitor modality influence on SSR amplitudes did not differ between reference modalities (interaction: $F(2,28) = 1.93$, $p = 0.16$).

As shown in Figure 4.2C and Tab. 4.2 (asterisks denote significant deviations from zero), while the presentation of same-modality or combined competitors led to suppression in the reference SSEP regardless of its modality, significant positive SSIs indicated amplification when a different-modality competitor was presented. Tactile SSEP amplitude was not systematically suppressed during combined competitor presentation (see Tab. 4.2). A post-hoc t-test against the SSI during same-modality competitor presentation, however, yielded no difference in suppression between conditions ($t(14) = 0.76$, $p = 0.46$). The same held true for a similar comparison between visual SSIs ($t(14) = -0.53$, $p = 0.60$).

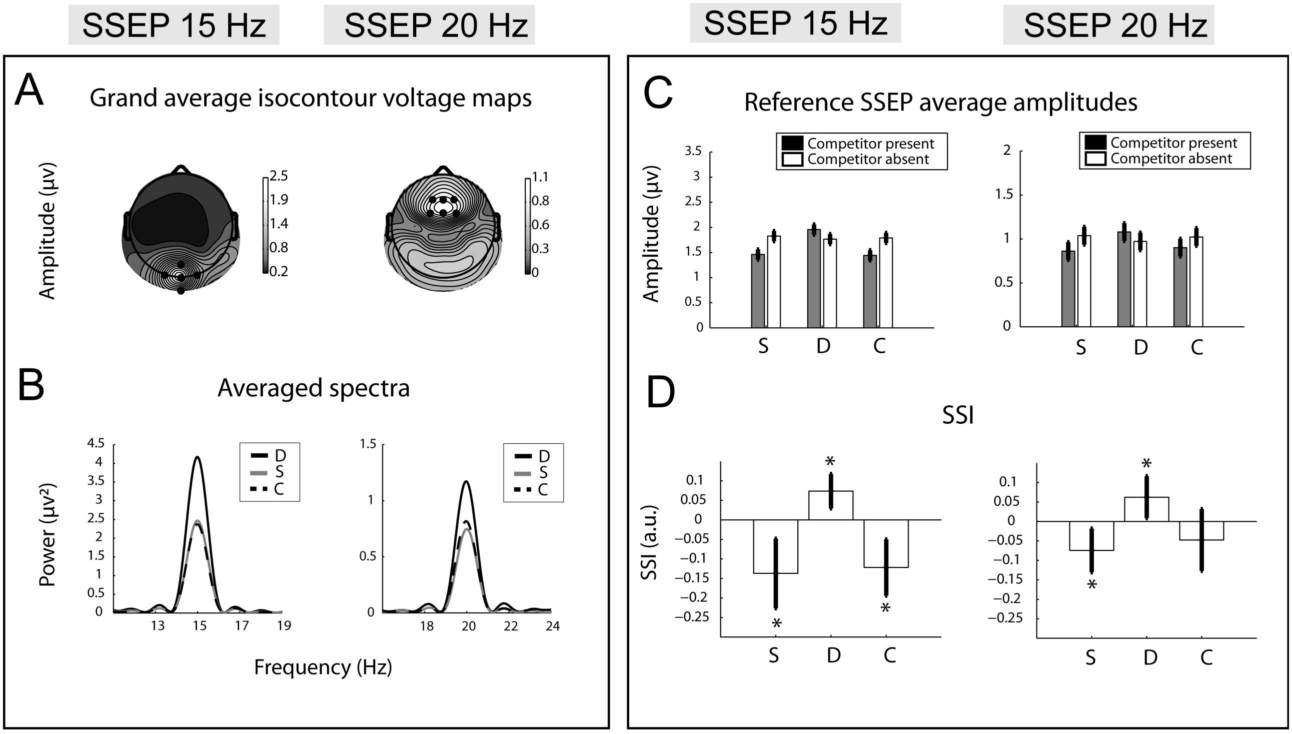

Figure 7: Reference SSEP results for Experiment 2

Figure 4.2 Reference SSEP results for Experiment 2. (A) Grand average isocontour voltage maps averaged across experimental conditions as well as competitor-present and competitor-absent periods for each reference SSEP. Highlighted sites indicate electrode clusters chosen for further analyses. (B) Grand average power spectra derived from the competitor-present period for each reference SSEP and respective conditions. Peaks correspond to the stimulation frequencies. (C) Bar plots allow for a comparison of absolute SSEP amplitudes between competitor-present and competitor-absent periods for each condition (**S** = same modality competitor, **D** = different modality competitor, **C** = combined competitors). Error bars show standard error of the mean. (D) Sensory suppression indices (SSIs) index normalized changes in reference SSEP amplitude in competitor-present relative to competitor-absent periods for each condition. Asterisks denote significant deviations from zero at the 0.05-α-level. Error bars show 95% confidence intervals.

Table 4.2 Experiment 2. Sensory suppression indices (SSIs) and results of t-tests against zero. N=15.

Table 2: Sensory suppression indeces - experiment 2

reference	competitor[1)]	*SSI*	*t(14)*	*p*
V	same	-.14	-3.31	<.01*
V	different	.07	3.58	<.01*
V	combined	-.12	-3.63	<.01*
T	same	-.07	-2.86	<.05*
T	different	.06	2.49	<.05*
T	combined	-.05	-1.29	.22

V = visual, T = tactile. 1) relative to reference modality. Asterisks mark significant results.

Competitor SSEPs

Scalp-topographical distributions of competitor-driven 24-Hz visual SSEP and 28-Hz tactile SSEP amplitudes showed maxima at similar sites as the reference SSEPs (see Fig. 4.3A). Hence, data of identical electrode clusters were used in statistical analyses of competitor amplitudes (see above). When the reference stimulus was presented in the same sensory modality as the competitor, SSEP amplitudes were generally smaller (visual SSEP: $t(14) = -2.27$, $p < 0.05$; tactile SSEP: $t(14) = -2.80$, $p < 0.05$; see Fig. 4.3B). Effects on visual SSEPs were topographically localized to occipital sites while effects on tactile SSEPs largely emerged at fronto-central sites (see Fig. 4.3B).

Furthermore, we tested whether above described differences varied with the competitor modality or with its mode of presentation (single vs. combined presentation). We found that SSEP amplitude differences between visual and tactile reference conditions did not depend on the modality of the competitor (main effect *competitor modality*: $F(1,14) = 0.09$, $p = 0.77$). Moreover, they did not vary between single and combined competitor presentations (main effect *competitor presentation mode*: $F(1,14) < 0.01$, $p = 0.95$). No specific combination of competitor modality and presentation mode led to a systematic effect on SSEP amplitude differences (interaction: F(1,14) = 0.02, p = 0.89).

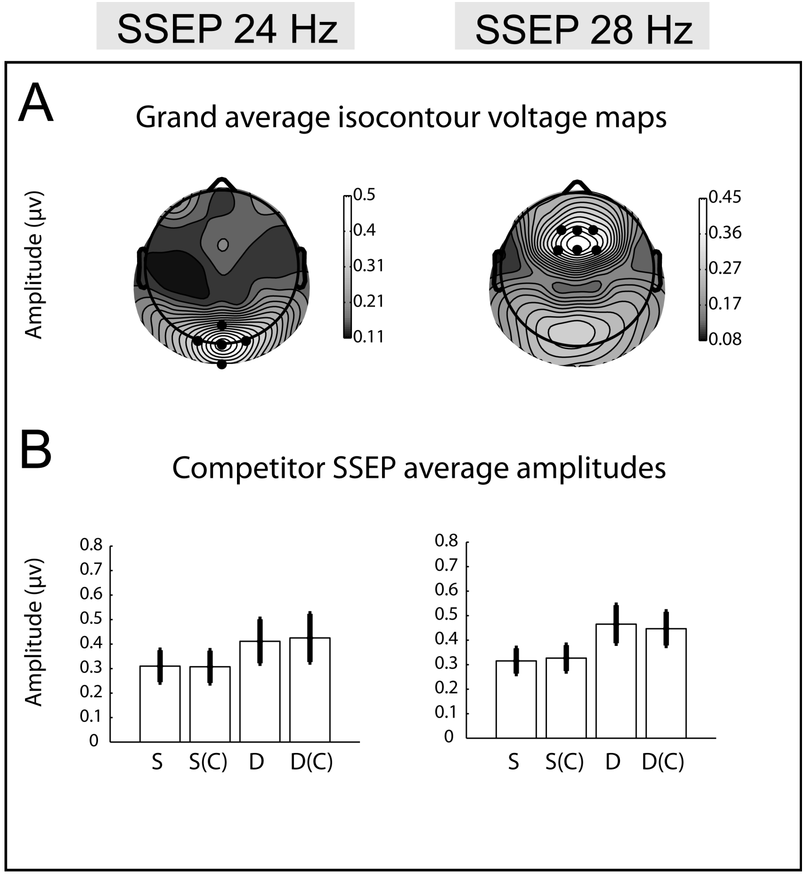

Figure 8: Competitor SSEP results for Experiment 2

Figure 4.3 Competitor SSEP results for Experiment 2. (A) Grand average isocontour voltage maps averaged across experimental conditions for each competitor SSEP. Highlighted sites indicate electrode clusters chosen for further analyses. (B)Bar plots depict the amplitude of competitor SSEPs for each condition (Amplitudes at **S(C)** and **D(C)** refer to conditions with combined competitor presentation). Error bars show 95% within-subject confidence intervals.

4.6 Methods Experiment 3

4.6.1 Participants

From a total of 17 recorded participants, data of 16 (age: 19 - 34 years, ten women, all right-handed) entered analyses. Data of one participant was excluded as she/he did not exhibit tactile SSEPs above general noise level. All participants reported normal or corrected-to-normal vision and normal hearing.

4.6.2 Stimuli and procedure

Experiment 3 investigated interactions between auditory and tactile stimuli. The auditory reference stimulus (Keitel et al., 2013, 2011) consisted of multi-speech babble (MSB) with a 40-Hz amplitude modulation. MSB can be considered as a type of broadband noise that closely resembles the spectral characteristics of human speech. We generated MSB from samples of eight different speakers (four women). Four different 10-s samples were extracted from continuous speech of each speaker. These samples were low-pass filtered with a cut-off frequency of 4 kHz and normalized in amplitude by a root-mean-square procedure to match intensities. The subsequent combination of individual samples yielded a signal with 32 simultaneously speaking voices. In earlier experiments, where participants had to attend to MSB, they reported consistently that it was impossible to extract a single speaker (Keitel et al., 2013, 2011). MSB stimulation was chosen for two reasons. First, it is maximally unrelated to the tactile stimulation, which reduces possible confounds with effects of audio-tactile integration. Second, its envelope shows little variance over time, which enables an amplitude modulation that elicits a stable auditory SSEP. We further chose a 500-Hz sine tone with a full 35-Hz amplitude modulation as the auditory competitor stimulus. Suppressive stimulus interactions in auditory cortex are a function of tonotopic distance between concurrent stimuli (see e.g. Jääskeläinen, Ahveninen, Belliveau, Raij, & Sams, 2007). Since ~90% of the MSB's spectral power are concentrated in the frequency band between 100 and 600 Hz, a tonotopically close but distinguishable pure 500-Hz tone provided a basis for suppressive stimulus interactions in early auditory cortex. Auditory reference and competitor stimulus streams elicited auditory SSEPs at 40 and 35 Hz, respectively. Headphones presented the reference stimulus to the left ear and the competitor stimulus to the right ear at a sound pressure level of 65 dB. Tactile stimulus presentation was similar to Experiment 2 with two exceptions. (1) We changed the flutter frequency of the tactile reference stimulus from 20 to 22 Hz to avoid a superposition of the first harmonic of its corresponding tactile SSEPs with the 40-Hz auditory SSEPs driven by the auditory reference stimulus. (2) Vibro-tactile stimulators were attached to index and ring fingers to minimize the risk of direct stimulator contact between adjacent fingers.

4.7 Results

4.7.1 Behavioral Data

Performance in the fixation cross task was monitored identically to Experiment 2. Hit rate did neither vary with the reference modality ($F(1,15) = 1.56$, $p = 0.23$) nor the competitor modality ($F(2,30) = 0.21$, $p = 0.80$). Furthermore, hit rates did not depend on a specific combination of both factors ($F(2,30) = 2.97$, $p = 0.08$, $\varepsilon_{GG} = 0.80$)(see Tab. 4.3).

Table 4.3 Correct responses for each condition averaged across participants in Experiment 3 (maximum correct responses = 70).

Table 3: Correct responses - experiment 3

Reference Competitor		Touch *S*	*D*	*C*	Audition *S*	*D*	*C*
Correct responses	*M*	62.2	63.5	63.0	62.8	62.8	61.6
	SEM	1.6	1.7	1.4	1.1	1.7	1.7

Competitor sensory modality: S = same as reference, D = different from reference, C = combined presentation; M = mean, SEM = standard error of the mean.

4.7.2 SSEP data

On average, across participants and conditions, we discarded 14% of epochs of the reference set and 9% of epochs of the competitor set due to artefacts (see General Methods for details on artefact detection).

Reference SSRs

22-Hz tactile SSEP amplitudes averaged across tactile reference conditions were maximal at a cluster of six frontal electrode sites (Fz, FCz, F1, F2, FC1, FC2; see Fig. 4.4A). 40-Hz auditor SSEP amplitudes averaged across auditory reference conditions revealed a slightly right-lateralized local maximum at a cluster of six fronto-central electrode sites (Fz, F2, F4, FCz, FC2, FC4; see Fig. 4.4A). Data averaged across respective electrode clusters were used in statistical analyses. Scalp maps in Figure 4.4A depict topographical distributions of amplitude differences between conditions.

Figure 4.4B shows grand average spectra during competitor presentation from each electrode cluster. Peaks correspond to the tactile flutter frequency and auditory amplitude modulation of driving reference and competitor stimuli. As in the previous experiments, SSEP amplitudes are generally smaller in conditions in which a competitor was presented to the same sensory modality as the respective reference stimulus.

A two-way repeated measures ANOVA of SSIs revealed that reference SSEP amplitude modulation was similar for tactile and auditory reference stimuli (main effect *reference modality*: $F(1,15) = 1.64$, $p = 0.22$). In contrast, whether the competitor was presented in the same or the other sensory modality influenced SSIs (main effect *competitor modality*: $F(2,30) = 7.09$, $p = 0.01$, $\varepsilon_{GG} = 0.67$, $\eta^2 = 0.15$). The influence of the competitor modality did not differ systematically between reference modalities (interaction: $F(2,30) = 1.40$, $p = 0.24$).

Figure 4.4D depicts contrasts of SSIs against zero for each condition. Asterisks denote significant deviations from zero. These comparisons indicated that only the presentation of a tactile competitor, either alone or in combination with an auditory competitor, led to a systematic suppression of the reference tactile SSEPs but not of the reference auditory SSEPs. Amplitude modulation of the auditory SSEPs showed a similar pattern, however, without reaching statistical significance (see Tab. 4.4). Post-hoc comparisons of SSIs between conditions with same-modality and combined competitors neither yielded systematic differences in touch ($t(15) = -0.47$, $p = 0.65$) nor in audition ($t(15) = 1.11$, $p = 0.29$).

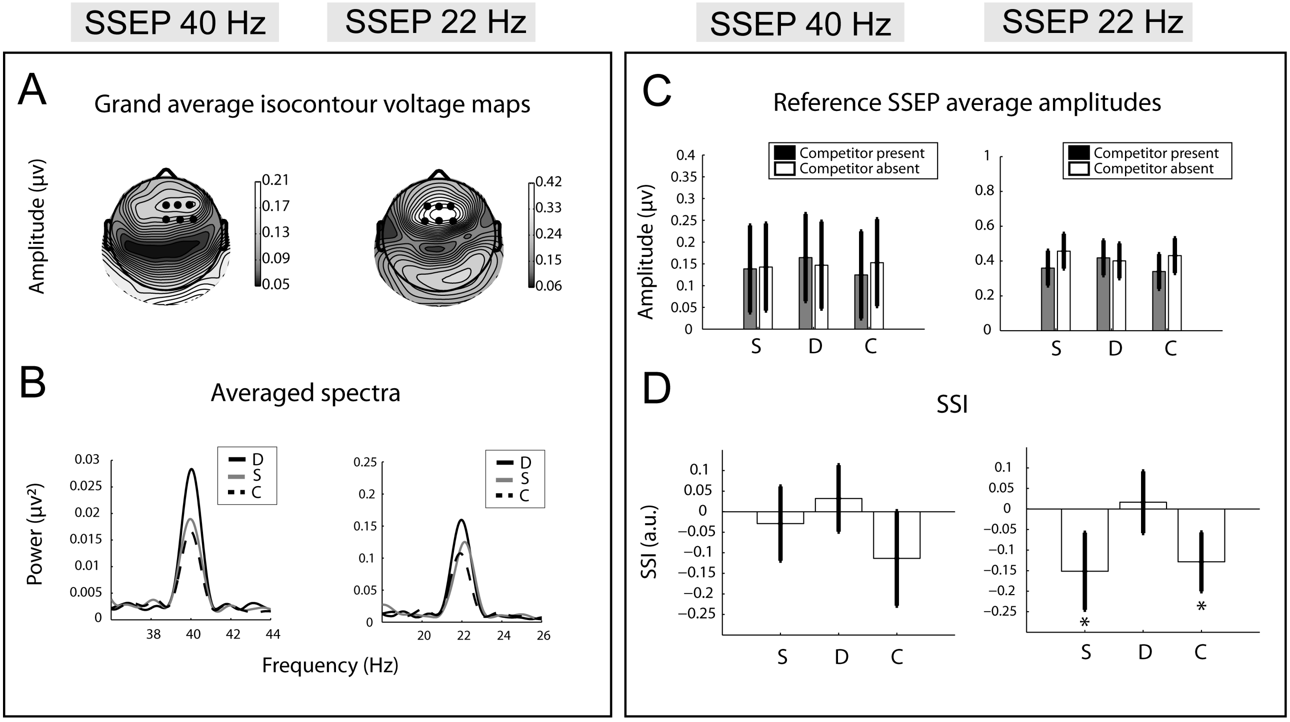

Figure 9: Reference SSEP results for Experiment 3

Figure 4.4 Reference SSEP results for Experiment 3. (A) Grand average isocontour voltage maps averaged across experimental conditions as well as competitor-present and competitor-absent periods for each reference SSR. Highlighted sites indicate electrode clusters chosen for further analyses. (B) Grand average power spectra derived from the competitor-present period for each reference SSEP and respective conditions. Peaks correspond to the stimulation frequencies. (C) Bar plots allow for a comparison of absolute SSEP amplitudes between competitor-present and competitor-absent periods for each condition (**S** = same modality competitor, **D** = different modality competitor, **C** = combined competitors). Error bars show standard error of the mean. (D) Sensory suppression indices (SSIs) index normalized changes in reference SSEP amplitude in competitor-present relative to competitor-absent periods for each condition. Asterisks denote significant deviations from zero at the 0.05-α-level. Error bars show 95% confidence intervals.

Table 4.4 Experiment 3. Sensory suppression indices (SSIs) and results of t-tests against zero. N=16.

Table 4: Sensory suppression indeces - experiment 3

reference	competitor[1)]	*SSI*	*t(15)*	*p*
A	same	-.03	-.68	.51
A	different	.03	.85	.41
A	combined	-.11	-2.11	.05
T	same	-.15	-3.45	<.01*
T	different	.02	.47	.65
T	combined	-.13	-3.83	<.01*

A = auditory, T = tactile. 1) relative to reference modality. Asterisks mark significant results.

Competitor SSEPs

As can be seen in scalp topographies in Figure 4.5A, 28-Hz tactile SSEP amplitude peaked at identical recording sites as the 22-Hz reference tactile SSEPs, which allowed performing statistical analyses on data from the above-defined electrode cluster. In contrast to the 40-Hz reference auditory SSEP, local maxima of 35-Hz competitor auditory SSEP amplitude showed a bilateral topography. Therefore, statistical analyses were performed on average data from two frontolateral 3-electrode clusters (F3, FC1, FC3 and F4, F6, FC4; see Fig. 4.5A). SSEP amplitudes were generally smaller when the reference stimulus was presented in the same sensory modality as the competitor (tactile SSEPs: $t(15) = -4.66$, $p < 0.001$; auditory SSEPs: $t(15) = -5.43$, $p < 0.001$). Effects on auditory and tactile SSEP amplitude were largest at fronto-central sites (see Fig. 4.5A).

SSEP amplitude differences between tactile and auditory reference conditions varied with the modality of the competitor (main effect *competitor modality*: $F(1,15) = 10.12$, $p < 0.01$, $\eta^2 = 0.21$), yet, did not depend on whether competitors were presented alone or in combination (main effect *competitor presentation mode*: F(1,15) = 0.61, p = 0.45). The influence of the competitor modality on SSEP amplitude differences was comparable for both competitor presentation modes (interaction: F(1,15) = 1.22, p = 0.29).

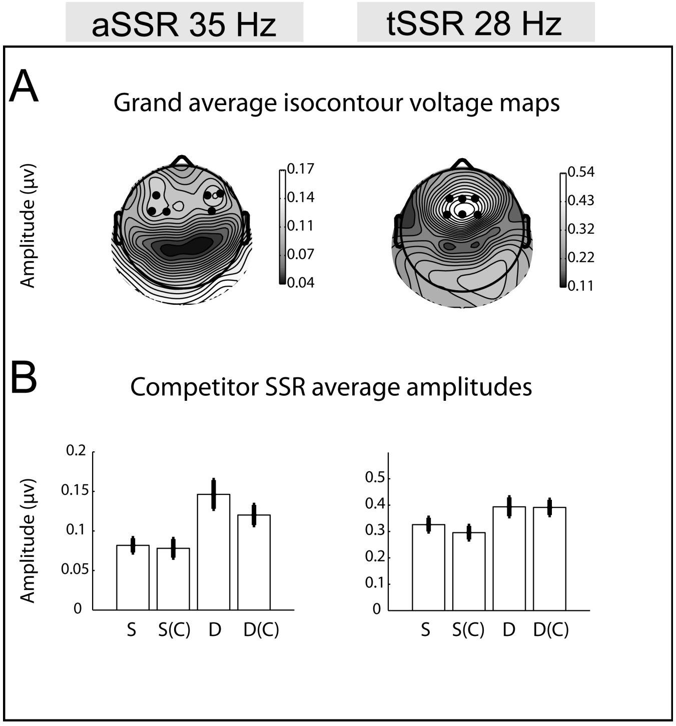

Figure 10: Competitor SSEP results for Experiment 3

Figure 4.5 Competitor SSEP results for Experiment 3. (A) Grand average isocontour voltage maps averaged across experimental conditions for each competitor SSEP. Highlighted sites indicate electrode clusters chosen for further analyses. (B)Bar plots depict the amplitude of competitor SSEPs for each condition (Amplitudes at **S(C)** and **D(C)** refer to conditions with combined competitor presentation). Error bars show 95% within-subject confidence intervals.

4.8 Discussion

The present study aimed to investigate whether visual, auditory and tactile stimuli compete for capacity-limited early sensory processing across sensory modalities. We conducted two experiments that probed putative visuo-tactile and audio-tactile stimulus interactions, respectively. Frequency-tagged continuous visual, auditory and tactile stimulus streams ('reference' stimuli) elicited oscillatory brain responses that indexed ongoing sensory processing in corresponding modalities. During the presentation of respective reference stimuli, we introduced frequency-tagged ‘competitors’, i.e. stimuli of the same and/or different sensory modalities. We compared amplitude changes of reference-driven SSEPs between *competitor-absent* and *competitor-present* periods. Decreased SSEP amplitudes in the competitor-present relative to the competitor-absent period would indicate suppression, the neural consequence of competition.

As expected and in line with previous work on competitive effects on SSEP amplitude in vision (Fuchs et al., 2008; Keitel et al., 2010) and touch (Severens et al., 2010), we observed reduced SSEP amplitudes during competitor presentation, only, when reference and competitor stimuli were presented to the *same* sensory modality in all but one specific case in Experiment 3 (auditory reference and competitor). In contrast, in none of the experiments did we find reduced amplitudes when reference and competitor stimuli were presented to *different* sensory modalities. These results strongly suggest that early sensory competition for processing capacity is exclusively modality-specific and does not extend across sensory modalities.

4.8.1 Competition within sensory modalities

To our knowledge, this is the first study to investigate early sensory competition – in the absence of attentional biases – in three sensory modalities by means of highly comparable paradigms. Our finding of suppression *within* each sensory modality supports the universal role of inter-stimulus competition as a consequence of limited processing capacities.

One may still argue that our findings were confounded with an inter-modal attentional bias by having participants perform a visual task in all experiments. It has been shown before that attention to stimulation in one modality may be detrimental to sensory processing in other modalities (Jennifer A Johnson & Zatorre, 2005; Laurienti et al., 2002). However, in all two experiments, we found that the processing of reference stimuli in each of the three senses showed comparable patterns of modulation by competition. More specifically, in none of the two experiments did SSEP amplitude modulation depend on the sensory modality of the reference stimulus. Furthermore, the same held true for effects of competition on the processing of competitors. Given these commonalities an inter-modal attentional bias towards processing of visual stimulation, if present at all, was negligible and did not systematically influence our results.

A closer look at specific results from Experiment 3 revealed that the presence of an auditory competitor did not suppress an auditory reference stimulus. This was surprising given that an auditory-auditory suppressive interaction was observed in a similar audio-visual experiment (Porcu, Keitel & Muller, in press) as well as in earlier studies (Kawase et al., 2012; Ross et al., 2012). We were not able to individuate a specific cause for the absence of this effect.

4.8.2 Influence of combined competitors

Each experiment included two conditions in which a competitor, presented to the same sensory modality as the reference stimulus, was combined with a competitor presented to the other sensory modality. Such combined competitor conditions aimed to assess whether the additional simultaneous presentation of a stimulus from a different sensory modality would modulate suppression. Note that these conditions involved the presentation of an additional stimulus, which rendered them physically dissimilar to the other conditions. Therefore, we interpreted respective results with caution.

We found that combined competitors did *not enhance* suppression of reference stimulus processing as compared with the presentation of a single competitor in the same sensory modality in any of the three experiments. Given the absence of competition across sensory modalities (see below), the suppression observed in the combined competitors conditions could thus be exclusively ascribed to the suppressive influence of competitors presented to the same sense as the reference stimuli. The fact that competitor processing during combined presentation was consistently comparable to competitor processing during single presentation (compare conditions S against S(C) and D against D(C) in Figures 4.3B and 4.5B) further supports this conclusion.

Taken together, presentation of combined competitors did not enhance suppression within sensory modalities, which emphasises the modality-specific nature of competition in early sensory processing.

4.8.3 Absence of cross-modal competition in early sensory cortices

Strikingly, in all two experiments, not one combination of reference and competitor stimuli from different sensory modalities gave rise to suppressive interactions that would have indicated cross-modal competition. Our results are well in line with earlier studies employing frequency-tagging paradigms to investigate early audio-visual interactions (Jacoby, Hall, & Mattingley, 2012; Parks, Hilimire, & Corballis, 2011b). Unlike the present investigation, however, these studies involved attentional biases of sensory processing. Specifically, participants attended to stimuli that elicited SSEPs. Our paradigm was designed to avoid sustained attentional influences on SSEPs. Therefore, we extend previous findings by demonstrating that cross-modal suppression cannot be observed even when inter-modal attentional biases are effectively abolished.

Notably, a recent line of functional neuroimaging studies nevertheless reported reduced activity (as measured by hemodynamic response changes) in sensory cortices corresponding to unattended sensory modalities (Jennifer A Johnson & Zatorre, 2005; Langner et al., 2011; Shomstein & Yantis, 2004). In contrast to our findings, this effect can be construed as a cross-modal suppression exerted by sensory cortices that corresponded to the attended modality. In these studies, however, participants again *attended* to stimulation in one or the other modality introducing an attentional bias. Therefore, it remained unclear whether lower cortical activity resulted from cross-modal competition per se or an attentional filtering mechanism that actively suppressed distracting input from unattended sensory modalities (Keitel et al., 2013). In the light of the present findings, the latter explanation appears the more likely.

Originally, inter-modal attention has been suggested as a mechanism that satisfies a fundamental capacity limit in sensory processing across sensory modalities. In terms of a putative biased competition account of inter-modal attention, concurrent stimuli in different sensory modalities are expected to enter a competition for common processing capacities. The complete absence of cross-modal competition in our experiments strongly challenges this notion. According to the original biased competition account, modelling mechanisms of attention in vision, competition takes place inside a neuron's receptive field (Desimone & Duncan, 1995; J H Reynolds, Chelazzi, & Desimone, 1999) and within neuronal populations across adjacent and/or overlapping receptive fields (Kastner, De Weerd, Desimone, & Ungerleider, 1998). Receptive fields thus provide a common space – a *map* (Franconeri et al., 2013) – on which competitive interactions take place as a function of distance between stimuli. Primary sensory cortices of different sensory modalities naturally miss a common amodal representation of space (Knudsen & Brainard, 1995). Considering that our SSRs were likely arising from respective primary sensory cortices (C.-M. Giabbiconi et al., 2007; Gutschalk et al., 1999; M M Müller et al., 1998b; Nangini et al., 2006), the lack of cross-modal competition might thus be easily explained by the absence of a common spatial map (see e.g. Franconeri et al., 2013).

Nonetheless, in the last couple of decades, a number of studies provided evidence for multisensory interactions in primary sensory cortices of different sensory modalities (for a review see Ghazanfar & Schroeder, 2006). Researchers identified several anatomical connections such as feed-forward projections from thalamic afferents (Hackett et al., 2007), feed-back connections from higher order multisensory areas (Macaluso et al., 2000) or lateral projections between primary sensory cortices (Cappe & Barone, 2005; Foxe & Schroeder, 2005; Iurilli et al., 2012a) as the neural substrate of early multisensory interactions. The exact functional role of the latter cortico-cortical connections remains debated (Lemus et al., 2010). Results from a study by (Iurilli et al., 2012a) still make them a prime candidate for conveying suppressive cross-modal influences in our experiments.

Iurilli et al. investigated auditory influences on stimulus processing in mouse primary visual cortex. Brief noise bursts were found to inhibit responses of visual neurons to concurrent dim light flashes via direct cortico-cortical connections between primary auditory and visual cortices. Such a cross-modal suppression contrasts with the present results. It has to be taken into account, however, that brief noise bursts constitute salient stimulation that likely trigger cross-modal attentional reorienting processes (Cate et al., 2009; Falchier et al., 2002). Therefore, suppressive effects reported by Iurilli et al. conflate pure sensory stimulus interaction and attentional influences in response to transient singular sensory events. It is possible, that in our experiments the onset of the competitor triggered such transient attentional reorienting as well. Yet, we focused our investigation on putative sustained cross-modal influences during processing of ongoing unrelated and unattended stimulation in different sensory modalities. To this end, in our analyses, we explicitly excluded competitor onset periods and, hence, putative effects of transient attentional reorienting towards competitors.

Given the above described neural inter-connectivity on the one hand and the lack of cross-modal competition on the other, it stands to question whether our approach was sensitive to cross-modal effects on sensory processing after all. In Experiment 2, we observed that whenever a single visual and a single tactile stimulus were presented simultaneously, regardless of which one acted as the competitor, the processing of the respective reference stimulus was enhanced. This facilitatory effect contrasts with our initial expectations of suppression between senses, yet, it demonstrates that ongoing stimulus processing in one sense can be influenced by the presence of a stimulus in another sense when both are unattended. A similar effect between concurrent visual and auditory stimuli, although involving attention to either vision or audition, has been observed by Jacoby et al. (2012).

Taken together, our results show that in the absence of attentional biases, early visual, auditory and tactile processing does not experience cross-modal suppression. Surprisingly, we found facilitatory interactions between visual and tactile stimuli. The lack of suppressive stimulus interactions and the presence of facilitatory effects suggest that cross-modal stimulus interactions in early sensory processing – absent attentional influences – might rather be tuned to facilitatory processes that subserve multisensory integration.

Summarising, we investigated competition for capacity-limited early sensory processing within and between visual, auditory and tactile modalities. In a series of experiments we found that concurrent unrelated and unattended stimuli enter a competition only when they were presented to the same sensory modality. Stimuli from different sensory modalities did not compete, although we observed cross-modal interactions of other types for specific stimulus combinations. Absent cross-modal competition is inconsistent with a fundamental capacity limit in sensory processing common to the three senses that we investigated here. This poses a challenge for a possible biased competition mechanism that is thought to govern attentional selection between senses. The finding of modality-specific competition only, however, corresponds well with the common finding of modality-specifc effects of inter-modal attentional selection on stimulus processing (Arrighi et al., 2011a; Keitel et al., 2013; Talsma et al., 2006b).

In contrast to our data, a number of studies have recently demonstrated cross-modal suppressive influences. Notably, these studies also involved the attentional modulation of stimulus processing. In the light of these studies, our results suggest that reported suppressive influences between senses rather reflect an attentional filtering-out of distracters than being a neural signature of cross-modal competition per se.

5. Experiment 4

5.1 Introduction

The absence of competitive interactions and additionally the mutual facilitatory interaction between vision and touch observed in Experiments 2 and 3 suggest a basic independence among different sensory modalities but at the same time a strong interplay (Eimer et al. 2003). In the present experiment, we aimed to investigate whether endogenous attention can trigger competitive interactions between visual and tactile signals, hence supporting the hypothesis of a supra-modal attentional control mechanism. To this end, we combined a classical dual task paradigm with the frequency-tagging method, which has been shown in the first experiment and in earlier works (Keitel et al., 2011a; Porcu, Keitel, & Müller, 2013; Saupe, Widmann, et al., 2009) to be a suitable means to explore inter-modal attention .

Crucially, unlike a previous audio-visual study (de Jong, Toffanin, & Harbers, 2010b) that employed both dual task and the frequency-tagging technique, we made sure that targets in both modalities were never presented synchronously. Such expedient was adopted to prevent subjects from coupling targets of different sensory modalities during the dual task (Charles Spence, 2008) and to avoid that the two modalities were treated as a unitary object, which most likely promotes multisensory integration.

Participants were randomly cued on a trial by trial basis to attend to either both modalities simultaneously (dual task) or one single modality (single task). We compared the SSEP amplitudes relative to the single task (*attend vision* or *attend touch*) with the amplitudes relative to the dual task (*attend vision & touch*). Two main scenarios could be expected: in the first scenario, if SSEP amplitudes relative to the dual task were lower than the SSEP amplitudes relative to the single task, this outcome would suggest the presence of a supra-modal attentional control mechanism. In the second scenario, if there were no amplitude differences between conditions, such result would suggest independent attentional control systems for vision and touch.

We observed that while tactile SSEP amplitudes did not show any significant differences across conditions, crucially visual SSEP amplitudes were significantly lower during the dual task condition than during the single task condition, indicating a possible supra-modal attentional system shared between modalities, moreover a further ERPs analysis showed lower amplitudes in the dual task condition as compared to the single task condition.

5.2 Methods

5.2.1 Subjects

Fifteen participants (range age: 19-34, 8 female) took part in the experiment. Subjects had normal or corrected to normal vision; none of them reported any neurological disease.

5.2.2 Procedure

Participants were comfortably seated in front of a 19 inch monitor (refresh rate: 60Hz; distance: 80 cm) inside an acoustically dampened and electromagnetically shielded chamber. Participant's hands – aligned with the sagittal midline of the participant's body – were positioned on a table above a flat flexible keyboard whose space bar served as response button. Both hands were placed right below the monitor in the same line as the visual stimulus. The distance between the hands was kept constant for all subjects (from left thumb to right thumb: 8 cm). Two small electromagnetic stimulators (Dancer Design, St. Helens, UK) were attached to the phalanges of both index fingers. Both hands were was concealed in order to avoid any influence caused by body sight.

Participants were randomly cued on a trial by trial basis to perform a single task - either visual or tactile - or a dual task, including both tasks together.

Each trial started with a visual symbolic cue (500 ms) displayed in the middle of the screen indicating what task had to be performed. The symbolic cue (see Figure 5.1) consisted of a black hand (tactile task) positioned 1.5 ° to the left of the fixation dot and a black eye (visual task) at 1.5 ° to the right of the dot. Whenever participants had to perform the visual task the eye symbol was presented with 100% of the contrast, while the hand contrast was reduced to 50% and vice-versa. When the dual task was to be performed, both figures were shown with 100% of the contrast. After cue presentation, the black fixation dot (0.15°) was present for 500 ms, then the visual and tactile streams were simultaneously present for 5 seconds. Each trial ended with a black “X” displayed for 1 second to allow subjects to blink.

The whole experiment was subdivided in 6 blocks, each block was composed of 54 trials. Events (targets plus distractors) were present in 50% of the trials and equally distributed between conditions within a time window between 500 ms and 4500 ms after stimulus onset. Events were randomized within each trial making sure that there was a minimum time difference of 800 ms between each event (either target or distractor). The number of targets or distractors within a trial varied randomly from 0 to 2 per modality (maximum 4 events per trial).

Visual stimulus and task: The visual stimulus consisted of a rapid serial presentation of grey letters (font size: 5° of visual angle) superimposed on a darker grey circle (diameter: 6° of visual angle) displayed at the centre of the screen (see Figure 5.1). Both letters and the grey circle flickered at a frequency of 6 Hz (5 on frames and 5 off frames per cycle) synchronized with the monitor refresh rate. Letters of the stream were randomly chosen from the English alphabet making sure that the same letter could never appear twice in a row. Subjects were asked to identify a brighter H (target brightness was adjusted during the training, see training section) among other letters with standard brightness. The task was made more demanding by adding two different types of distractors: a letter H with standard brightness and letters other than H with the same brightness as the target (the two kinds of distractors were randomly chosen in each trial). All events were presented within the letter stream for a duration of 83 ms (5 on frames).

Tactile stimulus and task: The tactile stimulus consisted in a 20 Hz amplitude modulated wave (AM, see section 2.4.2) obtained by a modulating sine wave of 20 Hz) and a carrier sine wave of 150 Hz (Figure 5.1). Left and right index fingers were stimulated with the same frequency to avoid any attentional bias to the left or to the right hand due to different physical differences of stimulation. Subjects were asked to discriminate a sudden increase in amplitude (duration: 200 ms) from a decrease in amplitude (200 ms) of the same intensity, randomly inserted within the vibrotactile stream.

Target intensity was adjusted for each subject during the training by means of a staircase procedure (see training section). The intensity of the events varied between 33% to 50% of the basic maximum intensity (~0.19 N). White noise was played through headphones in order to mask any sound the stimulators might have produced.

Dual task: During the dual task condition, subjects were asked to perform both the visual and the tactile task together. The number of targets and distractors was kept equal to the single task conditions, meaning that subjects had to detect up to 4 targets (2 visual and 2 tactile) per trial. Targets and distractors, were randomized assuring that subjects were unable to anticipate any event, additionally events never occurred simultaneously.

Training: Prior to the experiment, each participant was subjected to the following training procedure: 2 blocks per modality were reserved to set the individual task difficulty. To this end, a 3 down – 1 up staircase adapting procedure (Levitt, 1971) was applied. Once the subjective threshold (set at ~80% of correct responses) was established for both modalities, participants performed a maximum of two blocks of the actual experiment to familiarize with the procedure.

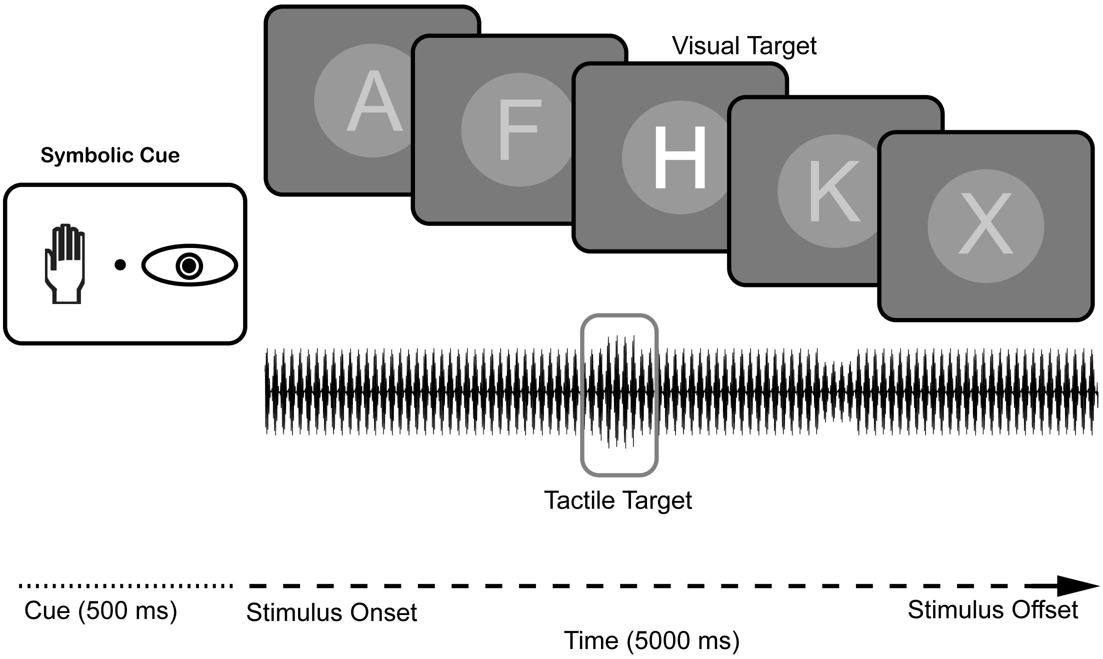

Figure 11: Schematic representation of typical trial

Figure 5.1 Schematic representation of typical trial. Symbolic representation of visual and tactile cues and examples of visual and tactile cues as a function of time.

5.3 Data analysis

5.3.1 Behavioural data analysis

Responses were judged as correct when the button press occurred between 200 and 800 ms after the stimulus onset. Reaction times (RT) and hit rates were then tested by means of two separated two way repeated measures ANOVA, with factors: '*modality*' and '*attention*'.

5.3.2 SSEPs analysis

Epochs of 5000 ms, starting with the onset of stimulus streams, were extracted from continuous data. We discarded epochs containing targets or distractors in order to avoid signal contaminations due to ERPs related to targets/distractors and corresponding motor responses in case of button presses.

Trials with blinks or eye movements exceeding a threshold of 19 µV (corresponding to a horizontal eye movement of about 1.5° of visual angle) were automatically rejected (on average, 20 % of trials was discarded). After averaging across all trials of the respective conditions, SSEP amplitudes for both modalities were computed at every electrode by applying a Fourier transformation to a time window of 4500 ms. The first 500 ms were not included in the analysis to avoid any influence of ERPs related to the stimulus onset. Amplitudes were quantified as the absolute value of the complex Fourier coefficients for each stimulation frequency. Figure 5.3B shows topographical distributions of visual and tactile SSEP amplitudes obtained averaging across the three conditions. Electrode sites showing maximum amplitudes were grouped in two clusters, one for each modality. The visual cluster was identified around the occipital area (PO7, POz, PO8, O2), the tactile cluster was instead localized in the fronto-central area (F1, F2, FCz, Fz). Averages across electrodes of each cluster for each modality were calculated to extract the amplitudes relative to the chosen frequencies (6 Hz and 20 Hz). Prior to statistical analysis, amplitudes for each subject were normalized to level out inter-subjects differences (see section 2.5.2 for a detailed explanation). Normalized amplitudes for both modalities and each condition were then subjected to two distinct one way repeated measures ANOVAs (one for each modality) with levels, for vision: *'attend vision' , 'attend touch' , 'attend both modalities' ;* for touch: *'attend touch'*, *'attend vision'* and *'attend both modalities'.*

5.3.3 ERPs analysis

A further analysis on EEG data was performed to extract ERP components related to visual and tactile targets. Prior to epoch selection, continuous data were band pass filtered (0.5-30 Hz, blackman windowed finite impulse response).

From continuous EEG data epochs were extracted from 100 ms before the target onset to 500 ms after the target onset. Artifacts rejection was performed following the same procedure applied to SSEP data (see previous section). Pre-stimulus baseline of 100 ms was subtracted from the following 500 ms after the target onset. Thus, data were re-referenced to averaged reference and epochs that belong to the same condition were then averaged. Due to the ongoing stimulation, reliable early ERP components could not be extracted, therefore we focused on later components such as the N140 for somatosensory evoked potentials (SEPs), N2 for visual evoked potentials (VEPs) and P3b for both modalities. As shown in earlier studies (Adler, Giabbiconi, & Müller, 2009; de Jong, Toffanin, & Harbers, 2010a), the ongoing oscillation normally causes a certain delay in the peak latencies and a substantial broadening of the components (Figure 5.4A).

Given that both hands received exactly the same stimulation, a bilateral cluster of electrodes (C5, CP5, C6, CP6, see Figure 5.4B) showing the maximum negativity was chosen to extract the first negative deflection (starting ~100 ms after the tactile target). Clusters of electrodes were chosen on the basis of previous studies (Martin Eimer & Forster, 2003; Katus, Andersen, & Müller, 2012). A similar approach was also adopted for visual ERPs to analyse the N2. Due to the central presentation of the stimulus a bilateral cluster was chosen. Electrodes (PO7, O1, O2, PO8, see Figure 5.4B) were chosen according to previous studies (Karns & Knight, 2009).

For statistical analysis two distinct time windows were subsequently extracted from the average of the chosen clusters, from 220 to 280 ms and from 140 to 300 ms after stimulus onset for vision and touch, respectively. A similar procedure was also adopted to extract data relative to the P3b in both modalities. Two electrodes (POz, Pz, see Figure 5.5B) for the visual P3b and a central cluster of electrodes for the tactile P3b (tactile cluster: Cz, Cpz, Pz, Poz, see Figure 5.5B) were chosen according to previous studies (Polish, 2007). Two further time windows relative to the P3b component (vision: 325 – 500 ms touch: 300 – 500 ms) were then extracted from the average of the respective clusters. As for the SSEPs statistical analysis, ERP data were then subjected to four distinct one way repeated measures ANOVAs; the first two including data from the N140 and N2 and the second two including data from both visual and tactile related P3b. In all the ANOVAs kept the same factors used in SSEP ANOVAs.

5.4 Results

5.4.1 Behavioural results

The ANOVA related to reaction times (see Figure 5.2) showed a significant main effect of *modality* (F(1,14) = 8.14, p <0.05) and *attention* (F(1,14) = 26.6 p <0.001), but no significant interactions (F(1,14) = 3 p = 0.1), post-hoc tests revealed that subjects were significantly slower in the dual task condition as compared to the single task condition both in vision (t(14) = -2.3, $p_{FDR} < 0.05$) and touch (t(14) = -4.2, $p_{FDR} < 0.05$).

The ANOVA conducted on hit rates (see Figure 5.2) showed significant main effects of 'modality' (F(1,14) = 14.4 $p < 0.005$) and 'attention' (F(1,14) = 5.5 $p < 0.05$), but no significant interaction (F(1,14) = 2.2 $p = 0.1$). Post-hoc t-tests revealed no significant differences between single task and dual task in both modalities, crucially the only significant difference was observed between visual dual task and tactile dual task (t(14) = 4.2, $p_{FDR} < 0.05$).

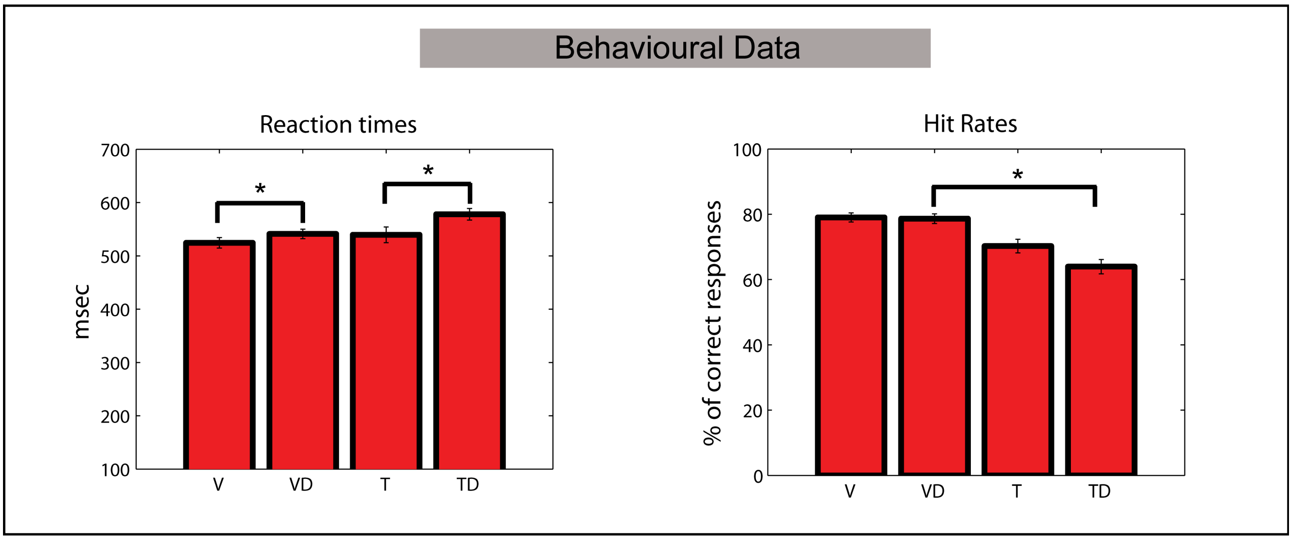

Figure 12: Behavioural results

Figure 5.2 Behavioural results. On the left, reaction times results relative to the respective conditions (V = attend vision, VD = Vision divided attention, T = attend touch, TD = Touch divided attention), Error bars indicate standard error of the mean (SEM). Asterisk indicates signficant difference ($p < 0.05$). On the right, Hit rates results according to specific conditions.

5.4.2 SSEP results

The ANOVA conducted on the visual SSEP amplitudes showed a main effect of attention (F(2, 28) = 6.980, $p < 0.005$). Post-hoc tests were then conducted to identify which condition contributed to this effect. As we expected, visual SSEP amplitudes for the attend vision condition were significantly higher compared to the attend touch condition (t(14) = 2.795, $p_{FDR} < 0.05$) and crucially it was also significantly higher as the attend both modalities condition (t(14) = 3.663, $p_{FDR} < 0.05$).

The ANOVA conducted on the tactile SSEP amplitudes, on the contrary, did not show any significant effect (F(2,28) = 0.216, p = 0.87). Tactile amplitudes did not differ between any condition (*attend touch* vs *attend vision*, t(14) = -0.4835, $p_{FDR} > 0.05$; *attend touch* vs *attend both modalities,* t(14) = 0.22, $p_{FDR} > 0.05$; *attend both modalities* vs *attend vision* t(14) = -0.5465, $p_{FDR} > 0.05$).

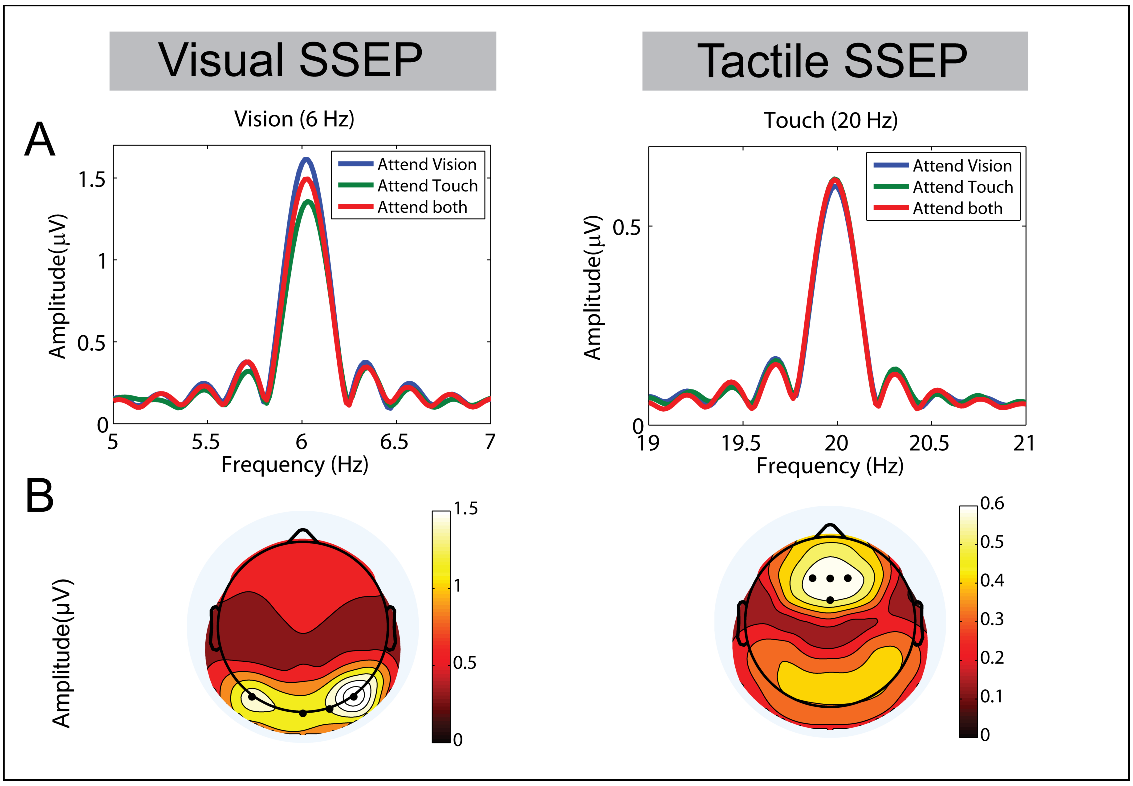

Figure 13: SSEP results

Figure 5.3 SSEP results. (A) indicates grand average of visual and tactile SSEP amplitudes relative to the respective conditions. (B) depicts grand average isocontour maps of visual and tactile amplitudes, black dots indicate chosen electrodes showing maximum amplitudes over the three conditions.

5.4.3 ERP results

The ANOVA conducted on the N2 component's data (see Figure 5.4A) showed a general effect of attention (F (2,28) = 8.581, $p < 0.005$). Paired t-tests showed that the attend vision condition was significantly different than the attend touch condition (t(14) = -5.5741, $p_{FDR} < 0.05$). Crucially *attend vision* was not significantly different than the *attend both modalities* condition (t(14) = -0.9, $p_{FDR} > 0.05$), while *attend touch* was significantly different to *attend both modalities* (t(14) = -4.247, $p_{FDR} < 0.05$).

The ANOVA relative to the N140 component (see Figure 5.4A) showed a significant effect of attention (F(2,28) = 26.253, $p < 0.05$). Following paired t-tests among all the comparisons revealed significant difference in any possible comparison (*attend touch* vs *attend vision,* t(14) = 7.678, $p_{FDR} < 0.05$; *attend touch* vs *attend both modalities,* t(14) = 3.5018, $p_{FDR} < 0.05$*; attend vision* vs *attend both modalities,* t(14) = -3.6462, $p_{FDR} < 0.05$).

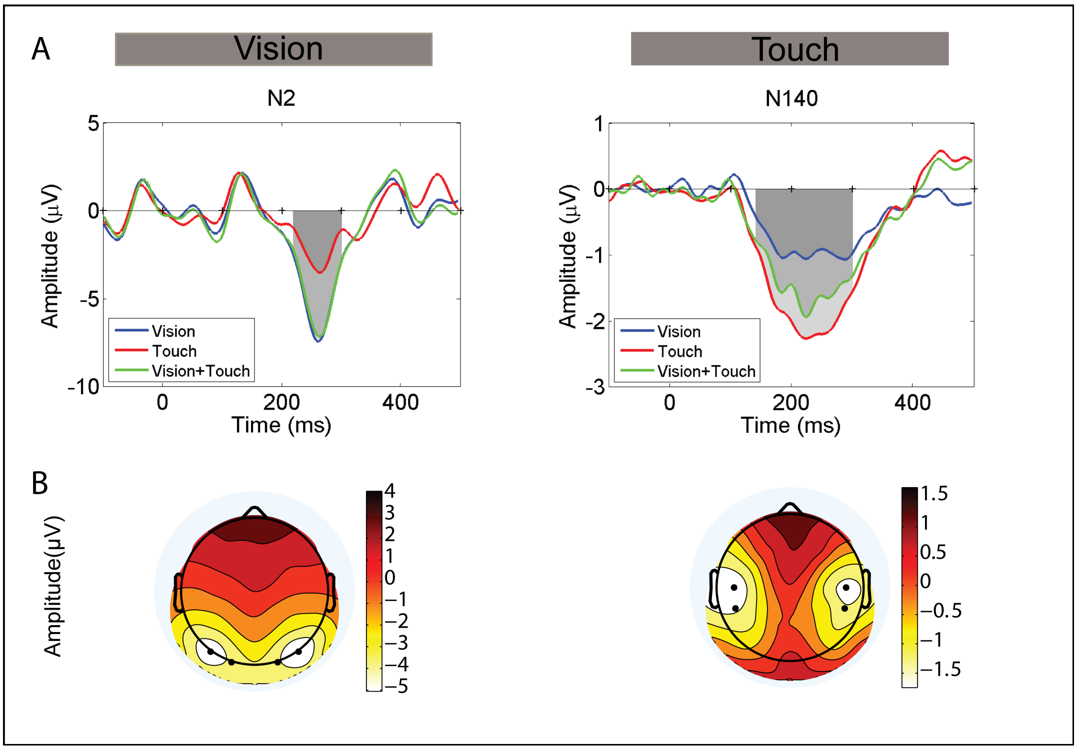

Figure 14: ERP results

Figure 5.4 ERP results. (A) shows grand average of N2 and N140 components in vision and touch, respectively, each line corresponds to a specific condition. (B) depicts grand average isocontour maps of visual and tactile amplitudes, black dots indicate chosen electrodes showing maximum amplitudes over the three conditions.

The ANOVA relative to the visual P3b (see Figure 5.5A) showed a significant attention effect ($F(2,28) = 8.581$, $p < 0.05$). Post-hoc paired t-test between *attend vision* and *attend touch* showed a significant difference ($t(14) = 3.2354$, $p_{FDR} < 0.05$), crucially a significant difference was observed also between *attend touch and attend both modalities* conditions ($t(14) = 4.6765$, $p_{FDR} < 0.05$). No significant difference was observed for the comparison *attend vision* and *attend both modalities* ($t(14) = 0.2264$, $p_{FDR} = 0.07$).

Concerning the tactile P3b (see Figure 5.5A), we observed a significant effect of attention ($F(2,28) = 18.487$, $p < 0.001$) and the following t-tests showed significant differences between all the possible comparisons (*attend touch vs attend vision* $t(14) = -5.2995$, $p_{FDR} < 0.05$; *attend vision* vs *attend both modalities,* $t(14) = -2.9755$, $p_{FDR} < 0.05$; *attend touch* vs *attend both modalities,* $t(14) = 3.6553$, $p_{FDR} < 0.05$).

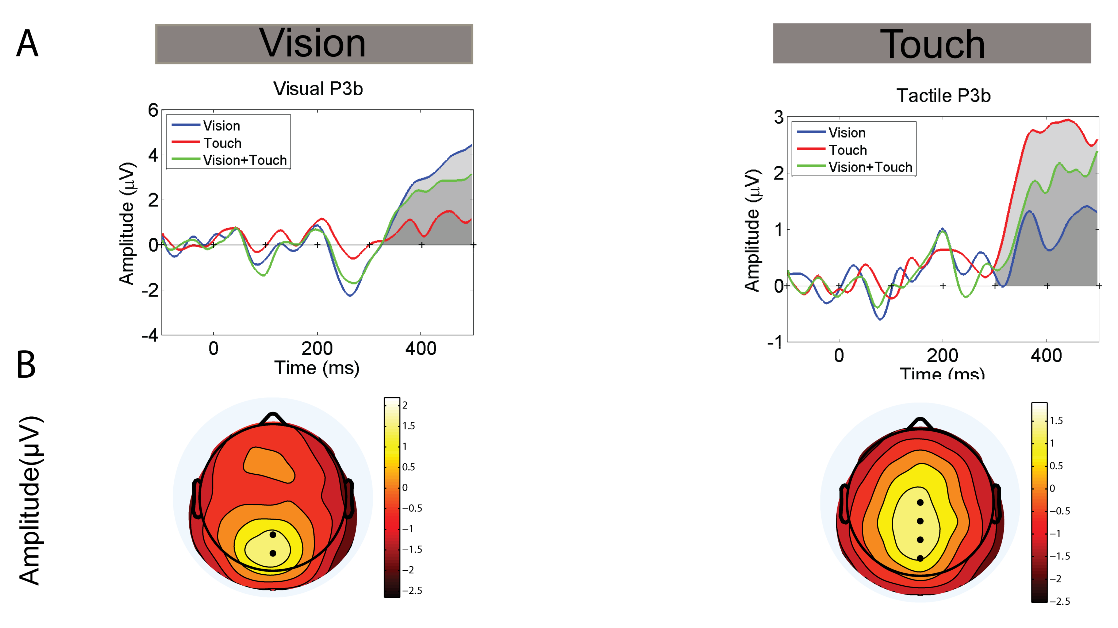

Figure 15: P3b results

Figure 5.5 P3b results. (A) shows grand average of P3b components in vision and touch, respectively, each line corresponds to a specific condition. (B) depicts grand average isocontour maps of visual and tactile amplitudes, black dots indicate chosen electrodes showing maximum amplitudes over the three conditions.

5.4.4 Tactile SSEPs exploratory analysis

A further investigation of single subject spectra revealed that 5 out of 15 subjects showed higher tactile SSEP amplitudes for the attend vision condition as compared to the attend touch condition. Figure 5.6 shows the attentional modulations of both modalities, calculated by subtracting normalized amplitudes of the unattended modality from the amplitudes of the attended modality. In a further step we focused on single trials analysis in order to investigate any potential trend of the tactile SSEPs and possible systematic tactile SSEPs variability related to the visual SSEPs. To this end, we used the same epochs previously extracted to analyse the SSEPs (see section 5.3.2), consequently we applied the Fourier transform on each single artifact-free epoch.

In order to test whether a change in tactile SSEP amplitudes coincided with a change in visual SSEP amplitudes, we conducted a Pearson's correlation between visual and tactile trials of the same condition for each subject.

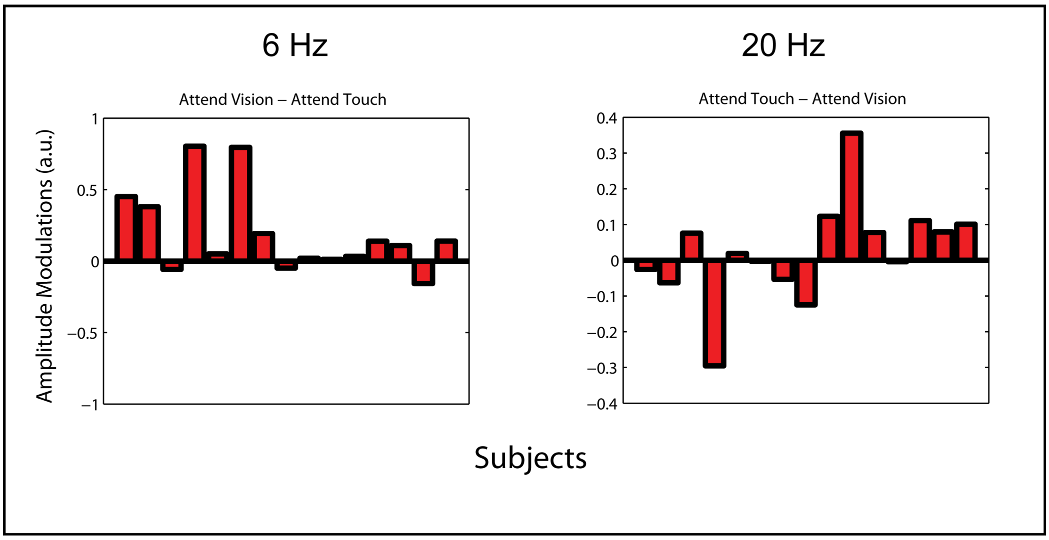

Figure 16: Attentional modulations

Figure 5.6 Attentional modulations. Depicts attentional effects for each subject and each sensory modality obtained by subtracting normalised amplitudes of ignored modality from normalised amplitudes of the attended modality, relative to each frequency.

Results single trials analysis: None of the conditions showed any systematic correlation between the visual and the tactile signals. In the *attend vision* condition we observed a significant correlation only in one subject. Notably we did not observe any specific trend in those subjects that exhibited higher tactile amplitudes in the attend vision condition as compared to the attend touch condition.

5.5 Discussion

The present study aimed to investigate whether visual and tactile selective attention is guided by a supra-modal attentional mechanism or whether each modality rely on a specific attentional control system. To address this issue, we compared effects of single and dual tasks on visual and tactile SSEP amplitudes. We hypothesised that if SSEP amplitudes relative to the dual task were lower than the SSEP amplitudes relative to the single task, such an outcome would suggest the presence of a supra-modal attentional system. On the contrary, if there were no amplitude differences between these two crucial conditions, such result would suggest independent attentional systems for vision and touch.

We observed lower visual SSEP amplitudes in the dual task condition as compared to the single task condition and additionally, in line with the first experiment, we observed significant higher amplitudes relative to the attend vision condition as compared to the attend touch condition. On the contrary, no significant differences were observed between tactile SSEP amplitudes across all the conditions. ERPs analysis showed almost exactly the inverse result: dual task related ERP amplitudes were reduced only in the tactile condition, both for the N140 and the p3b components. Concerning the visual ERPs, the dual task condition did not differ from the attend vision condition in both components. Concerning the behavioural data, we found slower reactions times in the dual task condition as compared to the single task condition in both modalities, thus suggesting a clear interference between visual and tactile tasks. Although our results are not entirely conclusive, in the following paragraphs we will explain why the present data point towards a supra-modal control system rather than a specific attentional system for each sensory modality.

The lack of consistent attentional modulations in tactile SSEPs resembles results observed in the first experiment (specifically relative to the 20 Hz signal) and in previous tactile SSEP studies (Adler et al., 2009; Katus et al., 2012). Although, the present data do not allow us to identify a specific factor that might account for such outcome, we try to rule out a few options (a more detailed discussion about tactile SSEPs can be found in section 5.5). Single subjects spectra revealed a huge variability across participants (see Figure 5.6) in line with data observed in Experiment 1 in the 20 Hz signal. As pointed out in the exploratory analysis section, 5 out of 15 participants showed higher amplitudes relative to the *attend vision condition* as compared to the *attend touch condition*. This variability, however, was not linked to any systematic drop in the tactile behavioural performance, therefore we could not relate tactile SSEP modulations to any systematic shifting of attention to the visual modality. Moreover, the correlations conducted on single trials did not reveal any mutual relation between the change of tactile and visual modulations, thus suggesting no evident influence of visual SSEPs on tactile SSEPs.

The consistent lack of tactile modulations led us to rely exclusively on visual SSEP and ERP data in order to interpret the present results. As shown by a previous cross-modal study (Talsma, Doty, Strowd, & Woldorff, 2006) visual SSEPs can be considered a reliable index of attentional resources allocation across different modalities and within the same modality (see Experiment 2 and 3, and also (Matthias M. Müller, Malinowski, Gruber, & Hillyard, 2003). Furthermore, ERP components relative to the tactile modality showed, on the one hand, that transient responses were consistently modulated by attention, hence suggesting that the lack of attentional modulations was confined to SSEP data. On the other hand, tactile ERP components exhibited lower amplitudes in the dual task conditions than amplitudes in the single task condition, therefore exhibiting the same pattern of modulations observed the visual SSEPs.

Notably, the P3b component, which has been previously shown to indicate the distribution of attentional resources in dual task (Polich, 2007), exhibited a strong reduction during the dual task in the tactile modality. Such a result shows once more that, despite the SSEP results, the tactile modality was consistently modulated by attention (a similar dichotomy among tactile SSEPs and ERPs can be found in Katus et al., 2012) and more importantly supports the hypothesis of a common attentional control system. On the contrary, visual P3b, even though showed a reduction in the dual task condition did not reach significance.

This result – together with the visual N2 data – can be ascribed to a potential priority that participants might have attributed to the visual task. Subjects focused significantly more on the visual target reducing consequently the difference between ERPs relative to the attend vision condition and the attend touch condition. This hypothesis seems to be supported by the higher hit rate in the visual dual task as compared to the tactile dual task. Although, participants were forced to simultaneously monitor both streams, it is plausible that participants were unable to optimally accomplish such a demanding task, thus giving the priority to the visual modality to the detriment of the tactile task. Consequently, the amplitude reduction, observed in the visual SSEPs in the dual task condition, partially represents the amount of attentional resources that were redrawn to perform the tactile task.

Besides the task demand, the spatial difference between tactile and visual stimuli might have contributed to bias the attentional resources to the visual modality. Although the space difference between stimuli was kept as minimum as possible, a small discrepancy was present in the vertical space. As our data clearly show, attention had to be spatially distributed between the two streams although giving the highest priority to the visual modality. Previous fMRI studies (e.g. Macaluso et al., 2000; Shomstein & Yantis, 2004) localized the posterior parietal cortex as a supra-modal area responsible to shift spatial attention among different sensory modalities, it's thus likely that the same network was involved in the attentional distribution in the present experiment.

Taken together, our results – although not entirely conclusive – seem support the hypothesis of a spatial supra-modal attentional system which leads the attentional focus in primary sensory areas, in order to optimize the behavioural performance and filter out potential distracting sensory modalities.

6. General discussion

The present work aimed to shed light on the ongoing debate concerning the distribution of processing resources among different sensory modalities. As already mentioned in the introduction (see section 1.5), a number of studies addressed this issue providing a multitude of seemingly conflicting results, mainly due to non comparable behavioural tasks and/or limitations inherent to the methods adopted. What stands out from the variety of these studies is the approach employed; the guiding idea behind these studies consisted mostly in dividing attention between two sensory modalities and then comparing the behavioural and/or physiological responses with a uni-sensory condition.

Thus, in order to overcome these potential issues, we tried to address this topic from a different prospective and only subsequently to adopt a more classical approach; Recently, Franconeri and colleagues (2013) proposed that classical two dimensional maps could be considered an appropriate locus where competitive interactions for resources processing might occur. As mentioned in section 1.7, such a view extends the main perspective behind the biased competition account, where two or more stimuli compete in order to gain a neural representation (Kastner et al., 1998). We adopted this essential idea and tested whether it could also apply to a cross-modal situation. We thus aimed to test basic competitive interactions between different sensory modalities – if present – regardless of attentional influences.

In order to investigate the distribution of processing resources in primary sensory cortices, we employed steady-state evoked potentials in various visual-tactile and audio-tactile experimental setting. In the *first experiment* (Porcu et al., 2013) we showed that, in line with previous visual and auditory studies (Saupe et al. 2009, Keitel et al. 2011), inter-modal attention affects both visual and tactile SSEP amplitudes. As already discussed in chapter 3, different frequency components were differently influenced, probably due to intrinsic physical features of the tactile and visual stimuli (see section 3.5). Besides the specific frequency modulations, the frequency tagging method proved to be a valuable approach to investigate sustained attention also between vision and touch, even tough with a reservation related to tactile SSEPs that will be further discussed in Section 5.5.

6.1 What does the lack of cross-modal competition tell us about processing resources?

The second and third experiment showed that – in absence of attentional influences – competitive interactions[1] among sensory modalities do not emerge, but they appear uniquely within single sensory modalities (with the exception of the auditory modality, see discussion in Section 4.8.1).

Does the latter result imply that *attentional processing capacities* between sensory modalities are distinct? The answer is no, *a*ttended stimuli require naturally extra resources as compared to ignored ones – for instance: firing rate increases when a stimulus is attended as compared to a non-attended one (e.g. Reynolds et al. 1999). Therefore, the present data would not allow us to infer how selective attention might impact the processing of two concurrent sensory modalities. However, we suggest that the lack of competitive interactions between sensory modalities necessarily implies an inherent *lower degree of interference* between sensory modalities as compared to a within modality condition (see Kastner et al. 1998), whether or not endogenous attention is directly involved in the processing.

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[1] The type of competitive interactions that we are considering here refers exclusively to basic interactions between stimuli completely unrelated to each other. We do not take into account competitive interactions due to the incongruence between information – such as, for example, the asynchronous movement of the lips relative to the voice.

A number of earlier studies has indeed reported no interference between sensory modalities (Arrighi et al., 2011; Duncan, Martens, & Ward, 1997; Keitel et al., 2013; Parks et al., 2011; Talsma et al., 2006). These results might be indeed ascribed to the lack of competitive interactions in early sensory areas.

Nevertheless, the absence of competitive interactions does not necessarily imply an absolute lack of interactions either in a facilitatory or suppressive fashion. As the second experiment demonstrated multisensory interactions can occur in early stages of processing in absence of attentional influences. Interactions between modalities can be considered as a continuum line where in the middle we can place a condition of *no competition* (e.g. experiment 3). This absence of competition probably it is not the norm in everyday life, given the sudden and dynamical saliency changes among sensory modalities.

Such a “*no competition”* status can be seen as a baseline condition subjected to changes induced by frequent interactions between modalities. The strength and the direction (facilitatory vs suppressive) of such interactions depends, on the one hand, on the degree of spatio-temporal coincidence between modalities that – in case of high congruency – it should promote facilitation. On the other hand, on the degree of saliency discrepancy between sensory modalities that in case of high discrepancy should promote suppression.

In the two following sections, I will discuss each one of these potential interactions.

6.1.1 Saliency discrepancies between sensory modalities

Recently, Iurilli and colleagues (2012) observed in mice subjects that varying the intensity level of an auditory stimulus (noise burst), the response of a neuron in primary sensory cortex to a visual stimulus could be inhibited via cortico-cortical connections. As mentioned in section 4.8.3, this result was possibly due to stimulus-driven attention, in other words, attention might have been redrawn from the visual stimulus to the auditory stimulus. Although at a first glance Iurilli's finding seems incompatible with our results, there is no actual contradiction. Whereas their suppressive interaction was driven by a saliency change in the auditory stimulus, in our experiments stimuli saliency was kept constant throughout the whole experiment, thus similar stimulus-driven processes were intentionally avoided. Additionally, in Iurilli's experiment, in order to obtain the visual inhibition, it was necessary to exceed a certain sound threshold (around 55-60 dB SPL), therefore it is plausible to assume that before reaching that specific threshold, inhibition was absent as we reported in our experiments 2 and 3.

Although, we did not control for possible small differences in saliency between sensory modalities, it is reasonable to think that even assuming saliency differences, such discrepancies were not strong enough to induce suppressive interactions. Moreover, if any effect of saliency differences might have occurred in our experiments, it should have been confined exclusively to the period relative to the competitor onset.

Hence, it is plausible to hypothesise that, contrary to within-modality competition where suppressive interactions occur regardless of saliency differences, in order to trigger cross-modal competition, it is necessary a top-down modulation or a bottom-up modulation such as sudden change in saliency. Although, we did not show any suppressive interactions between modalities, it is clear that saliency discrepancies would strongly effect attentional resources and show interferences both at a behavioural and physiological level.

6.1.2 Facilitatory multisensory interactions

In the second experiment we clearly observed a mutual facilitatory effect among tactile and visual responses. This results corroborates a recent SSEP study (Nozaradan, Peretz, & Mouraux, 2012) that was able to show multisensory integration among audition and vision.

Although we were unable to individuate the exact nature of these facilitatory modulations, we believe that subjects might have perceived visual and tactile stimuli as two linked objects, thus giving rise to multisensory interplay. An alternative explanation might be a spread of attention (see Busse et al. 2005), however, we observed this type of interplay exclusively in one experiment. If it had been an effect similar to a spread of attention, we should have observed it in the Experiment 3 as well, hence a sort of integration seems to be a more plausible mechanism. Additionally, the spatial proximity between tactile and visual stimuli might have promoted a better spatial alignment between the two modalities as compared to the visual and auditory stimuli, thus increasing the chance of visual and tactile stimuli to fall in the same receptive fields and thus to induce multisensory integration. Recently, Talsma and colleagues (2010), proposed that the interplay between multisensory integration and attention strictly depends on the strength of competition between sensory modalities. Specifically, if the degree of competition between sensory modalities is low – as in experiment 2 – multisensory integration can occur without/or with low attentional influence, on the contrary when competition between sensory modalities is high, such as when a voice and the movement of the lips are slightly out of synchronisation, top-down modulations are necessary to promote integration. Talsma's model seems to fit the data of the second experiment, corroborating the view that the temporal congruency between our stimuli was strong enough to promote integration.

6.2 The necessity of a supra-modal attentional control system

The aforementioned interactions between modalities inevitably influence the distribution of attentional resources, thus requiring an attentional control system to flexibly manage the overall limited processing resources (Lennie, 2003). As seen in the introduction, earlier studies proposed two main models of inter-modal attentional control: a supra-modal control model (M. Eimer & Schroger, 1998), a model in which each modality relies on its own attentional resources (Wickens et al. 2008) and two hybrid models in which modality are independent but linked to each other (see Alais, Newell, & Mamassian, 2010 for review). In the fourth experiment, we observed competitive interactions between modalities when subjects were engaged in a cross-modal dual task. This outcome – although not entirely conclusive – points towards a spatial supra-modal attentional control (Martin Eimer & Van Velzen, 2002; Jennifer A Johnson & Zatorre, 2005; Jolicoeur, 1999; Lakatos et al., 2007; Loose et al., 2003; Shomstein & Yantis, 2004; Soto-Faraco et al., 2002). Such a supra-modal system allows to control and distribute selective attention across early sensory modalities depending on two crucial factors: task demand and interactions occurring among sensory modalities. Although, this model seems to be in contrast with numerous studies (Arrighi, Lunardi, & Burr, 2011; Duncan, Martens, & Ward, 1997; Keitel et al., 2013; Parks, Hilimire, & Corballis, 2011; Talsma et al., 2006) which did not observe physiological and/or behavioural interferences between modalities, we think that our results might help to reconcile these conflicting results, as we will discuss in the following paragraphs.

Frequently we neglect that the overall amount of resources available to the human brain is limited (Lennie, 2003; see section 1.7 for more details), therefore attentional resources need inevitably to be flexibly distributed between cognitive processes, whether or not different sensory modalities share a common amount of processing resources. Hence, the conflicting results seen in previous studies, might be due to a supra-modal attentional control that dynamically recruits and redistribute processing resources according to task demand and/or modalities interaction. We suggest that according to the level of task demand of two concurring tasks, in case of high demanding tasks the system would recruit higher sensory areas (e.g. Shomstein and Yantis, 2004, Johnson and Zatorre, 2005) to balance the distribution of resources between sensory areas (Johnson et al. 2007). Specifically, in order to optimise the behavioural performance, the neural response of the sensory areas relative to the irrelevant modality might need to be suppressed, while the response of the sensory areas relative to the relevant modality need to be enhanced. On the contrary in case of low demanding tasks – such as detection tasks – the amount of processing resources might be below the overall limit, thus recruiting the specific early sensory areas which – according to results of experiments 2 and 3 – should exhibit virtually no interference and not requiring an active suppression of the irrelevant sensory areas. *What do we mean by task demand?* In agreement with Alais et al. (2009) a non demanding task might be a task involving primarily discrimination or detection of basic features such as pitch discrimination, contrast discrimination, bar orientation and so on, usually encoded by neurons in primary cortices. A high demanding task, instead, might involve language related tasks or generally tasks that involve higher cognitive processes and higher cognitive areas.

Concerning the interactions among senses, a strong saliency discrepancy between two modalities (as seen in Iurilli et al. 2012) seems as well to require a supra-modal system engagement in many situations. For instance, in order to suppress the most salient and irrelevant modality and boost the neural response of the less salient but relevant modality, a supra-modal control system appears to be the most appropriate architecture to balance the necessary processing resources. Of course task demand and sensory interactions can mutually influence each other, thus effect the distribution of attentional resources and requiring a balance between modalities.

Summarising, a supra-modal attentional control seems to be the optimal candidate to dynamically distribute the attentional focus according to task demand and stimuli interactions, in order to reach the optimal compromise between limited processing resources and behavioural success.

6.3 What do the present results tell us about tactile SSEPs and tactile attention?

Contrarily to visual SSEPs, tactile SSEPs did not provide consistent results across all the experiments. What is the cause of such discrepancy? Although the present data do not allow us to provide a definitive answer to this question, I will argue about potential causes in part strictly related to the tactile modality per se and in part related to the interplay between visual and tactile modalities.

As previous studies showed (Katus et al. 2012, Adler et al. 2009), tactile SSEPs are not consistently modulated by attention, although a few exceptions (Giabbiconi et al. 2007, Nangini et al. 2006) reported successful results. Adler and colleagues (2009) claimed that the lack of attentional modulations in SSEPs might be attributed to low perceptual load (Lavie, 2005). Although we did not explicitly tested this precise hypothesis, in the first experiment we adopted a detection task – usually considered as a low load task – while in the fourth experiment we employed a discrimination task that can be considered as a high load task. In both experiments, we did not obtained significant modulations at least in both fundamental frequencies. Hence, although we cannot completely rule out the influence of task demand, in the present work the perceptual load theory (Lavie, 2005) does not seem to account for our results.

A remarkable dichotomy can be immediately noticed throughout the present experiments: whenever attention was directed to the tactile stimulus, tactile SSEP modulations seemed no longer to behave in a fully predictable way.

Considering the first and the fourth experiment, we can clearly see that SSEP modulations were inconsistent and highly variable across subjects. Some subjects did not exhibit an attentional modulation, some others unexpectedly showed higher amplitudes relative to the attend vision condition as compared to the attend touch condition, while only a few subjects exhibited a clear attentional modulation (see Figure 3.2 and 5.6 for single subject spectra). On the contrary, in experiments two and three, tactile SSEPs showed equal suppressive and facilitatory interactions as the visual SSEPs, therefore displaying well predictable and robust patterns.

In agreement with previous tactile SSEP results (C. M. Giabbiconi, Dancer, Zopf, Gruber, & Müller, 2004; C.-M. Giabbiconi et al., 2007), we expected tactile SSEP attentional modulations to behave according to either a response gain modulation, exhibiting a multiplicative or an additive response. However, as we discussed in the introduction, attentional modulation it is not a linear process and the variety of results obtained in visual attention – especially in non-human primates (J H Reynolds, Pasternak, & Desimone, 2000) – demonstrates that attentional modulations can give rise to a multiplicative or additive gain response, a contrast gain response, or the combination of previous two main responses (for review see Reynolds and Heeger, 2009). Hence, tactile attentional modulations and more specifically SSEP modulations might actually behave as the visual modality (see section 1.2.1) and change responses according to different factors, such as, stimulated area, focus of attention and intensity. Very few studies have (e.g. Chapman & Meftah, 2005; Meftah et al., 2009) explicitly investigated how the attention influences the neural response and how these responses change as a function of intensity and cortical areas, namely S1 and S2 cortices. As emphasized in Section 1.3, Chapman and Meftah (2005) found response gain modulations exclusively in S2 cortex and none in S1. As

Nangini and colleagues (2006) first and Giabbiconi and colleagues (2007, see also Bardouille & Ross, 2008) later showed, tactile SSEPs seem to originate in S1 cortex, hence the lack of attentional modulation frequently observed in S1 might account for the variability across the present and previous results.

An additional source of variability might regard the stimulus intensity used in the present experiments. We kept supra-threshold stimuli across all the subjects, thus giving rise to potential response saturation (Tobimatsu et al., 1999) in some subjects and to a consequent absence of attentional modulation.

Besides the plausibility of the previous hypotheses, they do not seem to account for those subjects who exhibited higher tactile amplitudes relative to the attend vision condition. Single trial analysis (Experiment 4) showed that the response modulation across conditions was extremely stable – as well as the high inter-trial phase coherence measured in Experiment 1 – and the degree of variability of the tactile SSEPs was less than the one observed in visual SSEPs (see Figure 6.1). Hence, it seems that the higher tactile amplitudes relative to the attend visual conditions might be the result of a systematic process rather than a bi-product of random fluctuations.

An potential source of the tactile SSEP instability might have been the high visual saliency. Given its inherent high saliency, the flickering stimuli could transiently redraw attention from the tactile modality, thus – on average – lowering the signal modulation. However, we were not able to identify any systematic change in tactile SSEPs related to a change in visual SSEPs – as shown by the single trial analysis – or any drop in tactile hit rates. Of course, we cannot rule out the possibility that a simple correlation might not be able to capture less systematic, but yet effective visual-tactile interactions.

Future experiments might address some of the previous hypotheses, by measuring the tactile SSEP amplitudes and phase as a function of intensity and attention in order to investigate potential relation between intensity and attentional modulations. Moreover it would be profitable to investigate whether attentional models, such as the normalization model of attention (Reynolds and Heeger, 2009), might account also for the tactile attentional modulations.

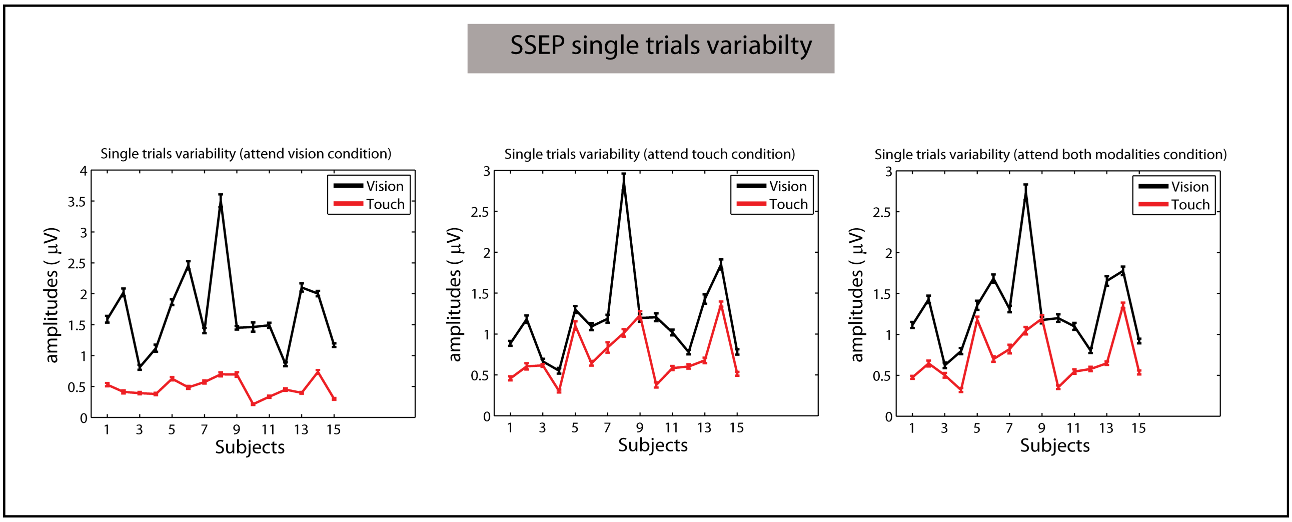

Figure 17: SSEP single trials

Figure 6.1 SSEP single trials. Indicate the average of single trials amplitudes for each modality and condition (relative to experiment 4), error bars indicate standard error of the mean (SEM). Attend vision: SEM vision = 0.05 SEM touch = 0.3; Attend touch: SEM vision = 0.05, SEM touch = 0.03; attend both modalities: SEM vision = 0.05, SEM touch = 0.03.

6.4 Taking all the results together

We might consider the interactions occurring between two or more sensory modalities as a sort of continuum line that illustrates the degree and the direction of such interactions. At the centre of this line, we see a virtual condition of equilibrium in which no competition for resources occurs between two sensory modalities. The absence of competition that we observed in Experiment 3 seems to be an ideal condition to optimize the interplay between modalities. If a strong competition – as the one present within a modality (Kastner et al. 1998, Keitel et al. 2010) – was present also between sensory modalities, processes like integration and the interplay between modalities would be for sure less flexible and efficient especially in terms of resources required to bind or link different modalities by means of top down modulations (Talsma et al. 2010).

The results of Experiment 3 can be placed in the middle of this line. As already emphasised, this finding supports the hypothesis that in primary sensory areas different sensory modalities have a lower degree of conflicting interaction (see Parks et al. 2011, Talsma et al. 2006 and Keitel et al. 2013 for similar results) if compared to single modalities where competition exerts a strong influence (see Kastner et al, 1998, Keitel et al. 2010). Specifically, we suggest that at early stage of processing (primary sensory areas), simple stimuli like ours do not compete and therefore they can be considered as a sort of baseline state. This state can then vary as a function of top-down (Johnson and Zatorre, 2005) and/or bottom-up modulations, such as saliency change (Iurilli et al. 2012). Hence it can result, on the one hand in suppressive interactions and on the other hand it can change as a function of 'congruency' between modalities, namely time and space coincidence, thus promoting in multisensory interplay as we have seen in Experiment 2.

Above this continuum line we can then place a supra-modal attentional system (see Experiment 4) that guides dynamically the stimuli selection in primary sensory areas, promoting both suppressive and facilitatory modulations in order to maximise the behavioural performance and filter out irrelevant modalities. Such a supra-modal attentional control might act according to task demand and the degree and type of interactions between sensory modalities.

Concluding, the most relevant finding of the present work pertains the absence of competitive interactions between sensory modalities. This result clearly points towards a low degree of interference between different sensory modalities in early sensory areas. Furthermore, we found evidence for a supra-modal attentional system which flexibly balance processing resources between modalities according to interactions between sensory modalities.

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List of Abbreviations

AM	amplitude-modulated
BOLD	blood oxygen-level-dependent
CRT	cathode ray tube
DFT	discrete Fourier transform
EEG	electroencephalogram
ERP	evoked related potential
FDR	false discovery rate
FFT	fast Fourier transform
fMRI	functional magnetic resonance imaging
GBR	gamma-band response
MSB	multi-speech babble
PET	positron emission tomography
PLF	phase locking factor
PPC	posterior parietal cortex
RF	receptive fields
RSVP	rapid serial visual presentation
RT	reaction times
SC	superior colliculus
SEM	standard error of the mean
SSEP	steady state evoked potential
SSI	sensory suppression index
STS	superior temporal sulcus
VIP	ventral intraparietal sulcus

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Summary

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Processing resources and interplay among sensory modalities: an EEG investigation

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Keeping track of multiple stimuli is a challenging task for the human brain. Despite the naïve impression that we are able to process the vast majority of information of the environment at a time, we are capable to deeply process only a small fraction of them. Our capacity to process stimuli is, indeed, highly limited (Broadbent, 1952), but at the same time very efficient. Such an ability implies that the human brain has developed throughout its evolution a number of ways to circumvent such resources constraints. Besides a remarkable ability to predict and recognize perceptual patterns, the most essential way the human brain "knows" to optimize processing resources is *selective attention*.

Selective attention has been conventionally studied and modelled within uni-sensory contexts (Desimone & Duncan, 1995; Reynolds & Heeger, 2009), only in the last three decades a growing number of studies has been devoted to the interplay among different sensory modalities and selective attention.

One of the most fundamental and yet debated questions within this matter regards how the human brain distributes limited processing resources among sensory modalities. Two main contrasting models have been proposed: a supra-modal attentional system in which different modalities share common processing resources and a second model which proposes independent processing resources for each sensory modality. Further hybrid

models propose a general resource independence between sensory modalities in early sensory stages, although maintaining supra-modal control system (Alais, Newell, & Mamassian, 2010).

Various studies addressed this topic providing a multitude of seemingly conflicting results (Alais et al., 2010), mainly due to non comparable behavioural tasks and/or restrictions inherent to the methods adopted. What stands out from the variety of such studies is the approach employed. The guiding idea behind these studies consisted mostly of creating the conditions to induce competitive interactions between two sensory modalities, usually by dividing attention between senses. Hence, physiological and/or behavioural indices were used to assess whether there was any difference between uni-modal and bi-modal presentations.

A critical issue – intrinsically related to this topic – concerns the lack of a well defined concept of processing resources. Recently Franconeri and colleagues (2013) sought to provide a more accurate definition and to individuate a “locus” for limited processing resources in attention and working memory. The authors rediscovered the classic concept of *maps* to indicate a precise anatomical space in which two concurrent stimuli can compete to each other. A map is a two-dimensional anatomical space characterized by *“a coherent spatial organization where the preferred stimuli of a neuron change smoothly from one location to the adjacent one”*. Thus, anatomical distance constitutes a flexible factor that influences the strength of competition between two stimuli therefore influencing the actual amount of processing devoted to a specific stimulus. Franconeri's hypothesis recalls one of the basic assumptions of the biased competition hypothesis originally proposed by Desimone and Duncan (1995). Biased competition hypothesis states that two visual stimuli can compete in order to gain a neural representation thus *“receptive fields* *can be viewed as a critical visual processing resource, for which objects in the visual field must compete"*. Moving from these assumptions, the primary aim of this work was to test whether competitive interactions between stimuli can also occur between stimuli presented in different sensory modalities in absence of any attentional bias. Consequently, we aimed to test how endogenous attention influences the concurrent resource distribution between two distinct sensory modalities.

In order to address these issues, we employed the so called frequency-tagging method based on a specific EEG response named steady state evoked potentials (SSEPs, e.g. Müller, Teder-Salejarvi, & Hillyard, 1998). Such a method was adopted to allow us to track distinct signals relative to each specific sensory modality and consequently to measure potential influences of attention and the interplay among modalities. We conducted four EEG experiments comprising visual, tactile and auditory stimuli.

Experiment 1. In the first experiment (Porcu, Keitel, & Müller, 2013), we aimed to test whether SSEPs were a suitable means to investigate inter-modal attention between vision and touch. We frequency-tagged a tactile stream (20 Hz) and a visual stream (7.5 Hz) and cued participants on a trial-by-trail base to attend either touch or vision for several seconds. As hypothesised, SSEP amplitudes were higher in both sensory modalities in the attend condition as compared to the non-attend condition. However, in the tactile modality the attentional modulation was exclusively present in the second harmonic (40 Hz) of the fundamental frequency. This outcome was likely due physical properties of the tactile target that led participants to focus on the carrier frequency (157 Hz) employed to generate the 20 Hz signal, while the 20 Hz signal acquired a minor relevance in the task performance.

Experiments 2 and 3. Experiments two and three (Porcu, Keitel, & Müller, 2014) constitute the core of the present work. We tested whether basic competitive interactions between stimuli, originally (Desimone and Duncan, 1995) confined to the visual modality, could be extended to a cross-modal context. The specific aim of these two experiments consisted of testing whether – in *early sensory areas* – potential competitive interactions are present between sensory modalities as well as within a single sensory modality (Kastner & Ungerleider, 2000) in absence of any attentional bias. To this end, we employed the same experimental paradigm in Experiments 2 and 3, although adopting different sensory modalities: touch vs vision and touch vs audition, respectively.

The fundamental procedure consisted of the concurrent presentation of a so-called *reference stimulus* and a *competitive stimulus*, both frequency tagged with a distinct frequency. In order to avoid any attentional bias, participants were engaged in a visual discrimination task on the fixation cross. Competitive stimuli could be presented either in the same modality as the *reference stimulus* or in a different modality.

In line with previous studies (Kastner & Ungerleider, 2000), we generally observed competition between stimuli in the same modality (with the exception of one of the auditory conditions), on the contrary no competition was present between different sensory modalities. Notably, in Experiment 2, we observed a mutual facilitatory interplay between visual and tactile modalities, which resulted in a significant increase of SSEP amplitudes relative to each modality.

Experiment 4. In Experiment four, we aimed to explicitly test whether, through the manipulation of the attentional focus between modalities we can find evidence of a supra-modal attentional system – despite the absence of competitive interactions (see previous section). To this end, we combined SSEPs with a classical dual task paradigm: participants were cued on a trial-by-trial base to attend to either a tactile and a visual stream simultaneously (both coded with specific frequencies) or to one of the two streams independently. We hypothesised that if a supra-modal attentional system controls resources distribution between the two modalities, we should observe lower SSEP amplitudes in the dual task as compared to the single tasks. SSEP results showed lower amplitudes in the dual task only in the visual modality, on the contrary tactile SSEPs did not exhibit any type of attentional modulation. However, tactile ERP components showed lower amplitudes in the dual task as compared to the single tasks.

Conclusions. Taken together, the aforementioned results point towards a hybrid model of inter-modal attention characterized by a general independence between processing resources among sensory modalities in early sensory areas (Experiments 2 and 3) and by a supra-modal control system. Such a supra-modal system flexibly balances the distribution of processing resources according to the interactions between sensory modalities (such as saliency discrepancies) and task demand. The absence of competitive interactions is fully in line with the predictions made by Franconeri and colleagues (2013), who suggested that anatomical distance and boundaries such as different sensory areas might reduce the competitive interactions between stimuli. Additionally, this lack of competitive interactions between – but not within – modalities supports previous studies (Keitel, Maess, Schröger, & Müller, 2013; Parks, Hilimire, & Corballis, 2011; Talsma, Doty, Strowd, & Woldorff, 2006) which reported independent processing resources when attention was biased toward two modalities or a unique modality. Even though we were not able to directly conclude from the present results that *attentional resources* are specific for each modality, our findings strongly suggest that even under an attentional bias condition, competitive interactions between modalities – in early sensory areas – should be largely reduced as compared to within modality interactions.

The present results provide a new prospective on the distribution of processing resources among different modalities and importantly help to reconcile previous apparently conflicting results where factors such as task demand or differences in saliency between modalities might have inevitably led to support one or the other model.

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Zusammenfassung

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Verarbeitungsressourcen und Wechselwirkungen zwischen sensorischen Modalitäten: Eine EEG-Untersuchung

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Das Nachverfolgen multipler Stimuli stellt für das menschliche Gehirn eine anspruchsvolle Aufgabe dar. Obwohl es unser naiver Eindruck sein mag, dass wir in der Lage sind, den überwiegenden Teil an Informationen, welche wir in einem bestimmten Moment aus der Umwelt empfangen, zu verarbeiten, sind wir faktisch nur zur tiefergehenden Verarbeitung eines kleinen Bruchteils von diesen imstande. Unsere Fähigkeit, Stimuli zu verarbeiten, ist in der Tat äußerst begrenzt (Broadbent, 1952), zur gleichen Zeit jedoch auch sehr effizient. Solch eine Fähigkeit lässt darauf schließen, dass das menschliche Gehirn im Laufe seiner Evolution eine Reihe von Mitteln entwickelt hat, derartige Ressourcenbeschränkungen zu umgehen. Neben dem bemerkenswerten Potential, Wahrnehmungsmuster vorauszusagen und wiederzuerkennen, liegt der wesentlichste Weg, welchen das Gehirn zur Optimierung der Ressourcenverarbeitung kennt, in *selektiver Aufmerksamkeit*.

Selektive Aufmerksamkeit ist konventioneller Weise in uni-sensorischen Kontexten erforscht worden (Desimone & Duncan, 1995; Reynolds & Heeger, 2009), erst während der letzten drei Jahrzehnte hat sich eine wachsende Anzahl von Studien den Wechselwirkungen zwischen verschiedenen sensorischen Modalitäten und selektiver Aufmerksamkeit gewidmet.

Eine der grundlegendsten und nichtsdestotrotz viel diskutierten Fragen in diesem Gegenstandsbereich ist jene nach der Art und Weise, in welcher das Gehirn beschränkte

Verarbeitungsressourcen zwischen sensorischen Modalitäten aufteilt. Zwei kontrastierende Hauptmodelle sind hier vorgeschlagen worden: Ein supra-modales Aufmerksamkeitssystem, in welchem verschiedene Modalitäten gemeinsame Verarbeitungsressourcen teilen, sowie ein zweites Modell, welches von einer unabhängigen Ressourcenverarbeitung in jeder einzelnen sensorischen Modalität ausgeht. Weitere, hybride Modelle legen eine generelle Ressourcenunabhängigkeit zwischen sensorischen Modalitäten in frühen sensorischen Stadien zugrunde, wobei sie jedoch das supra-modale Kontrollsystem (Alais, Newell, & Mamassian, 2010) beibehalten. Verschiedene Studien haben sich mit dem Gegenstandsbereich befasst und dabei eine Vielzahl scheinbar widersprüchlicher Ergebnisse geliefert (Alais et al., 2010), welche vor allem nicht vergleichbaren Verhaltensaufgaben und/oder den angewandten Methoden inhärenten Restriktionen geschuldet sind. Was diese verschiedenartigen Studien verbindet, ist jedoch der von ihnen verfolgte Ansatz. Die hinter ihnen stehende leitende Idee bestand in der Hauptsache darin, Bedingungen zu schaffen, welche kompetitive Interaktionen zwischen zwei sensorischen Modalitäten anregen, in der Regel durch das Teilen von Aufmerksamkeit zwischen diesen Modalitäten. Folglich wurden physiologische und/oder Verhaltens-Indizes benutzt, um festzustellen, ob ein Unterschied zwischen uni-modalen und bi-modalen Konditionen bestand.

Einen wichtigen, unmittelbar mit diesem Thema in Verbindung stehenden Aspekt stellt der Mangel an einem solide definierten Konzept von “Verarbeitungsressourcen” dar. In jüngerer Zeit haben Franconeri und Kollegen (2013) versucht, eine präzisere Definition bereitzustellen und einen “Locus” für beschränkte Verarbeitungsressourcen in Arbeitsgedächtnis und Aufmerksamkeit auszumachen. Die Autoren haben das klassische Konzept der *Maps* wiederentdeckt, um einen präzisen anatomischen Platz zu indizieren, in welchem zwei im “Wettstreit” stehende Stimuli mit einander konkurrieren können. Eine *Map* ist ein zweidimensionaler anatomischer Platz, welcher gekennzeichnet ist von einer *“coherent spatial organization where the preferred stimuli of a neuron change smoothly from one location to the adjacent one”*. Anatomische Distanz stellt also einen flexiblen Faktor dar, welcher die Stärke der Konkurrenz zwischen zwei Stimuli und demzufolge auch das effektive, einem bestimmten Stimulus gewidmete Maß der “Verarbeitung” beeinflusst. Franconeris Hypothese bezieht sich auf eine der Grundannahmen der *Biased Competition*-Hypothese zurück, welche ursprünglich von Desimone und Duncan (1995) vorgeschlagen worden ist. Die *Biased Competition*-Hypothese besagt, dass zwei visuelle Stimuli darum konkurrieren können, neurale Repräsentation zu erlangen; *“receptive fields can [thus] be viewed as a critical visual processing resource, for which objects in the visual field must compete”*. Ausgehend von diesen Annahmen war es das Hauptziel dieser Arbeit, zu testen, ob kompetitive Interaktionen zwischen Stimuli auch zwischen solchen Stimuli auftreten können, welche in *verschiedenen* sensorischen Modalitäten in Abwesenheit eines jeglichen *Attentional Bias* präsentiert werden. Im Folgenden zielten wir darauf, zu untersuchen, in welcher Weise endogene Aufmerksamkeit die konkurrierende Ressourcendistribution zwischen zwei verschiedenen sensorischen Modalitäten beeinflusst.

Um diesen Aspekten nachzugehen, haben wir dir sogenannte *Frequency-Tagging*-Methode angewandt, welche auf einer spezifischen EEG-Response namens *Steady State Evoked Potentials* (SSEPs, vgl. Müller, Teder-Salejarvi, & Hillyard, 1998) basiert. Die Anwendung dieser Methode ermöglichte es uns, unterschiedliche, einer jeweiligen spezifischen sensorischen Modalität zugehörige Signale zu verfolgen und folglich potentielle Einflüsse von Aufmerksamkeit sowie Wechselwirkungen zwischen Modalitäten zu messen. Wir führten vier EEG-Experimente unter Einbeziehung visueller, taktiler und auditiver Stimuli durch.

Experiment 1. Mit dem ersten Experiment (Porcu, Keitel, & Müller, 2013) zielten wir darauf, zu testen, ob SSEPs ein geeignetes Mittel für die Untersuchung inter-modaler Aufmerksamkeit zwischen Vision und Tastsinn darstellten. Mit der *Frequency-Tagging*-Methode markierten wir einen taktilen *Stream* (20 Hz) und einen visuellen *Stream* (7.5 Hz) und wiesen Teilnehmer an, auf einer *Trial-by-Trial*-Basis entweder Tastsinn oder Vision für mehrere Sekunden Aufmerksamkeit zu schenken. Wie von uns vermutet, waren die SSEP-Amplituden in beiden sensorischen Modalitäten in der Aufmerksamkeit schenkenden Kondition höher als in der keine Aufmerksamkeit schenkenden. Allerdings war in der taktilen Modalität die Aufmerksamkeitsmodulation ausschließlich in der zweiten Harmonischen (40 Hz) der fundamentalen Frequenz präsent. Dieses Ergebnis ist wahrscheinlich auf die physikalischen Eigenschaften des taktilen Targets zurückzuführen, welches Teilnehmer dazu veranlasste, ihre Aufmerksamkeit auf die Carrier-Frequenz zu richten (157 Hz), die verwendet wurde, um das 20 Hz-Signal zu erzeugen, während das 20 Hz-Signal eine geringere Bedeutung in der *Task*-Performanz erlangte.

Experimente 2 und 3. Die Experimente zwei und drei (Porcu, Keitel, & Müller, 2014) stellen das Herzstück der vorliegenden Arbeit dar. Wir untersuchten, ob grundlegende kompetitive Interaktionen zwischen Stimuli von ihrer ursprünglichen (Desimone and Duncan, 1995) Begrenzung auf die visuelle Modalität auf einen *cross*-modalen Kontext ausgedehnt werden könnten. Das konkrete Ziel dieser zwei Experimente bestand darin, zu untersuchen, ob – in *frühen sensorischen Arealen* – potentielle kompetitive Interaktionen zwischen sensorischen Modalitäten sowie innerhalb einer einzelnen sensorischen

Modalität in Abwesenheit jeglichen *Attentional Bias* bestehen (Kastner & Ungerleider, 2000). Hierzu wendeten wir in den Experimenten 2 und 3 das gleiche experimentelle Paradigma an, obwohl wir verschiedene sensorische Modalitäten einsetzten (Tastsinn vs. Vision beziehungsweise Tastsinn vs. Audition).

Das grundlegende Vorgehen bestand in der konkurrierenden Präsentation eines sogenannten *Reference Stimulus* und eines *Competitive Stimulus*, von welchen beide – gemäß der *Frequency-Tagging*-Methode – mit einer unterschiedlichen Frequenz markiert waren. Um jeglichen *Attentional Bias* zu vermeiden, wurden Teilnehmer mit einer visuellen *Discrimination Task* auf dem Fixationskreuz beschäftigt. *Competitive Stimuli* konnten entweder in der gleichen Modalität wie der *Reference Stimulus* präsentiert werden oder in einer anderen Modalität.

In Übereinstimmung mit vorausgehenden Studien (Kastner & Ungerleider, 2000) beobachteten wir allgemein Konkurrenz zwischen Stimuli in der gleichen Modalität (mit Ausnahme einer der auditiven Konditionen), andererseits war aber keine Konkurrenz zwischen verschiedenen sensorischen Modalitäten auszumachen. Bemerkenswerterweise beobachteten wir in Experiment 2 eine gegenseitige unterstützend-erleichternde Wechselwirkung zwischen visueller und taktiler Modalität, welche sich in einem signifikanten Anstieg der der jeweiligen Modalität zugehörigen SSEP-Amplituden niederschlug.

Experiment 4. Mit Experiment vier zielten wir darauf, zu testen, ob wir durch eine Manipulation des Aufmerksamsfokus zwischen Modalitäten Anhaltspunkte für ein supra-modales Aufmerksamkeitsmodell finden könnten – trotz der Abwesenheit kompetitiver Interaktionen (s. letzter Absatz). Zu diesem Zweck kombinierten wir SSEPs mit einem klassischen *Dual Task*-Paradigma: Teilnehmer wurden angewiesen, auf *Trial-by-Trial*-Basis entweder einem (jeweils mit bestimmten Frequenzen markierten) taktilen und einem visuellen *Stream* gleichzeitig oder aber einem der beiden *Streams* in unabhängiger Weise Aufmerksamkeit zu schenken. Wir vermuteten, dass wir in dem Fall, in welchem ein supra-modales Aufmerksamkeitssystem die Ressourcendistribution zwischen den zwei Modalitäten kontrollieren sollte, in der *Dual Task* niedrigere SSEP-Amplituden beobachten könnten als in den Single Tasks. Tatsächlich zeigten die SSEP-Ergebnisse niedrigere *Dual-Task*-Amplituden nur in der visuellen Modalität; taktile SSEPs wiesen im Gegensatz hierzu keinerlei Form von Aufmerksamkeitsmodulation auf. Taktile ERP-Komponenten hingegen zeigten in der *Dual Task* niedrigere Amplituden als in den *Single Tasks*.

Schlussfolgerungen. Zusammengenommen deuten die im Vorigen beschriebenen Ergebnisse auf ein hybrides Modell inter-modaler Aufmerksamkeit hin, welches von einer generellen Unabhängigkeit zwischen Verarbeitungsressourcen zwischen sensorischen Modalitäten in frühen sensorischen Arealen (Experiment 2 und 3) sowie von einem supra-modalen Kontrollsystem gekennzeichnet wird. Ein solches supra-modales System balanciert in flexibler Weise die Distribution von Verarbeitungsressoucen entsprechend der Interaktionen zwischen sensorischen Modalitäten (z.B. spezifischer Salienz-Unterschiede) und *Task*-Schwierigkeitsgrad aus. Die Abwesenheit kompetitiver Interaktionen steht in vollkommenem Einklang mit den Vorhersagen von Franconeri und Kollegen (2013), welche darauf hingewiesen haben, dass anatomische Distanz und Grenzen wie etwa verschiedene sensorische Areale kompetitive Interaktionen zwischen Stimuli zu reduzieren vermögen. Des Weiteren unterstützt dieses Nichtvorhandensein kompetitiver Interaktionen zwischen – aber nicht innerhalb – von Modalitäten vorhergehende Studien (Keitel, Maess, Schröger, & Müller, 2013; Parks, Hilimire, & Corballis, 2011; Talsma, Doty, Strowd, & Woldorff, 2006), welche unabhängige Verarbeitungsressourcen für den Fall nahegelegt haben, in welchem Aufmerksamkeit entweder auf zwei Modalitäten oder eine einzige Modalität gelenkt wurde. Obwohl wir aus den vorliegenden Ergebnissen nicht unmittelbar schließen konnten, dass für jede Modalität spezifische Aufmerksamkeitsressourcen existieren, weisen unsere Erkenntnisse stark darauf hin, dass selbst in einer Kondition des *Attentional Bias* kompetitive Interaktionen zwischen Modalitäten – in frühen sensorischen Arealen – im Vergleich zu Interaktionen *innerhalb* von Modalitäten weitgehend reduziert sein sollten.

Die vorliegenden Ergebnisse eröffnen eine neue Perspektive auf die Distribution von Verarbeitungsressourcen zwischen verschiedenen Modalitäten und verhelfen vor allem zu einer Zusammenführung früherer, scheinbar widersprüchlicher Ergebnisse, bei welchen Faktoren wie *Task*-Schwierigkeitsgrad oder Salienz-Unterschiede zwischen Modalitäten unvermeidlich dazu geführt haben mögen, entweder das eine oder das andere Modell zu stützen.

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Publications

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Part of the present thesis is based on the previous publications.

Poster presentations

Porcu, E., Müller, M. (September 2012) Steady state visual evoked potentials as an index of common attentional capacity between vision and touch. 5th International conference on Spatial Cognition (ICSC), Rome, Italy.

Porcu, E., Keitel, C., Müller, M. M. (June 2012) Steady state show no competition between vision and touch. Psychologie und Gehirn, 2012. Jena, Germany

Porcu, E., Keitel, C., Müller, M. M. (October 2011) Competition between unattended stimuli is modality specific. Rovereto Attention Workshop, Attention and Objects. Rovereto, Italy

Porcu, E., Müller, M. (July 2011) Effects of intermodal sustained attention on visual and tactile steady state evoked potentials. 2nd IMPRS Summer School, London, UK

Selbständigkeitserklärung

Hiermit erkläre ich,
Emanuele Porcu, geboren am 30.04.1978 in Oristano, Italien, wohnhaft in der Brockhausstrasse 52, 04229 Leipzig,
dass die vorliegende Arbeit ohne unzulässige Hilfe und ohne Benutzung anderer als der angegebenen Hilfsmittel angefertigt wurde, und dass die aus fremden Quellen direkt oder indirekt übernommenen Gedanken in der Arbeit als solche kenntlich gemacht worden sind.

Leipzig, 15.05. 2014 Emanuele Porcu