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Attentional Control Guides the Strategic Filtering of Potential Distraction as Revealed by Behavior and fMRI

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Summary

When dealing with significant sensory stimuli, performance can be hampered by distracting events. Attention mechanisms lessen such negative effects, enabling selection of relevant information while blocking potential distraction. Recent work shows that preventing the negative impact of forthcoming distraction is actively achieved by attentional selection processes. Thus, I hypothesize that the engagement of a distraction-filtering mechanism to counteract distraction, although indisputably beneficial when distraction occurs, also taxes cognitive-brain systems when distraction is expected but does not occur, leading to performance costs.

In my thesis, I seek the behavioral and brain signature of a mechanism for the filtering of potential distraction within and between sensory modalities. I show that, when potential distraction is foreseen in a stimulus-processing context, a cognitive mechanism is engaged for limiting negative impact of irrelevant stimuli on behavioral performance, yet its engagement is resource-demanding and thus incurs a performance cost when distraction does not occur. This cost consists of slower response times to a simple sensory stimulus when presented alone but in a potentially-distracting context, as compared to the same stimulus presented in a completely distraction-free context.

This cost generalizes across different target and distracters sensory modalities, such as touch, vision and audition, and to both space-based and feature-based attention tasks. The activation of the filtering mechanism relies on both strategic and reactive processes, as shown by its dynamic dependence on probabilistic and cross-trial contingencies. Probability of conflict substantially modulates the magnitude of the filtering cost, which

results larger in contexts where the probability of experiencing conflict is high. Crucially, across participants, the observed strategic cost is inversely related to the interference exerted by a distracter on distracter-present trials.

The strategic filtering mechanism is predominantly adopted as a longer-term, sustained, cognitive set throughout an extended time period. Its activation is associated with sustained brain activity in prefrontal areas and in the frontoparietal attentional network. Sustained brain activity in prefrontal areas correlates across participants with the filtering cost, thus confirming a close relationship between this sustained activation and the observed behavioral cost. I also show that the recruitment of the distraction filtering mechanism in a potentially distracting context guides attention and behavior through different top-down modulations. In fact, when potential distraction is foreseen, the activation of a filtering mechanism promotes both the attenuation of sensory representation of distracting stimuli in extrastriate visual cortex and the prevention of involuntary activations of conflict-driven motor responses in the premotor cortex.

These results attest to the existence of a system for the monitoring and filtering of potential distraction in the human brain that likely reflects a general mechanism of cognitive-attentional control.

Chapter 1

Introduction

1.1 Why studying attentional control?

In a world, which restlessly delivers a continuous bombardment of stimulation to human sensory systems, the event of being distracted is more like an inescapable fact than a mere eventuality. Therefore, the suppression of irrelevant information is as critical as the selection of relevant information for guiding efficient behaviors.

It is worth noting that the very same sensory stimulus might constitute a relevant target stimulus or an entirely irrelevant distracter depending on circumstances. Consider, for example, the case of a loud and sudden honk, which might be an extremely important alerting signal if we are driving a car, although it probably constitutes an undesired distraction when we sit at our office desk located alongside a busy road.

This simple example clarifies that the cognitive orientation towards specific goals also determines what sensory information is temporarily irrelevant and can be excluded from further processing. Moreover, it exemplifies that the attentional selection of relevant stimuli and the exclusion of irrelevant stimuli should take necessarily into account current behavioral goals. In fact, nothing else but current goals determine what is a *target* and what is a *distracter*.

Therefore, uncovering how the brain guides the selection of relevant stimuli while ignoring distracters represents a multifaceted challenge for cognitive neuroscientists. This includes the study of how current task goals are represented in a coherent cognitive set of instructions for the current task, how these instructions are used for guiding attentional orienting, how attention is directed towards relevant stimuli, and how the negative impact of distraction and conflict are limited in the brain.

1.2 Orienting attention towards relevant stimuli

In the cognitive neuroscience of attention, mechanisms for orienting towards relevant sensory inputs and for suppressing irrelevant distraction have been widely investigated both at behavioral and neural level and different models of attentional selection and attentional control have been proposed.

The *biased competition* theory provides evidence for a mechanism of attentional selection in the visual system (Desimone & Duncan, 1995; Desimone, 1998; Reynolds, Chelazzi, & Desimone, 1999). According to the biased competition model, which was initially proposed after neurophysiological studies in monkeys, a control is exerted by biasing competitive interactions among multiple stimuli in favor of the relevant one. Subsequent neuroimaging studies in humans provided converging evidence in favor of the biased competition model (see Kastner & Ungerleider, 2001, for a review). The effect of attention guides competitive spatial interactions in extrastriate visual cortex between target and distracters in spatial attention task by favoring spatial locations where target stimuli are presented (Kastner, De Weerd, Desimone, & Ungerleider, 1998). Suppressed processing of distracters is a direct consequence of such competitive unbalance. However, the biased competition model does not predict any specific and independent mechanism for the active filtering of distracting stimuli. Rather, it assumes that biasing competitive interactions toward target representations automatically determines the exclusion of distracters in spatial attention tasks. This view is coherent with studies suggesting that the enhancement of target representation in sensory areas might be the key element for guiding the selection of relevant information (Yeshurun & Carrasco, 1998; Carrasco, Penpeci-Talgar, & Eckstein, 2000).

The biased competition theory did not provide any insight about how these competitive interactions are generated in the brain. For example, one might wonder where these regulatory signals come from.

Studies of electrophysiology on monkeys have identified parietal and frontal regions that are involved in biasing sensory competition in sensory visual areas. In particular, the lateral intraparietal area (LIP) showed a role in the allocation of spatial attention towards the location of an expected target (Colby, Duhamel, & Goldberg, 1996), while the frontal eye field (FEF) was associated with visual responses in ventral visual area V4 (Moore & Armstrong, 2003; see also Buschman & Miller, 2007).

In humans, neuroimaging studies with cueing paradigms were typically used for investigating sources of attentional control over sensory areas. In fact, the study of brain responses during the cue-target delay permits to identify regions involved in attentional preparation for a target stimulus. A series of activations in superior frontal cortex, in inferior parietal cortex and in superior temporal cortex have been identified in preparation for the presentation of a target stimulus at a cued spatial location. The presentation of visual stimuli biased activity in extrastriate visual cortex in favor of target-representing regions (Hopfinger, Buonocore, & Mangun, 2000).

Attention-directing signals related to the presentation of an attentional cue originate in frontal and parietal areas, as elegantly demonstrated in a study combining psychophysiology and neuroimaging (Woldorff, Hazlett, Fichtenholtz, Weissman, Dale, et al., 2004). Lateral activations in prefrontal and parietal cortices were associated with the interpretation of a cueing signal, while more medial activations in frontal and parietal cortices were associated with attentional-directing signals.

Taken together, these studies provided with an innovative contribution for bridging the gap between the voluntary orienting of spatial attention and the stimulus-evoked responses in sensory brain areas.

1.3 Pushing attention away from distracting stimuli

The studied discussed so far focus on attentional control and its effects on the attentional selection by biasing representation in favor of relevant stimuli. However, this does not necessarily exclude the possibility that also active prevention of distraction might take place in the human brain. In fact, it appears reasonable hypothesizing that the guidance of appropriate behavior relies both on the selection of relevant information and on the inhibition of irrelevant information. The study of active processes for preventing distraction has gained interest in recent years. An early series of behavioral studies focusing on cognitive mechanisms for active dealing with distraction showed that different distraction filtering top-down settings are adopted depending on the probability of irrelevant noise in the visual scene (Awh, Matsukura, & Serences, 2003).

A considerable part of the investigation about active distraction suppression in cognitive neuroscience regards brain preparation mechanisms for dealing with upcoming distracters. Cueing paradigms are particularly suitable for this type of investigation because they allow making inferences about preparatory processes from responses evoked by cueing stimuli.

Effects of active distracter suppression in sensory areas have been evidenced in a study that used functional magnetic resonance imaging (fMRI) for identifying a distractersuppressive component of attentional selection in visual cortex (Serences, Yantis, Culberson, & Awh, 2004a). In this study, enhanced preparatory activity in response to a cue was observed in visual areas representing the spatial location where distracters were presented with high probability.

Further converging evidence has been provided by a study that explored preparation for lateralized targets and distracters suppression both in sensory areas and also in the brain regions that control the strategic deployment of attention (Ruff & Driver, 2006). This study evidenced enhanced anticipatory brain responses to expected distracter locations in the visual cortex. Moreover, an attentional preparation network was identified and areas within this network were functionally dissociated. Preparation for upcoming targets activated regions in the temporo-parietal junction of the right hemisphere. Differently, preparation for upcoming distracters activated the superior parietal lobule and frontal regions including the precentral gyrus and close to the putative location of human FEF (Ruff & Driver, 2006). This pattern closely resembles activations in the attentional control network identified in other studies (Hopfinger et al., 2000; Kastner et al., 1998; Macaluso, Eimer, Frith, & Driver, 2003; Capotosto, Babiloni, Romani, & Corbetta, 2009) and suggests that this frontoparietal network might be also involved in the preparatory stages of attentional deployment.

Recent evidences from human psychophysiology also support the idea that the suppression of distracting information is actively achieved in the human brain. With recordings of electroencephalogram (EEG), an event-related potential (ERP) component associated with the suppression of distracters has been identified (Sawaki & Luck, 2010). This component is observed both when the active inhibition of irrelevant sensory information is required and when the allocation of attention to a previously relevant sensory object must be terminated in preparation for the next trial (Sawaki, Geng, & Luck, 2012). Finally, it is worth pointing out that the preparation for the suppression of upcoming distracters is a time-consuming process, as demonstrated in a recent ERP study where long cue-target delays were associated with the prevention of distraction, while no evidence for active distracter suppression was found at short cue-target intervals (Horvath, 2013). Altogether, these findings corroborate the existence of active distracter suppression mechanisms in the human brain. These mechanisms can be recruited proactively in during the attentional preparation stage, rely on an attentional control network whose cortical substrate involves frontal and parietal regions, and exert an active inhibitory effect on sensory processing of distracting stimuli.

1.4 Attentional and cognitive control: the need for an integrate view

A model of attention proposed in the late 1980s by Posner and Petersen postulated the existence of two distinct systems, the anterior attentional system and the posterior attentional system (Posner & Petersen, 1989). According to this model, the anterior system includes prefrontal cortex and medial frontal structures, such as the anterior cingulate cortex, and executes the deployment of attentional control in conflicting tasks and the source of top-down processing in light of current behavioral goals. The posterior system, which includes the parietal cortex and the superior part of the frontal cortex (e.g., FEF), is involved in the orienting of visuospatial attention towards location of target stimuli. Casey and colleagues (Casey, Thomas, Welsh, Badgaiyan, Eccard et al., 2000) tested the functional dissociation between the anterior and the posterior attentional system with fMRI and an Eriksen flanker task (Eriksen, Coles, Morris, & O’Hara, 1985).

Regions of the anterior system were activated after the presentation of incompatible stimuli, suggesting a role of these areas in coordinating attentional responses and overriding distracting tendencies. Regions of the posterior system, including the superior parietal cortex and the superior frontal gyrus, were activated after prolonged sequences of incompatible trials, suggesting – according to the authors' interpretation – the attentional orienting towards relevant targets.

In the early 2000s, however, cognitive neuroscientists started focusing their research interest on either one of the two attentional systems proposed in the model by Posner and Petersen (1990). Consequently, two major and relatively independent lines of research developed, one focusing on cognitive control, conflict and response inhibition, and another one focusing on the orienting of visuospatial attention. These two lines of research developed relatively independently for the first decade of the new millennium.

In 2002, Corbetta and Shulman proposed an influential model of visuospatial attentional orienting systems in the human brain. According to this model, a frontoparietal dorsal network guides attention towards current goals (top-down attentional system), while a temporo-parietal ventral network (bottom-up attentional system) activates with abrupt onset of salient sensory stimulation and acts as a circuit-breaker on the top-down attentional system (Corbetta & Shulman, 2002). Recent evidence challenged the dichotomy between bottom-up and top-down attentional orienting and suggested prior history as an additional form of guidance in attentional selection, however the attentional guidance by current goals is still recognized as a key feature in guiding attention (Awh, Belopolsky, & Theeuwes, 2012).

On the other hand, studies relative to cognitive control mechanisms proceeded relatively independently from studies of visuospatial attention, notwithstanding cognitive systems that implement current goals likely communicate at some level with the top-down attentional network. Quite surprisingly, this issue has been discarded until recently (see, e.g., Walsh, Buonocore, Carter, & Mangun, 2011).

One of the key regions in the study of cognitive control and conflict processing is the anterior cingulate cortex (ACC). This region has been recently paralleled to Starbucks coffeehouses by Egner (2011), who observed that "like Starbucks coffeehouses, the dACC/mPFC has gained notoriety by ubiquity: it is hard to think of a common cognitive or affective experimental protocol that has not in fact been found to elicit activity in this region in human neuroimaging studies" (Egner, 2011). Whether one might agree or disagree with this provocative comment, the ACC undoubtedly plays a major role in the conflict monitoring theory in its more renowned formulations (Botvinick, Braver, Barch, Carter, & Cohen 2001; Kerns, Cohen, MacDonald, Cho, Stenger, & et al., 2004). According to this theory, dorsal ACC is specifically preponed to conflict detection, and its activation constitutes a regulatory signal for dorsolateral prefrontal cortex (DLPFC), which is in turn involved in implementing adaptive adjustments of cognitive control (Ridderinkhof, Ullsperger, Crone, & Nieuwenhuis, 2004). Moreover, the anterior cingulate cortex would exert a control on motor regions, by regulating the emission of behavioral responses in presence of conflicting response tendencies (Botvinick et al., 2001). It is worth noting that a recent account on the role of ACC questions the widely accepted notion that ACC activation reflects conflict processing. An alternative possibility is that ACC activity reflects time on task, and if this is the case the correlation between ACC activation and conflict would be merely incidental (Schmidt, 2013).

Although the exact role of ACC is a matter of debate in cognitive control literature, it is instead a matter of fact that in the last decade research on cognitive control and research on attention have been taken apart from each other quite substantially. Very recently, an fMRI study tried to reconcile the 'attentional perspective' with the 'cognitive control' perspective by hypothesizing that ACC interacts with the frontoparietal attentional network for modulating selective attention (Walsh et al., 2011). This study showed that cue-evoked preparation activates the frontoparietal network (Hopfinger et al., 2000; Woldorff et al., 2004), including FEF and superior parietal cortex. More interestingly, activity in the frontoparietal network increased after conflict trials and correlated with brain response in ACC in the preceding trial. Although some evidence for interactions between ACC activation and visual processing was documented already (Egner & Hirsch, 2005), these results establish for the first time a relationship between cognitive control and the frontoparietal attentional network. Further studies are needed, however, for clarifying the interplay of other structures involved in adjustments of control, in particular DLPFC, with the top-down attentional network.

A recently formulated model of cognitive control reconsiders the functional interplay between attentional and cognitive control. This model is known as the dual mechanisms of control (DMC) framework and proposes two forms of cognitive control: reactive control and proactive control (Braver, Paxton, Locke, & Barch, 2009; Braver, 2012; see also Ridderinkhof, 2002). Reactive control refers to a conflict-driven form of cognitive control. According to this model, in reactive control attention is recruited in a stimulus-evoked fashion and only when conflict is experienced. Proactive control, instead, is proposed "as a form of early selection in which goal-relevant information is actively maintained in a sustained manner, before the occurrence of cognitively demanding events, to optimally bias attention, perception and action systems in a goal-driven manner" (Braver, 2012; Miller & Cohen, 2001). Unfortunately, the DMC framework does not provide with a detailed neural architecture for reactive and proactive control systems. Instead, it suggests that common structures within the prefrontal cortex guide both proactive and reactive control. These prefrontal structures might switch between proactive and reactive control depending on context, task-goals, and inter-individual variability (Braver, 2012).

1.5 The relevance of strategic preparation for distracters

Most studies about how the brain actively prepares for upcoming distraction explore contingent aspects of dealing with distraction. In a typical paradigm, a cue is shown, and then the response to an event with or without the occurrence of distraction is studied. In real-life situation, however, it is not often the case that we see the abrupt appearance of colored dots in our visual receptive field preannouncing probable distractions. It is more likely that distractions have unpredictable and unexpected onsets. A situation that might be quite common in real-life is that the expectation of distraction can depend on the interaction between environmental circumstances and current goals. It is everyday-life experience that being distracted in a crowded environment is more probable than being distracted in a quiet environment. There are also more subtle situations. For example, try and think about the following one. You are a photographer and you decide to go to the Bird's Forest for trying to shot a rare migrating bird, the *Catchme* bird. You have a group of friends that really enjoy bird watching and they want to come with you. You know that capturing the *Catchme* bird in a photo shot requires both a total environmental stillness, a significant effort on attentional focusing and a high speed of motor (finger) reactions for shooting the picture just in the appropriate instant. This situation delineates then two possibilities: you agree to your friends coming with you, or you go by yourself. If you go to the Bird's Forest with your friends, you'll probably be a little bit edgy because you know that your friends are around and they might inadvertently make some distracting noise. Good for you, they are extremely silent and you don't hear them at all for the whole day. Nevertheless, and quite disappointingly, you miss the critical shot when you see the *Catchme* bird briefly appearing behind tree branches.

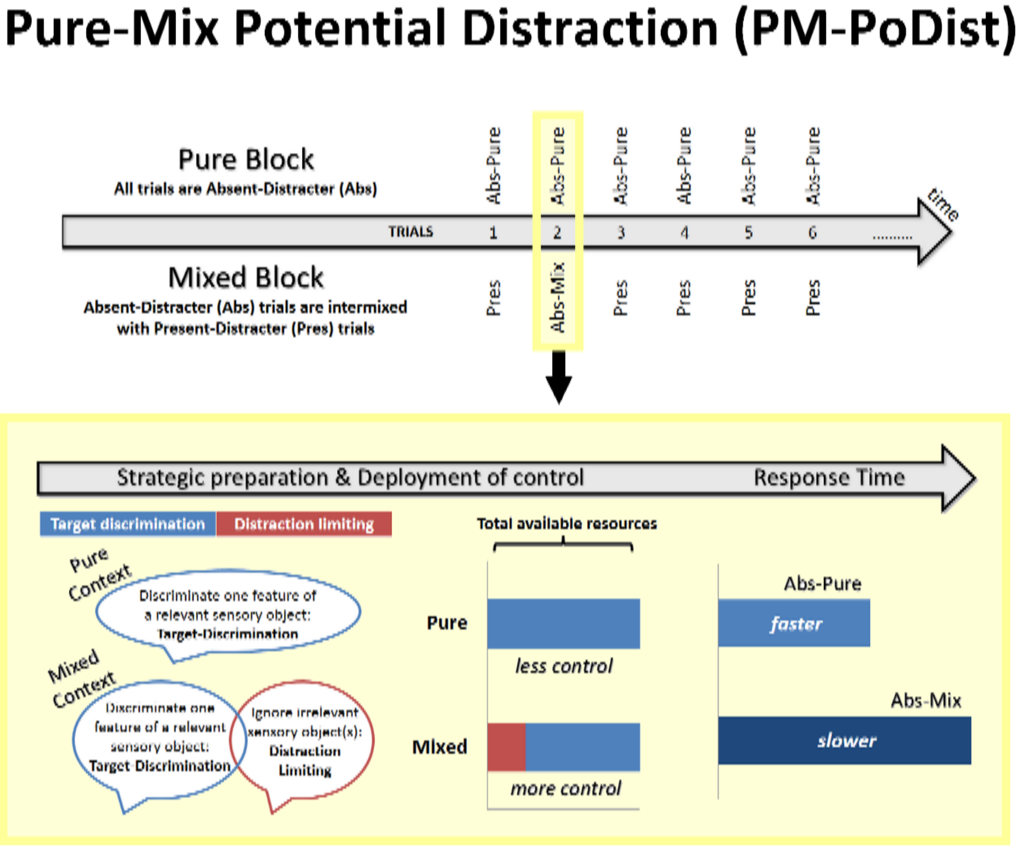
This exemplificative story poses the following question: is the mere expectation of distraction just distracting per-se? In other words, since you were expecting potential interference (e.g., from your friends' eventual noise), has your performance paid a cost even in absence of such interference, for example on response speed in the instant you needed to shot and catch the *Catchme* bird? From the scientific perspective of the cognitive neuroscience of attention and distraction, this question is complementary to the evidence that the brain can engage mechanisms for suppressing expected distracters, as reviewed earlier in this chapter. In fact, one might wonder whether context- and goal-driven attentional strategies might be proactively engaged for preventing potential distractions. In other words, when the brain deals with a task in which distraction is expected, one might wonder whether our cognitive systems are capable of adopting an attentional control strategy in order to actively suppress distraction and guiding behavior towards relevant stimuli. Although beneficial when expected actually occur, the engagement of such a strategy might be not so advantageous when expected distracters actually do not occur.

1.6 The Pure-Mix Potential Distraction (PM-PoDist) framework

The idea of the suppression of irrelevant distracters as an active process and the discussion about context-driven attentional strategies suggest the following hypothesis. When probability of being distracted is relatively high, a distraction-filtering mechanism is activated in a sustained fashion throughout the potentially distracting context. The activation of such a filtering mechanism is resource demanding and requires the engagement of sustained cognitive control, which in turn determines both a cost on behavioral performance when distraction is expected but currently absent and a measurable pattern of neural activations in the human brain. The entire work presented in this thesis is based on this hypothesis.

In Chapter 2, I will describe studies conducted with a novel paradigm that I designed for isolating and measuring the hypothesized behavioral distraction filtering cost. I termed this paradigm *Pure-Mix Potential Distraction* (PM-PoDist). The PM-PoDist paradigm includes two separate experimental blocks: the Pure block and the Mix block (Figure 1.1). In the Pure block, all stimuli are presented with no distracter (they are all absent-distracter stimuli: Abs-Pure). In the Mix block, some stimuli are presented with no distracters (absent distracter stimuli in the Mix block: Abs-Mix), while the remaining stimuli are presented with one (or more) simultaneous distracter(s) (present-distracter stimuli in the Mix block: Pres-Mix). Trials with present-distracters are useful for establishing the impact of concurrent irrelevant information on processing and responses to a target stimulus, but they are not the optimum for isolating the cost of the strategic engagement of a distraction-filtering mechanism.

Figure 1.1. Schematic reproduction of the rationale behind the experimental paradigm used for all studies presented in this thesis. The comparison between absent-distracter trials in a pure context with those in a mixed context permits to study strategic preparation for distraction. In a mixed context, distracter suppression is necessary and might be strategically recruited, although this would load cognitive control systems. According to my hypothesis, the proactive recruitment of a cognitive system for limiting distraction is achieved by increasing attentional and cognitive control. If this is the case, this will draw part of cognitive resources from those dedicated to target processing, as compared to a pure context, and will lead to the observation of a slower reaction time in Abs-Mix trials, as compared to Abs-Pure (see text for details).



To this aim, the critical comparison of interest is the one between Abs-Mix and Abs-Pure trials. Those trial types present exactly the same task, the same sensory stimulation (with no distracters), and the same required response.

However, they differ in *potential* distraction. In fact, the Abs-Pure trials is part of a block (or *context*, as I will use these two words interchangeably) where there is no possibility of distraction, while the Abs-Mix trial is part of a context where distraction will occur. Thus, Abs-Pure and Abs-Mix trials differ exactly in, and limited to, what I aim to measure: the absence and presence, respectively, of a potential for distraction. Any difference in responses to these two trial types will be then ascribed to a cognitive cost for dealing with context where potential distraction occur, namely, the distraction filtering cost. This cost is expected to reflect the sustained (or *strategic*, as I will use these two terms interchangeably) engagement of a *proactive* preparatory mechanism for limiting expected distraction (Figure 1.1).

A direct relationship between the filtering cost and its efficacy in limiting potential distraction will be proved by correlational analyses between the magnitude of the filtering cost and the magnitude of the interference exerted by distracters in trials were they actually occur. I will show a body of evidence for an inverse relationship between these two variables: the larger is the filtering cost, the smaller is the distracter interference, and vice versa. The presence of such an inverse relationship guarantees that the filtering cost truly reflects a strategic mechanism, which affects actual distracters processing and lessens their interference.

1.7 Overview of the studies

In Chapter 2, I will show that a distraction filtering cost is measured within and between different sensory modalities. In particular, the filtering cost is found when target and distracter belong to the same sensory modality (either touch or vision) and when they belong to different sensory modalities (vision and touch, audition and touch). I will show how the magnitude of the filtering cost changes depending on the probability of occurrence of distraction, with a smaller cost in a context where distraction occurs less frequently. By using cross-trial analyses, I will illustrate that the filtering cost is strategic in its nature; however its activation can be reactively modulated by contingencies in the trial sequence. The strategic activation is stronger in contexts where distraction occurs frequently, while reactive modulations are mainly observed in contexts where distraction occurs less frequently. The use of the PM-PoDist paradigm with a series of different tasks, from attentional capture to cognitive conflict, and the several replications of the filtering cost will prove the generality of the underlying mechanism, which configures as a general mechanism for attentional control in the human brain.

In Chapter 3, I will present a study that aimed at portraying the relationship between probability of *conflict* (rather than probability of distraction) and the strategic recruitment of the filtering mechanism. Moreover, this study also aims at extending the findings about a distraction filtering mechanism to a non-spatial attention task. The PM-PoDist paradigm is then used with two different experimental tasks, a visual arrow flanker task and a novel motion direction discrimination task with distraction. The peculiarity of this study is the manipulation of conflict probability. In addition to the Pure block, the PM-PoDist paradigm used in this experiment included two different types of Mix blocks, both with the same probability of distraction, but one with a high probability of conflict and one with a low probability of conflict. I will show that the filtering cost generalizes to the non-spatial task, however its magnitude does not depend on the probability of conflict in the non-spatial task. Rather, I will show that in the arrow flanker task the magnitude of the filtering cost depends on the probability of conflict. More precisely, when the occurrence of conflict is high, the filtering cost is larger, indicating a stronger recruitment of the filtering mechanism. Instead, when conflict probability is low, the filtering cost is still observed but with a reduced magnitude, indicating a lessened recruitment of the filtering mechanism.

In Chapter 4, brain mechanisms involved in dealing with contexts with different probability of conflict are investigated by means of functional MRI. Given that conflict probability modulates the filtering cost, as observed in Chapter 3, I will present an fMRI-compatible version of the PM-PoDist paradigm used for experiment in Chapter 3 (i.e., the arrow flanker task with the blocks with low and high probability of distraction).

In this study, my major interest is directed to studying strategic effects of distraction filtering, which might be identified as sustained activations in an fMRI experimental design, as well as in studying the contingent effect on stimulus processing and response execution evoked by the presentation of absent-, congruent-, and incongruent-distracter stimuli under different contexts (mixed block/event-related design: Visscher, Miezin, Kelly, Buckner, Donaldson et al., 2003; Petersen & Dubis, 2012). For illustrating context-driven attentional effects on stimulus processing in sensory areas in blocks with different probability of conflict, the study also included a functional retinotopic localizer. This allows identifying brain regions in the visual cortex, which responds to the retinotopic spatial locations of target and distracter stimuli, and thus permits studying whether such responses change in blocks with different probability of conflict.

In the results, I will highlight an increase in sustained activation of a series of frontal and parietal areas during Mix blocks, as compared to the Pure block. This sustained activity in dorsolateral prefrontal cortex, inferior and middle frontal gyrus, precentral gyrus, intraparietal sulcus, and superior and posterior parietal areas, clearly reflects the hypothesized strategic joint engagement of cognitive and attentional control systems.

From the analysis of event-related fMRI data, I will provide converging brain-behavior evidence by showing that the activity in frontal inferior regions is inversely correlated with the behavioral filtering cost. From the analysis of absent-distracter trials in Mix blocks, as compared to absent-distracter trials in the Pure block, I will present both an attenuated sensory processing of distracters under high conflict probability and a reduction in response preparation in the contexts where high conflict is expected. Finally, I will report activity in the anterior cingulate cortex, which is found for conflicting stimuli as compared to sensory-analogous non-conflicting stimuli, selectively for the context where the presence of conflict is low.

The behavioral and neuroimaging studies presented in this thesis, taken together, prove the existence of an attentional and cognitive control mechanism for the strategic filtering of potential distraction, and characterize its behavioral signature as well as its functional correlates in the human brain.

Chapter 2

The Costly Filtering

Of Potential Distraction:

Evidence For A Supramodal Mechanism

2.1 Aim of the study

This study is guided by the following hypothesis. In potentially distracting contexts, the brain is able to prevent interference from distracters by engaging a mechanism specifically aimed at filtering out forthcoming distracters. Then, the aim of this study is to disclose the behavioral fingerprint of an attentional control system that deals with forthcoming distraction. The activation of this putative filtering mechanism might require the allocation of attentional resources and increase the overall attentional load (Lavie, Hirst, de Fockert, & Viding, 2004), thus taking away resources from the primary task. Nonetheless, engaging this mechanism would be advantageous for behavioral performance, particularly when distraction is likely to occur. Consequently, such attentional filter might be engaged to different extents depending on the given circumstances, such as due to the likelihood of distracters occurrence. When forthcoming distraction is probable, this filtering mechanism might be strategically recruited throughout the whole task period, whereas when it is unlikely, reactive activation of the attentional filter upon detection of actual distraction might be a more convenient approach to achieve distracters suppression. I tested these two latter predictions in Experiments 1 and 2, respectively. Furthermore, in Experiments 3 and 4, I aimed at characterizing what aspect(s) of the distracting stimuli this mechanism is intended to deal with.

Finally, given that our environment is essentially multisensory and the brain is tuned to optimally combine cues from multiple sensory modalities (Stein & Meredith, 1993; Arrighi, Marini, & Burr, 2009), as well as to segregate them under certain circumstances (Calvert, Spence, & Stein, 2004; Kadunce, Vaughan, Wallace, Benedek, & Stein, 1997), a mechanism for the monitoring and filtering of forthcoming distraction is most likely to exert its influence over multiple combinations of stimuli and distracters from different sensory modalities. I reasoned that the context-driven activation of the mechanism in question is therefore likely to take place with distracters occurring both within and between sensory modalities and I thus developed a crossmodal visuo-tactile paradigm, since interactions between vision and touch have already been well established in spatial attention (Macaluso, Frith, & Driver, 2000; Macaluso, Frith, & Driver, 2002). I used tactile targets and visual distracters in Experiments 1-4. I then aimed at generalizing the results to different sensory modalities, in Experiment 5, and to a completely different experimental paradigm, in Experiment 6. Finally, in Experiment 7, I tested and rejected an alternative hypothesis for explaining these findings.

2.2 General Method

I used a paradigm where a distracter’s presence is not predictable. Therefore, an attentional system coping with forthcoming, potential distraction must deal with uncertainty. The experimental design followed the rationale of the Pure-Mix Potential Distraction (PM-PoDist) paradigm. This paradigm includes two separate blocks for each subject (see Figure 2.1, Panel B): one block (Pure block) comprised only absent-distracter unimodal trials (Abs-Pure), while another block (Mix block) contained absent-distracter unimodal trials (Abs-Mix) intermixed with present-distracter trials (Pres-Mix).

The rationale for this design is that the engagement of a strategic filtering mechanism could be masked on present-distracter trials, but it should lead to a measurable cost in distracter-free trials embedded within a potentially distracting context (i.e., Mix block), as compared to the same type of absent-distracter trials within an entirely distracter-free context (i.e., Pure block).

2.2.1 Participants

One hundred and twenty-six young healthy participants took part in Experiments 1-7. Ten participants were excluded from analysis because of their inability to use the foot-pedal response device (see below). Twenty subjects (age: 25.4 ± 5.7, 16 females, 19 right-handed) participated in Experiment 1. Sixteen subjects participated in each of Experiments 2 (age: 25.4 ± 5.7, 14 females, 14 right-handed), 3 (age: 25.7 ± 9.7, 12 females, 15 right-handed), 4 (age: 24.8 ± 7.1, 11 females, 14 right-handed), 5 (age: 25.4 ± 4.1, 12 females, 15 right-handed), 6 (age: 27.7 ± 9.5, 9 females, 15 right-handed), and 7 (age: 26.8 ± 2.7, 12 females, 14 right-handed).

All participants had normal or corrected-to-normal vision, were naïve as to the purpose of the research and the experimental procedure, and gave their informed consent to take part in the study. The study was approved by the ethical committee of the University of Milano-Bicocca and it was conducted in accordance with the Declaration of Helsinki (World Medical Organization, 1996).

2.2.2 Stimuli

The experimental apparatus for Experiments 1-4 consisted of a vertical panel in which two foam blocks (8 x 4 X 3 cm) were fixed to the left and the right side of a central fixation point, at a lateral distance of 25 cm. Two vibrotactile stimulators (custom-made electromagnetic solenoids, Heijo Electronics, Beckenham, UK; www.heijo.com) were embedded in each block, at the top and the bottom of the lateral side of the frontal aspect of each block. Visual distracters consisted of flashes from red light emitting diodes (LEDs). The experimental setup is represented in Figure 2.1, Panel A. Both vibrotactile and visual signals consisted of three 30ms single pulses interleaved with two 30ms off-phases, resulting in a total duration of 150ms for each stimulus. In all visuo-tactile experiments, visual stimulation led tactile stimulation by 30ms, as this stimulus-onset-asynchrony (SOA) was previously shown to be the most effective in a similar paradigm (Spence, Pavani, & Driver, 2004). The adoption of this small SOA is intended to achieve perceptual simultaneity for visual and tactile stimuli, as the visual system has longer transduction latencies than the somatosensory system (see Shore, Barnes, & Spence, 2006, for a discussion).

In Experiments 5 and 7, I modified the same apparatus by replacing the tactile stimulators with two loudspeakers, located one on the left and one on the right side of the central midline (eccentricity: 25 degrees), near the lateralized visual distracters, and occluded by an opaque shield. Visual stimuli were the same as previously described, while auditory stimuli consisted of three 30ms pure-tones (frequency: 587 Hz) interleaved with two 30ms silent periods, resulting in a total duration of 150ms for each stimulus. Auditory signals in Experiment 5 were completely lateralized (i.e., they came at 100% of intensity either from the left or the right speaker), while in Experiment 7 they were partially lateralized (i.e., a “right” stimulus came at 53% of intensity from the right speaker and at 47% from the left speaker, and vice-versa). In both experiments, auditory and visual stimuli were delivered simultaneously (SOA=0).

Experiment 6 used a computer-based arrow flanker task (e.g., Ridderinkhof, de Vlugt, Bramlage, Spaan, Elton et al., 2002) with visual stimuli presented on the computer screen (size: 17'', resolution: 1024x768, refresh rate: 60 Hz). Stimuli were up- or down-pointing arrows, presented centrally. A single target arrow was displayed in absent-distracter trials, while the target arrow was flanked by four simultaneous distracting arrows (two on the left and two on the right) in present-distracter-trials. The orientation of flankers could be either congruent or incongruent with respect to the direction of the central target arrow.

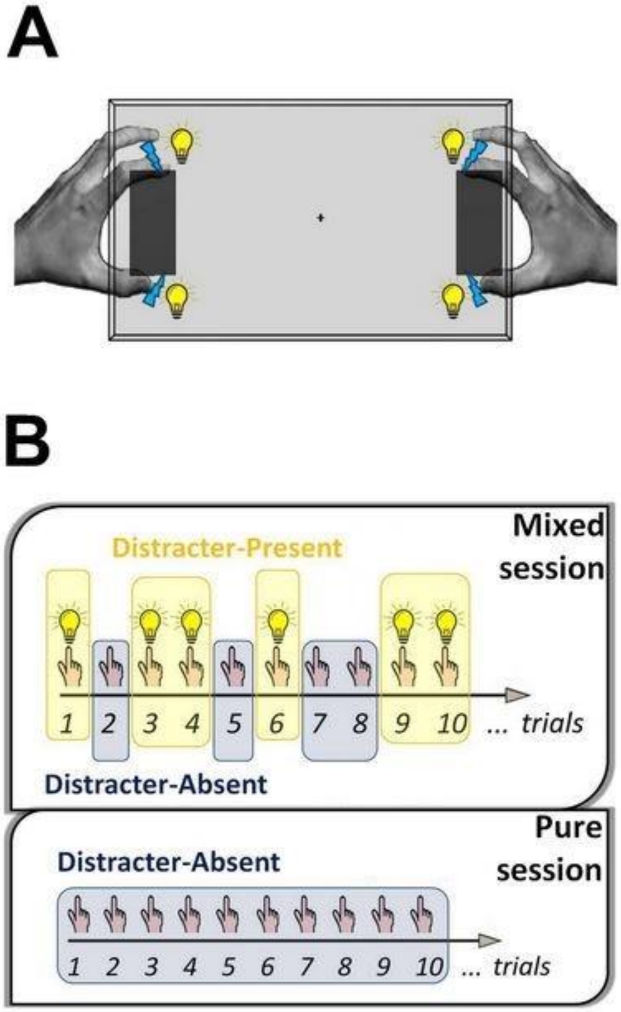
The orders of blocks, as well as the trial sequence within each block, were randomized. In present-distracter trials of all experiments, every possible spatial combination of target-distracter was delivered with equal probability. Presentation and timing of both the tactile and the visual stimuli were under computer control (through a custom-made I/O stimulator box, E-Studio software; Psychology Software Tools, Inc., Sharpsburg, PA, www.pstnet.com).

2.2.3 Task

Experiments 1-4

I ran a tactile elevation discrimination task in a similar vein to the one previously used to investigate the crossmodal congruency effect (Maravita, Spence, & Driver, 2003). Subjects sat in front of a table, at a distance of 57cm from the central fixation point. They placed their forearms on the table and held the foam cubes (one in each hand), keeping their index fingers on the upper vibrotactile stimulator and their thumbs on the lower stimulator. On each trial, subjects received vibrotactile stimulation at one out of four possible locations. They were asked to judge the elevation of the tactile stimulus (high/low), regardless of the stimulation side (left/right).

Figure 2.1. ***Panel A.*** Schematic representation of the experimental setup for Experiments 1 and 2. The blue dart symbols represent positions of the tactile stimulators. The yellow lamp symbols represent positions of the visual distracters. Subjects held two foam blocks (dark rectangles) with their left and right hands, by placing their index fingers on the upper tactile stimulators and their thumbs on the lower tactile stimulators. Only one tactile stimulation was delivered in each trial, accompanied by a visual distracting stimulation in distracter-present trials. ***Panel B.*** Examples of trial sequences in the two experimental blocks of all Experiments. The Mixed block comprised distracter-absent trials (trials 2, 5, 7 and 8 in the shown example) intermixed with distracter-present trials (trials 1, 3, 4, 6, 9 and 10 in the shown example). The Pure block was constituted by distracter-absent trials only. The ratio between absent- and present-distracter trials was 1:2 in Experiments 1, 3 and 4, and it was 2:1 in Experiment 2. The order of presentation was randomized.



Participants gave speeded elevation discrimination responses to the vibrotactile targets, while ignoring the distracters, if present. The visual distracters, when present, were equally likely to occur at the same or at a different elevation compared to targets, hence present-distracter trials (Pres-Mix) could contain either a congruent (Cong-Mix) or an incongruent (Inc-Mix) distracter, respectively.

The experimenter visually checked that participants maintained their eyes open and directed at fixation throughout all experiments. Responses were delivered through two foot pedals, one below the subjects' tiptoe and one below their heel, and subjects were to raise the tiptoe to respond "high" (index finger stimulus) or the heel to indicate "low" (thumb stimulus). The same foot-pedal method was used to collect responses in many previous studies using the same task (e.g., Spence et al., 2004; Heed, Habets, Sebanz & Knoblich, 2010).

Measures of response accuracy (Acc) and response times (RT) were collected. The total duration of the task was about 30 minutes.

Experiments 5 and 7

These experiments differed from Experiments 1-4 in that participants were required to indicate the side (right/left) of the auditory stimulus while ignoring any visual distracter that occurred either on the same (congruent, Cong-Mix) or on the opposite side (incongruent, Inc-Mix). Responses were delivered manually by pressing a key ("z" or "m") on the computer keyboard.

Accuracy and response times were recorded. The time required for completing the task was about 30 minutes.

Experiment 6

Participants were asked to report the orientation of a central arrow (pointing up or down) by pressing a key ("k" or "m") on the keyboard. In present-distracter conditions, the target arrow was flanked by either congruent or incongruent distracting arrows. I measured accuracy and response time. The global duration of this task was about 20 minutes.

2.2.4 Analysis

Statistical analyses were executed by means of two-tailed t-tests for pairwise comparisons, or ANOVA for cases with more than two levels in the independent variable. Accuracy values were preliminarily transformed into the arcsine of the square root by using the Freeman-Tukey correction (Freeman & Tukey, 1950). Response times were filtered to eliminate outliers, excluding all trials below values of 250ms (anticipatory responses) as well as all trials exceeding two standard deviations above the mean (late responses), computed separately for each subject and condition in log-values to overcome the typical asymmetry of the RT distribution (Ratcliff, 1993).

Possible speed-accuracy trade-offs were controlled for by calculating the inverse efficiency (IE) score (Townsend & Ashby, 1983), which has been extensively used in previous studies that used the crossmodal congruency paradigm (e.g., Holmes, Sanabria, Spence & Calvert, 2006; Marini, Tagliabue, Sposito, Hernandez-Arieta, Brugger, Estevez, & Maravta, 2013). Normality and kurtosis of the data distributions were checked and all values were < 2. When significant effects emerged, the effect size was computed by calculating the relative eta-squared index (η^2). In ANOVA, post-hoc comparisons, when appropriate, were conducted with the HSD-Tukey test.

2.3 Experiment 1

In this experiment, I aimed at testing whether, in a context in which visual distraction is likely, the attentional systems might engage a strategic mechanism to filter out forthcoming distracters, leading to a behavioral cost even when distraction is currently absent. The likely-distracting context was established by making the probability of distracter occurrence in the Mix block twice as high as the probability of distracter absence; specifically, Pres-Mix trials occurred twice as frequently as Abs-Mix trials (i.e., their proportion was 2:1).

First, I ran a direct comparison between trials with and without distracters from the Mix block, in order to verify that the distracting visual stimuli actually exerted a disturbing effect on tactile performance. Here, I used a one-way ANOVA factoring the type of trial in the Mix block (Abs-Mix, Cong-Mix, Inc-Mix), which turned out to be highly significant [F(2,38)=102.5, p<0.001]. The post-hoc analysis showed that, when incongruent distracters were present, responses to target stimuli were slowed down (Inc-Mix=559ms) as compared to both Abs-Mix (Abs-Mix=479ms) and Cong-Mix conditions (Cong-Mix=473ms) [p<0.001] (Figure 2.2, Panel A). No reliable difference between Abs-Mix and Cong-Mix conditions was observed. Here and in all subsequent experiments, I considered the difference in RTs between Inc-Mix and Cong-Mix trials as an index of *distracter interference* (mean distracter interference equaled to 86 ms in Experiment 1).

I also observed a main effect of *condition* within the Mix block in relation to accuracy [F(2,38)=74.1, p<0.001]. Post-hoc comparisons revealed that subjects were significantly more prone to making errors in Inc-Mix trials as compared to both Abs-Mix (p>0.005) and Cong-Mix trials ($p<0.005$). Mean error rates were 16.4% for Inc-Mix, 2.6% for Cong-Mix and 3.8% for Abs-Mix trials.

Given that the presence of measurable distracter interference was a prerequisite for the main hypothesis to be tested, I then compared the two distracter-free conditions belonging to different contexts, following the hypothesis of a selective cost in the Abs-Mix condition, relative to the Abs-Pure condition, due to the costly engagement of a distracter filtering mechanism in the former condition. As predicted, the potentially distracting context affected performance in Abs-Mix trials, compared to Abs-Pure trials, inducing an average RT cost of 40 ms (average: Abs-Pure=439ms, Abs-Mix=479ms) [$t(19)=4.43$, $p<0.001$, $\eta^2=0.71$][1]. Response accuracy was marginally higher for the Abs-Mix condition, compared to the Abs-Pure condition [$t(19)=2.23$, $p=0.04$, $\eta^2=0.45$] (Figure 2.2, Panel A). Since the latter result might suggest the existence of a speed-accuracy tradeoff, I also compared the inverse efficiency score and still found a significant cost under the Abs-Mix condition, compared to the Abs-Pure condition [$t(19)=3.14$, $p<0.01$, $\eta^2=0.58$], showing that the difference in RTs was not due to shifts in response criterion. However, it might be claimed that a possible criterion shift is masked by a ceiling effect in accuracy in the present experiment. Experiment 7 has been specifically designed to directly address this issue (see below).

Mean RTs and error rates for all experiments and conditions are shown in Table 2.1. If subjects had relied on enhanced target processing in order to deal with potential distraction, which should have led to an optimal performance in Abs-Mix trials,

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[1] NOTE: I re-analyzed the critical conditions (i.e., Abs-Pure and Abs-Mix) of this and the subsequent experiments (2-4) by filtering RTs with a superior cutoff of 4 SD above the mean (thus with a theoretical probability of excluding valid trials of less than 10^{-4}). Again, I found a significant difference between Abs-Pure and Abs-Mix conditions in all experiments (Experiments 1, 3, 4: *p*s < 0.01; Experiment 2: p=0.05).

compared to Abs-Pure ones. In fact, I observed the opposite pattern, with a relative cost in Abs-Mix trials, thus suggesting the involvement of a distracter suppression mechanism that also affected performance in distracter-free trials. These results demonstrate for the first time that the attentional processing of target stimuli is sometimes severely impaired when distraction is expected, but actually absent.

A candidate account of these findings relates to the notion of *post-error slowing* (Botvinick et al., 2001). Since error rates were globally higher in the Mix block (due to errors in Inc-Mix trials), I needed to examine whether the observed slowing-down of responses to Abs-Mix trials was a consequence of post-error slowing. In order to

Table 2.1. Mean response times (in ms) and error rates (in percentage, within brackets) for all experiments and conditions. *Note that in Experiment 3b distracters were neither congruent nor incongruent with the target elevation as there was a single distracter at fixation.

	Abs-Pure	**Abs-Mix**	**Cong-Mix**	**Inc-Mix**
Experiment 1	439 *(5)*	479 *(3.7)*	473 *(2.6)*	559 *(16.4)*
Experiment 2	457 *(4.7)*	483 *(3.8)*	490 *(2.6)*	586 *(15.4)*
Experiment 3a	426 *(8)*	468 *(8)*	449 *(4.6)*	521 *(25)*
Experiment 3b	426 *(8)*	460 *(8.1)*	452 *(13)* *	-
Experiment 4	433 *(3.8)*	466 *(3)*	482 *(3.2)*	561 *(16.8)*
Experiment 5	386 *(1.6)*	507 *(3)*	527 *(4.4)*	641 *(33.5)*
Experiment 6	380 *(3)*	410 *(1.9)*	425 *(1.6)*	467 *(6.1)*
Experiment 7	540 (*13.9*)	647 (*19.3*)	624 (*10.1*)	757 (*58.8*)

examine performance on trials that follow errors, I analyzed Abs trials (both in the Pure and in the Mix block) as a function of response accuracy in the previous trial. This originated a 2-by-2 ANOVA factoring *Block* (Pure/Mix) and *Previous Trial Response* (correct/incorrect). The analysis revealed a significant main effect of *Previous Trial Response* [F(1,19)=34.9, p<.001], with RTs to Abs trials after errors being longer than those after correct responses (*post-error slowing*).

Also the main factor *Block* was significant [F(1,19)=7.9, p=.01], confirming that Abs-Mix trials led to longer RTs compared to Abs-Pure trials. Crucially, no interaction was observed between *Block* and *Previous Trial Response* [F(1,19)=0.41, p=.71], indicating that the observed strategic cost (i.e., the slowing down of responses in Abs-Mix trials as compared to Abs-Pure) was independent of the preceding trial response. These results show that participants were overall slower after errors, as compared to correct responses, but also that post-error slowing does not account for the observed strategic cost[2].

At this point one may ask whether the observed cost on distracter-free trials in the potentially distracting context and the interference exerted by distracters (especially when incongruent) actually are the two faces of the same coin. If a filtering mechanism is engaged to cope with distraction, and that results in a cost even when distraction is expected yet currently absent, it should be possible to establish a relation between these two costs. In particular, subjects who strongly engage the filtering mechanism

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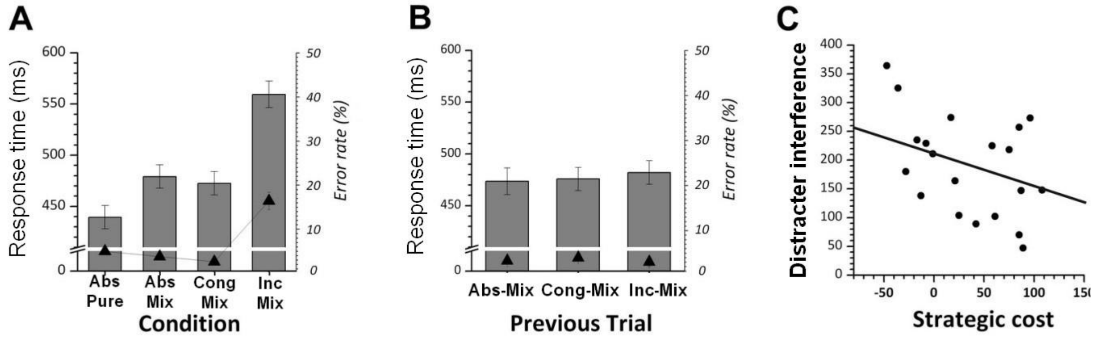
[2] NOTE: Since the number of Abs-Pure and Inc-Mix trials was the same, the whole Mix block was three times as long as the Pure block. In order to exclude a potential confound due to a decrease in sustained attention during the "long" Mix block, we split the Mix block in three parts and found that RTs became *faster* along the block (probably reflecting a learning process) and not slower, as a decrease in sustained attention would predict.

should suffer less from actual distracters compared to subjects recruiting this mechanism to a lesser extent.

I tested such prediction by means of a correlation analysis on a per-subject basis, directly comparing the *strategic cost*, defined as the difference between Abs-Mix and Abs-Pure trials, and the mean distracter interference, computed as described above. Since RTs and accuracy data showed a divergent tendency in this experiment, I choose to run the correlation analysis on inverse efficiency scores, which combine the two measures and

Figure 2.2. ***Panel A.*** Response times (represented by columns, left-side axis) and error rates (represented by triangles, right-side axis) in Experiment 1, separately for each condition: distracter-absent only (Abs-Pure), distracter-absent mixed (Abs-Mix), distracter-present congruent (Cong-Mix) and distracter-present incongruent (Inc-Mix). The difference between Abs-Mix and Abs-Pure (RTs: $p < 0.001$) is a measure of the strategic cost, while the difference between Inc-Mix and Cong-Mix (RTs: $p < 0.001$) indexes distracter interference. ***Panel B.*** Response times (represented by columns, left-side axis) and error rates (represented by triangles, right-side axis) to distracter-absent mixed trials in Experiment 1, separated on the basis of the preceding trial type: distracter-absent mixed (Abs-Mix), distracter-present congruent (Cong-Mix), distracter-present incongruent (Inc-Mix). No significant difference emerged. ***Panel C.*** Dots depict individual correlation points between the strategic cost and the distracter interference, as defined in the main text ($p < 0.05$). The solid line depicts the least squares fit for the data as calculated by means of a simple linear regression model. All values were computed as inverse efficiency (IE) scores.



therefore provide a more reliable overall index of performance. A significant inverse correlation emerged between these two variables [r(18)=-0.46, p<0.05], as shown in Figure 2.2, Panel C. It appears that, the more strongly one engages the mechanism to filter out potential distraction, the less his/her performance will be impaired when distraction actually occurs, and vice versa.

In order to explore whether activation of the filtering mechanism relies on truly strategic processes, I assessed its potential dependence on contingencies occurring along the trial sequence. In fact, results might reflect either a strategic or a contingent mechanism for the suppression of distracters. If the latter, the cost on Abs-Mix trials would likely increase in Abs-Mix trials following a Pres-Mix trial, compared to those following another Abs-Mix trial. Moreover, the greatest reactive activation should likely be observed after an Inc-Mix trial, since incongruent trials generate a higher degree of conflict for responding than Cong-Mix trials. I then sorted Abs-Mix trials based on the preceding trial type, subdividing Pres-Mix trials into Inc-Mix and Cong-Mix trials, and performed a one-way ANOVA factoring *Previous Trial* with three levels (Abs-Mix, Cong-Mix, Inc-Mix). This analysis showed that the preceding trial type did not reliably affect RTs in the Abs-Mix condition [F(2,38)=2.12, p=0.13] (Figure 2.2, Panel B, columns). I also found that the preceding trial type did not reliably affect error rates (Figure 2.2, Panel B, triangles), [F(2,38)=0.54, p=0.59].

Finally, I examined whether block order impacted performance by running an ANOVA on the Abs-Pure block factoring *Order* (first vs. second, between subjects) and *Mini-Block*[3] (1 to 6, within subjects). Both factors led to a significant main effect. More

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[3] NOTE: The Abs-Pure block (128 trials) was split into six subsequent mini-blocks, comprising 21 trials each.

specifically, *Order* revealed that the first block was slower than the second one [F(1,15)=11.9, p<0.005], reflecting a general practice effect. Also the factor *Mini-Block* was significant [F(5,75)=2.6, p<0.05]. Post-hoc analyses revealed that the first mini-block of each block was slower than the second one (p<0.05), yet it was not different from the subsequent four mini-blocks. No interaction was observed between *Order* and *Mini-Block* (p=0.92).

It thus appears that subjects adopted a strategy to deal with probable forthcoming distraction throughout the Mix block, by allocating part of their attentional resources to prevent interference. That strategy increases the attentional load (Lavie et al., 2004), thus reducing available resources for target processing, leading to the observed slowing-down of Abs-Mix responses. If so, the involvement of such strategy should be modulated by the distracters' probability, becoming less convenient when they are relatively unlikely to occur. I tested this prediction in the following experiment.

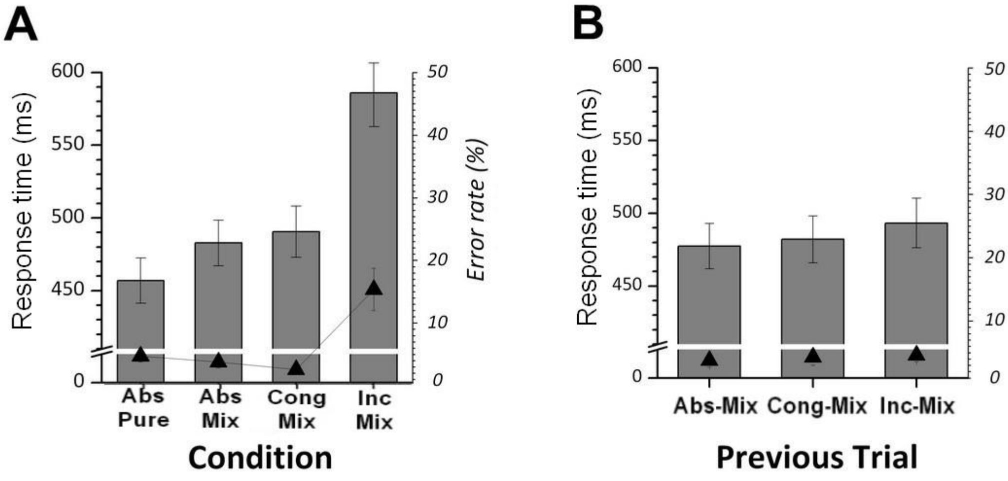
2.4 Experiment 2

One might conjecture that the absence of any contingent effect of the previous trial on Abs-Mix trials, as found in the previous experiment, can be explained by the relatively high frequency of Pres-Mix trials as compared to Abs-Mix trials. In this context, the best solution to cope with frequent distracters might well be to engage a strategic filtering mechanism along the whole block. However, when distraction is less likely, a reactive activation of the filtering mechanism upon detection of a distracter might be the optimal strategy.

The aforementioned prediction was tested in Experiment 2. I replicated the design of Experiment 1, introducing only one major change: here, Abs-Mix trials were embedded in a context with less likely distracters, since I reversed the number of Pres-Mix and Abs-Mix trials (i.e., their proportion is now 1:2). I hypothesized that, when distraction is less likely, the mechanism for distracters' filtering is engaged primarily through a reactive dynamics and perhaps to a lesser extent overall.

Results showed a moderate slowing-down of Abs-Mix responses as compared to Abs-Pure responses [Abs-Pure=457ms, Abs-Mix=483ms; t(15)=2.52, $p<0.05$, $\eta^2=0.55$] (Figure 2.3, Panel A), and the effect was weaker than in Experiment 1. No differences emerged

Figure 2.3. ***Panel A.*** Response times (represented by columns, left-side axis) and error rates (represented by triangles, right-side axis) in Experiment 2, for the two critical distracter-absent conditions, distracter-absent only (Abs-Pure) and distracter-absent mixed (Abs-Mix) (RTs: $p < 0.05$). ***Panel B.*** Response times (represented by columns, left-side axis) and error rates (represented by triangles, right-side axis) to distracter-absent mixed trials in Experiment 2, separated on the basis of the preceding trial type: distracter-absent mixed (Abs-Mix), distracter-present congruent (Cong-Mix), distracter-present incongruent (Inc-Mix). Responses were significantly slower following an Inc-Mix trial, compared to trials subsequent to both Abs-Mix ($p < 0.001$) and Cong-Mix ($p < 0.05$) trials.



in response accuracy [t(15)=1.77, p=0.11]. The mean distracter interference effect amounted to 96ms in this experiment [t(15)=9.87, p<0.001]. Noticeably, the RTs-cost observed in Abs-Mix trials compared to Abs-Pure trials did not emerge on IE scores [t(15)=1.50, p=0.15]. The latter measure, which allows to neutralize the potentially confounding effects of criterion shifts, is therefore revealing a null effect here (in contrast to Experiment 1), thus demonstrating that the filtering mechanism is recruited to different degrees depending on the probability of occurrence of distracters during the block. Therefore, this pattern of results fully confirms the hypothesis, highlighting that any strategic mechanism of distracters' filtering is more relaxed when distraction is still possible, but relatively improbable.

To explore whether the activation of this filtering mechanism under low distracters' probability primarily relies on a reactive dynamics, as hypothesized, I compared the cost of the mixed context (i.e., Abs-Mix minus Abs-Pure) on trials following either an absent-distracter or a present-distracter trial. I observed a significant effect of the main factor *Previous Trial* [F(2,30)=8.81, p<0.001] and post-hoc tests revealed a higher behavioral cost in Abs-Mix trials preceded by Inc-Mix trials compared to those preceded by both Cong-Mix (p<0.05) and Abs-Mix (p<0.001), whereas no difference was found between Abs-Mix trials preceded by Abs-Mix vs. Cong-Mix trials (p=0.41) (Figure 2.3, Panel B). Therefore, unlike what I found for Experiment 1, where I showed that the previous trial type did not reliably modulate the behavioral cost observed on Abs-Mix trials, the present results clearly demonstrate a difference in the behavioral cost depending on the type of the preceding trial, with the greatest cost following Inc-Mix trials. I then examined whether the mixed cost was still significant when contrasting Abs-Pure trials with Abs-Mix trials preceded by another Abs-Mix trial. This analysis aimed at testing whether a strategic activation of the filtering mechanism occurs when distracters are relatively infrequent, while discounting the reactive component of the filtering activation. This analysis did not reach significance level (p=0.08), showing that the observed mixed cost in Experiment 2 critically depends on the reactive engagement of the filtering mechanism.

Overall, these results clearly show that the filtering mechanism is activated in different ways and to differing degrees based on probabilistic information. They show that the filtering mechanism is predominantly recruited in a strategic manner when distraction is highly probable. Instead, when distraction is less likely, the system is more “relaxed”, and mainly relies on reactive activation of the filtering mechanism upon detection of a distracting event.

2.5 Experiment 3

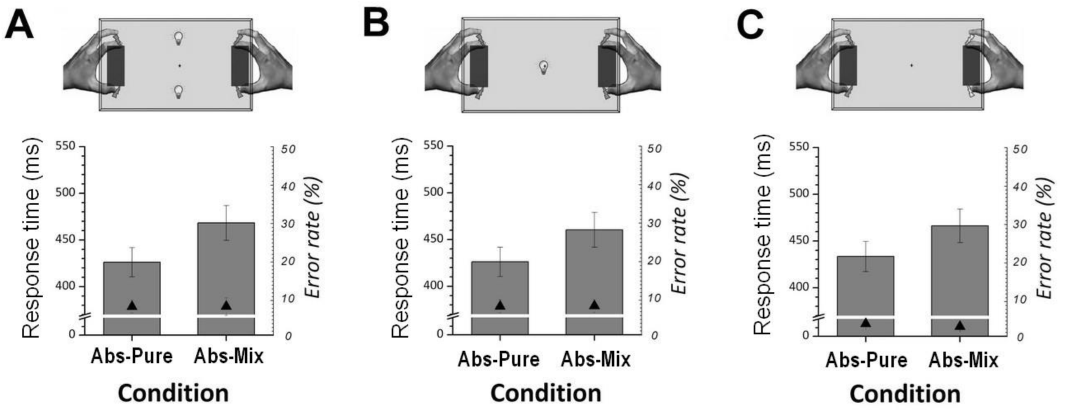
With the previous experiments, I provided solid behavioral evidence for the existence of an attentional mechanism that is engaged whenever I deal with potentially distracting contexts in order to counteract the cost on performance induced by distraction. I showed that, in a tactile discrimination task, the presentation of visual distracters determined a slowing-down of the elevation judgments when target and distracters occurred at opposite up/down locations (incongruent trials). Moreover, I disclosed that the human brain engages strategic and reactive filtering mechanisms aimed at preventing this behavioral cost. However, it is still not clear what perceptual or response-related properties of the distracting stimulus are essential to engage the latter mechanism.

When a distracter matches some perceptual properties of the target, or is somehow associated with a conflicting behavioral response, it induces greater interference, likely because of lower target discriminability and greater response competition, respectively (Eriksen, et al., 1985; Duncan & Humphreys, 1989; Desimone & Duncan, 1995; Serences, Shomstein, Leber, Golay, Egeth et al., 2005). In particular, given the typical features of the crossmodal congruency task, the critical distraction determined by spatially incongruent visual distracters on the tactile elevation judgment is known to be influenced by both spatial attention, being stronger when distracters are close to the hand receiving the touches, as compared to the contralateral hand, and response conflict (Spence et al., 2004; Forster & Pavone, 2008). Consequently, a mechanism for preventing such interference might depend on spatial-related characteristics, response-related characteristics, or both. I then planned to clarify whether the strategic filtering of potential distraction, as revealed by the previous experiments, depends on the spatial or the motor determinants of the critical stimulus/distracter conflict. More specifically, the filtering mechanism could be driven to suppress perceptual interference deriving from the sharing of spatial locations between targets and distracters. Alternatively, it might be aimed at optimizing the response selection stage, suppressing any response tendency evoked by the distracting stimulus. Recently, a preparatory mechanism for the suppression of forthcoming distraction has been identified in monkeys (Wardak, 2011). Such endogenous proactive inhibition prevents motor responses to a subsequent event and it is mediated by the activation of the supplementary motor area (SMA) (Wardak, 2011). A proactive mechanism for the preparatory inhibition of selective response tendencies has been identified also in humans (Cai, Oldenkamp, & Aron, 2011).

I set out to perform Experiment 3 in order to test whether spatial co-localization between targets and distracters or instead their response incompatibility plays a pivotal role in the recruitment of the strategic filtering mechanism. In this experiment, I modified the paradigm of Experiment 1 by including three blocks, randomly administered to participants. One block was the Abs-Pure block (condition A); in another block (condition B), the position of visual distracters was modified by placing them along the vertical meridian at a central high or low position, thus eliminating the spatial proximity with the tactile targets, but still maintaining an element of congruence (or incongruence) with the required elevation judgment (Figure 2.4, Panel A, upper part); in the remaining block (condition C), the position of distracters was again changed, by placing the distracter at a unique central location with middle elevation (i.e., superimposed to the fixation point), thus minimizing any spatial or response-related conflict (Figure 2.4, Panel B, upper part). Importantly, in Experiment 3 the proportion of present-distracter to absent-distracter trials was set to 2:1, as in Experiment 1.

If the filtering mechanism is intended to prevent any perceptual confusion between target and distracter at their respective spatial locations, disrupting their physical proximity – as I did in condition B, should be sufficient to prevent the filtering mechanism from being activated. Differently, if such mechanism is recruited to prevent distracter-driven response tendencies, the resulting cost should still be measured in the high-vs.-low distracter block (condition B), but it should be absent by presenting the distracter at the fixation point (condition C). Finally, if the filtering mechanism is activated to prevent a purely exogenous shift of attention caused by the mere

Figure 2.4. **Panel A** shows set-up and results for Experiment 3a, **Panel B** shows set-up and results for Experiment 3b, Panel C shows set-up and results for Experiment 4. The upper part of each panel depicts a schematic representation of the experimental setup, where the dart symbols represent the position of the tactile stimulators and the lamp symbols represent the position of the visual distracters (see also Fig. 1A). Lower graphs show RTs (columns, left-side axis) and error rates (triangles, right-side axis) for the two critical distracter-absent conditions: distracter-absent only (Abs-Pure) and distracter-absent mixed (Abs-Mix). Differences (p < 0.005 for all RTs pairs) index the cost of engaging the mechanism for the strategic filtering of potential distraction.



occurrence of a perceptual event in the visual field, the behavioral cost should be observed even in the latter condition.

The mean distracter interference effect amounted to 72 ms in block B [t(15)=4.48, p<0.001]. Of course, it was not possible to compute any distracter interference effect in block C, because there was no congruency/incongruency of distracters with respect to the target. However, if I compare RTs to Abs-Mix and Pres-Mix trials in block C I observe no significant difference [Abs-Mix=460ms; Pres-Mix=452; p=0.13].

Analysis of the comparison between block A and B revealed that responses for Abs-Mix trials (average RT: 468ms) were both slower [t(15)=4.60, p<0.001, corrected-α=0.0167,

$\eta^2=0.76$] (see Figure 2.4, Panel A, lower part) and higher in IEs [$t(15)=3.99$, $p<0.01$, corrected-$\alpha=0.0167$, $\eta^2=0.72$] than those for Abs-Pure trials (average RT: 426 ms), whereas this contextual effect was not modulated by the type of preceding trial [$F(2,30)=2.57$, $p=0.09$]. No differences between Abs-Mix and Abs-Pure trials were observed in terms of response accuracy ($p=0.49$). These results highlight that a strategic mechanism for the filtering of potential distracters is engaged even when target and distracting stimuli are spatially separated, thus such mechanism is likely not intended to prevent a potential perceptual integration between target and non-target stimuli (Spence et al, 2004).

However, since distracters could still be congruent or incongruent with respect to the targets in terms of response tendencies, it is possible that the functional significance of this filtering mechanism principally concerns the blocking of distracter-driven response tendencies. Consequently, in block C the distracter was rendered entirely irrelevant in terms of both spatial position and response compatibility, and therefore there should be no need for suppressing any competing motor response tendency and no need to call into play a mechanism for the proactive filtering of potential distraction. The comparison between blocks A and C showed that responses to absent-distracter trials were reliably faster in the Abs-Pure than in the Abs-Mix block (average RTs: 426ms vs. 460ms) [$t(15)=3.59$, $p<0.005$, corrected-$\alpha=0.0167$, $\eta^2=0.68$] (see Figure 2.4, Panel B, lower part) and such difference was also significant in terms of inverse efficiency scores [$t(15)=3.61$, $p<0.005$, corrected-$\alpha=0.0167$, $\eta^2=0.68$], while no significant differences emerged in accuracy ($p=0.90$). Again, there was no reliable effect of the type of preceding trial [$t(15)=0.46$, $p=0.65$].

I thus observed a cost of the distracting context in both blocks B and C, i.e. when distracters were spatially compatible or incompatible with the requested judgment and even when they consisted of a simple flash occurring at fixation. Consequently, the filtering mechanism does not seem to be primarily engaged either to avoid a perceptual integration of target and distracter stimuli because of their co-localization or to prevent a distracter-driven activation of conflicting response tendencies. Rather, its engagement seems to serve the primary role of counteracting an exogenous shift of spatial attention towards the irrelevant sensory information conveyed by the distracting visual stimulus.

2.6 Experiment 4

In the first three experiments, I showed that a strategic filtering mechanism prevents the cost of distraction in a crossmodal context where tactile targets are presented together with visual distracters.

One might wonder whether this crossmodal context is a special case, and whether or not present findings would generalize to contexts where distraction occurs within and not between sensory modalities. For example, it is conceivable that distraction arising from a sensory modality other than that of the target needs to be blocked by a specific mechanism of the kind I have characterized thus far, whereas within the same sensory modality a more flexible allocation of resources might entail no need to engage a specific distracting suppression mechanism. In other words, the strategic mechanism could be engaged selectively when a target from one sensory modality (i.e., tactile) competes with distracters from a different sensory modality (i.e., visual), and not when target and distracters belong to the same modality. An alternative possibility is that a within-modality distracter might compete even more strongly with target processing, because of the greater cognitive effort required to orchestrate concurrent attentional selection and filtering within the same sensory channel. If so, the occurrence of target and distracters within the same modality might lead to an even more pronounced filtering cost.

To examine whether a strategic filtering mechanism of potential distraction is recruited even within the same sensory modality, I replicated the paradigm of Experiment 1, but with both targets and distracters being tactile. In Experiment 4, one side of stimulation was assigned to targets and the opposite side to distracters, with target and distracter side being counterbalanced across participants (Figure 2.4, Panel C, upper part).

The mean distracter interference effect amounted to 80ms [t(15)=6.9, $p<0.001$]. Moreover, also within the tactile modality, I observed a cost exerted by the distracting context in Abs-Mix trials, compared to Abs-Pure trials, both in RTs (average RTs: 466ms and 433ms, respectively) [t(15)=3.08, $p<0.01$, $\eta^2=0.62$] (Figure 2.4, Panel C, lower part) and IEs [t(15)=2.44, $p<0.05$, $\eta^2=0.53$], whereas no difference in accuracy was observed between conditions ($p=0.36$). The previous trial type did not modulate such a cost [F(2,30)=0.91, $p=0.41$].

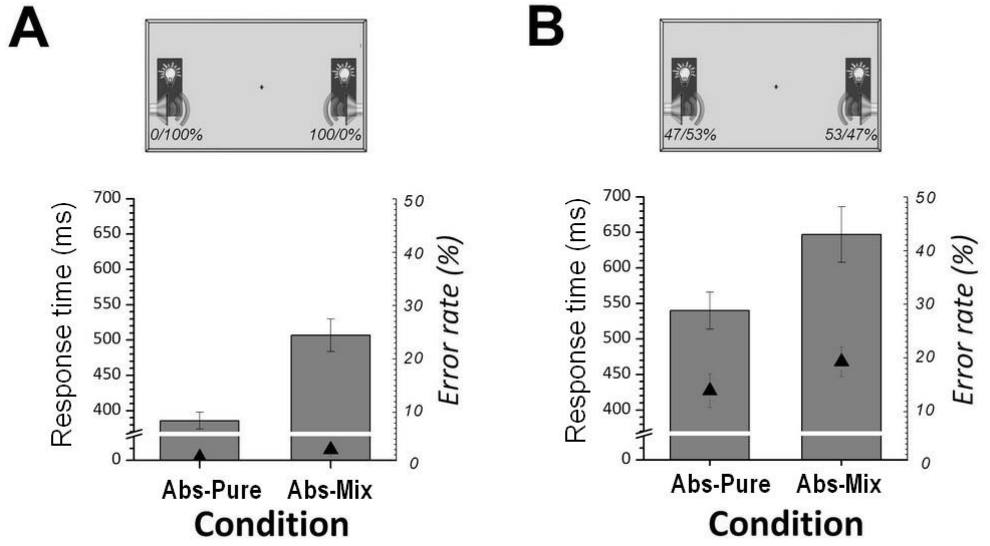
The above findings suggest that the mechanism I have uncovered is not specifically involved within bimodal contexts, where the segregation of input signals from different modalities is a pre-requisite for the attentional filtering to take place. Rather, the filtering mechanism is engaged also within unimodal contexts, for instance when targets and distracters are both tactile. Moreover, the effect size is quite comparable to the one observed in the preceding experiments, suggesting that the filtering of distracters in the same sensory modality as the target is not more resources-demanding than filtering between modalities, at least in the domain of spatial attention. Therefore, with this experiment, I confirmed the existence of an attentional mechanism strategically recruited in potentially distracting contexts, dealing with unimodal as well as multimodal contexts, whose primary function seems to be that of preventing a shift of attention from the target stimulus towards an expected, forthcoming distracter.

2.7 Experiment 5

I have provided solid evidence for a mechanism aimed at preventing potential distraction within and between sensory modalities. However, target stimuli were always tactile in the previous experiments, thus one might wonder whether these findings generalize to a different target modality. Therefore I reasoned that, in order to strengthen the claim of a truly supramodal nature of the strategic filtering mechanism, it was essential to perform an experiment where targets were delivered in a modality other than tactile. In addition, one might wonder whether these findings are replicated when eliminating the potential influence of other minor experimental factors such as the short physical asynchrony between target and distracting stimuli, as well as the somewhat unusual foot-response modality.

In this experiment, I planned to test whether the described results can be replicated when using a different crossmodal context (audio-visual), with a different target modality (auditory instead of tactile), a different response effector (the hand instead of the foot), and an exact synchrony between target and distracting stimuli (SOA=0). The experimental setup is represented in Figure 2.5, Panel A (upper part).

Figure 2.5. Panel A shows set-up and results for Experiment 5, **Panel B** shows set-up and results for Experiment 7. The upper part of each panel depicts a schematic representation of the experimental setup, where semi-transparent loudspeaker icons represent the position of the occluded loudspeakers and the lamp symbols represent the position of the visual distracters. Lower graphs show RTs (columns, left-side axis) and error rates (triangles, right-side axis) for the two critical distracter-absent conditions: distracter-absent only (Abs-Pure) and distracter-absent mixed (Abs-Mix). Differences ($p < 0.005$ for all RTs pairs) index the cost of engaging the mechanism for the strategic filtering of potential distraction.



Response times to Abs-Pure trials (mean: 386 ms) were significantly faster than those to Abs-Mix trials (mean: 507 ms), reflecting a dramatically high strategic cost [$t(15)=7.43$, $p<0.001$, $\eta^2=0.89$] (Figure 2.5, Panel A, lower part). In addition to this cost, also a significant distracter interference effect was observed [$t(15)=8.66$, $p<0.001$, $\eta^2=0.91$], with RTs to Inc-Mix trials being considerably slower than to Cong-Mix trials (641 ms and 527 ms, respectively). In terms of accuracy, performance was nearly optimal under both absent-distracter conditions, with mean error rates of 0.02 in Abs-Pure trials and 0.03 in Abs-Mix trials [$t(15)=1.80$, *ns*]. Also in Cong-Mix trials the subjects' performance was fairly good, with a mean error rate of 0.04, whereas performance was much worse when visual distracters were incongruent (error rate: 0.34) [t(15)=6.92, $p<0.001$].

These results replicated the finding of a strategic cost measured in absent-distracter trials within the context of a sound localization task with lateralized visual distracters. Akin to Experiments 1 and 2, I also performed an analysis of RTs by subdividing Abs-Mix trials based on the preceding trial type, in order to disentangle the relative contribution of strategic and reactive factors to the observed cost. The results of a one-way ANOVA revealed a significant main effect of *Previous Trial Type* [F(2,30)=82.3, $p<0.001$]. Post-hoc tests showed that all corrected pairwise comparisons differed from one another, with Abs-Mix trials preceded by another Abs-Mix trial being the fastest, those preceded by Cong-Mix trial being intermediate, and those subsequent to a Inc-Mix trial being the slowest (all *p*s<0.01). Crucially, however, one should note that even by considering only Abs-Mix trials preceded by another Abs-Mix trial and comparing them to Abs-Pure trials, a robust strategic cost is still obtained [t(15)=4.66, $p<0.001$, $\eta^2=0.77$].

While the general finding of a strategic cost was fully confirmed in the present experiment, here I also observed that a minor component of the cost measured in the Mix block was due to reactive engagement of the filtering mechanism following a present-distracter trial. Interestingly, not only Inc-Mix trials, but also Cong-Mix trials led to a significant slowing-down on the subsequent Abs-Mix trial.

2.8 Experiment 6

With the previous experiments, I provided compelling evidence in favor of a mechanism for the strategic filtering of potential distraction. Specifically, I demonstrated that the filtering mechanism is recruited to deal with probable forthcoming distraction both within and between sensory modalities, in tactile, visuo-tactile and audio-visual tasks. I claim that this filtering mechanism would be a general component of attentional control. With this experiment, I aim to support this claim by showing that strategic filtering occurs in the context of yet another target modality (visual) and, even more importantly, that it may be evidenced by applying the same logic as in the previous experiments to a well-established attentional task such as the arrow flanker task (e.g., Ridderinkhof et al., 2002; see Figure 2.6, Panel A).

Consistently with prior literature (Eriksen et al., 1985; Enns & Akhtar, 1989; Ridderinkhof et al., 2002), I measured a significant *distracter interference* effect, with RTs to Inc-Mix trials being slower than those to Cong-Mix trials (mean RTs: 467 ms and 425 ms, respectively) [$t(15)=8.07$, $p<0.001$, $\eta^2=0.90$]. Additionally, subjects were more prone to errors when they faced an incongruent, as compared to a congruent, distracter [$t(15)=3.46$, $p<0.005$].

Importantly, I measured a significant slowing-down of responses to distracters-absent trials when they were presented in the Mix (i.e., Abs-Mix trials; mean RT: 410 ms), as compared to the Pure (i.e., Abs-Pure trials; mean RT: 380 ms), block [$t(15)=5.62$, $p<0.001$, $\eta^2=0.82$]. No significant difference in accuracy was found between Abs-Pure and Abs-Mix conditions ($p=0.13$). The difference between Abs-Pure and Abs-Mix conditions was also highly significant when measured on inverse efficiency scores, rather than RTs, as the dependent variable [$t(15)=4.68$, $p<0.001$]. These results are represented in Figure 2.6, Panel B.

The difference in absent-distracter responses between the Pure and the Mix block (Abs-Mix minus Abs-Pure) was used as a measure of *strategic cost* because under the main hypothesis it reflects the engagement of an attentional mechanism intended to prevent interference exerted by forthcoming distraction.

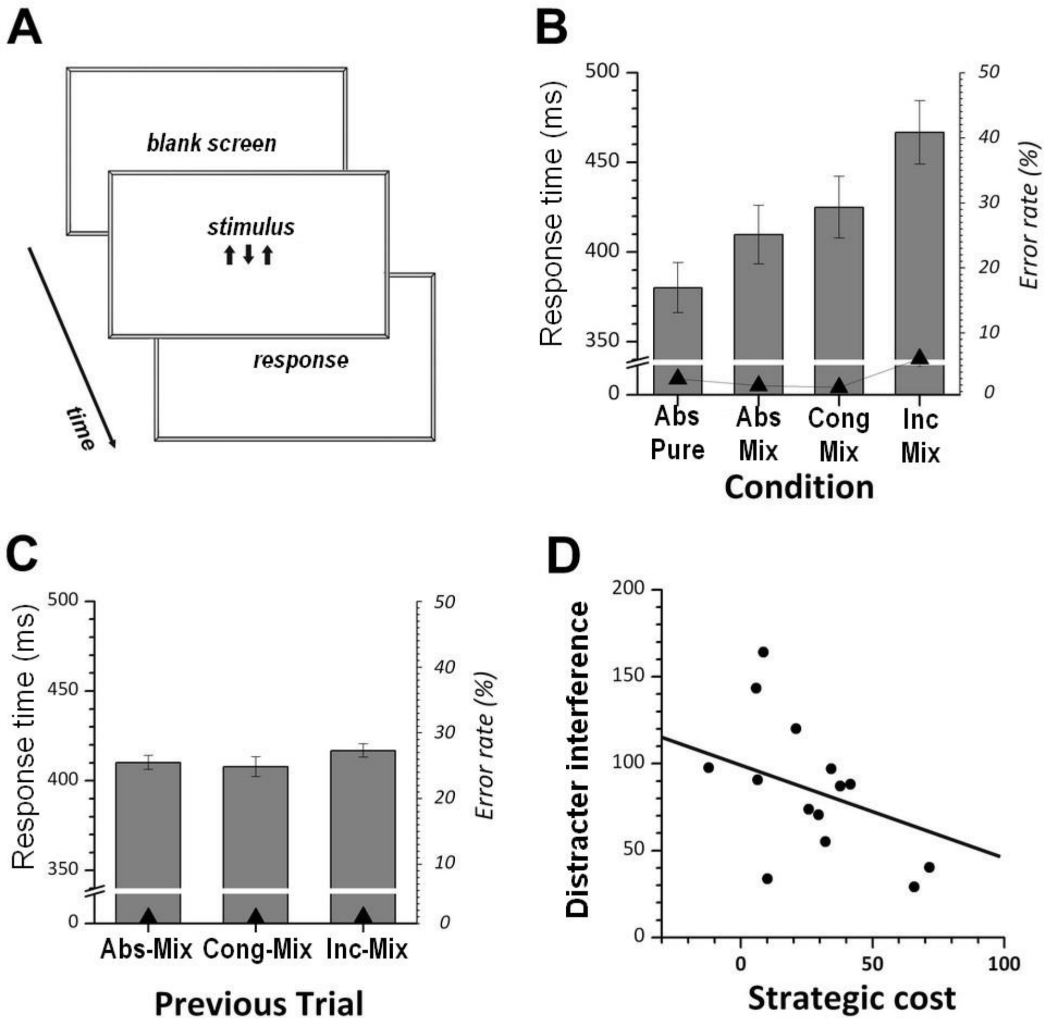
For providing further support for this view, I ran a correlation analysis between strategic cost and distracter interference, both computed as IE values to employ a more reliable index of performance, as I did for Experiment 1. I found a significant inverse correlation between these factors [r(14)=-0.57, p<0.05], fully replicating the pattern of Experiment 1 (Figure 2.6, Panel D).

Akin to Experiments 1 and 2, I also analyzed Abs-Mix trials by sorting them according to the preceding trial type. The related ANOVA resulted in a significant main effect of *Previous Trial Type* [F(2,30)=8.97, p<0.001, η^2=0.37], and post-hoc tests revealed that Abs-Mix trials preceded by incongruent distracter trials were slower than those preceded by a Cong-Mix (p<0.01) and by a Abs-Mix (p<0.05) trial (Figure 2.6, Panel C). However, differently from what observed in Experiment 2, where the strategic cost was abolished when considering only Abs-Mix trials preceded by another Abs-Mix trial, in the present experiment the strategic cost remained significant even when computed in this more stringent manner [t(15)=2.24, p<0.05, η^2=0.52].

Effect-size values indicate that, while the preceding trial type explains part of the variance, a significant amount of overall variance (namely, 52%) is still explained in this experiment by the "block" factor, even after having subtracted out the reactive component of the filtering activation.

This pattern of results clearly supports the idea that a distracter filtering mechanism is strategically engaged during the Mix block in Experiment 6.

Figure 2.6. ***Panel A***. Setup of the arrow flanker task of Experiment 6. For display purposes, an Inc-Mix trial is shown. In this trial, two incongruent distracters (upward arrows) flank a central target (downward arrow). In Cong-Mix trials, the flanking arrows were oriented the same way as the central target. In distracter-absent trials (Abs-Pure, Abs-Mix), only the central arrow was present. ***Panel B***. Response times (columns, left-side axis) and error rates (triangles, right-side axis) in Experiment 6, separately for each condition: Abs-Pure, Abs-Mix, Cong-Mix and Inc-Mix. The difference between Abs-Mix and Abs-Pure (RTs: $p < 0.001$) is a measure of the strategic cost, while the difference between Inc-Mix and Cong-Mix (RTs: $p < 0.001$) indexes distracter interference. ***Panel C***. Response times (columns, left-side axis) and error rates (triangles, right-side axis) to Abs-Mix trials in Experiment 6, separated based on the preceding trial type. Abs-Mix trials following a Inc-Mix trial were the slowest (p*s* < 0.05). ***Panel D***. Dots show individual correlation points between the strategic cost and the distracter interference, as defined in the main text ($p < 0.05$). The solid line depicts the least squares fit for the data as calculated by means of a simple linear regression model. All values are inverse efficiency (IE) scores.



2.9 Experiment 7

In Experiments 1-6, I provided solid evidence for the slowing-down of responses to stimuli from different sensory modalities in the absence of distraction when these stimuli are embedded in a potentially distracting context. I argued that such an impaired performance attests to the recruitment of a resource-demanding mechanism for the strategic filtering of upcoming distraction.

However, one could entertain an alternative interpretation of the results reported thus far. The RT cost in Abs-Mix trials, as compared to Abs-Pure trials, could be conceived as a form of strategic response procrastination within the Mix block in order to increase the level of cognitive processing of the given stimuli before response emission, thus contrasting more efficiently the disturbing influence of (potential) distracters and permitting the resolution of potential response conflicts. If this were the case, the longer time allotted for stimulus processing in the Mix (relatively to the Pure) block should result in more accurate responses for Abs-Mix trials than for Abs-Pure trials – a typical form of speed-accuracy trade-off. A limited increase in accuracy in absent-distracter trials in the Mix block was observed only in Experiment 1, but not in the subsequent experiments, suggesting *prima facie* that no substantial speed-accuracy trade-off was taking place overall across experiments. However, given that the mean accuracy was very high in both absent-distracter conditions of Experiment 1 (>95%), as well as of all other experiments, the hypothesized increase of accuracy in the Mix block might have been concealed by a ceiling effect, that is, by very high accuracy scores under both absent-distracter conditions. I then sought to test directly the aforementioned hypothesis by generally replicating the paradigm of Experiment 5 while increasing task difficulty, which was obtained by reducing the perceived spatial separation between left and right auditory stimuli. This manipulation, by increasing task difficulty, was expected to reduce mean performance accuracy, thus allowing the predicted change in accuracy to emerge. If the observed slowing-down of responses in Abs-Mix trials were due to a more cautious response setting adopted strategically throughout the Mix block, then the longer processing time should lead to better performance accuracy in Abs-Mix trials, as compared to Abs-Pure trials, in the present experiment. Conversely, if the observed RT cost in Abs-Mix trials were due to the strategic engagement of the postulated filtering mechanism, that should increase the cognitive load and in turn hamper performance globally, leading to longer RTs and reduced accuracy values. Therefore, any *increase* in accuracy for Abs-Mix trials compared to Abs-Pure trials would be compatible with the response procrastination hypothesis, while a *reduction* in accuracy for the same comparison would fully support the filtering hypothesis.

The experimental setup for this experiment is schematically reproduced in Figure 2.5, Panel B (upper part). Results showed that mean RTs for Abs-Pure and Abs-Mix trials in Experiment 7 were 540 ms and 640 ms, respectively [$t(15)=4.02$, $p<0.005$, $\eta^2=0.72$], replicating the finding of a filtering cost from the previous experiments (Figure 2.5, Panel B, lower part). Responses to Cong-Mix trials were reliably faster than those to Inc-Mix trials (624 ms and 750 ms, respectively) [$t(15)=6.91$, $p<0.001$, $\eta^2=0.87$]. More relevantly to the purpose of the present experiment, I observed a significant decrease in accuracy in Abs-Mix trials (80.7%), as compared to Abs-Pure trials (86.1%) [$t(15)=3.55$, $p<0.01$, $\eta^2=0.68$]. In addition, accuracy was higher for Cong-Mix trials (89.9%) than Inc-Mix trials (41.2%), where subjects appeared to respond more often to the visual distracter, probably because of audio-visual ventriloquism (Bertelson & Aschersleben, 1998).

These findings suggest that subjects were not able to use the prolonged delay before response emission in the Abs-Mix (as compared to Abs-Pure) condition for improving their performance, as predicted by the response procrastination account. Rather, participants slowed-down their responses and were more prone to errors in Abs-Mix trials, as compared to Abs-Pure trials. I argue that in the Abs-Mix condition subjects paid an overall cost in performance, as indexed by both RTs and accuracy data, because they were strategically adopting an attentional setting that caused a reduction of available cognitive resources for the main task, as compared to the Pure block. Then, these results strongly support the filtering hypothesis.

2.10 Conclusion

In Experiments 1-4, I disclosed and characterized a mechanism for the strategic filtering of upcoming distraction in a task with visual or tactile distracters and tactile targets. Since these two modalities are closely related (Macaluso, et al., 2000; Macaluso, et al., 2002), the observed results might be specific for visuo-tactile stimulus pairs. I ruled out this possibility by fully confirming the finding of a strategic cost in Experiment 5 and 7, where target stimuli were auditory rather than tactile. Incongruent visual distracters yielded greater interference in the auditory lateralization task of Experiments 5 and 7, as compared to the tactile elevation task of Experiments 1-4. Parallel to this more robust distracter interference effect, in Experiments 5 and 7 also the measured strategic cost was dramatically strong, likely because of the increased filtering demands determined by highly interfering visual distracters.

The claim of generality for the strategic filtering mechanism and its independence of the sensory modality and task procedures are further supported by Experiment 6. There, I applied the very same logic to a completely different paradigm (i.e., an arrow flanker task) and fully replicated findings from the preceding experiments. Remarkably, I provided further evidence for the close relationship between the strategic cost and the distracter interference, by showing once more with a correlation analysis that these two measures are inversely correlated.

The remarkably coherent pattern of results from all experiments combined fully supports the claim of a supramodal mechanism for the strategic filtering of distraction and provides compelling evidence that it represents a general and fundamental component of attentional control. Compatible evidence has been recently reported in a study by Wendt and colleagues (Wendt, Luna-Rodriguez & Jacobsen, 2012), where they show that context-dependent modulations of stimulus attributes (either spatial position or color) attest to perceptual filtering of distracter’s features.

A neurophysiological observation obtained with fMRI potentially related to the strategic filtering mechanism reported here is the increased preparatory activity (i.e., brain activity measured prior to stimulus onset in visual cortex) that is typically observed when interference from distracters is likely, rather than when it is unlikely (Serences et al., 2004a). Preparatory BOLD activity could reflect increased anticipatory inhibition of neural responses in brain areas representing distracters; thus, its enhancement might be a sign of increase in attentional control settings for distracters suppression. In the same study (Serences et al. 2004a), a null behavioral effect of distracters' probability is found on absent-distracter trials. Although that might appear to be in sharp contrast with present findings, in Serences and colleagues' study effects were assessed only in terms of changes in accuracy (whereas RTs were not analyzed), and I also do not observe changes in accuracy (except than in Experiment 7), whereas the cost I measure mostly emerges in response times. Of course, other differences in paradigm and methodology could also account for the apparent discrepancy between results from their study and the present one.

In a recent visuo-acoustic study (Weissman, Warner, & Woldorff, 2009), longer RTs were coupled with a reduction of activity in sensory-specific target-related areas as well as with an increase of activity in sensory-specific distracter-related areas and in frontal regions related to conflict representation and monitoring, including the anterior cingulate cortex. This suggests a potential failure in distracter suppression that in turn leads to longer RTs. Although this is a merely speculative argument at this point, it is tempting to hypothesize that the strategic filtering mechanism that I propose could rely on context-sensitive monitoring mechanisms involved in the control of spatial attention.

Chapter 3

Conflict Probability Modulates Cognitive Preparation For Filtering Out Spatial Distracters

3.1 Aim of the study

The behavioral cost for filtering out potential distraction cost was demonstrated for the first time in a series of studies that are described in Chapter 2 of the present thesis. When potential distraction is foreseen in a cognitive context, the activation of a mechanism for filtering out distracters across sensory modalities entails a cost on performance in terms of speed (and, limited to some circumstances, accuracy) of responses to target stimuli. This cost is measured on absent-distracter trials and is observed when those trials are presented in a Mix block (i.e., intermixed with some present-distracter trials), as compared to a Pure block (i.e., when distracters are never presented). With the term PM-PoDist (Pure-Mix Potential Distraction) I refer to an experimental paradigm where absent-distracter trials from a Pure block are compared to those from a Mix block. Previously described results showed that the filtering cost on response times is larger when present-distracter trials constitute the 66% (as compared to the 33%) of total trials (indexed by a decrease of .16 in η^2 effect size, see Experiments 1 and 2 in Chapter 2). Moreover, the filtering cost in the low-distraction block is not found on inverse efficiency (Townsend & Ashby, 1983), which is a measure unaffected by the speed-accuracy tradeoff (differently from simple response times). Sequential analyses also showed that in the low-distraction block the filtering cost is driven by cross-trial contingencies and thus it mainly activates with reactive, rather than strategic, dynamics (see Experiment 2 in Chapter 2).

However, in Experiments 1 and 2 of Chapter 2 two parameters were changed between the high-distraction (Experiment 1) and the low-distraction (Experiment 2) experiment, namely the proportion of occurrence of distracter-present trials (dropped from 66% to

33%) and the proportion of occurrence of conflict (dropped from 33% to 16.5%). Evidences from other experiments within the same study support the idea that the filtering cost can be driven by both conflict at response level (e.g., in Experiment 6) and by the mere presentation of a task-irrelevant and response-irrelevant distracting item (see Experiment 3, conditions B and C). Therefore, it cannot be univocally determined whether the observed reduction in the filtering cost between Experiment 1 and 2 is driven by the reduction in the proportion of irrelevant elements, by the reduction of conflict, or by both. I then aimed at disentangling this issue by selectively manipulating within-subjects and across different contexts the probability of conflict while leaving unaltered the probability of occurrence of irrelevant elements.

In this study, I primarily aimed at isolating the impact of conflict probability itself on the filtering cost. I investigated how the filtering cost varies as a function of conflict probability, with the idea of showing a larger filtering cost in high-conflict blocks as compared to low-conflict blocks. Accessorily, I expected to replicate results on proportion-congruent effect (Lowe & Mitterer, 1982; Jacoby, Lindsay & Hessels, 2003), with larger distracter cost in low-conflict blocks and smaller distracter cost in high-conflict blocks.

A parallel aim of the current study is further generalizing the filtering cost by exploring its occurrence in a new experimental paradigm. In Chapter 2, I studied a wide variety of experimental situations by means of visuo-tactile, audio-visual, tactile and visual experimental paradigms. In all these paradigms, however, target stimuli and distracters were presented at separate spatial locations. Thus, the supramodal mechanism for filtering out potential distraction might be space-based.

However, it is widely accepted that attention can be also directed towards specific objects (object-based attention: e.g., Duncan, 1984; Roelfsema, Lamme, & Spekreijse, 1998; Serences, Schwarzbach, Courtney, Golay, & Yantis, 2004b), and specific stimulus features (feature-based attention; see Maunsell & Treue, 2006, for a review), such as motion (Treue & Martinez-Trujillo, 1999), color (Andersen, Müller, & Hillyard, 2009), orientation (Liu & Hou, 2011), or contrast (Pashler, Dobkins, & Huang, 2004; Sani, Santandrea, Golzar, Morrone, & Chelazzi, 2013). I then aimed at exploring whether the filtering mechanism still engages during a non-spatial feature-based task.

Exploring the eventual occurrence of a filtering cost in a non-spatial task should allow shedding light into the filtering mechanism itself. In fact, if the filtering mechanism acts uniquely by suppressing information at locations of irrelevant stimuli, no filtering cost should be measured in a non-spatial task. Vice-versa, if the filtering mechanism can also prevent orienting attention towards irrelevant features, the filtering cost should be found in a non-spatial task. Finally, if the filtering mechanism is a higher-level cognitive system, which primarily prevents the emission of a response primed by the distracting stimuli, the filtering cost should be observed in any conflicting paradigm regardless of its spatial or non-spatial characteristics.

In the current study, I used two different tasks. In addition to the arrow flanker task (Spatial Task), here I introduced a novel task (Feature Task) where target and distracters are defined by different features, namely motion direction and object pointing direction. These two features of stimuli are processed independently in the brain at the level of high-level visual areas, since motion integration occurs in the dorsal stream in V5/MT+ (Huk & Heeger, 2002), while shape-object integration takes place in the lateral occipital complex (LOC; Kourtzi & Kanwisher, 2001). Therefore, in the feature-based task target and distracters share the same spatial location, are processed separately in the brain (in motion and shape-representation areas, respectively), but still conflict at the higher response-related level of processing. In the space-based task, instead, visual stimuli are processed in separate but adjacent position within the same retinotopic brain areas, have an analogous higher-level object representation, and conflict at the level of response selection.

3.2 Materials and Methods

3.2.1 Participants

Eighteen participants with no known neurological condition and with normal or corrected-to-normal vision participated in this study (mean age ± standard deviation: 21.3 ± 3, range 18-35, 12 females, 16 right-handed). All participants gave their informed consent to participate in the study and were paid 15 US dollars/hour. This study was approved by Duke University Institutional Review Board.

3.2.2 Experimental Design

For the entire duration of the study participants sat comfortably in a dimly illuminated room with their eyes at a distance of 57 cm from the central point of a 24'' computer screen (Asus VG248QE, 1920 x 1080 pixels, refresh rate 120Hz). The experimental paradigm was programmed ad-hoc using Matlab R2013a (Mathworks Inc.) with Psychtoolbox 3.0 (Kleiner, Brainard, Pelli, Ingling, Murray et al., 2007). Participants' responses were collected through button presses on a precision gamepad (Logitech Precision G-UG15).

The experiment included two different types of task, the *spatial task* (i.e., an arrow orientation discrimination task) and the *feature task* (i.e., a motion direction discrimination task), delivered in separate blocks of eight blocks each. Within each type of task, there were four different block types: the Pure block, in which all trials were absent-distracter trials (Abs-Pure); the Mix mostly Congruent block (mostCong), in which 60% of trials were congruent-distracter trials (Cong-mostCong), 20% of trials were incongruent-distracter trials (Inc-mostCong), and 20% of trials were absent-distracter trials (Abs-mostCong); the Mix mostly Incongruent block (mostInc), in which 60% of trials were incongruent-distracter trials (Inc- mostInc), 20% of trials were congruent-distracter trials (Cong- mostInc), and 20% of trials were absent-distracter trials (Abs- mostInc); the Mix mostly Neutral block (mostNeut), in which 80% of trials were neutral-distracter trials (Neut-mostNeut), and 20% of trials were absent-distracter trials (Abs- mostNeut). Both the order of blocks and the order of blocks within each block were counterbalanced across participants.

I used the rationale of the PM-PoDist paradigm, in which the Pure block serves as a reference context, while the other contexts (Mix blocks) provide with different levels of conflict probability but all include a small percentage of absent-distracter trials. No conflict was present in the mostNeut block, a low conflict probability was present in the mostCong block, and a high conflict probability was present in the mostInc block (i.e. 60%).

Participants received written task instructions and performed 20 practice trials for each type of task prior to the beginning of each block. Stimulus presentation time was 200 ms in the spatial task and 300 ms in the feature task. After each stimulus presentation, participants had a maximum time of 1500 ms for emitting their response. The subsequent stimulus onset occurred after an inter-trial interval varying in duration between 500 ms and 1000 ms.

Each participant completed 16 experimental blocks (8 blocks for each task type, adding up to 2720 single trials). The global duration of the experiment was about 1 hour and 30 minutes.

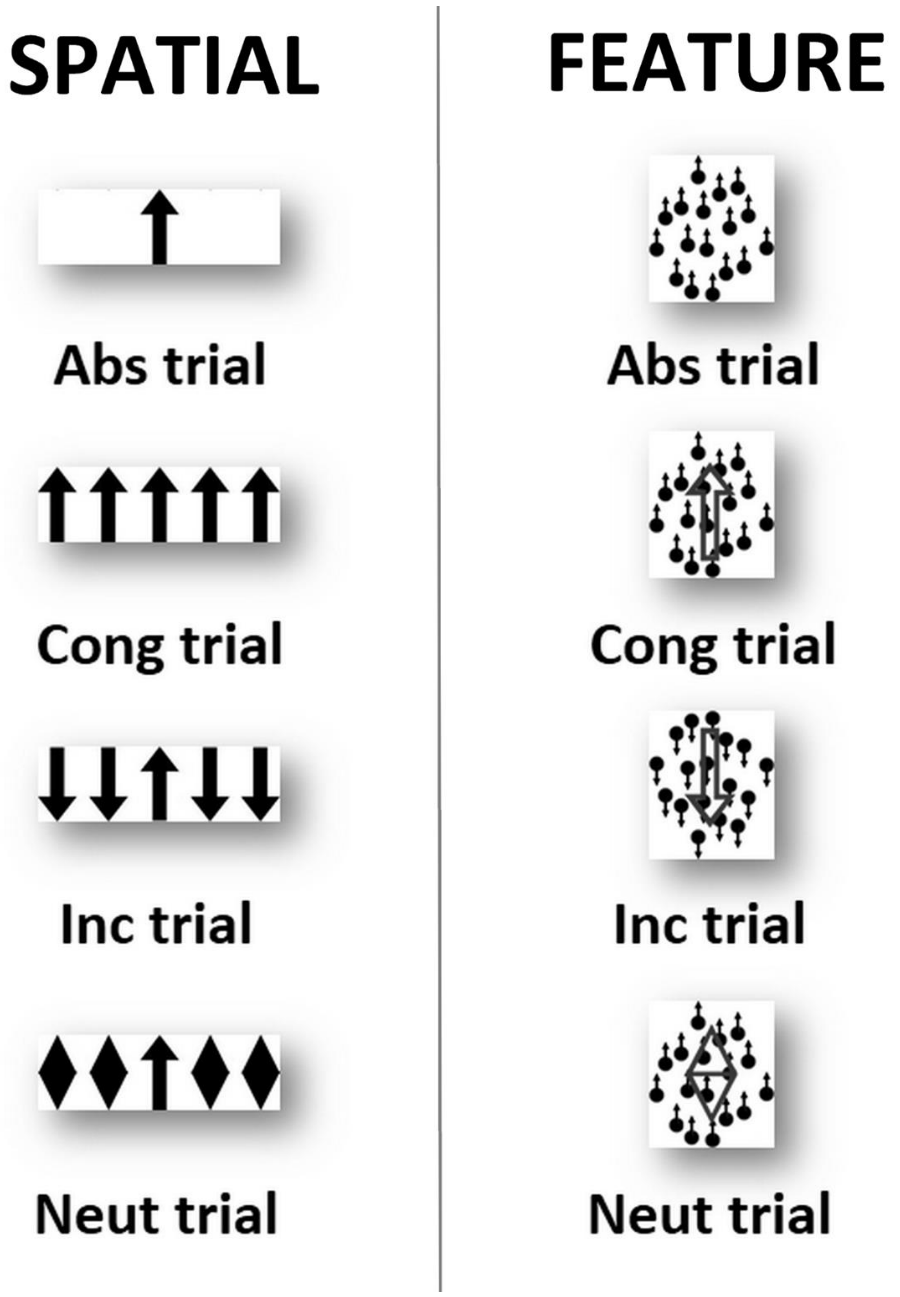
Spatial Task

Stimuli consisted in a horizontal array of five flanking arrows that were pointing either down- or upwards (all stimulus types are schematically reproduced in Figure 3.1). All arrows were presented in black on a medium-gray background in a central fixation position. Each arrow subtended a visual angle of 0.75 (vertically) by 0.5 (horizontally) degrees and the center-to-center distance between adjacent arrows was 0.75 degrees of visual angle.

The central arrow was the target while the four lateral arrows (two on each side of the target) were the distracters. In congruent trials, target and distracters pointed in the same direction (either up or down), while in incongruent trials target and distracters pointed in opposite directions (either target up and distracters down or vice-versa). In the mostNeut block, neutral distracters were diamond-like shapes (rather than arrows) presented in the same size, color, and spatial position as the distracting arrows in the other block types.

Participants were instructed to respond as quickly and as accurate as possible by pressing the gamepad button corresponding to the direction to which the target arrow was pointing while ignoring distracters.

Figure 3.1. *Schematic representation of stimulus types in the spatial task (left column) and in the feature task. Small arrows on each dot in the feature task represent direction of motion. The hollow arrow in the feature task was actually of the same color as the dots. According to their relative proportion, these stimuli made up four different block types. In the Pure block all trials were Abs. The mostCong block was constituted by 60% Cong, 20% Inc, 20% Abs trials. The mostInc block had 60% Inc, 20% Cong, 20% Abs trials. The mostNeut block included 80% Neut and 20% Abs trials.*



Feature Task

The target stimulus was a circular array of moving dots presented in the center of the screen (stimulus types are represented in Figure 3.1). The array had a radius of 2 degrees of visual angle and encompassed 100 dots (each with a radius of 0.1 degrees) moving either down or upwards at 100% coherence level. Motion speed values were randomly drawn for each dot from a uniform distribution on the interval between 3.6 and 5.4 degrees of visual angle per second.

The distracting stimulus was a hollow arrow, which was also presented in the center of the screen and subtended a visual angle of 3.6 degrees (vertically) by 2.4 degrees (horizontally). The distracting hollow arrow pointed either down or upwards. In congruent trials, motion direction was in the same direction as the hollow arrow orientation (either up or down), while in incongruent trials motion direction was in the opposite direction as the hollow arrow orientation (either motion up and arrow down or vice-versa). In the mostNeut block, neutral distracters was a hollow diamond-like shapes (rather than a hollow arrow) presented in the same size, color, and spatial position as the distracting hollow arrow in the other block types.

Participants were instructed to respond as quickly and as accurate as possible by pressing the gamepad button corresponding to the direction in which the dots were moving while ignoring distracters. Response times (RTs) and response accuracy were measured.

3.2.3 Analysis

The analysis aimed at assessing the cost of the distraction filtering mechanism and its consequent impact on the distracters cost in contexts characterized by different levels of conflict probability (no conflict in the mostNeut block, low conflict probability in the mostCong block, high conflict probability in the mostInc block). The behavioral cost of the distraction filtering mechanism (hence, the *filtering cost*) was computed as the normalized difference in response times between Abs-Mix trials and Abs-Pure trials, respectively. The behavioral cost associated with the presence of conflicting distracters (hence, the *distracters cost*) was calculated as the normalized difference in response times between incongruent and congruent trials, separately for the mostCong block and the mostInc block. In the mostNeut, where no conflict was present at all, a measure of distracter interference was calculated as the normalized difference between neutral-distracter (Neut-mostNeut) and absent-distracter (Abs- mostNeut) trials.

Given that results described in Chapter 2 showed that the filtering cost is represented optimally by response times values rather than by the percentage of accuracy, and given that those results also speak against a potential speed-accuracy tradeoff in this task (Experiment 7, Chapter 2), I used response times (RTs) as the main dependent variable of interest in the current study. Limited to the regression analysis and in accordance with the previous study (Experiments 1 and 6 in Chapter 2) for obtaining a more sensitive index of performance in the across subjects correlation I calculated the inverse efficiency score (Townsend & Ashby, 1983) and used it as the dependent variable.

Statistical analyses were carried out by means of repeated-measures Analysis of Variance (rmANOVA), general linear regression models, and t-tests. A preliminary paired samples t-test assessed whether any global difference on RTs emerges relatedly to the type of task (spatial task versus feature task). Then I conducted a comprehensive rmANOVA focusing on the overall analysis of the filtering cost and the distracters cost. This ANOVA had a 2×2×3 design factoring Task (spatial, feature), Cost (filtering cost, distracters cost) and Context (mostNeut, mostCong, mostInc). Another 2×2×3 rmANOVA used RTs to Abs-Mix trials for investigating sequential effects in Mix blocks by factoring Task (spatial, feature), Context (mostCong, mostInc), and Type of Preceding Trial (absent-distracter, congruent-distracter, incongruent-distracter). When significant interactions emerged in rmANOVAs, comparisons of interest were further explored by means of paired samples t-tests. The family-wise error rate (FWER) was controlled at significance level α = .05 by applying the Holm-Bonferroni method (Holm, 1979). I point out in the Results any p-value which did not hold significance level after FWER correction. All analyses were performed with Statistica for Windows release 6.0 (StatSoft Italia SRL) except for regression analysis which was conducted in R (R-Project, CRAN, www.r-project.org) and included the Bonferroni outlier test (Fox, 1997).

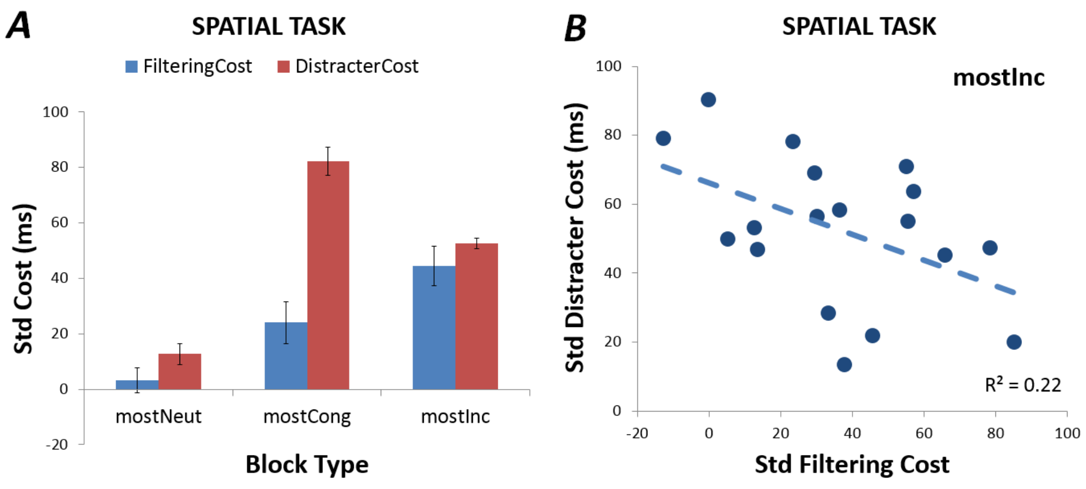
3.3 Results

A preliminary analysis aimed at investigating whether there are global differences in RTs between the spatial and the feature task by means of a paired samples t-test. Overall RTs were 394 ms and 420 ms for the spatial and feature task, respectively, but this difference was not statistically significant [t(1,17)=1.11, p=.28]. Thus, I report no significant difference in response times between the arrow orientation discrimination (spatial task) and the motion direction discrimination (feature task).

The rmANOVA on filtering cost and distracter cost as a function of context and type of task did not show a significant main effect of Task [F(1,17)=2.19, p=.16], coherently with the results of the overall t-test comparison on RTs between spatial and feature task. Instead, a significant main effect of Cost [F(1,17)=8.24, p<.05] and a significant main effect of Context [F(1,17)=85.92, p<0.001] were observed. The interaction between Task and Cost was significant [F(1,17)=6.81, p<.05] and the two-way interaction between Cost and Context was also significant [F(2,34)=12.61, p<0.001]. More relevant to the purpose of the current study, the three-way interaction between Task, Context and Cost was significant [F(2,34)=5.66, p<.01].

This latter interaction was further explored by running ad-hoc pairwise comparisons. First, I conducted pairwise comparisons in order to assess in what conditions a significant slowing-down on absent-distracter trials is observed in the mixed context as

Figure 3.2. **Panel A**: results of the spatial task. A significant filtering cost was observed in the mostCong and in the mostInc blocks (blue columns). A significant distracter cost (red columns) was observed in all blocks. The distracter cost was the smallest in the mostNeut block and the largest in the mostCong block. The filtering cost in the mostInc block was larger than in the mostCong block. **Panel B**: results of linear regression analysis between filtering cost and distracter cost. Across subjects, a significant negative correlation emerges, indicating that participants with larger filtering costs benefitted of a reduced interference from distracters, while participants with a smaller distraction filtering cost were slower when distraction was actually present.



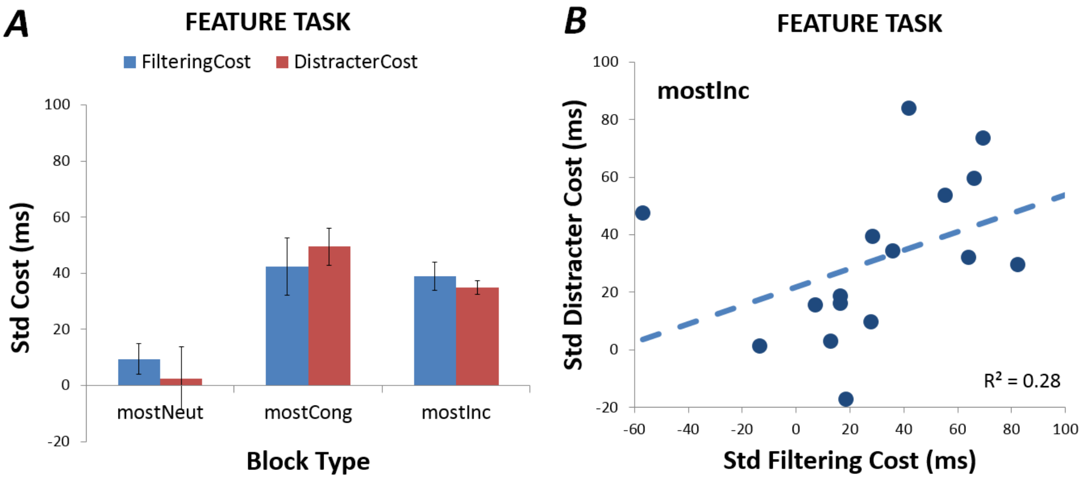
compared to the Pure block (i.e., the filtering cost). In the spatial task, absent-distracter trials showed longer RTs both in the mostCong (mean RT: 379 ms) and in the mostInc contexts (mean RT: 395 ms), as compared to the Pure block (mean RT: 361 ms) [t(17)=5.34, p<.001, and t(17)=5.74, p<.001, respectively]. No difference was observed between Abs-Pure (mean RT: 361 ms) and Abs-mostNeut (mean RT: 364 ms) trials [t(17)=0.79, p=.44]. In the feature task, absent-distracter trials showed longer RTs both in the mostCong (mean RT: 425 ms) and in the mostInc contexts (mean RT: 424 ms), as compared to the Pure context (mean RT: 386 ms) [t(17)=4.29, p<.001, and t(17)=2.79, p<.05, respectively]. No difference was observed between Abs-Pure (mean RT: 386 ms) and Abs-mostNeut (mean RT: 393 ms) trials [t(17)=1.63, p=.12]. These results attest to the presence of a significant filtering cost both in the spatial and in the feature task limitedly to contexts in which distracters show some degree of congruency (or incongruency) with the target stimulus. No filtering cost was observed when distracters were entirely irrelevant (e.g., they did not map into possible responses for the actual task).

Subsequently, I conducted another set of pairwise comparisons with the aim of investigating in what types of mixed contexts a significant distracter cost is found. In the spatial task, a significant distracter cost on RTs was observed both in the mostCong (mean RTs: Cong-mostCong=380 ms and Inc-mostCong=449 ms) and in the mostInc contexts (mean RTs: Cong-mostInc=400 ms and Inc-mostInc=443 ms) [t(17)=15.87, p<.001, and t(17)=10.73, p<.001, respectively]. A significant distracter cost was also exerted by neutral distracters trials (mean RT: 374 ms), with respect to Abs-mostNeut trials (mean RT: 364 ms), in the mostNeut context [t(17)=6.49, p<.001]. In the feature task, a significant distracter cost on RTs was observed both in the mostCong (mean RTs:

Inc-mostCong=470 ms and Cong-mostCong =418 ms) and in the mostInc contexts (mean RTs: Inc-mostInc=416 ms and Cong-mostInc=452 ms) [t(17)=3.94, p<.01, and t(17)=3.82, p<.01, respectively]. No significant distracter cost was found in the mostNeut context [t(17)=1.25, p=.23].

These results demonstrate the occurrence of a significant distracter cost both in the spatial and in the feature task in both types of conflicting contexts (i.e., mostCong and mostInc). When the distracter is neutral, an interference effect is present in the spatial task, but no interference is found in the feature task.

Figure 3.3. Panel A: results of the feature task. A significant filtering cost was observed in the mostCong and in the mostInc blocks (blue columns). A significant distracter cost (red columns) was observed in the mostCong and in the mostInc blocks (red columns). Both the filtering cost and the distracter cost were not significantly different in the mostCong and in the mostInc blocks. Neutral distracter did not elicit any significant cost. **Panel B**: results of linear regression analysis between filtering cost and distracter cost. Across subjects, a significant positive correlation emerges, indicating that participants with larger filtering costs also showed an augmented interference from distracters, while participants with a smaller distraction filtering cost were faster when distraction was actually present.



In order to assess whether each cost (i.e., filtering cost and distracter cost) is modulated depending on the probability of occurrence of conflict I ran a set of pairwise comparisons for specifically comparing the magnitude of the filtering and distracter cost between different contexts, separately for each task.

Previous analyses showed that in the spatial task a significant filtering cost emerged in the mostCong and in the mostInc contexts. The direct comparison between these two conditions showed that the filtering cost was larger in the mostInc context (mean: 44 ms) as compared to the mostCong context (mean: 24 ms) [t(17)=4.13, p<.001]. Conversely, the distracters cost was larger in the mostCong context (mean: 82 ms) as compared to the mostInc context (mean: 53 ms) [t(1,17)=5.77, p<.001]. The distracter cost measured in the mostNeut context was the smallest (mean: 13 ms) with respect to the mostCong and mostInc contexts [t(1,17)=18.61, p<.001, and t(1,17)=9.18, p<.001, respectively]. These results are shown in Figure 3.2, Panel A. This pattern of results clearly demonstrate that the filtering cost is larger as the probability of conflicting distracters increases, while the distracter cost exhibits the opposite pattern, thus being larger in the context where incongruent distracters occur less frequently.

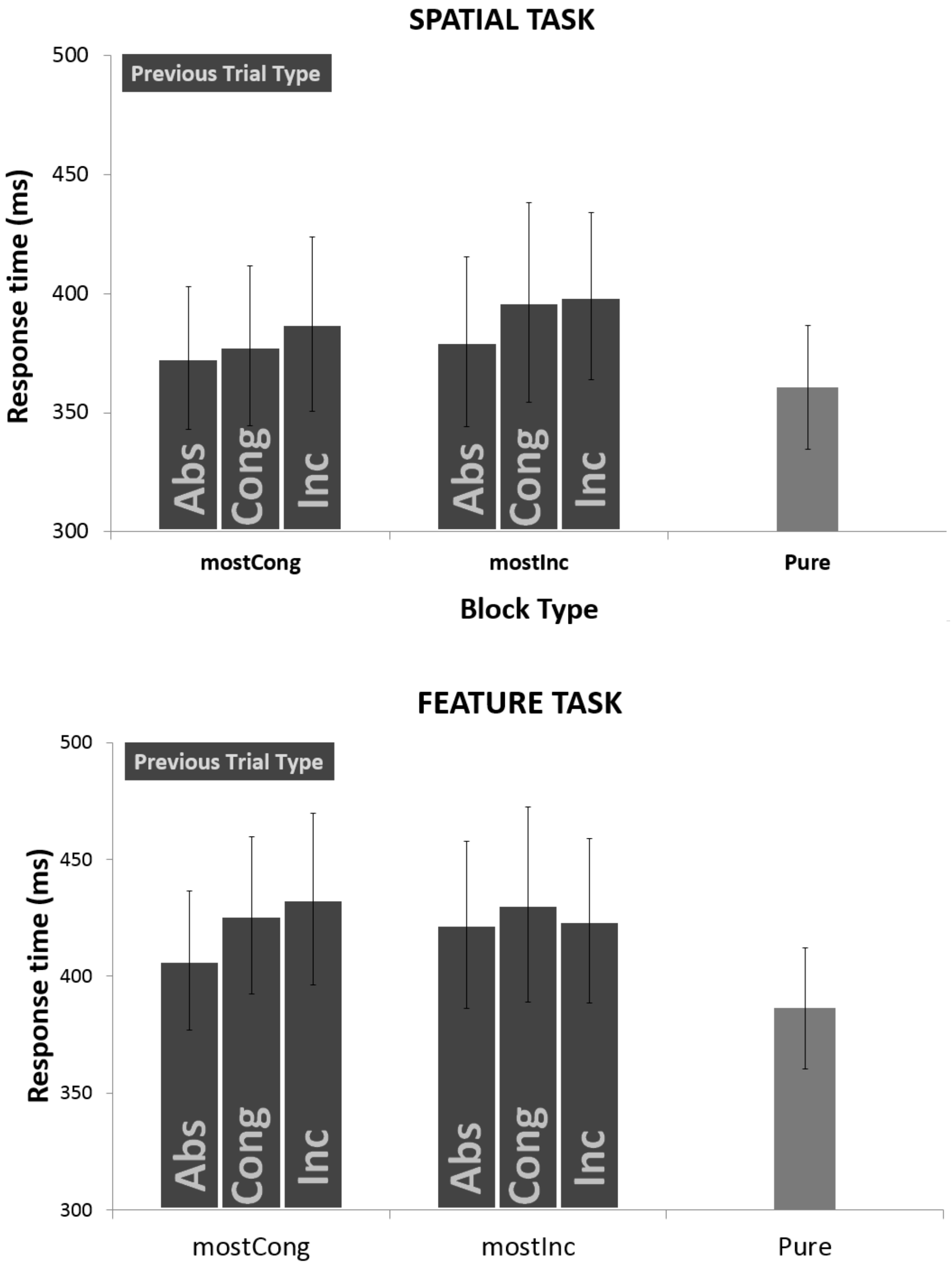
Then, analogous comparisons were performed within the feature task, because previous analyses have demonstrated the occurrence of a significant filtering cost and a significant distracter cost in the mostCong and mostInc context of the feature task too. The filtering cost did not significantly differ between the mostInc context (mean: 39 ms) and the mostCong context (mean: 42 ms) [t(17)=0.46, p=.64]. Similarly, the distracters cost was not statistically different in the mostCong context (mean: 49 ms) and in the mostInc context (mean: 35 ms) [t(1,17)=1.73, p=.10]. For these results, see Figure 3.3, Panel A. Differently from what observed for the spatial task, in the feature task the filtering cost and the distracter cost did not change depending on the probability of occurrence of conflicting distracters.

Correlation analyses in Experiments 1 and 6 of the previous study (Chapter 2) showed that the filtering cost is inversely correlated, on a per-subject basis, to the distracter cost. With the aim of exploring whether a similar relationship at the individual subject level is present in these data, a linear regression analysis was done. This analysis yielded to statistically significant results in the mostInc context of the spatial task and in the mostInc context of the feature task. Quite surprisingly, however, the sign of correlation coefficients was not the same for either case. In the spatial task, a significant *negative* correlation ($r=-.51$, adjusted-$R^2=.22$) was found [$F(1,17)=5.68$, $p<.05$] (Figure 3.2, Panel B), while in the feature task a significant *positive* correlation ($r=-.51$, adjusted-$R^2=.22$) was found [$F(1,17)=5.55$, $p<.05$] (Figure 3.3, Panel B).

Finally, I aimed at investigating to what extent (if at all) cross-trial contingencies modulate the magnitude of the filtering cost. In fact, previous data (Experiments 1 and 2, Chapter 2) evidenced that the filtering cost is mainly strategic in nature, although it shows some reactive modulations on a trial-by-trial basis.

The rmANOVA on sequential effects showed a significant main effect of Type of Preceding Trial [$F(2,34)=9$, $p<.001$]. Subsequent corrected comparisons revealed that Abs-Mix trials, which followed another Abs-Mix trial, were faster (mean RT: 395 ms) as compared to Abs-Mix trials following either a Cong-Mix (mean RT: 408 ms) or an Inc-Mix trial (mean RT: 411 ms) [$t(17)=2.85$, $p<.05$, and $t(17)=3.86$, $p<.01$, respectively] (Figure 3.4). I also investigated whether a significant strategic cost is observed when the reactive aspect of cross-trial dynamics is controlled.

Figure 3.4. Results of the sequential analysis. Absent-distracter trials in Mix blocks that were presented immediately after another absent-distracter trial were faster than those presented after a present-distracter trial. However, these absent-distracter trials were still significantly slower than absent-distracter trials in the Pure block, indicating that the filtering mechanism is modulated by cross-trial contingencies, but also that it is truly strategic in its nature.



To this aim, I compared Abs-Mix trials, which followed another Abs-Mix trial, with Abs-Pure trials, in both mostCong and mostInc contexts, separately for each tasks. For all comparisons, absent-distracter trials in the Pure block still showed faster RTs than Abs-Mix subsequent to another Abs-Mix trial in Mix blocks (all FWER corrected p-values <.05) (Figure 3.4). Even though the magnitude of the filtering cost reactively increased when the immediately preceding trial is present-distracter, this latter set of results strongly confirms that the filtering cost is truly strategic in its nature.

3.4 Conclusion

This study aimed at investigating whether conflict probability modulates the distracter filtering cost. The main result shows that in a spatial-based task, such as the arrow flanker task used here, the cost for filtering out potential distracters is strongly modulated depending on conflict probability. This adds to evidence from Chapter 2 in that not just the probability of distraction, but also more specifically the probability of conflict dramatically influences the magnitude of the distraction filtering cost. An accessory finding is constituted by the replication of the proportion congruent effect (Lowe & Mitterer, 1982; Jacoby et al., 2003; see Bugg & Crump, 2012, for a review). In fact, the cost of incongruent distracters was larger in the block where conflict is more probable and smaller in the block where conflict occurs less frequently.

In the feature task, results are substantially different. First, I still observe a significant slowing-down in absent-distracter trials in Mix blocks with congruent and incongruent distracters, as compared to the Pure block. However, the magnitude of this cost does not change depending on the probability of conflict. This is also the case for the distracter cost. A significant slowing down when conflicting distracters are presented actually occurs, but its magnitude is about the same in the two types of Mix blocks (mostCong and mostInc). This result differentiate the feature task from the spatial task and suggest that partly different mechanisms might be at play in determining the behavioral cost observed in the feature task.

Chapter 4

Sustained And Transient Brain Mechanisms For Dealing With Conflicting Distracters In Pure And Mixed Contexts

4.1 Aim of the study

This study aimed at investigating the brain processes involved in perceptual and attentional processes in contexts with different probabilities of conflicting distraction. As observed in Chapters 2 and 3, in potentially distracting contexts a strategic mechanism is activated for dealing with forthcoming distraction. In a spatial attention task, the activation of this distraction filtering mechanism becomes stronger as the probability of conflicting distraction gets higher (Chapter 3).

For studying brain structures correlated to the strategic distraction filtering, I conducted a functional magnetic resonance imaging (fMRI) study by replicating the experimental paradigm of the spatial task described in Chapter 3. I was interested in studying strategic brain activations, and more precisely context-related activations that are sustained for entire task blocks under different probabilities of distraction. I was also interested in studying how transient brain responses to the very same event type (for example, an absent-distracter trial, or an incongruent-distracter trial) change depending on the task context to which that specific trial belongs. From a methodological perspective, the present study used a mixed block/event-related experimental design (Visscher et al., 2003; Petersen & Dubis, 2012).

My primary interest was that of identifying brain regions that show greater activation in Mix blocks as compared to Pure blocks. I predicted to identify a series of regions of both the cognitive control and the attentional control network, in frontal and parietal lobes of the brain, which show enhanced sustained activity during potentially distracting contexts. Moreover, I aimed at establishing a relationship between this predicted strategic block-wise activity and the stimulus-evoked activity in absent-distracter trials during Mix blocks. A particular interest in the analysis of stimulus-evoked responses regarded the study of brain areas where stimulus processing changes depending on the context. For example, it is conceivable that in Mix blocks the attentional control network operates a bias on target's and/or distracters' sensory processing, for guiding appropriate behavior by modulating stimuli representations in visual cortex. This might assume the characteristics of an enhanced target representation, of a reduced distracter representation, or both.

In addition, a modulation by attentional and cognitive control systems for guiding correct responses and preventing the negative impact of conflicting stimuli might also be exerted at a relatively late processing stage, namely, at the response execution level. In this case, a reduced premotor representation of the response might be expected in the Mix blocks, particularly when conflict occur frequently, as compared to the rare-conflicting Mix block and to the Pure block. This hypothesized reduction in premotor activation, if confirmed, would reflect a more cautious response setting in blocks where conflicting distracters are frequent, for preventing the activation of distracter-driven response tendencies. Absent-distracter trials mixed in blocks with different probability of distraction are once again the ideal candidate for observing these predicted context-dependent modulations of brain responses.

As a corollary, I would also predict to observe context-dependent modulations in activity evoked by conflicting distracters. Coherently with the conflict monitoring model (Botvinick et al., 2001; Kerns et al., 2004) and with behavioral and neuroimaging studies of the proportion congruent effect (i.e., Grandjean, D'Ostilio, Phillips, Balteau, Degueldre et al., 2012), a stronger activation in dorsal anterior cingulate cortex (ACC) is expected in response to incongruent-distracter trials in a block with low conflict probability, as compared to a block with high conflict probability. This would reflect a less reactive activation to conflict in presence of a stronger proactive cognitive control during the highly conflicting block, as predicted by the dual framework theory of cognitive control (Braver, 2012).

4.2 Materials and Method

4.2.1 Participants

Twenty participants took part in this study (mean age ± SD: 26.2 ± 4.3, range 18-35, 10 females, all right-handed). All participants had normal or corrected-to-normal vision, normal hearing, and did not report any history psychiatric or neurological disorder. Participants gave their written informed consent to participate in the study in accordance with the Duke Institutional Review Board and they were compensated $20/hour for their participation.

4.2.2 Experimental paradigm

Visual stimuli were presented to participants in the bore of the scanner using a Hitachi CP X-505 video projector located at the back of the magnet room. This is a standard video projector that has a long lens that can focus its output onto a translucent plastic screen near the center of the magnet bore. The subjects viewed the screen when they were lying in the scanner using a 45 degree mirror (14.2 x 9 cm) mounted on the head coil.

The translucent plastic screen was 38 cm wide and the lens was adjusted so that the full projected image filled the screen. The full screen covered approximately 30 by 15 degrees of the visual field.

The experimental paradigm was programmed ad-hoc using Matlab R2013a (Mathworks Inc.) with Psychtoolbox 3.0 (Kleiner et al., 2007). Participants' responses were collected through button presses on button-box device (Current Design, Inc.). All participants used the index finger and the middle finger of their right hand for responding. The association of each response with a specific finger was counterbalanced across participants. Participants' alertness and gaze direction were visually checked by the experimenter for the entire duration of the experiment through an MR-compatible eyetracking miniature camera mounted inside the scanner (Resonance Technology Inc.) and connected to a control computer with the Viewpoint eyetracker software (Arrington Research, Inc.).

Participants received written task instructions and performed 50 practice trials outside the scanner and an additional 100 practice trials inside the scanner during the initial calibration phase.

The functional scans were divided into five runs. The first four runs ("task runs") had a duration of about 11 minutes and included 9 blocks (three of each type, see below) of the experimental task each. The fifth and last functional run ("retinotopic localizer") had a duration of about 12 minutes and was used to define regions of the visual cortex where visual stimuli were represented.

Task runs

The experiment included three different block types: the Pure block, in which all trials were absent-distracter trials (Abs-Pure); the Mixed Mostly Congruent block (mostCong), in which 60% of trials were congruent-distracter trials (Cong-mostCong), 20% of trials were incongruent-distracter trials (Inc-mostCong), and 20% of trials were absent-distracter trials (Abs-mostCong); the Mixed Mostly Incongruent block (mostInc), in which 60% of trials were incongruent-distracter trials (Inc-mostInc), 20% of trials were congruent-distracter trials (Cong-mostInc), and 20% of trials were absent-distracter trials (Abs-mostInc).

Akin to studies described in Chapters 2 and 3, I used the PM-PoDist paradigm. The Pure block served as a reference context, while the mostCong and the mostInc blocks (i.e., Mix blocks) constituted contexts with different levels of conflict probability. A low conflict probability was present in the Mixed Mostly Congruent block (i.e. about 23%), while a high conflict probability was present in the Mixed Mostly Incongruent block (i.e. about 54%). Each Mix block type contained the same amount of absent-distracter trials (i.e., about 23%).

Stimuli consisted in a horizontal array of five flanking arrows that pointed either down or upwards. The arrows were presented for 200 ms at each trial in a central fixation position and were colored in black on a medium-gray background. Each arrow subtended a visual angle of 0.75 (vertically) by 0.5 (horizontally) degrees and the center-to-center distance between adjacent arrows was 0.75 degrees of visual angle.

The central arrow was the target while the four lateral arrows (two on each side of the target) were the distracters. In congruent trials, target and distracters pointed in the same direction (either up or down), while in incongruent trials target and distracters pointed in opposite directions (either target up and distracters down or vice-versa). Participants were instructed to respond as quickly and as accurate as possible by pressing the button corresponding to the direction to which the target arrow was pointing while ignoring distracters.

Stimulus sequence was pre-determined by using a genetic algorithm (Optimize GA; Wager & Nichols, 2003) for creating a pseudo-random sequence with a variable inter-trial jittering. This method allowed optimizing design efficiency and hemodynamic response function estimation while controlling counterbalancing and frequency of different trial types. Because of the sequence and jittering optimization performed by the genetic algorithm, subsequent trials were presented at SOA ranging from 1.5 s to 9 s. The duration of each block was fixed for the entire experiment, with Mix blocks having a duration of 70.5 s and Pure blocks having a duration of 28.5 s. Blocks were separated by pauses with durations ranging from 12 s to 16.5 s. During each pause, the fixation cross changed to a white color to inform participants of the occurrence of a pause. Prior to the beginning of the subsequent block, participants were visually cued about the type of block that was about to start (either Pure, mostCong, or mostInc) and the fixation cross became black as an alerting signal.

Retinotopic localizer run

A functional retinotopic localizer run was conducted in order to identify regions of the visual cortex where the position of target stimuli and the positions of distracting stimuli are represented. Blocks with a duration of 15 s each were alternated with inter-block pauses of 15 s. In the target block, an arrow flashed at a frequency of 8 Hz in the spatial position of the target, while in the distracter block four arrows flashed at a frequency of 8 Hz in the position of the distracters. The direction of the arrows (up/down) changed every 1000 ms. Participants were engaged in a simple task for keeping them alert for the entire duration of the retinotopic localizer run. The fixation point briefly changed its color to a light grey every 12-18 s and participants were required to press a button with their right index finger every time this color change occurred. The global duration of the experiment was about 1 hour and 30 minutes.

4.2.3 fMRI acquisition

MR images were recorder on a 3T GE MR750 scanner. Functional images were acquired with the spiral sensitivity encoding (SENSE) technique and using the following parameters: horizontal FOV=19.2 cm, vertical FOV 13.6 cm, TE=28ms, TR=1500ms, flip angle 75 degrees. The resulting voxel size was 3x3x4 mm with no slice gap. Anatomical series were acquired both at the same resolution and with the same parameters of the functional images (co-planar) and at high resolution with a voxel size of 1x1x1 mm (horizontal FOV 25.6 cm, vertical FOV 19.2 cm). Intensity correction was applied with Clairview.

4.2.4 Behavioral analysis

The analysis aimed at assessing the cost of the distraction filtering mechanism and the differences in the distracters-related cost in contexts characterized by different levels of conflict probability (low conflict probability, high conflict probability). The filtering cost was computed as the normalized difference in response times between Abs-Mix trials and Abs-Pure trials, respectively. The behavioral cost associated with the presence of incongruent distracters (hence, the *incongruency cost*) was calculated as the normalized difference in response times between incongruent (Inc) and congruent (Cong) trials, separately for the Mixed Mostly Congruent Distracter block (mostCong) and the Mixed Mostly Incongruent Distracter block (mostInc).

Similarly to studies in Chapters 2 and 3, I used response times (RTs) as the main dependent variable of interest in the current study. I excluded from behavioral analyses all responses faster than 200 ms and slower than a cutoff value calculated on a per-subject basis with the method suggested by Ratcliff (1993) (i.e., the superior cutoff is equal to the third quartile of the reaction time distribution plus 1.5 times the interquartile range). Limited to the regression analysis and in accordance with the previous studies (Chapters 2 and 3) for obtaining a more sensitive index of performance I used the inverse efficiency score (Townsend & Ashby, 1983) as the dependent variable. In the regression analysis the eventual presence of outliers was evaluated with the Bonferroni method (Fox, 1997) as implemented in R software package (R-project, CRAN).

Statistical analyses on behavioral data were carried out by means of planned comparisons with paired samples t-tests and general linear regression. The family-wise error rate (FWER) was controlled at significance level α =.05 by applying the Holm-Bonferroni method (Holm, 1979). I point out in the Results any p-value which did not hold significance level after FWER correction.

4.2.5 fMRI analysis

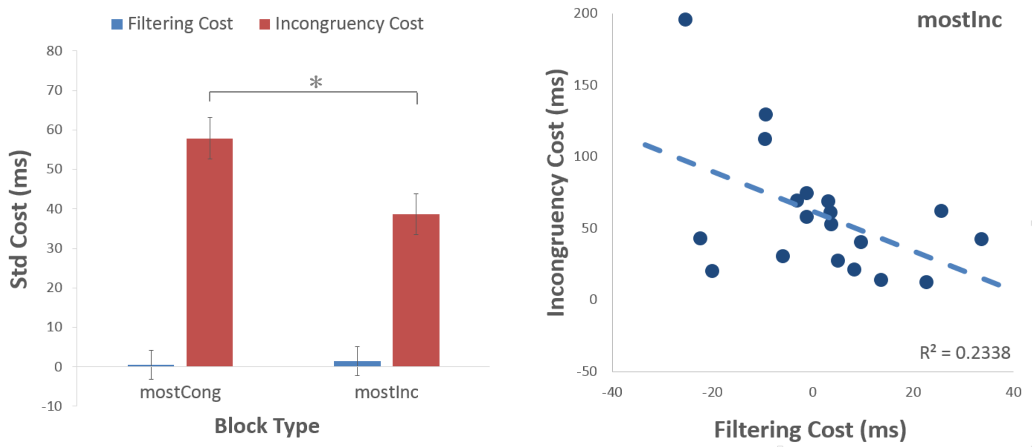
Brain analyses were conducted with FSL 5.0.1 software package (FMRIB's Software Library; Jenkinson, Beckmann, Behrens, Woolrich, & Smith, 2012; Woolrich, Jbabdi, Patenaude, Chappel, Makni et al., 2009; Smith, Jenkinson, Woolrich, Beckmann, Behrens et al., 2004). Initially, the brain-scalp segmentation was carried out on functional and anatomical images with BET (Brain Extraction Tool; Smith, 2002). The first six volumes of each functional time-series were discarded to allow for magnetic saturation effects. Time-series were high-pass filtered with a cutoff of 215 s. Functional images were then corrected for interleaved slice acquisition and pre-whitened using FILM (FMRIB's Improved Linear Modelling). A spatial smoothing was conducted by applying a three-dimensional Gaussian kernel (FWHM: 8 mm for task runs and 5 mm for the retinotopic localizer run). Motion correction was applied with FLIRT tool (Jenkinson, Bannister, Brady, & Smith, 2002) and motion estimates were subsequently included as nuisance regressors in the statistical model.

The statistical whole-brain analysis was carried out with the general linear model (GLM) implemented in FEAT (FMRIB's Expert Analysis Tool) by using custom regressors. A mixed block/event-related design was used (Visscher et al., 2003; Petersen & Dubis, 2012). Sustained activity was modeled by entering block regressors (Pure, mostCong, mostInc) with the shape of a canonical gamma hemodynamic response function (HRF) and with the duration of a whole task block each. Transient (event-related activity) was modeled by using a finite impulse-response (FIR) model (Dale, 1999; Ollinger, Shulman, & Corbetta, 2001; Visscher et al., 2003). The temporal derivative was included in the model for all block regressors. In this model, no predetermined shape for the HRF is assumed. Rather, a pre-established number of time-points in the peristimulus interval are entered in the general linear model and for each time-point the parameter estimates are calculated. Each of the nine different event types (Abs-Pure, Abs-mostCong, Cong-mostCong, Inc-mostCong, Abs-mostInc, Cong-mostInc, Inc-mostInc) was modeled with 10 time-points starting 3 s before the stimulus onset and terminating 10.5 s after the stimulus onset. A series of contrasts on parameter estimates of both block and event-related regressors was set up in the model and fed to higher-level analyses. The reported event-related contrasts are calculated on the average BOLD signal of three peri-peak time-points of the FIR model corresponding to the temporal window between 3 s and 6 s after stimulus onset. Functional images were first co-registered to the high-resolution anatomical image of each subject and then standardized to the Montreal Neurological Institute (MNI) 2mm standard brain template by using FLIRT registration tool (normal linear search with DOF=6 for co-registration and with DOF=12 for standardization). Limited to the retinotopic localizer run, a mask of the occipital lobe was created on the MNI 2mm standard brain template with WFU Pickatlas (Maldjian, Laurienti, Kraft, & Burdette, 2003). This mask was used in the pre-thresholding stage for eliminating contributions from all voxel outside the occipital lobes. The whole-brain voxelwise analysis and the analysis of the retinotopic localizer run were performed at the group level with FLAME (FMRIB's Local Analysis of Mixed Effects) mixed-effects model in FEAT. Statistical images were corrected for family-wise error rate (FWER) by using cluster thresholding with a Z-value of 2.33 and a cluster threshold p = 0.05.

4.3 Behavioral results

I first compared the RTs in Abs-Pure trials with those in Abs-mostCong and in Abs-mostInc contexts for evaluating the presence of a behavioral filtering cost, but none of these comparisons yielded any significant result [t(19)=0.17, p=.86, and t(19)=0.34, p=.73, respectively]. One possible reason for the lack of a behavioral filtering cost is the slower pace of advancement in the stimulus sequence as compared to previous studies.

Figure 4.1. Behavioral results. A significant incongruency cost on response times (Incongruent trials minus Congruent trials) was observed in both types of Mix blocks (red columns, left panel). The proportion congruent effect was also found (i.e., larger incongruency effect in the mostCong block; see Bugg & Crump, 2012, for a review). No significant filtering cost was found (blue columns, left panel). However, a significant across-participants correlation was identified between the filtering cost and the incongruency cost (right panel).



This slower pace is required by a methodological optimization for the fMRI experimental design. A control experiment was conducted for further investigating this aspect[4].

I then examined the presence of a distracter cost in the two mixed contexts separately. In the mostCong context, a significant distracter cost emerged [t(19)=12.03, p<.001], with responses to Incongruent trials being slower than responses to Congruent trials (median RTs: 626 ms and 701 ms, respectively). Also in the mostInc context a significant

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[4] The control experiment was conducted behaviorally and included two different stimulus presentation sequences. The first sequence exactly replicated the timing of the in-scanner sequence, i.e. inter-trial intervals (ITIs) were jittered up to 9 s. I expect to replicate the null filtering cost with this sequence. A second sequence differed only because all ITIs had a maximum duration of 1.5 s. This second sequence had a much faster pace, similarly to all my previous studies where the filtering cost has been observed. Thus, I expect to find a significant filtering cost. Results confirmed both predictions. With the slow-paced sequence, no significant filtering cost was observed [mostCong: t(16)=0.76, p=.46; mostInc: t(16)=0.97, p=.35], while with the fast-paced sequence a significant filtering cost emerged [mostCong: t(13)=3.17, p<.01; mostInc: t(13)=6.84, p<.01]. These results are commented in the Discussion.

cost of distracter was measured [t(19)=8.65, p<.001], with Incongruent trials eliciting slower responses than Congruent trial (median RTs: 632 ms and 680 ms, respectively). I then compared the distracter cost in the mostCong context with the distracter cost in the mostInc context. The distracter cost was significantly larger in the mostCong context than in the mostInc context [t(19)=6.24, p<.001]. This result replicates results described in Chapter 3 and previous findings described in the existing literature (Lowe & Mitterer, 1982; Jacoby et al., 2003; Grandjean et al., 2012; Bugg & Crump, 2012).

Although a significant filtering cost on RTs was not found in the present study, it is still possible that such null result derives from averaging a pool of positive (RT costs) and negative (RTs advantages) values across subjects.

Like I did in previous experiments, I then calculated the difference in absent-distracter trials between Mix and Pure blocks and used these filtering "cost" values in a regression analysis.

Analogously to what I found in previous studies (see Chapters 2 and 3), I aimed at testing whether the filtering cost is correlated, across subjects, to the distracter cost.

In the mostCong context the regression analysis did not produce any significant result. In the mostInc context, instead, a significant inverse correlation (r=-.48, adjusted-R^2=.19) between the filtering cost and the distracter cost was found [F(1,18)=5.18, p<.05]. Both the absence of a correlation in the mostCong context and the presence of an inverse correlation in the mostInc context replicate previous findings with similar (see Experiment 6, Chapter 2 and Spatial Task, Chapter 3) and different paradigms (see Experiment 1, Chapter 2).

4.4 fMRI results

4.4.1 Sustained activity

Mixed blocks > Pure block show a widespread increase of sustained activity

Sustained brain activity in Mix blocks was compared with sustained brain activity in the Pure block. This comparison allowed identifying brain regions that show a selective increase in sustained activation in contexts with potential conflicting distraction, as compared to a completely distracter-free context. With this analysis several foci of activation were identified in the frontal, parietal, temporal, and occipital lobe (see Table 4.1 for the complete list).

Largest Z-scores were measured in frontal and parietal lobe. In the frontal lobe, significant activation was found in left dorsolateral prefrontal cortex (DLPFC) in Brodmann areas 9 and 46 (see Figure 4.2, Panel A, coronal view and Panel B, axial view). Another focus of activity was identified in the left inferior frontal gyrus (IFG) at level of the pars opercularis (see Figure 4.2, Panel A, sagittal view).

Additional frontal activations were found bilaterally in the middle frontal gyrus (MFG) in the left hemisphere close to the frontal pole (Figure 4.2, Panel A, axial view) and in the right hemisphere in a dorsomedial location (Figure 4.2, Panel B, axial view). Regions of the right medial frontal gyrus corresponding to Brodmann area 8, the putative location of human frontal eye fields (FEFs; Paus, 1996; Amiez & Petrides, 2009), were also activated.

In the parietal lobe, activations included a peak in left superior parietal lobule (SPL) which extended to the adjacent intraparietal sulcus (IPS) (see Figure 1, Panel B, sagittal view).

Figure 4.2. Sustained activity in Mixed blocks minus Pure block. In contexts with probability of conflicting distraction, sustained activations were observed in a widespread set of brain regions. Frontal regions included the left inferior frontal gyrus (IFG), the left dorsolateral prefrontal cortex (DLPFC), and middle frontal gyrus bilaterally (MFG). Parietal activations included the superior parietal lobule (SLP), the intraparietal sulcus (IPS) and the precuneus. Additional foci of activity were identified in the fusiform gyrus (FG), in the inferior temporal gyrus (ITG), and in the occipital pole.

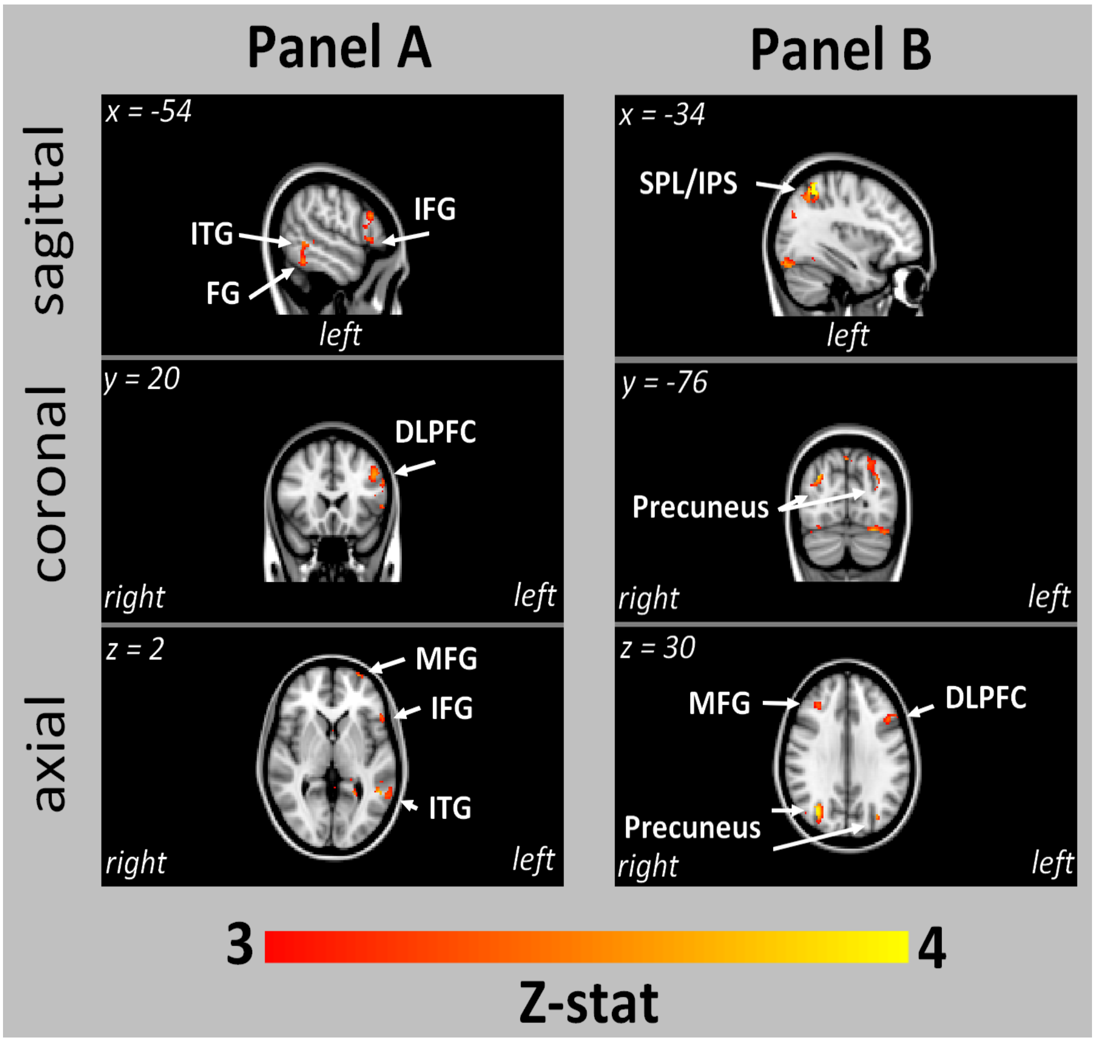


Table 4.1. Brain regions that showed peaks of sustained activity in Mix blocks relatively to the Pure block. Cluster size (CL-size) is expressed in voxels and the reported *p*s are FWER-corrected with the cluster method (CL-p). Coordinates are in MNI space and Brodmann areas (BA) labels refer to the nearest grey matter (within 5mm).

CL-size	*CL-p*	*Z-value*	*X*	*Y*	*Z*	*Side*	*Region*	*Area*
15586	$<10^{-10}$	4.4	-34	-54	54	L	Superior Parietal Lobule	BA 7
15586	$<10^{-10}$	3.99	-22	-72	50	L	Precuneus	BA 7
15586	$<10^{-10}$	3.94	-4	-72	46	L	Precuneus	BA 7
15586	$<10^{-10}$	3.94	-60	-54	-8	L	Middle Temporal Gyrus	BA 37
15586	$<10^{-10}$	3.94	-42	-56	-14	L	Fusiform Gyrus	BA 37
3041	<0.001	3.71	-52	24	26	L	Inferior Frontal Gyrus	BA 9
3041	<0.001	3.65	-46	20	34	L	Middle Frontal Gyrus	BA 9
3041	<0.001	3.65	-44	28	18	L	Middle Frontal Gyrus	BA 46
3041	<0.001	3.57	-28	64	2	L	Middle Frontal Gyrus	BA 10
3041	<0.001	3.44	-54	20	4	L	Inferior Frontal Gyrus	BA 45
3041	<0.001	3.43	-52	24	2	L	Inferior Frontal Gyrus	BA 45
1426	<0.05	3.56	54	40	18	R	Middle Frontal Gyrus	BA 46
1426	<0.05	3.48	32	34	32	R	Middle Frontal Gyrus	BA 9
1426	<0.05	3.29	24	32	38	R	Middle Frontal Gyrus	BA 8
1426	<0.05	3.19	54	40	22	R	Middle Frontal Gyrus	BA 46
1426	<0.05	3.18	8	38	40	R	Medial Frontal Gyrus	BA 8
1426	<0.05	3.14	14	34	44	R	Medial Frontal Gyrus	BA 8

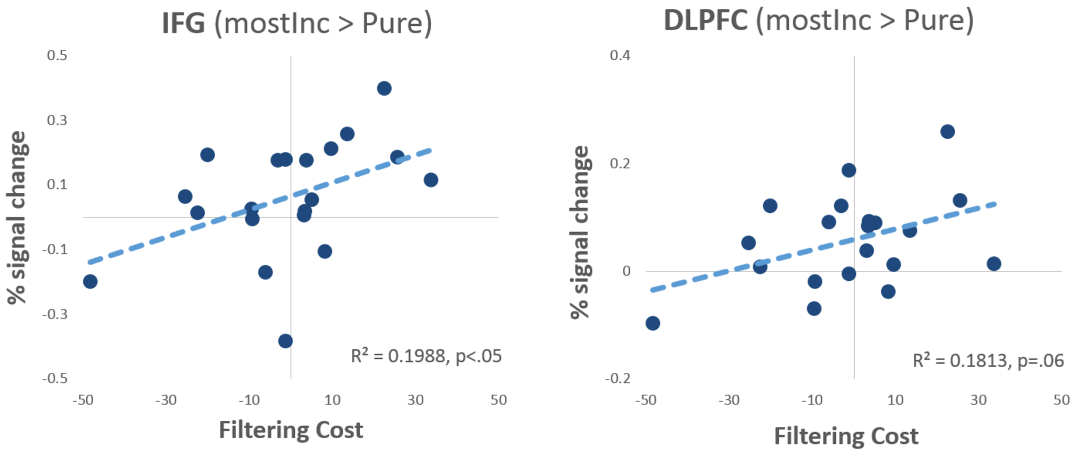
Another region of activity in the parietal lobe was found bilaterally in the precuneus (BA 7) (see Figure 4.2, Panel B, coronal and axial view). Finally, an additional focus of activity was isolated in the left temporal lobe with peaks in the middle temporal gyrus (MTG), in the inferior temporal gyrus (ITG) and in the fusiform gyrus (FG) (see Figure 4.2, Panel A, sagittal view).

No significant differences between Mix block types

Direct contrasts between the two types of Mix blocks did not yield any significant result. For further exploring differences between Mix block types, four regions of interest (ROIs) were created in correspondence of the peaks identified in the previous analysis (Mix blocks > Pure block). Two spherical ROIs with radius of 6 mm were created with centers in left IFG, one in a relatively dorsal location compared to the other more ventral location (ventral IFG: x =-54, y=20, z=4, and dorsal IFG: x =-52, y=24, z=26, respectively). Two spherical ROIs with a radius of 6 mm were created with centers in left DLPFC, one in a relatively anterior location compared to the other more posterior location (anterior DLPFC: x =-44, y=28, z=18, and posterior DLPFC x =-46, y=20, z=34, respectively).

These regions showed more sustained activity in Mix blocks than in the Pure block. With the aim of assessing potential differences between the two different types of Mix blocks, I extracted average COPE values (Contrasts Of Parameter Estimates) within each ROI from the contrast mostCong > mostInc. In this analysis, positive values would reflect greater activation the mostCong block than in the mostInc, while negative values would reflect greater activation in the mostInc block than in the mostCong. In this analysis, however, I did not find any significant result.

Figure 4.3. Across-subjects correlations between BOLD signal in two frontal ROIs (left IFG and left DLPFC) and the behavioral filtering cost. The average BOLD signal change in regions of the cognitive control network showed a significant positive correlation with the observed behavioral filtering cost. Larger increases of brain activity in IFG (and, with marginal statistical significance, in DLPFC) were associated with a larger slowing-down in Abs-Mix trials. These results are compatible with the association between brain activity in prefrontal areas and the recruitment of a sustained distraction-filtering mechanism in Mix blocks.



Sustained frontal activity correlates with behavioral filtering cost

One of the aims of the current study is testing the hypothesis of a parallel between a behavioral cost for filtering out potential distracters and the implementation of a strategic cognitive set in the frontal areas of the frontoparietal attentional network.

At behavioral level, I did not find a significant filtering cost, however I evidenced an inverse correlation across subjects between the magnitude of the filtering cost and the magnitude of the interference exerted by incongruent distracters.

This result supports the idea that different participants adopted (or did *not* adopt) strategies for dealing with potential distracters when there is a relatively high probability of incurring in conflicting distracters.

I then aimed at investigating whether these individual differences in the implementation of the filtering mechanism were reflected by different level of brain activity in areas of the frontoparietal attentional network that I identified as more active in the mixed contexts at the group level.

To this aim, I conducted four separate correlation analyses within each of the ROIs described in the previous paragraph (ventral IFG, dorsal IFG, anterior DLPFC, posterior DLPFC), across subjects, between the filtering cost and the average COPE values. These analyses were conducted in mostly incongruent blocks, which are the blocks with the greatest conflict level and thus with the greatest predicted strategic filtering level.

I found a significant positive correlation ($r=.45$, adjusted-$R^2=.15$) between activity in the dIFG ROI and the behavioral filtering cost [$F(1,18)=4.47$, $p<.05$] and a trend towards a positive correlation ($r=.43$, adjusted-$R^2=.14$) also in the aDLPFC ROI [$F(1,18)=3.99$, $p=.06$] (See Figure 4.3).

4.4.2 Stimulus-evoked activity

Context-related effects on absent-distracter trials

The first aim of the analysis of transient activity was the identification of brain areas that are activated in the stimulus processing phase of an absent-distracter trial in contexts with potential distraction as compared to a context with no potential distraction. Thus, I contrasted transient activity evoked by an Abs-Mix trial with transient activity evoked by an Abs-Pure trial.

Figure 4.4. Transient activity evoked by absent-distracter stimuli in Mix blocks minus absent-distracter stimuli in the Pure block. Abs-Mix trials evoked larger parietal and occipital activations in Mix blocks than in the Pure block. Peaks of activity were observed bilaterally in the superior parietal lobule (SPL), in the precuneus and in the middle occipital gyrus. These results might indicate a strengthened attentional orientation to targets in Mix blocks.

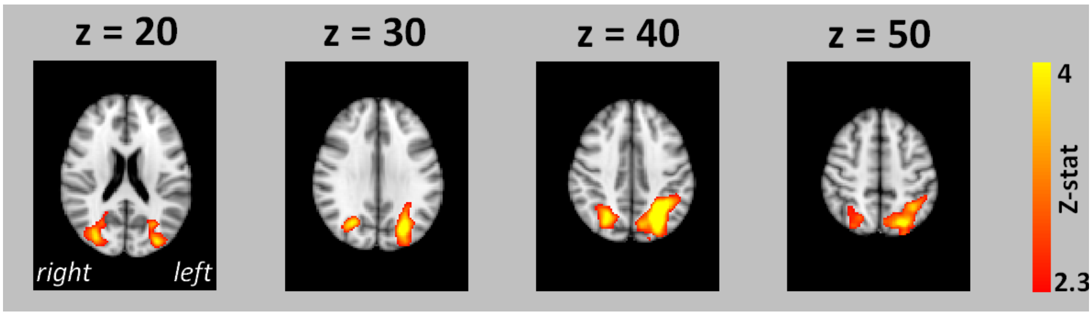


Table 4.2 The Table reports global and local peaks of activity. Cluster size (CL-size) is expressed in voxels and the reported *p*s are FWER-corrected with the cluster method (CL-p). Coordinates are in MNI space and Brodmann areas (BA) labels refer to the nearest grey matter (within 5mm).

CL-size	*CL-p*	*Z-value*	*X*	*Y*	*Z*	*Side*	*Region*	*Area*
3995	<0.01	4.38	-32	-84	22	L	Middle Occipital Gyrus	BA 19
2272	<0.05	3.9	32	-80	20	R	Middle Occipital Gyrus	BA 19
2272	<0.05	3.48	42	-72	14	R	Middle Occipital Gyrus	BA 19
2272	<0.05	3.2	32	-84	8	R	Middle Occipital Gyrus	BA 18
2272	<0.05	3.07	38	-78	4	R	Middle Occipital Gyrus	BA 19
3995	<0.01	4.93	-26	-72	30	L	Precuneus	BA 31
3995	<0.01	4.8	-32	-54	40	L	Angular Gyrus	BA 39
3995	<0.01	4.96	-26	-70	38	L	Precuneus	BA 19
3995	<0.01	3.97	-10	-72	44	L	Precuneus	BA 7
2272	<0.05	4.25	26	-62	38	R	Precuneus	BA 7
2272	<0.05	2.62	30	-68	58	R	Precuneus	BA 7
3995	<0.01	4.26	-22	-72	52	L	Superior Parietal Lobule	BA 7

Bilateral brain activity was identified in extrastriate visual cortices in the middle occipital gyrus (BA 18, BA 19). Other activations were observed in parietal lobe, in the left and right precuneus (BA 19, BA 7), in the left superior parietal lobe (BA 7), and in the left angular gyrus (BA 39). A summary of activations for this contrast is reported in Table 4.2 and showed in Figure 4.4.

Conflict-related effects in present-distracter trials

For identifying conflict-related effects, I compared activity evoked in congruent-distracter trials with activity evoked in incongruent-distracter trials, separately for the two types of Mix blocks (mostCong and mostInc). Differences in brain activations between congruent- and incongruent-distracter conditions are likely to reflect conflict processing.

In the mostCong block, incongruent distracters elicited significant bilateral activations in the frontal cortex, particularly in the dorsal part of Anterior Cingulate Cortex (ACC), in DLPFC, in the medial frontal cortex and in the precentral gyrus. Bilateral parietal activations were observed in the superior parietal lobule (SPL) and in the intra-parietal sulcus (IPS) extending caudally and ventrally to the precuneus. Other areas of activation were found in the right fusiform gyrus and bilaterally in the occipital lobe (see Table 4.3 and Figure 4.5, left panel).

In the mostInc block, brain activity associated with incongruent distracters was observed bilaterally in the precentral gyrus, in the inferior parietal lobule (IPL) and in the precuneus. Additionally, I observed activity in the right posterior cingulate cortex (PCC) and bilaterally in the occipital lobe in the middle and inferior occipital gyrus (see Table 4.4 and Figure 4.5, right panel).

Table 4.3. Peaks of transient activity evoked by incongruent-distracter minus congruent-distracter stimuli in the mixed mostly Congruent block. Cluster size (CL-size) is expressed in voxels and the reported *p*s are FWER-corrected with the cluster method (CL-p). Coordinates are in MNI space and Brodmann areas (BA) labels refer to the nearest grey matter (within 5mm).

CL-size	*CL-p*	*Z-value*	*X*	*Y*	*Z*	*Side*	*Region*	*Area*
13075	$<10^{-10}$	6.72	40	36	24	R	Middle Frontal Gyrus	BA 9
13075	$<10^{-10}$	6.54	28	-4	48	R	Middle Frontal Gyrus	BA 6
13075	$<10^{-10}$	6.19	36	46	18	R	Middle Frontal Gyrus	BA 10
13075	$<10^{-10}$	6.11	50	6	36	R	Precentral Gyrus	BA 6
13075	$<10^{-10}$	6.11	46	4	38	R	Precentral Gyrus	BA 6
13075	$<10^{-10}$	5.87	6	12	46	R	Medial Frontal Gyrus	BA 32
27890	$<10^{-17}$	5.59	42	-68	-12	R	Fusiform Gyrus	BA 19
27890	$<10^{-17}$	7.75	42	-44	44	R	Inferior Parietal Lobule	BA 40
27890	$<10^{-17}$	7.42	28	-62	46	R	Superior Parietal Lobule	BA 7
27890	$<10^{-17}$	6.74	28	-66	36	R	Precuneus	BA 7
27890	$<10^{-17}$	6.57	52	-56	-10	R	Fusiform Gyrus	BA 37
1591	<0.05	4.41	-42	24	34	L	Precentral Gyrus	BA 9
1591	<0.05	4.05	-44	52	6	L	Middle Frontal Gyrus	BA 10
1591	<0.05	4.03	-32	46	20	L	Middle Frontal Gyrus	BA 10
1591	<0.05	3.67	-32	52	0	L	Middle Frontal Gyrus	BA 10
1591	<0.05	3.4	-20	46	12	L	Medial Frontal Gyrus	BA 9
1591	<0.05	3.32	-26	58	-6	L	Superior Frontal Gyrus	BA 10
27890	$<10^{-17}$	6.64	-42	-40	42	L	Inferior Parietal Lobule	BA 40

Table 4.4. Peaks of transient activity evoked by incongruent-distracter minus congruent-distracter stimuli in the mixed mostly Incongruent block. Cluster size (CL-size) is expressed in voxels and the reported *p*s are FWER-corrected with the cluster method (CL-p). Coordinates are in MNI space and Brodmann areas (BA) labels refer to the nearest grey matter (within 5mm).

CL-size	*CL-p*	*Z-value*	*X*	*Y*	*Z*	*Side*	*Region*	*Area*
4933	$<10^{-4}$	5.19	16	0	70	R	Superior Frontal Gyrus	BA 6
3113	<0.01	3.89	28	-74	20	R	Precuneus	BA 31
3113	<0.01	3.61	22	-72	36	R	Cuneus	BA 7
4933	$<10^{-4}$	5.44	12	-46	64	R	Precuneus	BA 7
4933	$<10^{-4}$	5.43	22	-44	68	R	Superior Parietal Lobule	BA 7
3113	<0.01	4.5	56	-28	32	R	Inferior Parietal Lobule	BA 40
3113	<0.01	4.49	54	-44	16	R	Superior Temporal Gyrus	BA 13
3113	<0.01	3.94	46	-60	-6	R	Middle Temporal Gyrus	BA 37
3113	<0.01	3.78	50	-68	10	R	Middle Temporal Gyrus	BA 37
1469	<0.05	3.65	-58	-2	28	L	Precentral Gyrus	BA 6
2879	<0.01	5.36	-40	-72	14	L	Middle Occipital Gyrus	BA 19
2879	<0.01	4.25	-14	-76	36	L	Cuneus	BA 7
2879	<0.01	3.97	-20	-74	24	L	Precuneus	BA 31
2879	<0.01	3.61	-42	-86	-2	L	Inferior Occipital Gyrus	BA 19
2879	<0.01	3.3	-30	-88	8	L	Middle Occipital Gyrus	BA 18
2879	<0.01	3.24	-50	-70	-4	L	Middle Occipital Gyrus	BA 37
4933	$<10^{-4}$	5.14	-8	-46	64	L	Precuneus	BA 7
4933	$<10^{-4}$	4.97	-14	-42	64	L	Precuneus	BA 7
4933	$<10^{-4}$	4.78	-18	-56	64	L	Precuneus	BA 7
1469	<0.05	4.02	-50	-32	34	L	Inferior Parietal Lobule	BA 40
1469	<0.05	3.93	-64	-36	30	L	Inferior Parietal Lobule	BA 40
1469	<0.05	3.93	-52	-42	32	L	Inferior Parietal Lobule	BA 40
1469	<0.05	3.81	-54	-28	32	L	Inferior Parietal Lobule	BA 40
1469	<0.05	3.69	-56	-28	44	L	Postcentral Gyrus	BA 2

Figure 4.5. Transient activity evoked by incongruent-distracter trials (minus congruent-distracter trials) in the mostly Congruent block (left column) and in the mostly Incongruent block (right column). In the mostly Congruent block, conflicting distracter trials activated the left dorsolateral prefrontal cortex (DLPFC), the left and right superior parietal lobule (SPL), the left and right dorsal anterior cingulate cortex (ACC), the left and right precentral gyrus, the left and right precuneus, and the left and right intraparietal sulcus. In the mostly Incongruent block, conflicting distracters activated the left and right precentral gyrus, the left and right inferior parietal lobule (IPL), the left and right precuneus, and the left and right posterior cingulate cortex (PCC).

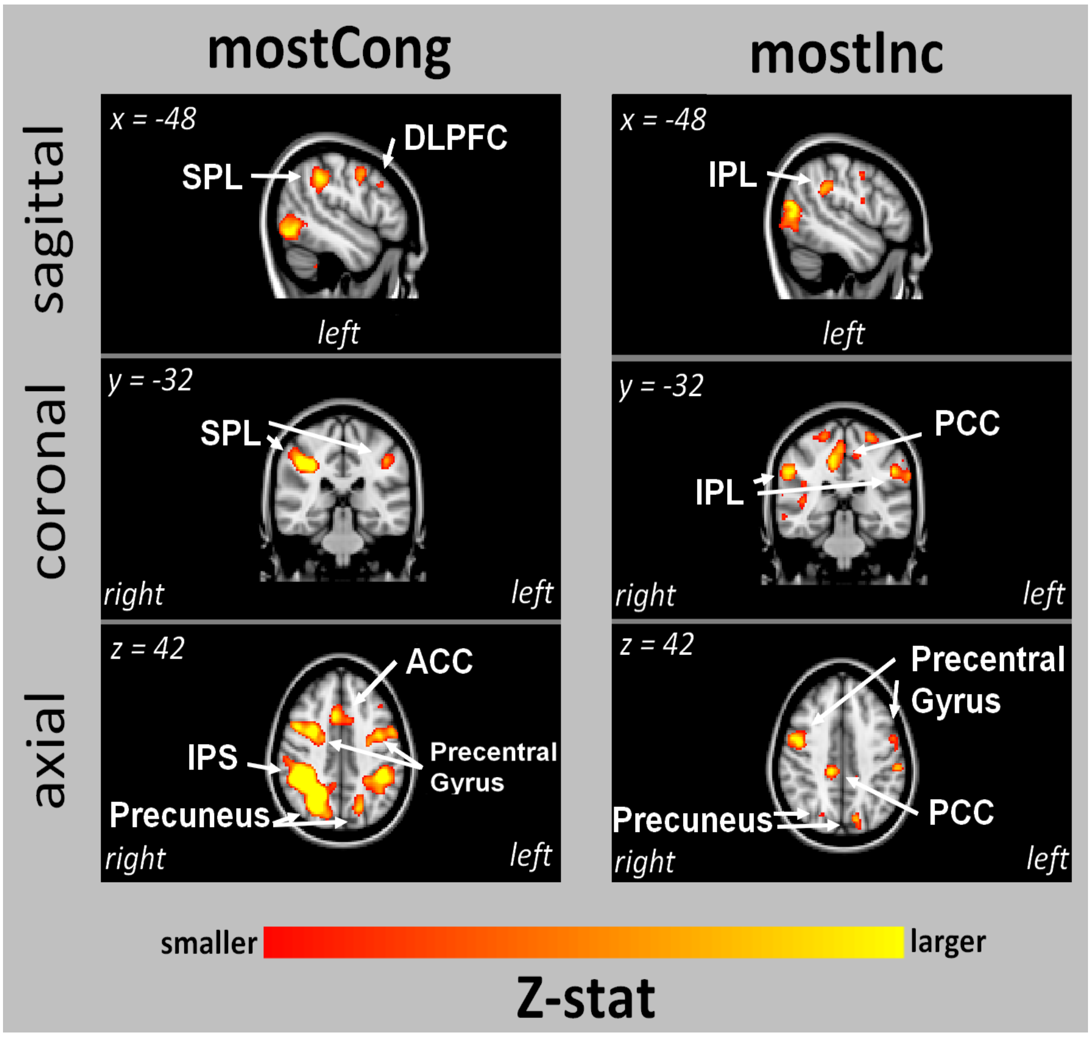
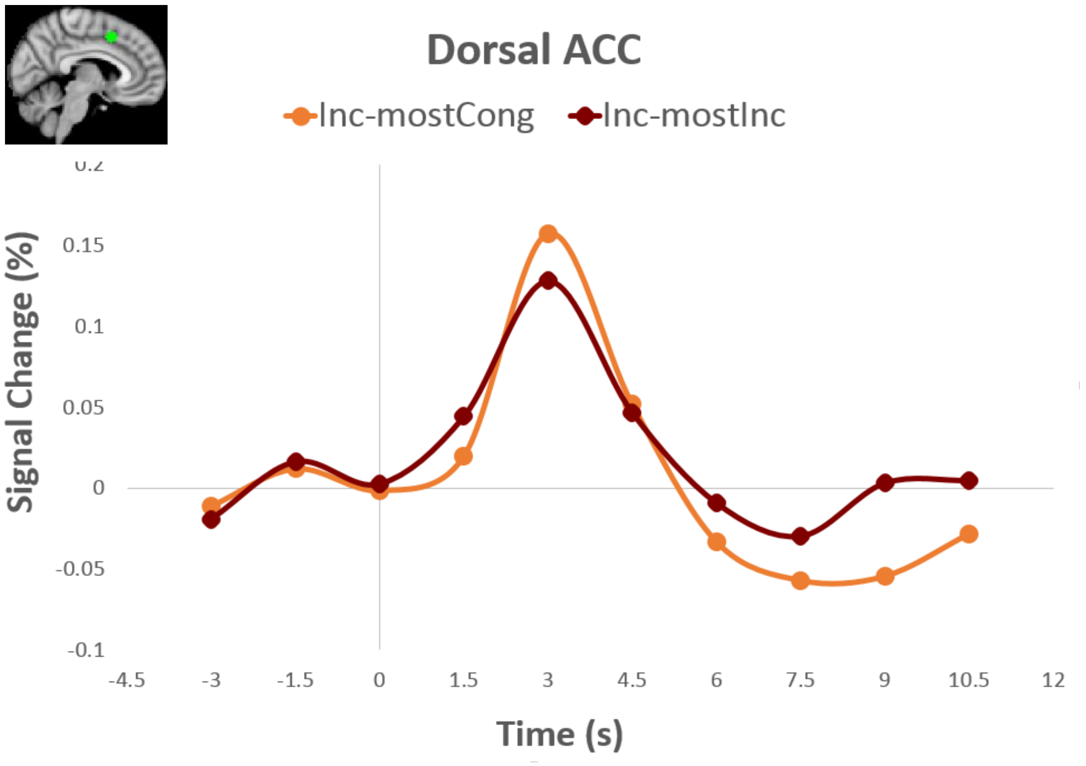


Figure 4.6. Hemodynamic response to incongruent-distracter stimuli in the dorsal ACC ROI during the mostly Congruent block (Inc-mostCong, orange line) and the mostly Incongruent block (Inc-mostInc, red line). Coherently with the existing literature (e.g., Botvinick et al., 2001; Kerns et al., 2004), conflict-driven responses were observed in ACC, with the highest peak of activity in the mostly Congruent block (Grandjean et al., 2012).



For representing conflict-related responses in the anterior cingulate cortex, a spherical ROI was created with a radius of 6mm and centered in the peak of Z-stat within ACC as identified by the voxelwise analysis (MNI coordinates: x = 6, y = 12, z =46). The average hemodynamic response function was extracted from this region for all types of congruent and incongruent stimuli (Figure 4.6).

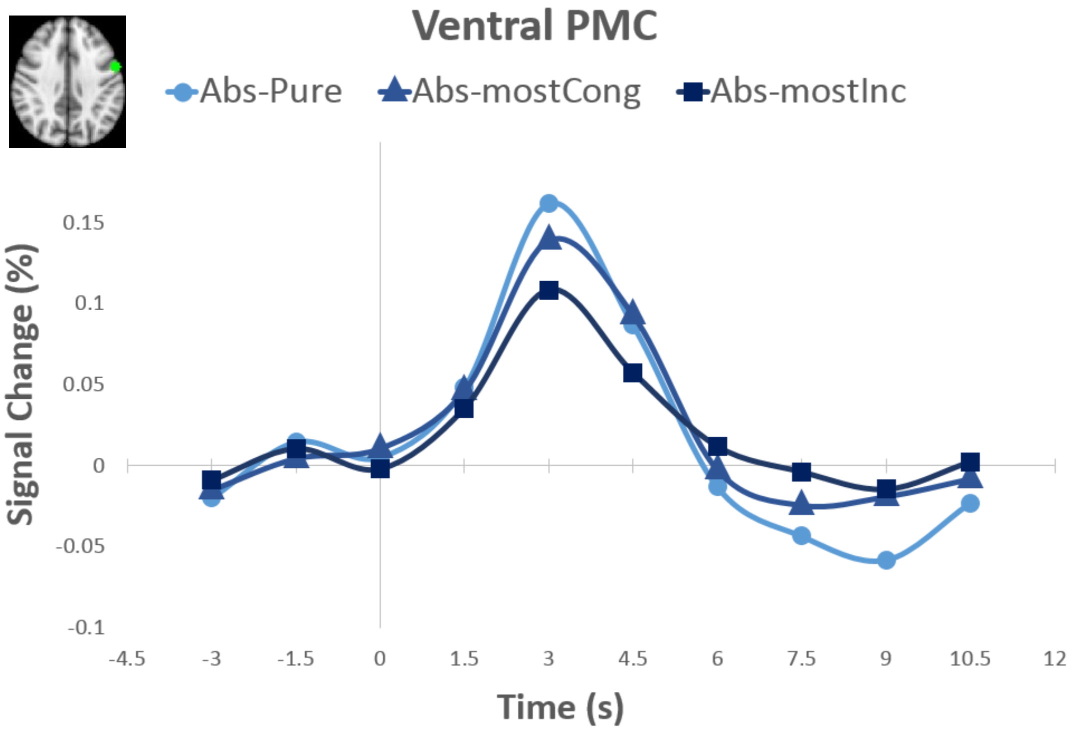
Response readiness for Absent-distracter trials in different contexts

One possible function of the filtering mechanism is preventing erroneous responses primed by distracters (rather than correctly driven by target stimuli). If so, in contexts where distracters are more frequent, erroneous response tendencies need to be controlled more often. This might be implemented in the brain at the neural stage of the preparation for the execution of a motor response. The most cautious response setting would need to be adopted in the context where incongruent distracters occur more frequently and it would prevent the too-fast emission of a potentially wrong, distracter-driven motor response. When incongruent distracters occur in a minority of trials, there is still need for some cognitive control over response tendencies, even thought to a lesser extent than in the mostly incongruent situation. The context where distraction never occurs would need the least degree of control and, consequently, the highest response readiness (since the execution of a response cannot be erroneously deviated by the presence of any conflicting stimulus). For examining response readiness across contexts with different probability of conflicting distracters, I focused my analysis on the left premotor cortex (since all participants used their right hand for the response). Given that the key prediction is that the mechanism for dealing with potentially distracting contexts is implemented in a sustained fashion for complete experimental blocks, I also expect that a different "response readiness set" is implemented as a cognitive strategy along an entire block. Thus, once again absent-distracter trials constitute the ideal means for probing response readiness levels in different contexts.

Then, I defined regions of the premotor cortex with a significant response in absent-distracter trials under the three different conflicting contexts. Then, I individuated the peak of the overlapped activation, which was located in the precentral gyrus (BA 6) in the lateral premotor cortex (MNI coordinates: x = -56, y = 2, z = 36).

I created a spherical region of interest (premotor-ROI) with a radius of 6 mm from which I extracted the average BOLD signal for Abs-Pure, Abs-mostCong and Abs-mostInc trials (all versus the fixation baseline) from individual participants' data. Finally, I calculated

Figure 4.7. Hemodynamic response to absent-distracter target stimuli in the premotor cortex ROI. The strongest activation was observed in the Pure block and the weakest in the mostly Incongruent block. In the mostly Congruent block, the peak of the response was at an intermediate level. This differences might reflect a modulation over response tendencies with the greatest control in the context with frequent conflicting distracters. In the Pure block, there is no conflict and thus no need for preventing any conflict-induced response tendency. Given that these differences are all observed in absent-distracter trials, they might derive from a strategic preparatory bias executed by frontal areas (such as IFG and DLPFC) over the premotor cortex.



the base-to-peak response for each context type and conducted paired t-test contrasting different contexts. A larger base-to-peak difference in the hemodynamic response function was observed in both the Pure and the mostly Congruent block as compared to the mostly Incongruent block [$t(19)=2.17$, $p<.05$, and $t(19)=2.4$, $p<.05$]. No differences were found between the Pure and the mostly Congruent block. These results attest to a stronger premotor activation in contexts where most of the trials represent the correct response with no conflict, and to a reduced premotor activation in the context where most trials present a response conflict between target and distracters. These results are represented in Figure 4.7.

4.4.3 Retinotopic effects in the visual cortex

Areas responding to the spatial position of targets were identified in the visual cortex with the subtraction between target and distracter blocks, respectively, in the retinotopic localizer run. This contrast originated a region of interest corresponding to areas of the visual cortex where targets are processed (target-ROI). The target-ROI included the right middle occipital gyrus (BA18), part of the left and right inferior occipital gyrus (BA18) and part of the left lingual gyrus (BA17). Areas responding to the spatial position of distracters were identified in the visual cortex with the subtraction between distracter and target blocks, respectively, in the retinotopic localizer run. This contrast originated a region of interest corresponding to areas of the visual cortex where distracters are processed (distracter-ROI). The distracter-ROI included several peaks of activity in the left and right lingual gyrus (BA17). Target and distracter ROIs are represented in Figure 4.8 and peak activations are reported in Table 4.5.

Distracter-ROI

The primary interest of this analysis was comparing responses to distracters under different conflict probability, with the hypothesis that sensory representations of distracters in the visual cortex are more suppressed in the high-conflict context as compared to the low-conflict context. In principle, this distracter suppression might be specific for incongruent distracters or extended to both congruent and incongruent distracters.

Since I hypothesized that distracter suppression is driven by a strategic setting of a top-down attentional control mechanism and essentially relies on sustained activity, I expect that this suppression is directed towards the spatial location of potential distracters and affects indistinctively both congruent and incongruent distracting stimuli.

A different hypothesis of a larger activation in distracters-ROIs in the mostly congruent block might be proposed if one considers that this type of distracters occurs rarely in the mostly congruent block and then tend to be more perceptually salient. If this is the case, however, a relative reduction in responses in the mostly incongruent block, as compared to the mostly congruent, should be selective for incongruent-distracter trials.

Finally, it is also possible formulating an alternative hypothesis, with an enhancement of the distracter representations in the high-conflict probability block as compared to the low-conflict probability block. In fact, when distracters occur more frequently, they become less salient and interfere less with behavior, thus there is no need for a stronger sensory suppression. Instead, the strongest suppression would occur when distracters are less probable and more interfering with behavior.

Figure 4.8. Target ROI (green) and distracter ROI (red) in visual cortex as derived from Target > Distracter and Distracter > Target contrasts, respectively, in the retinotopic functional localizer run. Overall, these ROIs mainly occupy extrastriate visual cortices, even though there are a few peaks in the primary visual cortex as well. Distracter (i.e., peripheral) ROIs were found medially from the ventral the dorsal portion of the occipital lobe, whereas target (i.e., foveal) ROIs were identified in lateral locations mainly in the ventral occipital lobe. This medial-lateral pattern resembles findings from previous studies (see, e.g., Levy et al., 2011, Fig. 7B).

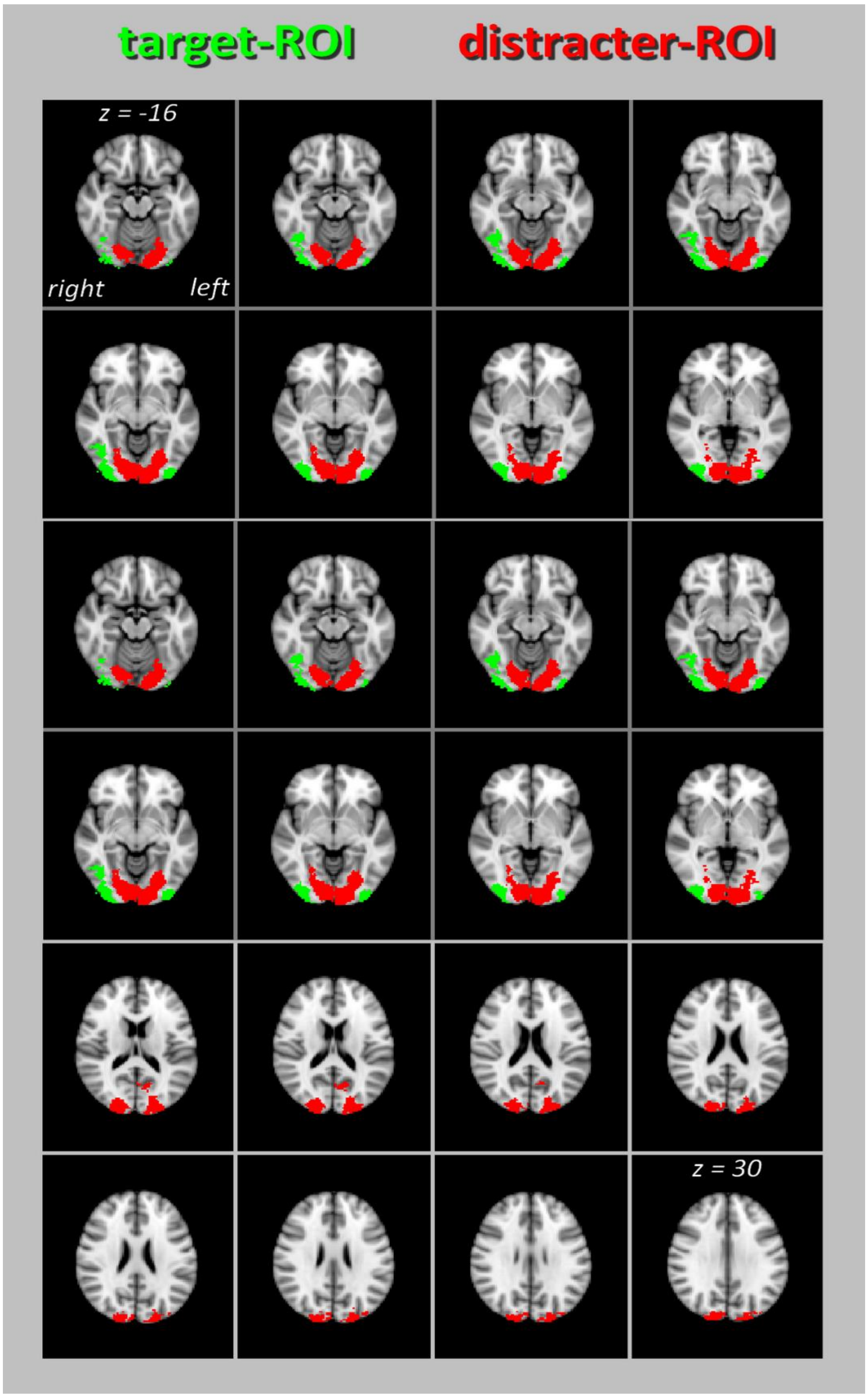


Table 4.5. Peak locations of the hemodynamic response within target and distracters clusters in the functional localizer run. The reported *p*s are FWER-corrected with the cluster method (CL-p). Coordinates are in MNI space and Brodmann areas (BA) labels refer to the nearest grey matter (within 5mm).

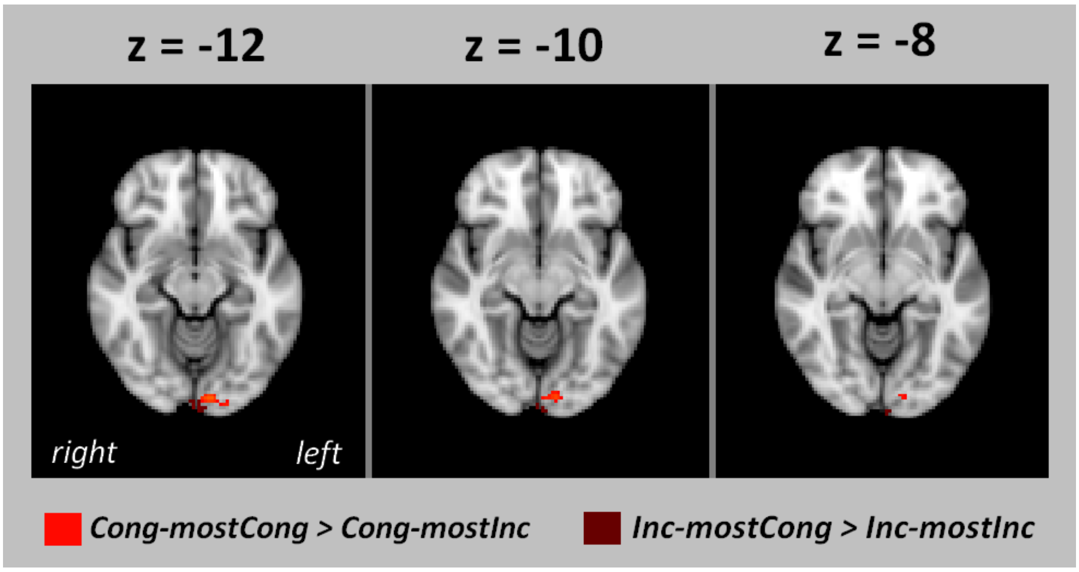
ROI	*CL-p*	*Z-value*	*X*	*Y*	*Z*	*Side*	*Region*	*Area*
Target	$<10^{-7}$	3.94	34	-88	-4	R	Infer. Occipital Gyrus	BA 18
Target	$<10^{-7}$	3.91	36	-90	-10	R	Infer. Occipital Gyrus	BA 18
Target	$<10^{-7}$	3.87	34	-84	0	R	Middle Occipital Gyrus	BA 18
Target	$<10^{-7}$	3.78	24	-102	-10	R	Lingual Gyrus	BA 17
Target	$<10^{-7}$	3.67	38	-86	-12	R	Infer. Occipital Gyrus	BA 18
Target	<0.01	4.47	-34	-94	-10	L	Infer. Occipital Gyrus	BA 18
Dist	$<10^{-30}$	5.21	-12	-94	-10	L	Lingual Gyrus	BA 18
Dist	$<10^{-30}$	5.18	-16	-98	2	L	Lingual Gyrus	BA 17
Dist	$<10^{-30}$	4.91	-20	-96	0	L	Lingual Gyrus	BA 17
Dist	$<10^{-30}$	4.81	14	-96	2	R	Lingual Gyrus	BA 17
Dist	$<10^{-30}$	4.81	-18	-90	6	L	Lingual Gyrus	BA 17
Dist	$<10^{-30}$	4.76	18	-88	-6	R	Lingual Gyrus	BA 18

Under the theoretical guidance of the aforementioned hypotheses, I focused on four contrasts of interest: Cong-mostCong > Cong-mostInc, Cong-mostInc > Cong-mostCong, Inc-mostCong > Inc-mostInc, and Inc-mostInc > Inc-mostCong. I conducted a voxelwise analyses within the distracter-ROI, as defined after the analysis of the retinotopic localizer data. Cluster of activation were identified by thresholding the images corresponding to contrasts of interest at a Z-value of 1.64 (corresponding to p=.05) and with a cluster size threshold of 50 contiguous active voxel.

No cluster was identified in sensory areas for being significantly more active in response to distracting stimuli, either congruent or incongruent, in the context with high-probability of conflict as compared to the context with low conflict probability (Cong-mostInc > Cong-mostCong and Inc-mostInc > Inc-mostCong). This result clearly attests that visual distracters do not have a stronger sensory representation in the mostly incongruent block than in the mostly congruent block.

The analysis on the remaining two contrasts, which aimed at identifying regions more activated by distracters in the mostly congruent than in the mostly incongruent block, identified two significant clusters. One cluster in the left lingual gyrus showed significantly more activity for congruent trials in the mostly congruent block than in the mostly incongruent block (Cong-mostCong > Cong- mostInc; Table 4.6). A different cluster, centered in the right lingual gyrus but also extending to the left lingual gyrus, showed significantly more activity for incongruent trials in the mostly congruent block than in the mostly incongruent block (Inc-mostCong > Inc-mostInc; Table 4.6). These results attest to a relative reduction of distracter-related activity in the mostly incongruent context as compared to the mostly congruent context. Because these results show that the sensory representation of distracters was stronger in the mostly congruent block and weaker in the mostly incongruent block, they comply with the hypothesis of a greater distracter suppression in the context with high probability of conflicting distracters. The greater suppression in the mostly incongruent block was found for both congruent and incongruent distracters.

Figure 4.9 / Table 4.6. Voxelwise analysis within distracter-ROI and target-ROI. No significant context-related modulations of responses in absent-distracter trials were found within target-ROI. Two separate areas in the lingual gyrus showed larger response to congruent and incongruent distracters, respectively, in mostCong block as compared to the mostInc block. This result might indicate an attenuated sensory representation (and thus a stronger suppression) of distracters in the mostInc block. Coordinates (in MNI space) indicate the center of gravity of the activated cluster and Brodmann areas (BA) labels refer to the nearest grey matter (within 5mm).



Contrast	*Z-value*	*X*	*Y*	*Z*	*Side*	*Region*	*Area*
Cong-mCong > Cong-mInc	3.24	-8	-90	-6	L	Lingual Gyrus	BA17
Inc-mCong > Inc-mInc	2.39	10	-88	-14	R	Lingual Gyrus	BA18

This finding clearly speak against the possibility of a contingent increase of response for rare incongruent-distracter trials in the mostly congruent block. Rather, this finding is in line with the idea of a generalized attenuation of sensory input from spatial locations representing distracter, independently of the actual distracter type, in the mostly incongruent block as compared to the mostly congruent block.

Target-ROI

Analysis in the ROI representing target aimed at identifying any difference in sensory processing of target stimuli in absent-distracter trials depending on the pure or mixed context to which these trials belong. One might expect an enhanced processing of targets in the contexts, where more effort is produced for focusing on task-relevant information and thus the representation of target becomes more efficient than in a pure context. An alternative view predicts the opposite pattern, namely, an augmented sensory representation of targets in the Pure block, due to the lack of any potential distraction in a pure context, which prevents the potential draw of attentional resources away from the target stimulus.

These hypotheses were investigated by focusing on four contrasts of interest: Abs-Pure > Abs-mostCong, Abs-Pure > Abs-mostInc, Abs-mostCong > Abs-Pure, and Abs-mostInc > Abs-Pure. I conducted a voxelwise analyses within the target-ROI, as defined after the analysis of the retinotopic localizer data. Cluster of activation were identified by using the same thresholding procedure described for the distracter-ROI. No significant difference emerged in any of these contrasts. There was a trend for a higher activation for absent-distracter trials in the mostly congruent block than in the Pure block; however, the resulting cluster included only 40 voxels and thus did not reach the threshold criterion.

Therefore, I did not find any significant different in target sensory processing in visual areas between the pure and the mixed contexts.

4.5 Conclusion

In this study, I investigated sustained and stimulus-evoked brain mechanisms for dealing with potentially distracting and conflicting contexts. I identified a series of regions, mostly located in – but not limited to – frontal and parietal lobes, that showed enhancements in sustained activation throughout blocks with conflicting distracters, as compared to blocks with no occurrence of distraction.

The activated regions included areas implicated in cognitive control, such as the dorsolateral prefrontal cortex, and in the inhibition of conflicting response tendencies, such as the inferior frontal gyrus. Moreover, the activated regions included areas belonging to the top-down attentional network, such as medial frontal areas, including the putative human frontal eye field, and the intraparietal sulcus and superior parietal regions, that play a role in attentional orienting to target stimuli.

The analysis of transient brain responses to absent-distracter stimuli in different contexts highlighted a reduction in premotor activity and an increase in posterior parietal activity. The magnitude of both this premotor reduction and this parietal enhancement is stronger when the probability of conflict is high. Modulations of responses evoked by present-distracters stimuli were also observed. In particular, incongruent distracters elicited larger activity in the dorsal portion of the anterior cingulate cortex than congruent distracters. This difference was larger in the mostly congruent block.

Finally, in extrastriate visual regions representing distracters, a reduction of activity was found in the mostly incongruent block as compared to the mostly congruent block. This reduction was unspecific for the type of present-distracter trial and likely indicated a preparatory suppression of distracter sensory representations selective for the context with high probability of conflicting distraction.

Chapter 5

General Discussion

5.1 The behavioral cost for strategic filtering of potential distraction

In the present thesis, I wished to uncover and characterize the behavioral and brain correlates of a cognitive mechanism that is recruited in order to prevent interference from irrelevant distracters in potentially distracting and conflicting situations.

I hypothesized that when probability of distraction is high a distraction-filtering mechanism is activated in a sustained fashion throughout a potentially distracting context. I demonstrated that this mechanism is resource demanding in that it requires the recruitment of cognitive control processes and therefore its activation leads to a sizable performance cost when distraction is likely, yet currently absent. Accordingly, I showed that the engagement of the distraction filtering mechanism in potentially distracting contexts leads to a measurable pattern of neural activations in the human brain.

In Chapters 2 and 3, by running a series of behavioral experiments with a novel paradigm guided by the theoretical rationale of *potential* distraction (Pure-Mix Potential Distraction paradigm), I showed that the speeded processing of a sensory stimulus (either visual, tactile or auditory) in a simple discrimination task is severely slowed-down in potentially distracting contexts. Crucially, this happens in a block where distraction is expected but does not occur (i.e., absent-distracter trials in the Mix context), as compared to a block where the probability of distracters' occurrence is null (i.e., absent-distracter trials in the Pure context).

Preliminary converging evidence can be found in a prior study in the domain of developmental psychology (Enns & Akhtar, 1989), where a mean RT cost of 32 ms was obtained for younger adults performing absent-distracter trials in Pure and Mix blocks.

Incidentally, in that study the cost in the mixed condition was even larger in children. That observation supports the existence of a context-sensitive mechanism for the filtering of potential distraction that might be present even early during development.

Critically, if one considers absent-target trials where that cost is observed, there are no differences at all (e.g. in terms of sensory stimulation, single-trial attentional demands, and task requirements) between Pure and Mix blocks. When one instead considers the global context, one comes to realize that trials with slowed-down responses (Abs-Mix) were embedded in a trial-sequence where most trials contained a concurrent distracter (e.g., Chapter 2, Experiments 1 and 3-7), whereas in the Abs-Pure block distraction never occurred. It appears therefore reasonable to hypothesize that the observed cost is driven by the global context.

The main question then becomes what kind of specific mechanism the brain must engage during the execution a perceptual task in a potentially distracting context. It is likely that its functional role should be related to the effort to optimize resources and performance in the specific task and within the given context, in particular by preventing interference from irrelevant distracters. This intriguing hypothesis is fully supported by the finding that the observed slowing-down in the Mix block (as compared to the Pure block) is intimately related to the blocking of interference from distracters, when they occur. In fact, a series of correlation analysis (first reported in Chapter 2, Experiment 1; then replicated in: Chapter 1, Experiment 6; Chapter 3, Spatial Task; Chapter 4, behavioral results) showed that these two measures (i.e., filtering cost and distracter interference) are inversely correlated: the greater the filtering cost, the lower the actual interference, and vice-versa. This result provides strong evidence that the filtering cost truly reflects the activation of a mechanism whose purpose is filtering-out distracters, and thus fully confirms the proposed interpretation.

Interestingly, the inter-subject variability in the magnitude of the strategic cost might be related to differences in the individual effort and/or ability to activate the strategic filtering mechanism, although it might also depend on the total amount of resources available to the single individual. In particular, the recruitment of a strategic mechanism for attentional control has been related to working memory (WM) capacity. Individuals with higher WM capacity mainly use proactive control, while individuals with lower WM capacity mainly rely on reactive processes for dealing with incompatible distracters in a Simon task (Gulbinaite & Johnson, 2011).

5.2 Can different interpretations account for the observed results?

In principle, the observed slowing-down of responses in Abs-Mix trials, compared to Abs-Pure trials, is not sufficient to guarantee that the filtering mechanism is tonically active throughout the potentially distracting experimental block. Response time experiments with conflicting stimuli typically highlight a slowing-down of responses in trials immediately following trials with conflicting stimuli (*post-conflict slowing*; e.g., Verguts, Notebaert, Kunde, & Wühr, 2011). A perhaps analogous increase in response latency is also observed immediately after errors, and it has been termed *post-error slowing* (Botvinick et al., 2001). These effects represent behavioral adjustments due to inter-trial contingencies and they are supposed to rely upon reactive adjustments of cognitive control. I considered post-error slowing and post-conflict slowing as possible determinants for the observed cost. For further investigating the role of reactive adjustments of cognitive control in my studies, I conducted a series of analyses on trial sequences and cross-trial effects in the Mix blocks (Chapter 2, Experiments 1 and 6; Chapter 3, Spatial and Feature Task). A major goal of these analyses was establishing whether a significant filtering cost is still observed when taking apart cross-trial sequential effects by calculating the filtering cost only on absent-distracter trials preceded by another absent-distracter trial in the Mix block, with respect to absent-distracter trials in the Pure block.

The analysis in the first experiment of Chapter 2 confirmed the occurrence of post-error slowing, but also revealed that this phenomenon does not account for the observed strategic cost. As regards post-conflict slowing, it is worth noting that, when comparing response times in Abs-Mix trials as a function of the previous trial type, I found that the latter does not modulate the behavioral cost when distracters were highly probable (Chapter 1, Experiment 1 and Experiments 3-4). Subjects were not reliably slower after incongruent trials compared to congruent or absent-distracter trials. A significant preceding-trial effect was indeed observed in Experiments 5 and 6 of the first study (Chapter 2). However, further analyses showed that the strategic cost in these two experiments was still observed even after subtracting out any reactive component.

Analyses conducted on Experiment 6 (Chapter 2) and on the Spatial and Feature Task (Chapter 3) replicated the finding of a maintained filtering cost even excluding cross-trial dynamic effects from its calculation. In fact, in mixed contexts absent-distracter trials that followed another absent-distracter trial were faster than absent-distracter trials that followed a present-distracter trial (either congruent or incongruent). This was observed in the study described in Chapter 3 independently from the type of task and indicates that the filtering mechanism is modulated by cross-trial contingencies, because its cost is attenuated after absent-distracter trials. Interestingly, the net cost of the filtering mechanism is still present in both task types (spatial-based and feature-based task) and contexts (mostly congruent and mostly incongruent) even when considering only absent-distracter trials that followed another absent-distracter trial. In other words, after excluding the impact of cross-trials effects, a significant filtering cost was still found also in the spatial/feature study (Chapter 3). This finding confirms the truly strategic nature of the distraction filtering mechanism.

Globally, the notions of post-error slowing and post-conflict slowing seem inadequate for fully accounting for my results. Sequential analyses confirmed the intuition that the mechanism for the filtering of upcoming distraction is engaged on a strategic basis and is sustained along the potentially distracting block.

Finally, another possible interpretation should be considered for the slowing-down of responses observed in mixed contexts. In Mix blocks, participants are more exposed to errors because of incongruency and might strategically procrastinate their responses in order to accumulate more confidence in the correctness of their decision. This particular strategy may be conceived as a shift of response criterion in the Mix block, as compared to the Pure block, resulting in a form of speed-accuracy trade-off (e.g., Wickelgren, 1977). The eventual adoption of a higher response threshold in Mix blocks would allow deeper and more accurate sensory processing, at the cost of longer RTs (Ratcliff, 2002; Brown & Heathcote, 2008). Accordingly, if the slowing-down I observed in Abs-Mix trials were due to strategic response procrastination, an increase in accuracy should be observed as well in the same condition. In Experiment 7 (Chapter 2), which was specifically designed to test this hypothesis, I actually measured the reverse pattern, in that subjects were both slower and less accurate in absent-distracter trials of the Mix (as compared to the Pure) block. Thus, present data allow us to reject the speed-accuracy trade-off hypothesis and instead fully support the costly filtering hypothesis.

It is then possible concluding that, within the context of a perceptual discrimination task, which is not highly demanding in terms of attentional resources, a mechanism preventing the negative impact of distracters is strategically engaged throughout the potentially distracting block. This sustained process entails increased activity in cognitive control systems, diminishing available cognitive resources for processing and responding to the target stimulus and therefore causing the observed slowing-down of responses in Abs-Mix trials.

5.3 Strategic filtering and distraction probability

At this point, it is worth noting that when distraction is expected only in a minority of total trials, a sustained activation of the filtering mechanism might be disadvantageous, because it leads - as I found - to consistent overall behavioral costs. With possible, yet improbable, distraction, the activation of the mechanism for filtering-out distracters might more conveniently rely on reactive, rather than strategic, processes (Morishima, Okuda, & Sakai, 2010; Braver, 2012). In keeping with that prediction, in Experiment 2 (Chapter 2), where distraction probability was reduced to one third, I found only weak evidence for the activation of the strategic mechanism, as reflected by the fact that the filtering cost was only marginally significant. This is in line with previous research showing that manipulations of distracters' probability lead to different patterns of interference: the lower the distracters probability, the higher the actual interference they engender, and vice-versa (Geyer, Müller, & Krummenacher, 2008). That study varied the probability of distracters across blocks, with 20%, 50% and 80% of present-distracter trials in different blocks, showing that RTs in present-distracter trials did not differ from RTs in absent-distracter trials in the 80% condition. Under such a high probability of distraction, it is likely that a filtering mechanism was fully operating at all times to prevent interference, but the cost resulting from its engagement cannot be assessed because a pure absent-distracter condition was not included in their experimental design. Moreover, a previous-trial analysis performed by Geyer and colleagues (Geyer et al., 2008) revealed that distracter interference was reduced in trials immediately subsequent to a present-distracter trial, compared to trials following an absent-distracter trial. Interestingly, this dependence of RTs upon events in the preceding trial was much higher under low distracters probability and it was largely reduced when distracters were 80% present. This is quite reminiscent of findings in Experiments 1 and 2 of Chapter 2. While in Experiment 1 (with high probability of distraction) the type of the preceding trial did not reliably affect performance in the next Abs-Mix trial, in Experiment 2 (with low probability of distraction) a selective slowing of Abs-Mix responses after incongruent-distracter trials was observed. This finding raises the possibility that the occurrence of a highly distracting event (i.e., the incongruent present-distracter trial) would act as a trigger signal in preparation for the immediately upcoming trial, inducing the subject to re-activate dynamically the distracter filtering process. This is also in line with the idea that observers enhance their on-line cognitive control over distracter interference in a certain trial because they have encountered a distracter in the preceding trial (Geyer et al., 2008). In Experiment 1, I also performed a sequence analysis in order to examine: a) whether block order impacted performance, and b) whether there was a carry-over of the strategic settings in the initial part of the

Pure block in those subjects who encountered it after the Mix block. Coherently with previous studies (Müller, Geyer, Zehetleitner & Krummenacher, 2009), I found a robust practice effect, indicating that subjects were overall slower in the first Pure block as compared to the same block performed as the second one. I also observed that the first mini-block in each block was slower than the second one. This latter result might reflect some form of within-block task practice and it is not due to carry-over effects. In fact, carry-over effects should have been observed only in subjects who performed the Pure block after the Mix block, but data show that the interaction between *Order* and *Mini-Block* was very far from significance (p=0.92).

5.4 Strategic filtering and conflict probability

Differences between Experiments 1 and 2 of the first study (Chapter 2) changed the probability of distraction. However, in this regard a critical point might be raised. Since present-distracter trials were equally distributed in those experiments between incongruent-distracter and congruent-distracter trials, not only distraction probability changed but also incongruence (i.e., conflict) probability changed. More specifically, the proportion of occurrence of present-distracter trials dropped from 66% to 33% and the proportion of occurrence of conflict dropped from 33% to 16.5%. Therefore, it cannot be univocally established what of those factors (i.e., reduction in distraction probability and reduction in conflict probability) actually determined the reported reduction of the filtering cost. The study in Chapter 3 helps clarifying this topic. In fact, that study specifically investigated whether *conflict* probability modulates the distracter filtering cost in a spatial-based and in a feature-based conflict tasks.

It is known from existing literature that the negative impact on performance of incongruent distracters is larger when conflict probability is relatively low. This is the so-called *proportion congruent effect* (Lowe & Mitterer, 1982; Jacoby et al., 2003; see Bugg & Crump, 2012, for a review). One recently proposed interpretation (Grandjean et al., 2012) of the proportion congruent effect suggests that in high-conflict situations the frequent need to inhibit incompatible stimuli is implemented in a proactive cognitive control set that promotes the activation of goal-relevant information (Ridderinkhof, 2002; Kerns et al., 2004; Braver, 2012). In low-conflict situations, conversely, all stimuli provide compatible information for most trials, then cognitive control is predominantly reactive and conflict is counteracted just in the moment of its occurrence (Ridderinkhof, 2002; Grandjean et al., 2012; Braver, 2012).

My study in Chapter 3 presented a different characteristic than most studies on the proportion congruent effect because it used a context-level manipulation of proportion congruent effect (Crump, Gong, & Milliken, 2006, Bugg, Jacoby, & Toth, 2008), rather than a cue-based manipulation (see Bugg & Crump, 2012, for a review). Nonetheless, a proportion congruent effect was observed in the spatial-based conflict task (Chapter 3), thus confirming and extending existing findings that were obtained with the Stroop task (Jacoby et al., 2003; Grandjean et al., 2012). The novel feature-based conflict task (Chapter 3), instead, showed only a non-significant tendency to a modulation of the incongruency cost by the proportion of conflicting trials in a given context. The lack of a statistically significant proportion congruent effect might stand because the motion discrimination task is by far a more complex task than the arrow orientation discrimination task (for example, because of the need for motion integration). This implies that the motion task requires more attentional load on targets and in parallel the impact of distracters decreases, as predicted by Lavie's theory of selective attention and cognitive load (Lavie & Cox, 1997; Lavie et al., 2004; Kelley & Lavie, 2011). Modulations of distracters' interference effect depending on the conflicting context might be reduced in the feature-based task for this reason.

More relevantly to the theoretical interest of the present thesis, the study in Chapter 3 clearly demonstrated that in a spatial-based task, such as the arrow flanker task, the magnitude of the filtering cost significantly depends on conflict probability. This adds to the evidence from Chapter 2 in that not just the mere probability of *distraction*, but also – and even more precisely – the probability of *conflict* significantly modulate the magnitude of the strategic filtering cost in a visuospatial attention task.

5.5 Potential implications for existing literature

The combined measurement of the proportion congruent effect with the filtering cost (Chapter 3) permits to open a new perspective on the interpretation of the proportion congruent effect itself. In fact, my results reveal an interesting parallel between the filtering cost and incongruency-driven interfering effects in different contexts. In the mostly congruent block, participants pay a small cost for preventing distraction. This seems reasonable given that conflicting distraction occurs in a limited number of trials. However, when distraction actually occurs, it has a dramatic impact on performance, as demonstrated by the very large cost of incongruent distracters. In the mostly incongruent block, instead, the opposite pattern takes place. Conflicting distracters are presented in the majority of trials and, accordingly, participants have a robust filtering cost, which is associated with a high effort in preventing the negative impact of incongruency, as demonstrated by the smaller distracter cost in the mostly incongruent block. Additionally, the inverse correlation across subjects between the filtering cost and the distracter cost, also found in the previous study (Experiments 1 and 6, Chapter 2), has been replicated in the spatial task (Chapter 3). These results thus suggest that the differential magnitude of the incongruency effect depending on the probability of distraction – i.e. the proportion congruent effect – might be the consequence of a differential strength of engagement of a distracter filtering mechanism under different contextual circumstances.

It is well known that contextual circumstances may well play a widespread role in modulating attentional settings. For example, previous experience can lead to the sustained suppression of irrelevant stimuli by means of the prolonged activation of distracter suppression processes (Dixon, Ruppet, Pratt, & De Rosa, 2009). The mechanism for the filtering of potential distraction I describe in this thesis appears well characterized as a context-sensitive process. A context where distraction is likely leads to the strategic recruitment of the filtering mechanism, while in contexts where conflicting distraction is relatively infrequent the mechanism is engaged less strongly (Chapter 3, spatial task) and through reactive dynamics (Chapter 2, Experiment 2).

The aforementioned interpretation also fits well with two well-known phenomena: *post-error reduction of interference* (Ridderinkhof et al., 2002; Danielmeier & Ullsperger, 2011) and *pre-error speeding* (Eichele, Juvodden, Ullsperger, & Eichele, 2010). Post-error reduction of interference was originally described using either a flanker task (Ridderinkhof et al., 2002) or a Simon task (Ridderinkhof, 2002), and consists in a reduced cost caused by incongruent distracters after an error trial. Such effect is thought to depend on cognitive control (King, Korb, von Cramon, & Ullsperger, 2010). Within the theoretical framework of distraction filtering that I propose in this thesis, a reactive engagement of the filtering mechanism following an error provides a highly compatible account of the existing results. In addition, it has been recently observed that, in a modified flanker task, participants' responses become increasingly faster over the five trials before an error is committed (Eichele et al., 2010). In agreement with my hypothesis, this progressive speeding observed prior to an error might be indicative of a gradually weakened engagement of the filtering mechanism. In that situation, cognitive control would release distraction-filtering resources, leading to faster responses to targets, until the filtering mechanism is so feeble that the occurrence of a distracter causes a wrong response.

5.6 In the search of a supramodal filtering system

Data from the seven experiments of the first study (Chapter 2) support the idea that the filtering mechanism acts at a supramodal level. I measured the strategic cost in visuo-tactile (Experiments 1-3) and visuo-acoustic (Experiments 5 and 7) conditions, and within the tactile (Experiment 4) and the visual (Experiment 6) modality. Interestingly, it has been documented that, in an audio-visual selective attention task, brain representations of visual distracters are susceptible of different degrees of attenuation depending on the sensory modality of the target (Ciaramitaro, Bucaras, & Boynton, 2007). However, as shown by results of the study described in Chapter 2, the cost ensuing from the strategic activation of distracter-filtering mechanisms occurs both within and between sensory modalities. Thus, it is likely to reflect supramodal attentional (and not sensory-specific) processes. Even if current data do not permit to positively determine that the *same* filtering mechanism is operating within and between modalities, my results are fully compatible with the notion that the filtering mechanism is supramodal in nature.

5.7 The filtering cost might underlie different strategies

The lack of a proportion-congruent effect in the feature task (Chapter 3) and the lack of modulations on the filtering cost depending on distracter probability in the same task suggest that partly different mechanisms might be at play as compared to the spatial task (Chapter 3). Moreover, in the feature task the correlation between the filtering cost and the distracter cost shows a significant *positive* trend, which clearly differs from previous evidences (Chapter 2, Experiments 1 and 6, and Chapter 3, Spatial Task) where a *negative* trend was observed. In the feature task, some participants showed a generalized slowing-down in Mix blocks. This slowing-down regarded both absent-distracter and present-distracter trials. Instead, other participants showed a generalized speed-up, which also regarded both absent-distracter and present-distracter trials. This result hardly reconciles with the idea that the filtering cost and the distracter cost observed in the feature task are two sides of the same coin. Rather, it seems that in the feature task the mixed context adds complexity to the task regardless of the probability of conflict. This is in line with the generalized increase in complexity in the motion discrimination task already mentioned earlier in this chapter. Results of the feature task indicate that some participants are more efficient than other while dealing with this complexity. Nevertheless, all participants used the strategy of a generalized and prudential slowing down, for dealing with Mix blocks as compared to the Pure block.

This slowing-down drives to the same direction both the filtering cost and the incongruency cost. Therefore, there is the possibility that the strategy of a more cautious response setting is predominantly adopted in Mix blocks during the feature task. Under this view, it appears reasonable hypothesizing that those participants who are strategically cautious in the Mix block become even more cautious when encountering a conflicting distraction. Although additional evidence is needed for further confirming this point, the parallel tendency between the cost of mixed absent-distracter trials and the cost of incongruent distracters trials observed in the feature task seem to be in line with the aforementioned hypothesis.

5.8 The filtering mechanism as a task-dependent gating system

Having shown that in potentially distracting contexts a strategic mechanism is recruited for blocking forthcoming distraction, now an intriguing question regards which characteristic(s) of distracters this mechanism is actually intended to suppress. Distracters can interfere with the target discrimination task at different levels. When target and distracting stimuli are located in close spatial vicinity and the distracter is incongruent in terms of elevation (Chapter 2, Experiment 1), a phenomenon of target mislocalization might occur. In a visuo-tactile task similar to the one I adopted for initial experiments (Chapter 2, Experiments 1-4), it has previously been shown that a sort of ventriloquism effect (i.e., the capture of the perceived position of the tactile stimulus by the visual distracter) might partly explain the resulting interference (Spence et al., 2004). Moreover, in visual brain areas, evoked responses to a distracter from the same or another sensory modality relative to the target show an enhancement when distracter and target are in the same, compared to different, spatial location (Ciaramitaro et al., 2007). Given the above evidence, the strategic filtering mechanism might serve to prevent the perceptual integration of the two stimuli and thus reflect the effort to impede that the location of the visual distracter captures the location of the tactile target. Experiment 3A (Chapter 2) tested this possibility and results clearly showed that a strategic filtering mechanism is active even when tactile targets and visual distracters are placed in different and distant spatial locations. That finding challenges the hypothesis that the filtering mechanism is primarily aimed at preventing a visuo-tactile ventriloquism effect.

An event-related potentials study has shown that the crossmodal congruency effect reflects a form of response-conflict interference, that is, a competition between responses instantiated by target and distracter in incongruent conditions (Forster & Pavone, 2008). Based on that evidence, the strategic filtering mechanism might primarily operate for attenuating or completely disabling the distracter-driven behavioral response. Recent research has provided substantial evidence for a control mechanism aimed at preventing and suppressing response tendencies, a phenomenon termed *proactive inhibition* (e.g., Jaffard, Benraiss, Longcamp, Velay, & Boulinguez, 2007). Proactive inhibition in the brain involves the activation of the prefrontal cortex (Jaffard, Longcamp, Velay, Anton, Roth et al., 2008; Boulinguez, Ballanger, Granjon, & Benraiss, 2009) and determined a modulation over premotor motor regions, including the primary motor cortex and the premotor cortex in humans (Jaffard et al., 2008), with converging evidence for the supplementary motor area in the macaque (Wardak, 2011). Proactive inhibition can be sustained during task execution, starting in a preparatory fashion even before any stimulus is presented (Cai et al., 2011). It is important to note that a key requirement for proactive inhibition of motor responses is that a sensory stimulus should tend to evoke by itself a specific motor response. This is the case in most experiments described in this thesis, particularly for experiments that focused on conflict (Chapters 3 and 4). However, in one experiment (Chapter 2, Experiment 3B) I showed that the strategic filtering mechanism is engaged even when the distracter is entirely task irrelevant and is not associated to any behavioral response code. The notion of proactive inhibition might account for the filtering cost observed in Experiment 1, 2 and 3A (Chapter 2) and for the filtering cost observed in the study described in Chapter 3. However, this notion fails to explain results from Experiment 3B (Chapter 2). Rather, results from Experiment 3B suggest that the filtering mechanism is still active when the distracter is a flashing light shown at fixation. Under such circumstances, the only way in which the distracter can conceivably interfere with the main task is via a bottom-up attentional capture mechanism. At present, it is still hotly debated whether attentional capture is susceptible to top-down modulations: some studies have found no evidence in that direction (e.g., Koelewijn, Bronkhorst, & Theeuwes, 2009); however, other recent research has reported some form of control over the exogenous capture of attention (Eimer & Kiss, 2008; Chisholm, Hickey, Theuwees, & Kingstone, 2010). Findings from Experiment 3B could nicely fit with the idea that a strategic setting of cognitive control is adopted for preventing the exogenous capture of attention by a salient, yet irrelevant, distracter, in turn leading to an appreciable behavioral cost when the distracter is absent. However, further replications of the finding of a filtering cost in absence of response competition might be needed for confirming this result.

It is worth pinpointing that results of Experiment 3B do not necessarily exclude that the filtering mechanism might prevent both mechanisms, namely that irrelevant distracters capture attention (for example, by spatiotopically attenuating their sensory salience) and that conflict-primed responses lead the execution of an inappropriate motor response. In fact, it is completely plausible hypothesizing that the cognitive control systems might orient the filtering mechanism towards different stages of stimulus processing (i.e., response-related, or attentional-perceptual aspects) depending on the task type and task demands.

5.9 The behavioral filtering cost requires speeded tasks

The fMRI experiment described in Chapter 4 is essentially an in-scanner replication of the spatial task described in Chapter 3. However, a major difference was observed in behavioral results between these two studies. In fact, the in-scanner behavioral data did not show a significant filtering cost on response times. Thus, one might wonder whether a filtering mechanism was engaged at all by participants during the execution of the task in the scanner. There is some behavioral evidence in favor of the hypothesis that the filtering mechanism was indeed recruited, even though its behavioral signature did not show up in the scanner. In fact, I found a significant across-subjects correlation between the filtering cost and the incongruency cost during the in-scanner task. The finding of an inverse relationship between these two behavioral measures clearly demonstrates that the cognitive mechanism for filtering out potential distraction was activated anyways. Additionally, a significant brain-behavior correlation showed that across participants the filtering cost was paired with activity in specific brain areas (see the next paragraph for an extensive discussion). Then, one might wonder why behavioral data on response times collected in the scanner failed to identify the filtering cost. To shed light into this aspect, I replicated the in-scanner experimental sequence in a behavioral setting. It is worth noting that the in-scanner sequence differed from the stimulus presentation sequence used in the earlier behavioral study (Chapter 3) because I optimized the stimulus sequence for in-scanner presentation with an ad-hoc genetic algorithm procedure (see Chapter 4, Material and Methods). The major difference consists in the slower pace in the sequence of trials in the scanner, as compared to the behavioral study in Chapter 3. This had fundamental methodological advantages for the fMRI data (i.e., it favored the estimation of the hemodynamic response function and strengthened the statistical power of contrast detection); however, as a side effect, it critically decreased the cognitive load on control systems (Lavie et al., 2004). A fast pace of stimuli presentation allows to keep the participant constantly engaged in the task and, even more relevantly, requires a continuous deployment of cognitive resources. Since one of the hypothesized dynamics that drive the filtering cost is the reduction of available cognitive resources in the mixed context, it is clear how fundamental a constant task engagement actually is for the finding of a significant behavioral cost with the PM-PoDist paradigm. Instead, such a constant engagement does not take place when the inter-stimulus interval might be as long as 9 s (as in the fMRI task). The control behavioral study, which replicated the in-scanner sequence, also replicated the in-scanner behavioral results. In fact, it failed to show a behavioral filtering cost. In a second behavioral control experiment, I changed the in-scanner sequence by removing all inter-trial intervals longer than 1.5 s. Quite remarkably, results of this second control experiment showed a significant filtering cost.

These two control experiments confirm that when the inter-stimulus interval is long, as it is in the scanner, the behavioral cost is not observed. Consequently, they provide support to the hypothesis that a constant load on cognitive control is determinant for exacerbating a behavioral filtering cost. However, another behavioral signature of the filtering cost, namely the inverse relationship with the distracter interference effect, was still found even at low-pace of presentation. This guarantees that a filtering mechanism was indeed recruited by cognitive brain systems for dealing with potential distraction during Mix blocks in the fMRI task.

5.10 Prefrontal brain areas control strategic filtering in Mix blocks

I studied strategic and stimulus-evoked brain mechanisms that differentiate mixed contexts from pure contexts in the fMRI experiment described in Chapter 4. A distributed network in frontal and parietal lobes showed increased sustained activity in Mix blocks as compared to Pure blocks. Two regions of particular interest in this network are the left dorsolateral prefrontal cortex (DLPFC) and the inferior frontal gyrus (IFG). These areas have been proposed as key regions in the implementation of attentional and cognitive control (i.e. Posner & Petersen, 1989; Kerns et al., 2004; Hampshire, Chamberlain, Monti, Duncan, & Owen, 2010). Their functional role appears related to the maintenance of task-relevant information (Casey et al., 2000) and to the inhibition of inappropriate responses (Brass & von Cramon, 2002; Boehler, Appelbaum, Krebs, Hopf, & Woldorff, 2010), respectively.

I propose that DLPFC and IFG activations constitute the brain signature of the activation of a mechanism for the strategic filtering of potential distraction, as demonstrated by the direct relationship – which I found in the regression analysis across participants –

between the increase of BOLD signal in lateral and inferior prefrontal areas and the magnitude of the filtering cost.

The sustained activation in DLPFC is consistent with the hypothesis of a strategic engagement of cognitive control in Mix blocks. The DLPFC is part of the anterior attentional system (Posner & Petersen, 1989; Stuss, Shallice, Alexander, & Picton, 1995). One key feature of this system is coordinating attentional orienting by controlling the activation of appropriate responses and the suppression of conflicting responses (Casey et al., 2000). Across subjects, we observed that the changes of BOLD responses in left DLPFC are directly correlated to the magnitude of the strategic filtering cost. Another region whose activation individuated a significant brain-behavior correlation with the filtering cost is the left inferior frontal gyrus (IFG). This area have been identified in a series of previous studies about interference resolution (see Nee, Wager, & Jonides, 2007, and Derfuss, Brass, Neumann, & von Cramon, 2005, for reviews) and is considered as a key region in inhibition and attentional control (Aron, Fletcher, Bullmore, Sahakian, & Robbins, 2003; Hampshire et al., 2010). These results are thus compatible with the idea of a key role of DLPFC and IFG in implementing the control settings of the strategic filtering mechanism. One possible operational mechanism for this implementation by left DLPFC and left IFG is the control over stimulus-response rules. In particular, these areas might both exert an inhibitory control over incompatible response tendencies and in parallel prevent an inappropriate attentional allocation to distracters.

Previous studies showed that greater activation in DLPFC is associated with task-setting maintenance and augmented control over stimulus-response association (Stuss et al., 1995; Vallesi, McIntosh, Alexander, & Stuss, 2009; Floden, Vallesi, & Stuss, 2011). In a study of mixed and pure contexts with preparatory cues, it has been proposed that a control function of prefrontal areas might be biasing the precentral gyrus for the enhancement of task-related response sets (Vallesi et al., 2009). However, the authors' interpretation substantially differs from what I suggest here. In fact, they claim that in mixed and non-cued blocks (i.e., in maximum uncertainty conditions) the DLPFC acts as a completely stimulus-driven mechanism (i.e., *reactively*), while my study strongly supports the idea that in mixed contexts DLPFC is *proactively* engaged, as demonstrated by the finding of enhanced sustained activity.

The left DLPFC activation has been associated with the implementation of a task-setting in task *preparation*, as indicated by findings of cue-related activity in this region (i.e., Fassbender, Foxe, & Garavan, 2006). However, previous studies about attentional preparation did not separate sustained from stimulus-evoked activity. Thus, cue-related activity found in previous studies might reflect either a contingent task-set implementation in response to a cue, or a more sustained task-set implementation that is observed in absence of target items. My data clearly support this latter hypothesis. The observed activations in frontal brain areas seem to reflect a preparatory mechanism for dealing with potential distraction. I propose that augmented cognitive control is strategically implemented in potentially distracting contexts for guiding appropriate behavior, possibly by exerting a control over the execution of motor responses and by regulating the top-down attentional network.

The analysis of stimulus-evoked responses elicited by absent-distracter trials in different contexts showed significant differences in the left premotor cortex (please note that all participants used their right hand for responses). In particular, the higher premotor activation was found in the Pure block and the lesser activation was found in the mostly incongruent block, with an intermediate level of premotor activation in the mostly congruent block. It is worth underlying that these responses – even though they are stimulus-evoked – are all referred to absent-distracter trials and thus reflect genuine differences in the preparatory and strategic settings depending on the *context*, rather than being the correlate of different *stimulus* demands. These results are consistent with the idea of a gating of motor responses activated – likely by frontal control regions such as the left DLPFC and IFG – for the strategic filtering of irrelevant distracter-driven response tendencies.

In addition, some recent studies suggested a role for inferior parietal cortex in the proactive inhibition of motor responses (Jaffard et al., 2008; Boulinguez et al., 2009). As mentioned earlier in this discussion, the study by Jaffard and colleagues (2008) showed some interesting similarities with my study because it also used mixed and pure contexts. However, that study used baseline activation as an index of sustained and proactive control. This design raises some methodological issues. In fact, activity at rest might reflect the so-called default mode network, rather than some sustained motor inhibition as assumed by these authors (Jaffard et al., 2008). Rather, in my design sustained activity was modeled as a long block-wise regressor and was independent from baseline activity, which was not explicitly modeled (Friston, Holmes, Worsley, Poline, Frith et al., 1994; Friston, Zarahn, Josephs, Henson, & Dale, 1999). Additionally, the use of baseline activity for identifying sustained inhibition postulates that inhibition cannot occur as a stimulus-evoked process, as recognized by authors themselves (Jaffard et al., 2008). However, this assumption appears incompatible with the renowned findings of stimulus-evoked inhibition (e.g., Carter, Macdonald, Botvinick, Ross, Stenger et al., 2000; Botvinick et al, 2001; Bugg & Crump, 2012). In my study, I identified some brain areas in the inferior parietal lobule (IPL) that responded to incongruent events in the mostly incongruent block. These regions might exert an inhibition over response tendencies, as proposed by Jaffard and colleagues (2008). Nevertheless, my study shows that the IPL activation is clearly reactive rather than proactive. Differently from medial frontal regions such as anterior cingulate cortex (ACC), which is activated by *rare* conflict, IPL activity is associated with *frequent* conflict.

This finding also helps in differentiating the functional role of conflict under different contexts. When the probability of conflict is low, I observed strong ACC activation in response to conflict, accompanied by DLPFC and superior parietal activations, as commonly found in cognitive conflict studies (Botvinick et al., 2001; Kerns et al., 2004; Grandjean et al., 2012; see Schmidt, 2013, for a critical review). This pattern of transient activity might reflect conflict-evoked adjustments in cognitive control. As demonstrated in my former behavioral study (Chapter 2, Experiment 2), the engagement of the filtering mechanism is driven by reactive dynamics in a context where conflicting distraction is present in a minority of trials. The transient re-activation of DLPFC found for rare incongruent trials is fully compatible with this view. This result is also consistent with a previous study that found DLPFC and ACC activity for incongruent distracters in mostly congruent blocks (Grandjean et al., 2012). Even though DLPFC shows reactive bursts of activation when highly conflicting stimuli are detected in a low-conflict context, the global analysis of Mix blocks revealed that tonic DLPFC activity is sustained throughout potentially distracting contexts as compared to the Pure block. Instead, I did not observe DLPFC activity evoked by incongruent distracters in the mostly incongruent block. Differently, the ACC was also activated by frequent conflict, although much less strongly than by rare conflict. Indeed, frequent conflict probability activated IPL more strongly than rare conflict, possibly indicating response inhibition (Jaffard et al., 2008). These patterns of activity clearly differentiate conflict processing and cognitive control under different contexts in frontal and parietal areas.

5.11 Attentional and cognitive control act in concert for guiding the strategic filtering of potential distraction in the human brain

My data suggest that the gating on motor responses might not be the unique control function implemented by the distracter filtering mechanism. In a fMRI study of the flanker task (Durston, Davidson, Thomas, Worden, Tottenham et al., 2003), it has been shown that the prefrontal cortex (including dorsolateral areas) is involved in adjustments in control that subsequently lead to top-down biasing in the superior parietal cortex. Coherently with that study, my data suggest that cognitive control determines a sustained activation in the dorsal attentional network (left DLPFC and IFG) not only for modulating response readiness but also for implementing top-down modulations from frontal onto parietal and posterior sensory areas (Corbetta & Shulman, 2002; Szczepanski, Konen, & Kastner, 2010; Asplund, Todd, Snyder, & Marois, 2010; Esterman, Chiu, Tamber-Rosenau, & Yantis, 2009; Greenberg, Esterman, Wilson, Serences, & Yantis, 2010). These modulations might eventually result in an enhanced attentional orienting to targets and/or in an inhibitory modulation of the distracters' representation.

In my study, sustained and stimulus-evoked activity in the frontal lobe were not limited to the cognitive control network (ACC, DLPFC, IFG), but also showed enhanced sustained activation in the frontoparietal attentional system (Hopfinger et al., 2000; Woldorff et al., 2004; Slagter, Giesbrecht, Kok, Weissman, Kenemans et al., 2007). The finding of complex activation patterns that involve both conflict-related and attentional control systems has been also reported in a recent study that offers an integrate view by proposing that conflict detection triggers an enhancement of control in the frontoparietal attentional network for appropriate attentional preparation (Walsh et al., 2011). In that study, a cue signaled the predicted level of conflict (low, medium, high) in the upcoming trial. Higher conflict expectation led to increased activity in ACC during the cue-target delay and triggered an enhancement of activity in FEF and in the posterior parietal cortex (Walsh et al., 2011). However, that study used a cueing paradigm for manipulating conflict expectation and did not make a distinction between sustained and stimulus-evoked patterns of activity in the brain. As noted in the previous paragraph, brain activity measured in the cue-target delay period might be either cue-triggered or sustained. With the mixed block/event-related experimental design, I could genuinely isolate sustained activations for identifying the strategic and proactive components of cognitive and attentional control. Additionally to DLPFC and IFG activations, which have been already discussed in the previous paragraph, I also identified brain areas of the frontoparietal attentional network that were more active in Mix blocks than in the Pure block. In particular, sustained activity in mixed contexts was observed in the middle frontal gyrus (MFG) and in the medial frontal gyrus (MeFG), as well as in the intraparietal sulcus (IPS) and in the occipito-temporal-parietal junction, including portions of the precuneus and portions of the angular and lingual gyri. Posterior temporo-parietal areas have a determinant role in the attentional preparation network (Ruff & Driver, 2006). These regions typically show preparatory activity for suppressing irrelevant visual distracters in a variety of visuospatial attention studies (e.g., Hopfinger et al., 2000; Ruff & Driver, 2006) and are considered as parts of a network for directing attention towards the relevant locations in the visual field (Corbetta & Shulman, 2002; Egner & Hirsch, 2007). Critically, in my study the sustained activation of these posterior regions during Mix blocks might be related to the allocation of spatial attention towards the relevant parts of the visual field (i.e., target locations). Coherently with this suggested view, I observed an increase in occipito-parietal activity evoked by absent-distracters stimuli in Mix blocks (as compared to the Pure block). This finding might indicate an enhancement of attentional orientation to targets in potentially distracting contexts.

In previous studies, posterior parietal activity has been associated with augmented attentional orienting activity in frontal areas of the frontoparietal attentional system, particularly in FEFs (Hopfinger et al., 2000; Hung, Driver, & Walsh, 2005). Remarkably, I observed a significant sustained activation in FEF during Mix blocks. Although the role of FEF in visuospatial attention is still a matter of debate, this region seems to play a role in controlling the top-down orienting of attention (Corbetta & Shulman, 2002) by biasing activity in posterior brain regions and in visual sensory cortices towards stimuli that are relevant according to current task-set and goals. In particular, FEF might be engaged in a sustained fashion throughout a visual task for guiding attention to targets and for maintaining task-relevant information in the working memory (Offen, Gardner, Schluppeck, & Heeger, 2010).

The role of the frontoparietal attentional system is guiding visuospatial attention in the selection process, by both orienting towards task-relevant targets and by inhibiting the attentional orienting towards task-irrelevant distracters (Serences & Yantis, 2006; Kelley, Rees, & Lavie, 2013). Distraction suppression is now widely recognized as an active process that guides the attentional selection of relevant items by avoiding irrelevant distractions (Serences et al., 2004a; Ruff & Driver, 2006; Sawaki et al., 2012;

Payne & Allen, 2011). The suppression of distracters might take place at the sensory level in the visual cortex (Serences et al., 2004a; Ruff & Driver, 2006).

Recent studies indicate that the suppression of irrelevant distracter can occur at two stages: an initial stage in the precuneus where upcoming demands for distracter suppression are anticipated and a subsequent stage where processing of distracters is inhibited (Payne & Allen, 2011). Quite interestingly, I observed a significant brain activity in the precuneus in Mix blocks as compared to the Pure block. This precuneus activity was observed as both sustained and transient (i.e., block-wise in mixed contexts and event-related in response to absent-distracter stimuli).

The increase in precuneus activation during Mix blocks might indicate an anticipatory preparation for the inhibition of distracter representation (Payne & Allen, 2011). Coherently with this view, I provided evidence for the attentional suppression of distracter representations in extrastriate visual cortex in the mostly incongruent block. When the probability of distraction is high, and distracters always occur at the same retinotopic locations, sensory responses evoked by conflicting distracters are lessened as compared to a context with low probability of distraction.

Although I cannot establish a direct causal relationship between the recruitment of the filtering mechanism and retinotopic effect of distracter inhibition, it is tempting hypothesizing that this distracter suppression is driven by the recruitment of the filtering mechanism as indicated by simultaneous sustained activations in the frontoparietal network of cognitive and attentional control.

5.12 Conclusion

In my thesis, I proposed a novel theoretical framework, accompanied by an ad-hoc experimental manipulation (Pure-Mix Potential Distraction), for the investigation of the strategic mechanisms of attentional control. Guided by the proposed framework and by using the potential distraction paradigm, I demonstrated the existence of a cognitive-attentional mechanism for the strategic filtering of potential distraction in the human brain. I conducted a series of behavioral studies that demonstrate the generality of this mechanism, by showing its supramodal nature, and that characterized its reactive and proactive dynamics depending on contextual circumstances. I showed that this filtering mechanism is recruited in a variety of attentional situations, from capture by an irrelevant, salient stimulus, to more complex manipulations of conflict probability in spatial and non-spatial tasks.

Finally, I described the brain areas and networks involved in the recruitment of the filtering mechanism, thus completing the characterization of the proposed strategic filtering mechanism with neuroimaging methods. In particular, I showed that in Mix blocks a wide set of brain regions sustain the successful performance of excluding conflicting distracters and orienting visuospatial attention toward target stimuli. These regions includes DLPFC and IFG, which are thought to exert a different degree of cognitive control depending on probability of distraction by strategically gating response tendencies in PMC, and regions of the frontoparietal attentional network such as FEF and IPS, which are thought to bias brain activity in extrastriate visual cortex both for orienting towards targets and for retinotopically suppressing distracters-evoked activity. These results accomplish both the objective of identifying the functional brain network for dealing with potentially distracting contexts and the aim of correlating activity in these networks with their behavioral effect on stimulus-processing and stimulus-response associations depending on the context. I showed that prefrontal and frontal brain areas, commonly referred to the cognitive control system, such as DLPFC, IFG and ACC, might act in a sustained fashion and in concert with the frontoparietal attentional system. These mechanisms guide the control of behavior and the exclusion of irrelevant distracters in wide variety of control-demanding attentional tasks.

This thesis invests a topic of particularly broad interest and these results are of interest to both basic and applied scientists. In fact, the knowledge about brain mechanisms for dealing with distraction might be used in a wide set of everyday-life situations. In particular, potential implications of this study regards all those professional figures whose jobs require optimal attentional and cognitive performance in presence (either *actual* or *potential*) of distracting and conflicting stimuli. Such professional figures include, but are not limited to, photographers, athletes, air traffic controllers, and jet pilots.

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