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Composite targets in the Attentional Blink: New insights into the neural substrates of expectations, interference, switching & consolidation by means of MEG.

Sarah Mohammed

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School of Psychology
College of Science and Engineering
University of Glasgow

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Abstract

Top-down expectations allow us to quickly filter relevant events from the continuous stimulation by the environment. The Attentional Blink (AB) paradigm simulates such taxing situations in the laboratory (Raymond et al., 1992). For the first time, I employed composite events as targets in an AB paradigm. A first target (T1) was defined as 3 consecutive digits, while a second target (T2) was an ‘X’. In this way, unfulfilled expectations regarding T1 could be elicited by presenting partial targets, containing only 1 or 2 digits. My paradigm was specifically developed to allow the manipulation of global and local expectations independently. While global expectations are induced by relative trial frequencies and modulate target expectations prior to a trial, local expectations are induced by the consecutive presentation of digits that raise the expectation for a full target as a trial unfolds.

I predicted that, when expectation for the full target was globally high and locally raised to a maximum, disappointing these expectations would result in an AB in itself without a full T1 being presented (i.e. with 2 digits). Possibly, this AB could be even larger in magnitude than when expectations are met (with 3 digits). This was indeed the case when 3 digit trials were the most frequent event (Experiments 1, 3, 4 and 5). When global expectations for 3 digits were high, I observed the strongest AB with 2 digits, greater even than with the full T1. This suggests that maximally raised but violated expectations (with 2 digits) have a more detrimental effect on subsequent T2 processing than fulfilled expectations for the full target (3 digits).

I subsequently showed that this pattern could not simply be explained by enumeration of the digits (Experiment 2). Counting the digits was associated with the same blink magnitude with 1, 2 and 3 digits, suggesting that counting involves consolidation of digits into working memory as targets, a process unaffected by global expectation of trial types or the quantity of digits.

I then investigated the role of bottom-up signals in switching from raised expectations for the T1 to T2. I considered the roles of the post digit mask (Experiment 3), and of colour- (Experiment 4) and sound-based (Experiment 5) switching signals which marked the end of the digit event. Performance was improved considerably by removing the lag 1 mask after partial targets (1 digit and 2 digits), but not after full targets (3 digits). For partial targets, the

presence of a mask seems to conflict with the expectations for another digit, and the knock-on effect could be a delay in switching to T2. The AB magnitude for full targets is unaffected by the mask, suggesting consolidation of T1 and switching to T2 occurs immediately after the 3rd and final digit. On the other hand, marking the final digit with a colour or sound did not influence the AB in any digit condition. Taken together, this suggests that in this paradigm, top-down expectations play a much stronger role than bottom-up factors.

I then manipulated the relative frequencies of the digit events to investigate how top-down global and local expectations contributed to the AB magnitudes. In Experiments 6 and 7, the 3 digit event became increasingly rarer as the 2 digit event became more frequent. Overall, I found a reversal of the previous pattern: The AB with 3 digits became increasingly stronger than the AB with 2 digits. My findings suggest that global expectations influence the build up of local expectation increments with each presented digit, yet this occurs in a non-linear fashion.

Two MEG experiments further show that raised and subsequently violated expectations for T1 have a distinct neural signature (MEG Experiment 1), which cannot be accounted for by the act of counting the digits (MEG Experiment 2). In particular, beta-band oscillations seem to code for both the target processing and the rapid changes in local expectations during the trial. A key finding from MEG Experiment 1 was the similar widespread beta power decrease for 2 digits and 3 digits until 0.6 s, when the conditions dissociated into a frontal power increase for 2 digits while the 3 digit power decrease continued. Tentatively, I suggest that this could represent the building of expectations for the full target (power decrease) and the subsequent violation of expectations (frontal power increase) in the 2 digit trials.

An M300 to each digit suggests that all digits enter the global workspace and are consolidated into working memory; a finding which is corroborated by the theta-band results. Meanwhile, alpha oscillations were more posterior and appear to code for the processing of full targets only (3 digits in MEG Experiment 1, and 1, 2 and 3 digits in MEG Experiment 2).

To summarise, my key finding is that an AB can be elicited without a T1 actually occurring. Building up expectations about the T1 event within a trial can alone induce an AB. Furthermore, built and subsequently violated expectations for the T1 event seem to be coded in the brain by widespread

modulations of beta oscillations. I discuss the findings with relation to several models of the AB. In particular, my behavioural and MEG findings fit well with the “Robust State” hypothesis (Kessler et al., 2005a), set within the wider “Global Workspace” framework (Dehaene et al., 2003a), which accounts for the dynamic interaction of top-down expectations with bottom-up visual processing. I envisage this novel aspect of expectations complementing the growing knowledge of the AB and emphasising the importance of network dynamics as a metaphor for the parallel distributed processing in the brain.

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Abbreviations

α	Alpha
ß	Beta
γ	Gamma
θ	Theta
AB	Attentional Blink
ACC	Anterior Cingulate Cortex
BA	Brodmann Area
BB	Boost and Bounce model of AB
CSD	Cross-Spectral Density
CCNi	Centre for Cognitive Neuroimaging, at Glasgow University
DLPFC	Dorsolateral Prefrontal Cortex
EEG	Electroencephalography
ERF	Event-Related Field
ERN	Error-Related Negativity
EPSP	Excitatory PostSynaptic Potential
eSTST	episodic Simultaneous Type, Serial Token model of AB
fMRI	functional Magnetic Resonance Imaging
fT	femto Tesla ($1fT=10^{-15}T$)
GW	Global Workspace model of the AB
HIPS	Horizontal segment of the IntraParietal Sulcus
ICA	Independent Component Analysis
ISI	Inter-Stimulus Interval
MANOVA	Multivariate Analysis of Variance
MEEG	Magnetoencephalography and electroencephalography
MEG	Magnetoencephalography
ns	not significant
PFC	Prefrontal Cortex
PPC	Posterior Parietal Cortex
RS	Robust State hypothesis of AB
RSVP	Rapid Serial Visual Presentation
SD	Standard Deviation
SNR	Signal-to-Noise Ratio
SOA	Stimulus Onset Asynchrony
SQUID	Superconducting Quantum Interference Device
STST	Simultaneous Type, Serial Token model of AB
T	Tesla (Measure of magnetic field strength)
T1	First target
T2	Second target
T2|T1	Performance on T2, given T1 was correct
TLC	Temporary Loss of Control account of AB
TFR	Time-Frequency Representation
TTI	Target-to-Target Interval

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Author’s Declaration

I declare that this doctoral thesis is my original work, unless otherwise referenced in the text.

Chapter 1 - General Introduction

Temporal Attention

The outside world provides a continuous flow of almost infinite information. We would be completely overwhelmed were we not capable of rapidly selecting relevant information from background noise, as well as chunking relevant events together based on our past experience and current goals. Research into temporal attention investigates how we cope with multiple concurrent stimuli and rapid switching from one task to another. Performing two tasks within a short time period is taxing: For example, trying to recall a telephone number while entering your PIN number into a bank machine is tricky. Temporal attention has been investigated experimentally by presenting stimuli within a rapid serial visual presentation (RSVP) stream, asking participants to report or respond to several targets. Dual target deficits, in particular, are studied using the Attentional Blink (AB), Repetition Blindness (RB) and Psychological Refractory Period (PRP) paradigms.

The Attentional Blink

In a standard AB paradigm, two targets must be detected or identified within RSVP streams of around 10 items per second. If the first target (T1) is successfully reported, the following target (T2) is often missed when the targets are presented within 500 ms of each other (Raymond et al., 1992, Broadbent and Broadbent, 1987, Weichselgartner and Sperling, 1987). Performance is high when the interval between targets is increased, and when only one target must be reported. This suggests it is the need to attend to two separate targets in a short amount of time that underlies the AB. Current models of the AB are described later in this chapter.

In a typical AB paradigm, there is no task switch between T1 and T2 (e.g. both targets belong to the same category of “letters”). Lag[1] 1 sparing is observed in such situations: this refers to the high performance for T2 when it immediately follows T1 (Raymond et al., 1992). Visser and colleagues (1999)

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[1] In the standard AB paradigm, “lag” refers to the temporal position of T2 relative to T1. E.g. T2 is at lag 1 when it immediately follows T1, while a distractor occurs between the targets when T2 is at lag 2.

performed a systematic review of the literature involving over 100 experiments. They concluded that lag 1 sparing occurs when T1 and T2 are similar, in paradigms without a task switch and those involving a one dimensional task switch (e.g. a switch in category between T1 and T2). Lag 1 sparing is frequently absent when a multi-dimensional switch is required (e.g. changing task and category).

There has been some debate about whether the T2 deficit in paradigms employing a task switch should be called an “AB”. Switching between tasks takes time, even with predictable switches (Rogers and Monsell, 1995): the cost of switching relates to the need to reconfigure the task set. Potter and colleagues (1998) suggested that the term “AB” should be reserved for tasks without a switch, where lag 1 sparing was present. When lag 1 sparing was absent, they argued that the deficit on T2 was not a pure AB. Instead it could result from a mixture of the AB and a task switch, or purely a task switch. On the other hand, Kawahara and colleagues (2003) argued that the term “AB” could encompass tasks with and without a switch, suggesting that a task switch simply increased the delay in attending to T2. In agreement with this is Marti and colleagues’ (2012) interpretation of Peterson and Juola’s (2000) findings. T2 performance was compared between switch (switching between spatially different RSVP streams) and no-switch (single RSVP stream) conditions. The AB magnitude was identical with a Stimulus Onset Asynchrony (SOA) greater than 240 ms (lag 2). Conditions differed only in terms of lag 1 sparing: sparing was present in the no-switch condition and absent in the switch condition (Peterson and Juola, 2000, Experiment 1). Taken together with Visser’s (1999) review, this suggests that the term “AB” is suitable when a task switch is present, with task switching mainly affecting performance at lag 1.

Typically an AB is induced when 10 items per second are presented in the RSVP stream (SOA = 100 ms). However several groups have found an AB with slower presentation rates. Using standard visual AB paradigms, Gross and colleagues (2004) used an SOA of 146 ms, while Potter and colleagues (1998) presented items every 120 ms or 135 ms. Experiments with more complex targets have also used relatively slow RSVP streams. In a study where targets were words and the task included spatial aspects, Duncan et al, (1997) used an

SOA of 250 ms. In an experiment with pictures as stimuli, the SOA was 144 ms (Trippe et al., 2007).[2]

Repetition Blindness

Repetition Blindness (RB) is a reduced performance for reporting the second repetition of a target within RSVP streams (Kanwisher, 1987). An example from everyday life is failing to notice the repetition of a word when reading a sentence. The deficit on the repeated target is found with various stimuli (e.g. words, letters and pictures), and when targets are specifically defined (e.g. the letter "A") or belong to the same category (e.g. a vowel) (Kanwisher et al., 1996). The "Type-token" theory relates RB to a failure to individuate the second repetition of the target (Kanwisher, 1987). Each target is identified as a "type" (e.g. an "A"). However, only the first instance of the "A" is episodically labelled as a "token". Therefore the second repetition is not consciously perceived. RB and the AB are similar phenomena, with a strong T2 deficit when targets are presented within a short time interval. However, the effects are dissociable (Chun, 1997, see Arnell and Shapiro, 2011 for a recent review).

Psychological Refractory Period

The Psychological Refractory Period (PRP) refers to the response delay for a second task when performing two tasks within a short time period (Pashler, 1994). Like the AB, the deficit lasts for several hundred milliseconds. Unlike the AB and RB paradigms where responses are made after the trial, PRP tasks require speeded responses to the tasks. Online response selection is therefore a key determinant of the PRP (cf. Jolicoeur, 1999b). In a comparison between PRP and AB, Jolicoeur (1999a, b) showed that the complexity of the response to T1 influenced performance when the T1 response was speeded (PRP) but not when it was unspeeded (AB). This replicated the finding by Ward and colleagues (1996) that the difficulty of the T1 response (2 vs. 4 alternative discrimination task) did not modulate the AB magnitude. A task switch, often between modalities, is also used in PRP paradigms. It has been suggested that the AB and PRP are highly related phenomena, reflecting different aspects of the same

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[2] The SOA I used is within this range: SOA is 186 ms in Behavioural Experiments 1-7 (Chapters 2-7) and 150 ms in the behavioural pilot for the MEG (Chapter 8).

deficit: the delay in processing a T2 (PRP) could relate to a blinking of a T2 (AB) (Jolicoeur et al., 2000, Marti et al., 2012).

The Current Paradigm

The paradigm used in the following behavioural experiments is based on an AB paradigm, yet with a complex multi-part T1 and a task switch. Participants attend to an RSVP stream of letter distractors (SOA = 186 ms), imbedded with digits (0, 1, 2 or 3 digits) which may be following by the letter X. The majority of experiments (Behavioural Experiments 1, 3-7) involve target detection: The task involves participants responding whether or not they saw 3 digits (T1) and the letter X (T2). In the counting experiment (Behavioural Experiment 2) participants count the digits (T1) and detect the letter X (T2). Unspeeded responses are made to the targets. The T1 digit event requires a 2 alternative-forced choice (AFC) response (3 digits/not 3 digits) in the detection experiments, and a 4 AFC response (0/1/2/3 digits) in the counting experiment. Although my task is designed to be an AB experiment, it could involve aspects of both RB and PRP. The repetition of digits within the T1 event could result in RB. The task switch between T1 and T2 could lead to a delay in processing T2 at short lags. Yet since participants respond after the trial in my task and performance is expressed in terms of accuracy (not reaction time), the findings are more likely to mirror the AB rather than PRP literature.

Expectations and the Attentional Blink

I will now focus on the AB, since my paradigm most closely resembles an AB paradigm, firstly by the need to attend to 2 targets which are temporally separated by various lags and secondly by the unspeeded response after the trial. Specifically, I will discuss the influence of target expectations on performance in the AB.

Perception is strongly guided by top-down expectations induced by current goals and previous experience of the outside world. But how do expectations influence performance when we are highly taxed, for example having to select relevant information at high speed? How quickly can we chunk information together and how fast can we switch between different target events? Furthermore, what happens when top-down influences have biased us towards anticipating a particular event, yet our expectations are disappointed? Will there be downstream effects for processing subsequent information?

Expectations about task difficulty have been previously shown to modulate the AB magnitude. When conditions were presented in blocks and participants informed of the difficulty of the upcoming T1 task, there was a greater magnitude AB in the hard condition than both the easy and medium conditions (Shore et al., 2001). However, when conditions were mixed and unannounced, T1 difficulty did not affect AB magnitude (McLaughlin et al., 2001, Experiment 1). Counter-intuitively, the AB magnitude was larger when participants could anticipate the upcoming difficulty in blocked trials than when preparation was not possible in mixed trials. When participants anticipated a hard target, it seems that they focussed more narrowly on the detection of this target, naturally assuming this strategy would aid their performance. However, when unaware of difficulty, they perhaps allocated attention more diffusely. This fits with recent work which suggests that “overinvestment” in the form of a highly focused mental state, dedicated to finding targets, contributes greatly to the AB impairment (Taatgen et al., 2009, Olivers and Nieuwenhuis, 2005, Olivers and Nieuwenhuis, 2006, Arend et al., 2006, Wierda et al., 2010).

Further studies suggest that unexpected T1 events induce a greater blink than if they are expected (Crebolder et al., 2002, Martens et al., 2006). Oddball events strongly capture attention (see Ranganath and Rainer, 2003 for a review) which is beneficial for processing the unexpected target itself. But within a dual target setting such as the AB, subsequent targets suffer from the excessive attention to T1. Accordingly, infrequent T1s were associated with a greater AB magnitude than frequent T1s (Crebolder et al., 2002, Experiment 5). Likewise when the identity of T1 was invalidly cued before a trial (in 25% of all trials), generating false expectations about target identity, there was a greater blink than on valid trials (Martens et al., 2006). It seems likely that participants learned to anticipate the frequent validly-cued targets. When the T1 event deviated from their frequency-based global expectations, perhaps the enhanced capture of attention by that target contributed to the larger magnitude AB.

Expectations developed prior to a trial can clearly modulate visual processing within the AB. However, the visual attention system is highly adaptable and we can react to rapidly changing events as they unfold. So what will happen if expectation for an event is gradually built up over time within a trial? If expectations for T1 are incrementally raised, yet the final event deviates from these expectations, will there be a consequence for T2? Could these unfulfilled expectations interfere with processing of a subsequent target? I aimed to shed light on these issues by employing a composite first target. That is, T1 was defined as 3 consecutive digits so that unfulfilled target expectations could be elicited by presenting partial targets containing only 1 or 2 digits. Expectations are influenced by top-down signals relating to the target template. At the start of the experiment, expectations for the target may be strongly guided by task instructions: In this paradigm, the goal for the T1 task is to find 3 consecutive digits. As the participant gains practice during the experiment, they may learn the relative probabilities of the digit conditions, which could in turn influence expectations for the full T1.

This paradigm provided a novel way to investigate the role of target expectations under high temporal processing pressure, especially with respect to the question of whether it is particularly difficult to switch away from high but unfulfilled expectations. In other words: would it be particularly hard ‘to let go’ when high expectations remained unfulfilled? This paradigm further allowed varying local and global expectations independently. While local expectations refer to the build-up of target expectations in a given trial with each additional target increment (digit) presented, global expectations refer to factors like relative trial frequency (or pre-trial cueing), which I expected to globally modulate the local build-up rate. That is, in an experiment where target events (3 digits) are very frequent the build-up rate of local expectations should be high, whereas in an experiment where 3 digit events are rare the build-up rate should be low.

Current models of the AB

Expectations have been tentatively explored within the AB literature and it seems that globally raised and subsequently disappointed expectations induce a stronger AB (e.g. Martens et al., 2006). However, existing accounts of the AB were not designed to incorporate global expectations, let alone incrementally increasing local expectations. My novel paradigm differs from a standard AB paradigm in 2 ways: T1 is revealed over time, and there is a task switch between T1 (digits) and T2 (letter). As such, it is impossible to make firm predictions regarding my paradigm without extending the existing accounts. I will, however, draw tentative predictions from some AB accounts as a starting point for my rather exploratory paradigm. It is noteworthy that the temporary loss of control (TLC) account (Di Lollo et al., 2005) was designed to explain the absence of an AB with 3 or more consecutive targets (i.e. “spreading the sparing”, Olivers et al., 2007). Several studies found that no AB occurs when reporting the identities of 3 or more consecutive targets, providing they are of the same category and not separated by distractors (Di Lollo et al., 2005, Kawahara et al., 2006, Kihara et al., 2008, Nieuwenstein and Potter, 2006, Olivers et al., 2007). It is an extension in time of lag 1 sparing (Raymond et al., 1992). This phenomenon suggests that the visual attention system can handle multiple target items presented in sequence. This is relevant for my paradigm, suggesting that consecutive target information - T1 composites in this case - can be processed in sequence without generating an AB per se.

The TLC account focuses on the control over the configuration of the current input filter (Di Lollo et al., 2005). While the central processor is busy with targets, it cannot send maintenance signals to the filter. So configuration of the filter can be disrupted by subsequent items which are categorically different from T1. There is agreement that in the AB, delaying T2 processing leads to the T2 representation either decaying or being substituted by following distractors at a pre-conscious, perceptual level (Enns and Di Lollo, 2000, Giesbrecht and Di Lollo, 1998, Vogel and Luck, 2002). Although it explains “spreading the sparing”, the TLC account does not incorporate increasing expectations with each additional target. The loss of control which causes the blink is the result of the T1 backward mask, which is indistinguishable between digit levels in my paradigm. Hence, the TLC account in its present form would suggest an equal sized AB for all digit events, disregarding the number of digits and their status as full T1 (3 digits) or partial T1 (1 or 2 digits).

Limited capacity accounts of the AB in general propose that T1 processing depletes cognitive resources, resulting in fewer resources available for T2 (see Shapiro et al., 1997 for reviews, Dux and Marois, 2009). For example, in the 2 stage model (Chun and Potter, 1995), after initial rapid detection of target features, a capacity-limited processing step is necessary to consolidate targets into working memory. During RSVP conditions, a bottleneck develops in the 2nd stage with T2 consolidated only once T1 consolidation is complete. I can draw 2 alternative predictions from this consolidation-based account. If partial targets could be immediately filtered out as non-targets online, I envisage that only the full target condition (3 digits) would induce an AB. Alternatively, 1 and 2 digit events could also be consolidated as partial targets and the decision about target vs. non-target could be conducted offline before responding. Partial targets would then also induce an AB that would correlate with the duration of consolidation, i.e., a strong AB with 3 digits, a moderate AB with 2 digits and a mild AB with 1 digit. However, capacity-limited accounts fail to explain some recent AB findings including “spreading the sparing” and “over-investment”(see Martens and Wyble, 2010 for a recent review). While it is clear there are capacity-limitations in working memory (Miller, 1956), they may not be the root cause of the AB. Therefore, I think it unlikely that a monotonic AB magnitude will be seen with increasing digit level.

The initial AB theory, however, placed emphasis on the brief suppression of information processing to distractors which followed T1 (the Temporary Suppression model, Raymond et al., 1992). The suppression was the result of interference between the leading target and the next distractor. Recent accounts (the Robust State hypothesis, Kessler et al., 2005a; the Boost and Bounce model, Olivers & Meeter, 2008; the Episodic Simultaneous Type, Serial Token model, Wyble et al., 2009) have built on this, suggesting it is the dynamic interaction between the inhibition and excitation which causes the blink, although the sources of the inhibition and excitation differ between accounts.

The Robust State (RS) hypothesis (Kessler et al., 2005a) of the AB is based on recurrent spreading of activation within networks (cf. Houghton and Tipper, 1996, Rumelhart and McClelland, 1986). The RS hypothesis evolved from neurophysiological findings regarding the dynamics of excitation and inhibition within attentional networks (Gross et al., 2004, Hommel et al., 2006, Kessler et al., 2006). Here the enhancement of T1 is the direct result of the interference from the post-T1 mask. The network reacts to the mask by suppressing all non-T1 activity, which enhances the representation of T1, but results in a stable suppressive state. However, it is this stability which hampers the transition to T2 processing. The basic concept of RS implies two important things. Firstly, the transition between stable states naturally incorporates task-switching: If T2 is further away from T1 in state-space (e.g. different category and colour) then the transition will be more effortful. Secondly, the T1-mask may not be the only factor in generating a robust state that is hard to perturb and induces an AB (Kessler et al., 2005a, p. 1038).

The Boost and Bounce (BB) account (Olivers and Meeter, 2008) uses a computational model to explain the AB, and extends the “over-investment” hypothesis (Olivers and Nieuwenhuis, 2005, Olivers and Nieuwenhuis, 2006, Shapiro et al., 2006). Boosting (or enhancing) of target representations activates gate neurons above threshold so targets can enter working memory. Meanwhile, distractors are bounced (or inhibited) to prevent their entry. The RS and BB accounts both explain why over-emphasis on T1 may result in a processing problem for T2. In both accounts, over-emphasis on T1 results in enhanced T1 processing which subsequently leads to a more robust suppressive state or a stronger bounce, respectively, during the AB period. As described above, quite counter-intuitively, a slight distraction from the task leads to a smaller AB (Arend et al., 2006, Taatgen et al., 2009, Olivers and Nieuwenhuis, 2005, Olivers and Nieuwenhuis, 2006), while knowing that a hard T1 will occur enhances the AB (Shore et al., 2001). If I extrapolate these considerations to target expectations in this paradigm, then partial targets could pre-activate or boost the T1 representation in anticipation of the full 3 digit event, which could then hamper the switch to T2 (cf. Kessler et al., 2005a, Kessler et al., 2006). In agreement with the cueing effects reported by Martens and colleagues (2006), this could be especially hard when the final 3rd digit does not arrive to complete the target; maximally raised expectations (i.e., strongest pre-activation) are violated during the time period when the cognitive system has to switch to T2.

The Episodic Simultaneous Type, Serial Token (eSTST) (Wyble et al., 2009) and the earlier STST computational models (Bowman and Wyble, 2007) propose that attention allocation is determined by competition between excitation from incoming targets and inhibition from encoding targets in working memory. This dynamic interplay acts to encode targets into separate attentional episodes (cf. Wyble et al., 2011) or event files (cf. Hommel and Akyurek, 2005). Several successive targets are encoded in a single attentional episode, which explains “spreading the sparing”. This aspect of the eSTST model is particularly relevant to my paradigm, where consecutive digits could be encoded into a single episode for consolidation into working memory.

The Global Workspace (GW) theory of the AB, implemented as a computational model by Dehaene and colleagues (Dehaene et al., 2003a, Sergent et al., 2005, but also see Baars, 1997, , 2005), reveals how widespread broadcasting across the brain is necessary to consciously report targets. It could be regarded as the wider framework for the RS hypothesis (Kessler et al., 2005a). Like the RS hypothesis, it is based on the idea of recurrent activation within networks, and links neurophysiological findings with conscious reports. While masks play a key causal role in the AB in the RS hypothesis, competition between T1 and T2 is at the heart of the GW model. In the GW theory, all targets initially cause bottom-up activation in low-level visual cortex. If activation exceeds a threshold, target information enters the global workspace. Activated workspace neurons in the temporary global network suppress their neighbours, and recurrent processing within the workspace (cf. development of a robust suppressive state, Kessler et al., 2005a) leads to a broadcasting of information. This 2nd top-down amplification step is crucial for the large-scale integration between specialised processors in distant brain regions, including the parietal and frontal cortex. In the AB, T2 is blinked because it cannot enter the global workspace: The broadcasting of T1 inhibits T2 access. The P300, in this model, is associated with the "global access" of targets (Dehaene et al., 2003a, p8520), in keeping with the replicated findings that the P300 is absent when T2 is not consciously perceived (i.e. when T2 is blinked). It should be stated that, in its present form, the GW computational model (Dehaene et al., 2003a) cannot account for lag 1 sparing or spreading the sparing (cf. Martens and Wyble, 2010), because of the inherent capacity limitation of the GW. However, this model provides a framework for the dynamic interaction between bottom-up and top-down processing, and as such, is highly relevant to my investigation into the role of top-down expectations in temporal attention.

Neural correlates of the Attentional Blink and Expectations

Neurophysiological findings provide further evidence for such a dynamic equilibrium between excitation and suppression in the AB (see Kessler et al., 2006 for reviews, Janson and Kranczioch, 2011), as suggested by RS, BB and eSTST accounts (Kessler et al., 2005a, Olivers and Meeter, 2008, Wyble et al., 2009). For example, the P300 (and the M300, its magnetic counterpart) is thought to reflect consolidation into working memory (Donchin and Coles, 1988, Verleger, 1988) or access to the global workspace (Dehaene et al., 2003a), and is greatly modulated by AB manipulations (Arnell et al., 2004, Kessler et al., 2005a, Kessler et al., 2005b, McArthur et al., 1999, Shapiro et al., 2006, Vogel et al., 1998, Wierda et al., 2010). Counter-intuitively, in trials where a mask followed T1, the M300 to T1 peaked earlier than in unmasked trials (Kessler et al., 2005a), while the T2-M300 was delayed in keeping with previous findings (Vogel and Luck, 2002). These results suggest that excitation by T1 can even be boosted (reduced latency) by the occurrence of a mask. Yet this occurs at the expense of increased suppression, resulting in a highly stable suppressive state that is the direct consequence of the competition induced by the T1-mask. This robust state would have to be actively perturbed to switch to T2. The efficiency to accomplish this perturbation will determine performance on T2, hence the T2-M300 is even delayed on trials with no blink.

Furthermore, it has been proposed that communication between distant parts of attentional networks occurs via neural synchrony (Fries, 2005; Fries et al., 2001; Varela et al., 2001). Within a target-related network, AB performance was directly related to the synchronization status of the network within the beta (β) band (Gross et al., 2004, Kranczioch et al., 2007). In trials without a blink there was enhanced synchronization to T1 reflecting a stable processing state which, according to the RS hypothesis (Kessler et al., 2005a), would have to be perturbed (i.e. de-coupled; see Rodriguez et al., 1999 for a similar notion) in order to switch to T2. This prediction was supported by the enhanced desynchronization before a successful synchronization was observed for T2. Together with the T1-T2 M300 findings, this is substantial support for a dynamically changing equilibrium between excitation and suppression, including a need for active perturbation as proposed by the RS hypothesis.

Temporal expectations are also reflected in the oscillatory activity of the brain, particularly in the alpha (α) and beta (β) bands. Several studies into visual expectations have revealed anticipatory α power decreases (Bastiaansen and Brunia, 2001, Klimesch et al., 1998, MacLean and Arnell, 2011, Rohenkohl and Nobre, 2011), which may reflect increased thalamocortical transfer (cf. Hanslmayr et al., 2011). Priming the cortex in this way would be advantageous if the stimulus arrives as expected, as processing may be quick and efficient (cf. Bastiaansen and Brunia, 2001).

Under RSVP conditions, expectations set up before the trial (MacLean and Arnell, 2011) and those which build within the trial (Gross et al., 2006) can modulate oscillatory activity. Anticipatory α power decrease before the RSVP stream was related to performance on the AB (MacLean and Arnell, 2011). On blink trials where T2 was presented at short lags, there was an α decrease. Likewise, anticipatory α decreases were observed for long lags where both targets were successfully reported. This concurs with over-investment theories of the AB, and further suggests that global expectations are beneficial when there is sufficient time to process both targets (long lag trials). In the ß band, the predictability of the target onset was associated with phase synchronization within the AB target-related network (Gross et al., 2006). As the likelihood of a single target occurring increased within a trial, there was a greater difference between synchronization to the target and desynchronization to the pre-target distractor. Local expectations for the occurrence of a target are thus reflected in the ß band synchronization profile, which is highly relevant to my paradigm. The network may become increasingly pre-activated by expectations, while distractors are suppressed. Again, such priming of the network would aid processing of the expected target. That said, within an AB setting, stability to a highly expected T1 could delay switching to T2, as it would be necessary to actively de-couple the stable state in order to switch.

Aims of the current study

My main hypothesis is that expectations of a composite T1 could be a major top-down influence that enhances the robustness of the T1 event, and I predict that this stability will be reflected in the underlying neural pattern. In the behavioural experiments, I focused on the implications of partial T1 events that maximally raise but subsequently disappoint the participant’s expectations, in contrast to fulfilled expectations with full T1 events. Accordingly, with the first experiment I aimed to investigate whether it was at all possible to obtain a stronger AB effect with a partial target than with a 3 digit full T1. To this end, global target expectations were raised by making 3 digits the most frequent digit event. It was thought that, in turn, a 2 digit partial target would maximally raise local expectations in form of pre-activation yet, in the absence of target completion, this strong pre-activation would have to be suppressed in order to allow for a switch to T2. I expected that this could result in higher costs for T2 processing than the actual consolidation of a highly anticipated full T1 event.

Chapter 2 - Behavioural Experiment 1: Consolidation versus unfulfilled expectations

For the first time, I investigated the impact of a composite T1 on the AB. The general method for all experiments employed an RSVP stream consisting of targets among capital letter distractors. The T1 task was to detect the presence of 3 consecutive digits. Importantly, to build up expectation for a full T1 (3 digits) within the trial, 1 and 2 digit events were also presented. I stressed to participants that 1 and 2 digit sequences did not constitute a target. Correct responses on T1 were "T1" on 3 digit trials and "no T1" on 1 and 2 digit trials. The standard T2 task involved detecting the letter X. In the first 5 behavioural experiments, I kept the number of full target trials (full T1: 3 digits) equal to the number of partial target trials (partial T1: 1 digit and 2 digits). Crucially, the task required solely the detection of the full T1: Identification of each individual digit could result in a higher working memory load with increasing levels of T1 compositionality. Since the focus here was on the role of target expectations, it was important to balance memory load across digit conditions.

Although no existing account makes specific predictions for the paradigm employed here, some tentative hypotheses can be extrapolated. To recap from Chapter 1, I can draw 2 alternative predictions from accounts based on capacity-limitations in working memory (eg. the 2 stage model, Chun and Potter, 1995, see Shapiro et al., 1997 for a review), depending on whether partial targets enter working memory. If only the 3 digit event enters working memory, bottleneck accounts might predict an AB solely with a full 3 digit T1, and not with partial T1s (1 digit and 2 digits). However, all digits could be consolidated in working memory as potential parts of the full target. In this case, capacity limitation accounts would predict that a stronger AB magnitude with increasing size of the T1 composite event; i.e. largest AB with 3 digits, moderate AB with 2 digits and mild AB with 1 digit. The TLC account (Di Lollo et al., 2005) in its present form would likely predict an equally sized AB with 1, 2 and 3 digits. Based on the general idea of the RS account (Kessler et al., 2005a), one would predict a strong AB with a partial target of 2 digits when expectations are maximal; possibly even a larger AB than with the full target (3 digits). Regarding the AB size in these two conditions there is a 'race' between consolidation vs. unfulfilled expectations. Does consolidation of the full T1 event and subsequent switching to a letter T2 take longer than switching away from maximally raised but disappointed expectations? In this experiment, the most frequent event was 3 digits (same trial frequency as 1 + 2 digits), allowing for practice and therefore efficient consolidation of the full T1. This enabled us to test under favourable conditions whether switching away from maximally raised but disappointed expectations (with 2 digits) could actually generate a stronger AB than efficient consolidation of a full T1 (3 digits).

Method

Participants

Twenty participants (10 male, 24.52 years ± 7.74) were recruited from the University of Glasgow community. Different participants took part in each experiment. In all experiments, participants reported normal or corrected vision. The studies were conducted in accordance with the declaration of Helsinki and were approved by the local ethics committee. Participants provided written informed consent, and received either payment or undergraduate course credits.

Apparatus and stimuli

All experiments were designed using E-Prime (Version 1.1; PST Inc., Pittsburgh, PA, USA) and run on a standard PC (refresh rate 59.973 Hz, 19 inch monitor, resolution 1024 x 768 pixels). Viewing distance was 55 cm and stimuli subtended an angle of 3°. Testing took place under dimmed lighting conditions. Stimuli were presented in black 64 point Geometric 231 Light BT font in the centre of a grey screen (RGB 65, 65, 65). Once initiated by the participant, a fixation cross was presented centrally for 800 ms, followed by a 200 ms blank screen. The subsequent RSVP stream consisted of 15 single items (letters and digits) occurring serially with SOA of 186 ms (ISI=106 ms). Distractors were capital letters, drawn from the alphabet without replacement. Certain letters (B, D, I, J, K, O, S, Z) were excluded as they resembled digits or the letter X. The composite T1 comprised 1, 2 or 3 consecutive single digits, which included numbers between 1 and 8, e.g. a 3 digit T1 could be “2-8-5”. The order of the digits was randomly selected, however the same digit was not repeated within a sequence (e.g. “1-4-1” was not possible). T2 was the letter X, which could appear at lag 1 (186 ms final digit onset asynchrony), lag 2 (372 ms), lag 3 (558 ms), lag 4 (744 ms) and lag 5 (930 ms) (Figure 1). Lag refers to the position of T2 with respect to the onset of the final digit, irrespective of whether there was a full T1. T1 had 6 possible starting positions, between the 2nd and 7th position in the stream, ensuring targets did not occur in the first or final position. Trials of the different conditions were presented in a randomised order.

Procedure and design

Participants made an unspeeded response on the keyboard at the end of the trial to the question: “How many types of targets did you see? 0, 1 or 2”. If they answered 1 target, they were asked: “Did you see: 3 digits in a row or the letter X?” A key point is that I required participants to simply detect the presence of 3 digits and the X, not to remember the identity of the digits. I stressed the importance of accuracy.

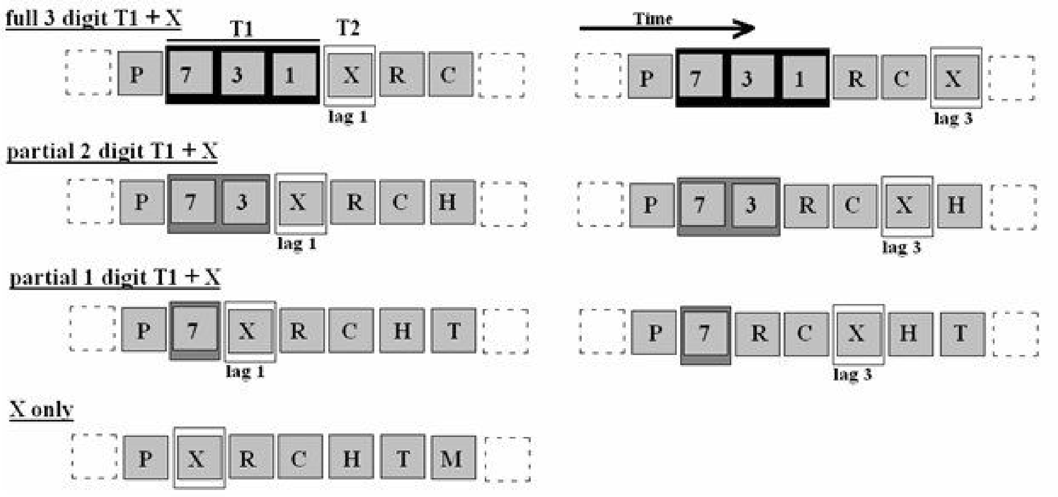

Figure 1 – Behavioural experimental conditions. Full T1 & T2 (3 digits + X), partial T1 & T2 (2 digits + X; 1 digit + X) & T2 only (0 digits + X) conditions. T2 is shown at lag 1 (left) & lag 3 (right). Full 3 digit T1 highlighted in black, partial T1s in grey & T2 in white.

It was a 4x5 repeated measures design with 2 factors – condition (3 digits + X, 2 digits + X, 1 digit + X and 0 digits + X (i.e. T2 only baseline)) and lag (lags 1-5) (Figure 1). Additional conditions without a T2 were trials containing only 3 digits, 2 digits, 1 digit or distractors. The dependent variable was performance on T2, given T1 was correct (T2|T1) in trials with digits and T2, and percent correct on the target in T2 only (0 digits + X) trials.

In Experiments 1 to 5, trials containing digits and a T2 were equalled in number for those with a full T1 (3 digits) versus those with a partial T1 (1 and 2 digits). The number of trials in all conditions is detailed in Table 3 in the Appendix A. There were 12 trials per lag in the 3 digits + X condition, 6 trials per lag with 2 digits + X, 6 trials per lag with 1 digit + X and 12 trials per lag with 0 digits + X[3]. The global probability of seeing 3 digits is 0.4, 2 digits is 0.17 and 1 digit is 0.17. The conditional probability of seeing the full T1 (3 digits) increases from 0.55 after a 1st digit has been presented (P(3 digits|1 digit)) to 0.71 after a 2nd digit (P(3 digits|2 digits))[4]. The conditional probability of seeing a 2nd digit after 1 digit is 0.77 (P(2nd digit|1 digit). Participants completed 14 practice trials and 300 experimental trials. Short breaks could be taken as needed and the experiment lasted approximately 40 minutes.

For statistical analysis of each experiment, MANOVAs were first applied to individual accuracy percentages (T2|T1) to investigate T2 performance over lags at 4 levels of T1 compositionality (3, 2, 1 and 0 digits). MANOVAs were used rather than repeated measures ANOVAs since there were violations to the assumption of sphericity (Mauchley test, $p < .05$) in all experiments. MANOVA does not assume sphericity between the multiple repeated measures, and so is preferable to the ANOVA in this situation (see O'Brien and Kaiser, 1985). I used planned comparisons at lag 1 (Experiment 1 only), lag 2 and lag 3 as a measure of performance within the blink period. Planned comparisons were used to compare digit conditions to the T2 only baseline (0 digits + X) to determine whether a blink had occurred. Average accuracy on T2 only trials was above 85% in all 7 behavioural experiments. I then compared digit conditions with planned comparisons to reveal the relative magnitudes of the AB. I also analysed performance on the composite T1 in trials with digits and a T2[5]. In other words, I analysed whether participants correctly reported a T1 on 3 digit trials and no T1 on 1 and 2 digit trials, irrespective of their performance on T2.

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[3] Although the number of trials per lag is quite low in this experiment, the same data pattern was replicated in Experiments 3 (masked condition), 4 and 5.

[4] See Figure 33 in the General Discussion for an illustration of the conditional probabilities for the full T1. Also see Table 4 in Appendix A for calculations of the probabilities.

[5] This corresponds to T1 performance analysis in a standard AB paradigm

Results

T2|T1 Performance

For T2|T1 performance, the 4x5 MANOVA revealed significant main effects of condition (F (3, 17)=31.61, p< .0001, η_p^2 = 0.6680) and lag (F (4, 16)=23.74, p< .0001, η_p^2 = 0.7084) and a significant interaction of condition and lag (F (12, 8)=8.69, p< .01, η_p^2 = 0.3018) (Figure 2A).

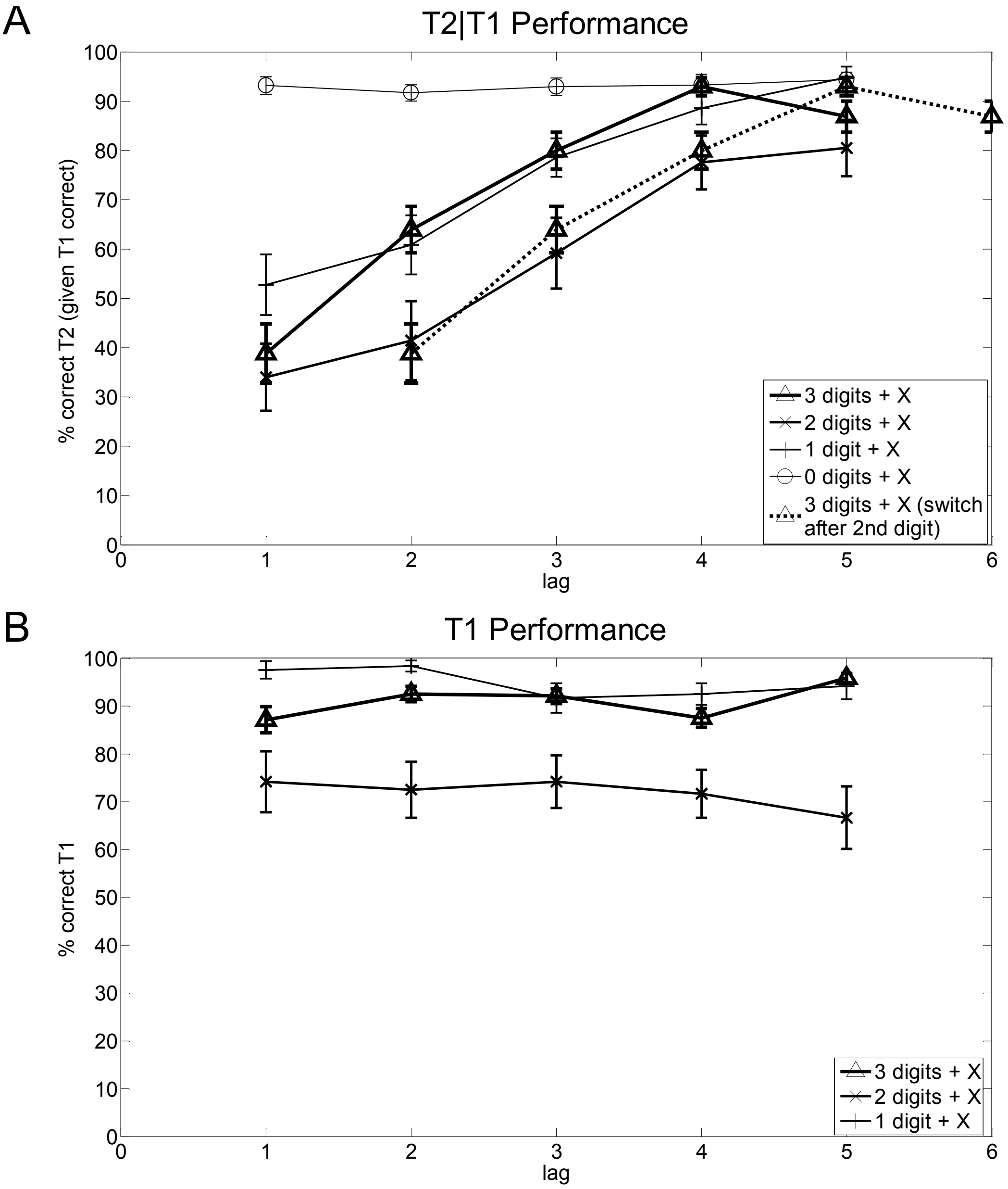

Figure 2 - Experiment 1: Consolidation versus unfulfilled expectations. A) T2|T1 performance at various levels of T1 compositionality. B) T1 performance at various levels of T1 compositionality. Error bars in all graphs show +/- 1 standard error of the mean

An attentional blink occurred with all partial (1 digit and 2 digits) and full T1s (3 digits). Performance with 1, 2 and 3 digits was significantly lower than baseline (0 digits + X) at lag 1 (all $p < .00001$), lag 2 (all $p < .001$) and lag 3 (all $p < .01$). In terms of relative blink magnitudes, 3 digit performance was lower than 1 digit at lag 1 ($p < .05$) while performance did not differ at lags 2 and 3. Two digit performance was below 1 digit at lags 1, 2 and 3 (all $p < .05$). Performance with 2 digits was below 3 digits at lag 2 ($p < .01$) and lag 3 ($p < .05$), while performance did not differ at lag 1. Lag 1 sparing was not observed in any digit condition, most likely due to the need for multidimensional switches between targets (Visser et al., 1999): Here participants must switch from detecting digits (T1) to a letter (T2), as well as from detecting 3 occurrences of the target feature (T1) to 1 occurrence (T2). I did, however, observe better lag 1 performance with 1 digit (53%) than with 2 digits (34%) and 3 digits (39%), while 2 and 3 digit performance was equally low.

To investigate whether participants learnt the probabilities of the digit events during the experiment, I divided T2|T1 data between the first and second halves of the experiment. Each half contained 150 trials. The 2x4x5 MAVOVA consisted of half (1^{st}, 2^{nd}), condition (4 digit levels) and lag (lags 1-5). The significant main effect of half (F (1, 19)=18.94, $p < .001$, $\eta_p^2 = 0.4992$) was driven by better performance in the 2^{nd} half of the experiment. The 2-way and 3-way interactions involving the factor “half” were not significant (all $p > .1$). Additionally, the main effects of lag and condition, as well as the interaction of lag with condition, were significant, as described in the T2|T1 statistics performed across the whole experiment.

Performance on digit-events

For composite T1 performance (correctly reporting ‘no T1’ on 1 and 2 digit trials, and correctly reporting ‘T1’ on 3 digit trials) in trials with digits and X, a 3x5 MANOVA consisted of condition (3 digits + X; 2 digits + X ; 1 digit + X) and lag (1-5). It revealed a significant main effect of condition (F (2, 18)=16.37, $p < .0001$, $\eta_p^2 = 0.4569$) and an interaction of condition and lag (F (8, 12)=3.39, $p < .05$, $\eta_p^2 = 0.1023$) (Figure 2B). Collapsed over all lags, 2 digit T1 performance (72%) was lower than 3 digits (91%; p< .01) and 1 digit (95%; p< .001), while 1 digit and 3 digits did not differ. The interaction of condition with lag was driven by lower performance with 3 digits than 1 digit at lags 1 and 2 (both $p < .01$), while there was no difference at lags 3, 4 and 5. Also 2 digit performance was below 3 digits at lags 2, 3, 4 and 5 (all $p < .05$) but not at lag 1, while 1 digit performance was above 2 digits at all lags (all $p < .01$).

Mistakes on T1 included reports of 'no T1' on trials with 3 digits (miss) and reports of 'T1' on trials with 1 digit or 2 digits (false alarms). The low performance on T1 in trials with 2 digits and X (Figure 2B) reflects a high rate of false alarms. When there were only 2 digits, participants reported that they had seen 3 digits 28% of the time (collapsed across lags). False alarms on T1 were less frequent in trials with 1 digit and X (only 5%). Misses of T1 in trials with 3 digits and X were also low, with participants saying they had not seen a full T1 only 9% of the time.

Accuracy on trials with a full T1 only (i.e. 3 digits, no X) was also high, with an overall performance of 91%. The high performance detecting 3 consecutive digits mirrors "spreading the sparing" findings (Di Lollo et al., 2005, Kawahara et al., 2006, Kihara et al., 2008, Nieuwenstein and Potter, 2006, Olivers et al., 2007), further suggesting the AB is not primarily caused by an inability to identify target information in a sequence.

False alarms on the digit event

In the current experiment, participants made many T1 false alarms on trials with 2 digits and X, often reporting they saw the 3 digit full T1. More T1 false alarms were made with 2 digits than with 1 digit. This gives some indication that participants may strongly expect a 3rd digit after they have seen a 2nd digit, while these expectations may be weak after the 1st digit. However, to investigate AB performance it is important that participants are as accurate as possible on the T1 event. Therefore, in Experiments 3 to 7 I gave visual feedback when false alarms were made on T1 to encourage participants to be vigilant in reporting the occurrence of the T1. Participants were informed after the trial when they incorrectly said they had seen 3 digits on trials with only 0, 1 or 2 digits. To anticipate the effect of feedback, T1 false alarms on 2 digit trials were reduced by an average of 40% (across all experiments and lags). Note that no feedback was given on other trial outcomes (e.g. misses of T1 on trials with 3 digits, or misses or false alarms on T2), as I did not want to affect the AB magnitudes.

Discussion

An AB occurred whenever T2 was displayed after a full T1 (3 digits) or partial T1 (1 or 2 digits). I had suggested that built-up expectations for a full digit target could be sufficient to induce an AB. In fact, a more pronounced, longer lasting AB was observed with 2 digits than with 3 digits, though at lag 1 performance was equally low in both conditions. A moderate AB was also observed with just 1 digit. The magnitude of the AB did not correlate with the number of presented digits, as predicted by capacity limitation accounts (e.g. the 2 stage model, Chun and Potter, 1995). Neither was there a fixed AB magnitude irrespective of the quantity of digits, as the TLC account (Di Lollo et al., 2005) might predict. Rather there was a greater AB with 2 digits than 3 digits – an outcome anticipated by the general idea of the RS account (Kessler et al., 2005a).

I therefore suggest that the high global expectation for 3 digit events (most frequent trial type: P(3 digits) = 0.4) leads to a strong, incrementally increasing pre-activation of the digit representations in anticipation of the final (3rd) digit, along with suppression of distractors. If this expectation is fulfilled, the system seems to switch quickly to T2, through rapid digit matching and efficient consolidation. Frequent practice of the 3 digit full target may lead to efficient consolidation in working memory. Furthermore, with the long SOA (186 ms), T1 consolidation could have less of a detrimental impact on T2 than in a typical AB paradigm (with an SOA of 100 ms). On the contrary, a distractor following 2 digits is relatively unexpected, and I propose there is strong competition between highly activated digit representations and the suppressed distractor letters. It would take time and effort for the letters to “win” so the cognitive system could switch to T2. Thus, the 2 digit AB (at lags 2 and 3) was more pronounced and longer lasting than with the 3 digit full target. Similar performance for these two conditions at lag 1 seems to suggest that the advantage of faster consolidation and switching with a full T1 is not yet reached at lag 1 – as the activation of digit representations remains strong. This result is compatible with the RS account and my interpretation of the BB account (Olivers and Meeter, 2008), that take the detrimental effect of over-emphasis on T1 into consideration, as well as with notions that focus on the ease of transition from T1 to T2 attentional states, which is proposed in the eSTST

(Wyble et al., 2009) (re-engagement of attention) and RS (transition between stable states) accounts.

Finally, it was not the case that only the full target (3 digits) induced an AB, which was a possible hypothesis drawn from capacity limitation accounts. My findings suggest that 1 digit and 2 digits were processed as partial targets (i.e. as potential parts of the full target), rather than rapidly discarded as non-targets. Three digit trials were the most frequent event (P(3 digits = 0.4) as there were equal numbers of trials with full targets versus partial targets. The conditional probability of seeing the full T1 increases from 0.55 after a 1st digit has been presented (P(3 digits|1 digit)) to 0.71 after a 2nd digit (P(3 digits|2 digits)) (Table 4 in Appendix A). The incrementally raised expectations (with each digit) for the full T1 could have consequences for T2, such that an AB occurred with partial targets: Strongest with 2 digits due to maximally raised expectations, but still present even with only 1 digit.

In terms of practice, AB performance in all digit conditions improved equally from the first 150 trials to the second 150 trials. As there was no interaction of practice with digit condition, the pattern of relative blink magnitudes did not change between the first and second halves of the experiment. This suggests that participants quickly learnt the global probabilities of the digit events, since there was an effect of global target expectations on the AB within the first half of the experiment.

There are two alternative explanations for the findings – switching after the 2nd digit, and counting the digits. Firstly, participants may not wait for the 3rd digit to complete the full T1 event before they switch to detecting T2. The conditional probability of seeing 3 digits, given you have seen 2 digits (P(3 digits|2 digits)=0.71) is high: i.e. If you see 2 digits there will be a full T1 on 70% of trials. Therefore participants may switch from digits to T2 after seeing 2 digits rather than waiting for the 3rd digit. Indeed, for T1 performance in trials with 2 digits + X, participants made many false alarms, saying they had seen the 3 digit full T1 ~30% of the time (Figure 2B). If participants switch after the 2nd digit, an extra lag is introduced (during the presentation of the 3rd digit), which would shift the 3 digit + X T2|T1 performance to the right (Figure 2A, dotted line). This would result in a similar sized AB for 2 digits and 3 digits.

However this explanation of an early switch cannot account for my findings. In the following target detection experiments (Behavioural

Experiments 3 – 7), I provided feedback after the trial when participants made a false alarm (saying “T1”) on partial target trials (with 1 digit or 2 digits). As well as improving accuracy on the T1 event, this could also encourage participants to wait for the 3rd digit before switching to T2, despite the high likelihood of a 3rd digit occurring after a 2nd digit. In experiments with the same global frequency as Experiment 1 (Experiments 3 (masked), 4 and 5), the T1 performance for 2 digits + X improved to over 85%, suggesting that feedback encouraged participants to attend to the whole digit event before switching. If the early switch explanation was correct, one might expect the 3 digit AB to be stronger and longer-lasting when feedback was given, leading to an equal AB for 2 digits and 3 digits (as with the dotted line in Figure 2A). However a stronger AB was observed with 2 digits than 3 digits in Experiments 3 (masked), 4 and 5, matching the T2|T1 pattern from Experiment 1. This overall pattern of results renders the early switch explanation unlikely.

Another alternative explanation is that participants could simply count the digits, which would induce an AB as all digit events are consolidated as targets. The variations in the AB magnitude could reflect relative trial frequencies, not in terms of expectations but rather in terms of processing difficulties. Rare target events could simply be perceived as more difficult. In order to test this alternative, I conducted a ‘counting’ experiment (Behavioural Experiment 2), while using the same relative trial frequencies. If this alternative explanation is true, I should obtain exactly the same result as in Experiment 1.

Chapter 3 - Behavioural Experiment 2: Digit enumeration

So far it is unclear exactly how participants regard partial targets of 1 digit and 2 digits. They represent part of a larger target, and all digits seem to enter the T1 input filter (Di Lollo et al., 2005), evident by the finding of a blink with partial targets in Experiment 1. But are partial targets processed to the same degree as a full target of 3 digits? In other words, are 1 digit and 2 digits automatically consolidated into working memory as potential targets? That being the case, each digit would enter working memory as it was perceived. Alternatively, consolidation could begin only once there is ample evidence for the presence of the full target (e.g. as the 3rd digit flashes on the screen).

Furthermore, could the findings in Experiment 1 be explained simply by the act of counting the digits in the T1 event? Counting 2 digits could result in a larger blink than with 3 digits as they are an odd-ball event and, thus, more difficult to process. In Experiment 2, I asked participants to report the quantity of digits in the T1 event (0, 1, 2 or 3) and detect T2 (the letter X). If I observed the same pattern as in Experiment 1 of a maximal AB with 2 digits, I could conclude that participants consolidated all digits as targets and that counting the T1 event in combination with the odd-ball status of the 2 digit events had caused the result. However, if a different pattern emerged, I could conclude that, although some kind of enumeration is involved in the task, it is not the primary factor influencing the AB. Such a finding would corroborate my interpretation of Experiment 1, in terms of incrementally raised expectations that can ensure efficient processing when fulfilled but are especially hard to overcome when disappointed.

Method

Participants

Twenty participants (8 males, mean age 24.10 years ± 6.47 SD) were recruited.

Apparatus, stimuli, procedure and design

The experimental design was identical to Experiment 1, but with a different task instruction. Participants counted the number of digits (T1 task) and detected the letter X (T2 task). After the RSVP stream, participants were asked “How many digits did you see? 0, 1, 2 or 3”, then “Did you see the letter X? yes or no”. T2 was presented at lags 2-5. The dependent variable was performance on T2, given T1 (number of digits reported) was correct.

It was a 4x4 repeated measures design with 2 factors: condition (3 digits + X; 2 digits + X; 1 digit + X; 0 digits + X) and lag (2-5). Trials containing digits and a T2 were equalled in number for trials with 3 digits versus those with 1 digit and 2 digits. Participants completed 11 practice trials and 360 experimental trials. There were 18 trials per lag in the 3 digits + X condition, 9 trials per lag with 2 digits + X, 9 trials per lag with 1 digit + X and 18 trials per lag with 0 digits + X (see Table 3 in the Appendix A for the number of trials in all conditions). The global probability of seeing 3 digits is 0.4, 2 digits is 0.17 and 1 digit is 0.17. The conditional probability of seeing a 2nd digit after 1 digit is 0.77 (P(2nd digit|1 digit) while the conditional probability of a 3rd digit occurring after a 2nd digit is 0.71 (P(3 digits|2 digits)) (See footnote 4 on p30). The experiment lasted approximately 40 minutes.

Results

T2|T1 Performance

For T2|T1 performance, the 4x4 MANOVA revealed significant main effects of condition (F (3, 17)=4.57, $p<$ .05, η_p^2 = 0.2590) and lag (F (3, 17)=13.51, $p<$ .00001, η_p^2 = 0.6336) and a significant interaction effect of condition and lag (F (9,11)=3.48, $p<$ .05, η_p^2 = 0.2568) (Figure 3A). I repeated the MANOVA without the baseline condition (0 digits + X) to investigate the effect of actively counting digits on the AB. The 3x4 MANOVA revealed only a significant main effect of lag (F (3, 17)=12.12, $p<$ .001, η_p^2 = 0.6160). The main effect of condition was no longer significant (p=0.1), although there was a trend towards an interaction of condition and lag (F (6, 14)=2.72, p= .06, η_p^2 = 0.0806). Comparing digits, there was no difference between performance with 1, 2 and 3 digits at lag 2 (all $p>$

.7). At lag 3, 2 digit performance did not differ from 1 digit (p= .3). However, performance at lag 3 was greater with 3 digits than with 1 digit (p< .01), while there was a trend towards higher performance with 3 digits than 2 digits (p= .06).

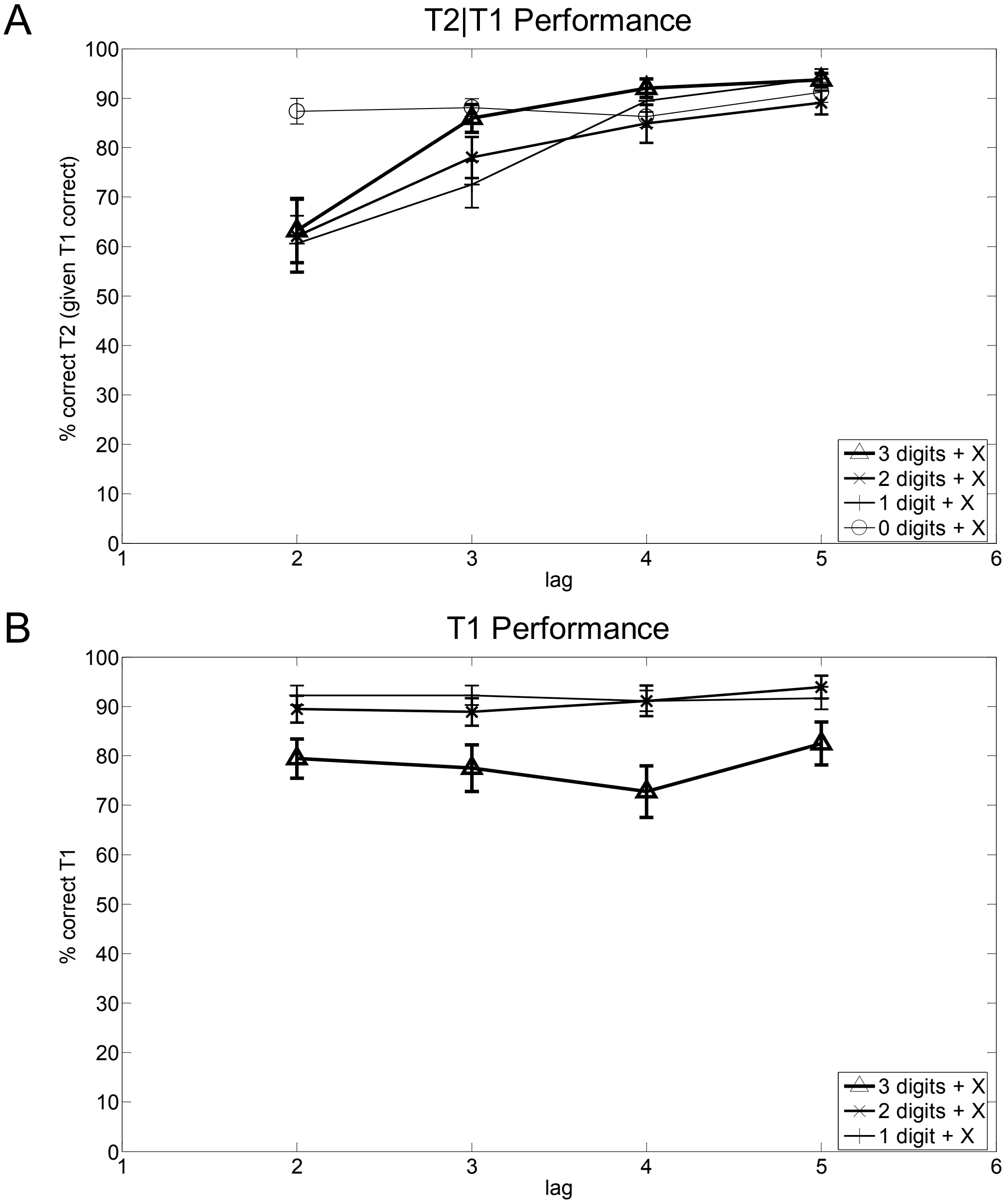

Figure 3 - Experiment 2: Digit enumeration. A) T2│T1 performance and B) T1 performance at various levels of T1 compositionality. Error bars show +/- 1 standard error of the mean

I compared T2|T1 performance in the first and second halves of the experiment to investigate the effect of learning. Each half contained 180 trials. The 2x4x4 MANOVA consisted of half (1^{st}, 2^{nd}), condition (4 digit levels) and lag (lags 2-5). The significant main effect of half (F (1, 19)=15.89, p< .001, η_p^2 = 0.4554) was driven by better performance in the 2^{nd} half. The significant interaction of half with lag (F (3, 17)=12.02, $p< .001$, $\eta_p^2 = 0.1957$) was driven by greater performance in the 2nd half than the 1st half at lag 2 ($p< .0001$), lag 3 ($p< .01$) and lag 4 ($p< .05$) while there was no difference at lag 5 ($p= .59$). Neither the interaction of half with condition nor the 3-way interaction were significant (all $p> .2$). Additionally, the main effects of lag and condition, as well as the interaction of lag with condition, were significant, as described in the T2|T1 statistics performed across the whole experiment.

Performance on digit-events

For digit-event (T1) performance in trials with digits and X, a 3x4 MANOVA consisted of condition (3 digits + X; 2 digits + X ; 1 digit + X) and lag (2-5). It revealed a significant main effect of condition (F (2, 18)=6.65, $p< .01$, $\eta_p^2 = 0.3751$) (Figure 3B). This was driven by significantly lower performance in the 3 digit condition (78%) than in both 2 digit (91%) and 1 digit (92%) trials, collapsed over all lags (both $p< .01$), while performance in 1 and 2 digit trials did not differ. The mistakes made on T1 in trials with 3 digits and X were typically reports of 2 digits (20% of the time), with fewer reports of 1 digit (2%) or 0 digits (<1%).

Discussion

An AB of similar magnitude occurred with 1, 2 and 3 digit levels, with no significant differences at lag 2. The 3 digit AB was in fact attenuated compared to 1 and 2 digits at lag 3, while at the same time T1 only performance on 3 digits was poorer than on 1 and 2 digits over all lags. In contrast, in Experiment 1 the 2 digit AB was of greater magnitude at lag 2 than the AB with 3 digits and 1 digit although the trial frequencies were identical in both experiments (i.e. 3 digits were the most frequent event). The only difference was that in Experiment 1 the task involved detecting the 3 digit target event. In the current experiment, the necessity to quantify the digit events granted all digits with a "target" status, such that all digits may be consolidated into working memory. Counting sequential items and confining the result to memory appears to require a set amount of time. The duration of this process does not linearly increase with the number of the counted items, and is only marginally influenced by relative condition frequencies. Once this set period is over, a task switch to T2 can occur. Based on the qualitatively different patterns in Experiment 1 and 2, I conclude that the task in Experiment 1 involved a different or addition process than simply counting the digits.

There was a main effect of practice on the AB magnitude. Performance in all digit conditions improved equally from the first 180 trials to the second 180 trials. The interaction of half with lag shows that practice improved T2 performance within the AB period (lags 2-4), while performance at lag 5 was high throughout the experiment.

The main aim of this experiment was to test whether the act of counting together with the relatively rare nature of 2 digit events could account for the pattern observed in Experiment 1. I have shown that this is not the case. Therefore, my interpretation of Experiment 1 was supported, where I proposed that the incremental build-up of expectations for the 3 digit full target accounted for the differences in AB magnitude, with the strongest effect in the 2 digit condition when expectations are maximally raised but unfulfilled.

In the next experiment, I focussed on the impact of the T1 backward mask. Somewhat paradoxically, in the present paradigm the mask does not simply interfere, but also provides bottom-up evidence about the end of the digit event (especially in the 1 and 2 digit conditions) and could actually trigger the switch to T2. In the following experiment, I therefore investigated how raised expectations might interact with the digit-event mask and which factor might have the stronger impact on AB magnitudes.

Chapter 4 - Behavioural Experiment 3: Expectations and the digit-event mask

In this and the following behavioural experiments I return to the original task of detecting 3 digit events. Post-target distractor masks play an important role in the AB, as discussed below. However, with a composite T1, the role of the mask is of particular interest. When 1 digit or 2 digits are presented, the lag 1 mask is the visual evidence that a full T1 will not occur, i.e. the mask defines it as a “partial target”. Hence, an unresolved question is whether the mask following a composite T1 predominantly helps participants to switch their expectations from T1 to T2 (i.e. a “switching-signal”) or whether it primarily interferes with the processing of T1 composites.

With standard AB paradigms, replacing the distractor after T1 with a gap typically attenuates the blink magnitude (Chun and Potter, 1995, Grandison et al., 1997, Kessler et al., 2005a, Seiffert and DiLollo, 1997, Raymond et al., 1992), although a strong AB has been shown when an unmasked T1 is followed by a briefly presented T2 (duration of 58 ms rather than 100 ms) (Nieuwenstein et al., 2009). This suggests the mask causes interference with target processing, but it is still unclear whether the mask plays a direct or indirect role in causing the AB (cf Nieuwenstein et al., 2009). Physiological evidence from EEG and MEG studies illustrates that the P300s (and M300s) elicited by both T1 and T2 are modulated by masking (see Kessler et al., 2006 for a review). The P300 is thought to reflect a target being processed and consolidated into working memory (Donchin and Coles, 1988, Verleger, 1988) or accessing the global workspace (Dehaene et al., 2003a), and is greatly modulated by AB manipulations (Arnell et al., 2004, Kessler et al., 2006, Kessler et al., 2005a, Kessler et al., 2005b, McArthur et al., 1999, Shapiro et al., 2006, Vogel et al., 1998). The T2-related P300 is suppressed when T2 is missed (Kessler et al., 2005a, Shapiro et al., 2006, Vogel et al., 1998), yet, when T2 is unmasked, although no AB is observed, the T2-related P300 is delayed for short lags (Vogel and Luck, 2002). In addition, a mask after T1 leads to an earlier T1-M300 peak in prefrontal areas compared to unmasked trials, while delaying the T2-M300 peak (Kessler et al., 2005a). According to the RS account, competing representations between the disturbing mask and T1 can actually boost T1 through the suppression of distractor representations and anything else not compatible with T1. This enhancement of T1 comes at a cost to subsequent target processing: the resulting robust suppressive state to T1 has to be actively perturbed before a switch to T2 can occur (Kessler et al., 2005a, Gross et al., 2004, Gross et al., 2006, Kessler et al., 2006). The authors stressed, however, that any factor (not just the T1 mask) that influences the equilibrium between activation of T1 patterns and suppression of other patterns can modulate the AB (Kessler et al., 2005a, p. 1038). In Experiments 1 and 2, I found evidence that raised expectations can constitute such an influence, especially when expectations remain unfulfilled while one has to switch to T2: in Experiment 1 I found the strongest AB with a 2 digit partial T1. I therefore predict that the T1-mask would have the most detrimental effect in the 2 digit condition, and so omitting the T1 mask should attenuate the AB primarily in these trials. The RS (Kessler et al., 2005a) and eSTST (Wyble et al., 2009) accounts postulate that the mask can interfere with consolidation of T1, so the 3 digit AB could be modulated by removing the mask.

Additionally, this experiment will allow us to test an alternative explanation for my findings. It is possible that the 2 digit AB was maximal in Experiment 1 due to basic discrimination difficulties, as 2 digits lies between 1 digit and 3 digits[6]. If that is the case, I would expect performance on 2 digit events (i.e. T1 performance, irrespective of T2 performance) to improve when unmasked, given the increased time after the digits for discrimination. To anticipate, the results speak against this alternative. Overall, Experiment 3 allowed us to investigate the relative importance of the T1 mask as a bottom-up switching signal and/or source of interference, and to compare its effect to top-down target expectations.

Method

Participants

Twenty participants (7 male, mean age 23.20 years ± 4.18 SD) were recruited.

Apparatus, stimuli, procedure and design

There were 2 masking conditions: T1 masked and T1 unmasked. A single gap after T1 in unmasked trials could have acted as a perceptual marker for T1. Also the cognitive load in unmasked trials could be lower than masked trials, since unmasked streams contained 1 less item. To control for this, 2 gaps (of duration 186 ms) were introduced to the RSVP streams of all conditions (Figure 4). The unmasked condition contained the critical gap at the T1+1 position, and a control gap before or after the targets. The masked condition contained a distractor in the T1+1 position (like previous experiments) with 2 control gaps either side of the targets. Restrictions for the placement of control gaps included: Gaps could not occur between targets or directly next to a target (i.e. at the T1-1 or T2+1 positions); 2 adjacent gaps were not allowed; and gaps could not occur at the start (position 1) or end (position 15) of the stream. Control gaps were distributed pseudo-randomly throughout the stream. Trials of the different masking conditions were presented in a randomised order.

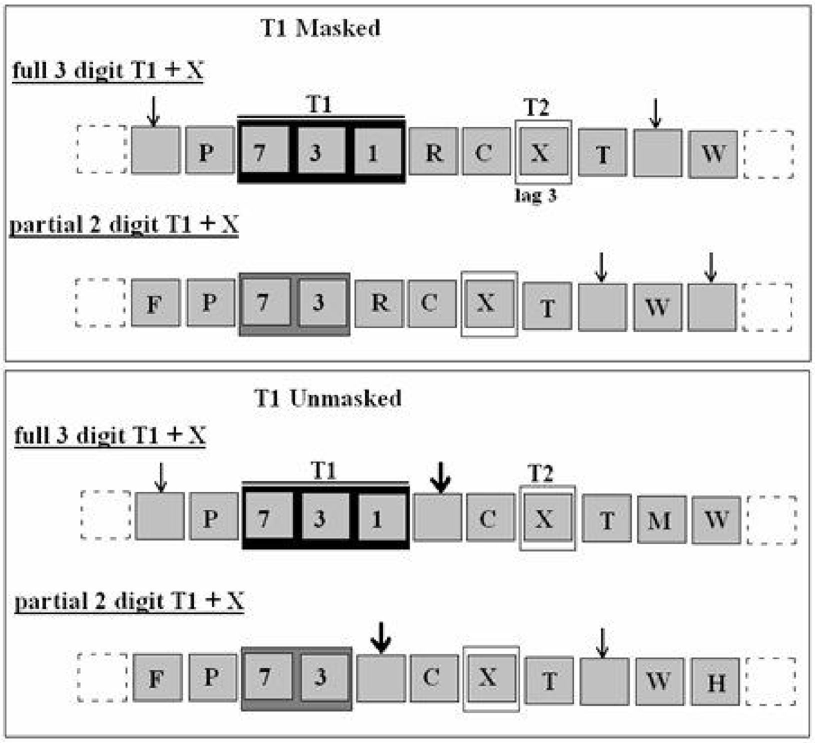

Figure 4 - T1 masked & unmasked trials, shown for 3 digits + X & 2 digits + X. Blank squares highlighted with arrows denote a gap. The critical gap (lag 1 position in unmasked trials) is shown by thick arrow. Control gaps are shown by thin arrows.

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[6] I would like to thank Chris Olivers for pointing out this alternative explanation.

The overall design of the paradigm was similar to Experiment 1, with the following exceptions. T2 was presented at lags 2-5, but not at lag 1, since there was a gap at lag 1 in unmasked trials. Participants received visual feedback ("Error, there was no number target"), following reports of 3 digits when this was not the case. This was to encourage participants to be more vigilant about seeing and reporting full T1s, following the large number of T1 false alarms on 2 digit trials in Experiment 1.

It was a 2x4x4 repeated measures design with 3 factors – mask (masked, unmasked), condition (3 digits + X; 2 digits + X; 1 digit + X; 0 digits + X) and lag (2-5). The relative frequencies of conditions matched Experiments 1 and 2, with trials containing digits and T2 balanced in frequency between those with a full T1 (3 digits) versus those with a partial T1 (1 and 2 digits). Participants completed 11 practice trials and 240 trials in each masking condition, with a total of 480 experimental trials. In each masking condition, there were 12 trials per lag in the 3 digits + X condition, 6 trials per lag with 2 digits + X, 6 trials per lag with 1 digit + X and 12 trials per lag with 0 digits + X (see Table 3 in the Appendix A for the number of trials in all conditions). The global probability of seeing 3 digits is 0.4, 2 digits is 0.17 and 1 digit is 0.17. The conditional probability of seeing the full T1 (3 digits) increases from 0.55 after a 1st digit has been presented (P(3 digits|1 digit)) to 0.71 after a 2nd digit (P(3 digits|2 digits)). The conditional probability of seeing a 2nd digit after 1 digit is 0.77 (P(2nd digit|1 digit) (See footnote 4 on p30). Participants were given a short break every 15 minutes and the experiment lasted approximately 1 hour.

Results

T2|T1 Performance

For T2|T1 performance, the 2x4x4 MANOVA revealed significant main effects of mask (F (1, 19)=9.61, $p< .01$, $\eta_p^2 = 0.3359$), condition (F (3, 17)=6.69, $p< .01$, $\eta_p^2 = 0.3111$) and lag (F (3, 17)=5.69, $p< .01$, $\eta_p^2 = 0.3918$), a significant interaction effect of mask and lag (F (3, 17)=4.26, $p< .05$, $\eta_p^2 = 0.2454$), while there were trends towards interaction effects of condition and lag (F (9, 11)=2.73, $p= .06$,

η_p^2 = 0.2134) and of mask by condition by lag (*F* (9, 11)=2.49, *p*= .08, η_p^2 = 0.1137).

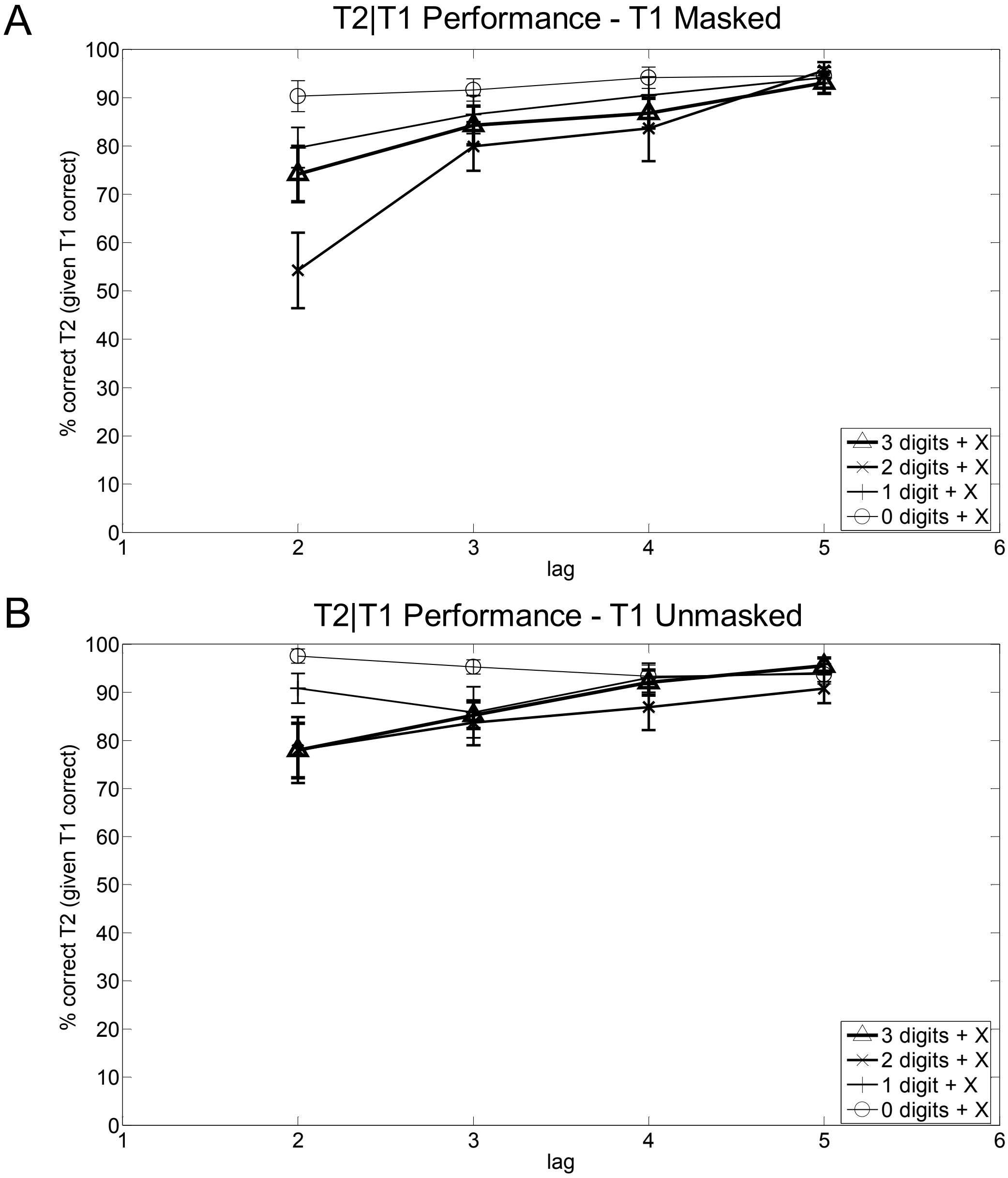

Figure 5 - Experiment 3: Expectations and the digit-event mask. T2│T1 performance at various levels of T1 compositionality for A) masked and B) unmasked conditions. Error bars show +/- 1 standard error of the mean.

A similar pattern emerged in masked (Figure 5A) and unmasked trials (Figure 5B): there was an AB with all digit levels. In both masking conditions, 1 digit performance was significantly below baseline at lag 2 (both *p*< .05) but not at lag 3. With 3 digits, performance was below baseline at lag 2 (*p*< .01) but not at lag 3 in masked trials, and at lags 2 and 3 in unmasked trials (both *p*< .01). Two digit performance was below baseline at lag 2 and 3 in masked and unmasked trials (all *p*< .05). In masked trials, 3 digit performance did not differ from 1 digit at lag 2 or 3, while 3 digit performance was significantly lower than

1 digit at lag 2 in unmasked trials ($p < .05$). Two digit performance was lower than 1 digit at lag 2 in both masked and unmasked trials (both $p < .01$), while performance did not differ at lag 3. When masked, performance with 2 digits was lower than 3 digits at lag 2 ($p < .01$) but not at lag 3. However, when the post digit mask was removed, 2 digit performance did not differ significantly from 3 digits at lag 2 or lag 3.

Comparing masking conditions, there was no difference in AB magnitude (at lag 2 or 3) for 3 digit trials. However, the AB at lag 2 was significantly stronger in masked than unmasked trials (both $p < .01$) with 1 digit (masked 80%, unmasked 91%) and 2 digits (masked 54%, unmasked 87%), while there were no differences at lag 3.

I compared T2|T1 performance in the first and second halves of the experiment to investigate the effect of learning. Each half contained 240 trials, divided equally between masked and unmasked conditions. The 2x2x4x4 MANOVA consisted of half (1st, 2nd), mask (masked, unmasked), condition (4 digit levels) and lag (lags 2-5). The significant main effect of half (F (1, 19)=13.24, $p < .01$, $\eta_p^2 = 0.4107$) was driven by better performance in the 2nd half. The significant interaction of half with condition (F (3, 17)=8.17, $p < .01$, $\eta_p^2 = 0.1955$) was driven by higher performance in the 2nd than the 1st half for 1 digit ($p < .01$) and 2 digits ($p < .01$) while there was no learning effect for 3 digits ($p = .78$) or 0 digits ($p = .13$). The trend towards an interaction of half with lag (F (3, 17)=2.81, $p = .071$) was driven by better performance in the 2nd than the 1st half at lag 2 ($p < .001$), where there were no significant differences at lags 3, 4 or 5 (all $p > .1$). Additionally, there were significant main effects of mask, condition and lag, and significant interactions of mask by lag, and mask by condition by lag (all $p < .05$), and a trend towards an interaction of digit by lag ($p = .07$), as described in the T2|T1 statistics performed across the whole experiment.

Performance on digit-events

For composite T1 performance in trials with digits and X, a 2x3x4 MANOVA consisted of mask (masked; unmasked), condition (3 digits + X; 2 digits + X; 1 digit + X) and lag (2-5) (Figure 6). The significant main effect of condition (F (2, 18)=12.59, $p < .001$, $\eta_p^2 = 0.2572$) was driven by better performance in 1 digit (98%) than both 2 digit (87%) and 3 digit (92%) trials, collapsed across lag and masking conditions (both *p*< .05). T1 performance did not differ between 2 and 3 digits.

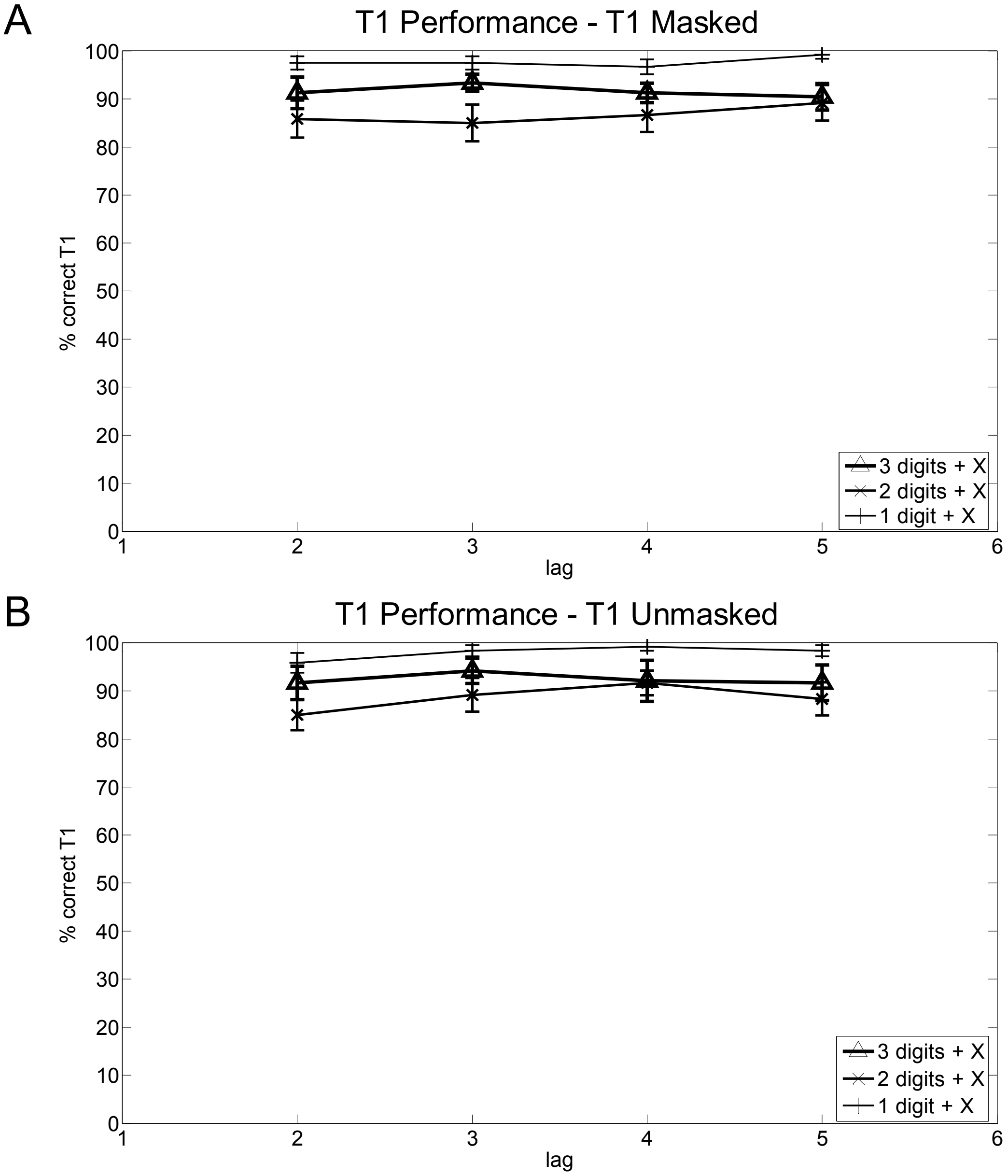

Figure 6 - Experiment 3: Expectations and the digit-event mask. T1 performance at various levels of T1 compositionality for A) masked and B) unmasked conditions. Error bars show +/- 1 standard error of the mean.

Finally, I specifically compared performance on 2 digit events with and without a mask, allowing us to test an alternative explanation: 2 digits could be more difficult to discriminate than 1 digit or 3 digits, resulting in the maximal AB with 2 digits. If that was the case, omitting the mask would surely improve performance on the digit-event as a direct reflection of improved discriminability. However, I did not observe such an improvement at lag 2 (*p*= .85) or at lag 3 (*p*= .31). Thus, the data reveal dissociation in the 2 digit condition between the AB magnitude and performance on the digit-event: While the AB was attenuated by removing the mask, performance on the digit event was not influenced. This renders the discriminability explanation unlikely.

Discussion

An AB occurred with the full T1 (3 digits) and partial T1s (1 and 2 digits) in both masked and unmasked conditions. When masked the 2 digit partial T1 condition again displayed the greatest blink magnitude, larger than with 3 digits. There was a subtle effect of removing the post digit mask. In contrast to the prediction from the RS account (Kessler et al., 2005a), removing the mask after 3 digits did not alter performance, while removing the mask after 1 digit attenuated the AB. Most importantly, omitting the mask after 2 digits attenuated the AB, so that performance matched the 3 digit AB. With respect to the role of the mask in this paradigm, I can conclude that although the mask may serve as an indication of the end of the digit event, it causes interference at the same time. This is especially apparent when expectations are maximal (i.e. with 2 digits). Resuming my discussion of why 2 digits induced an even stronger AB than a 3 digit full T1, it seems likely that a mismatch between high expectations and the mask delayed switching to T2.

The mask seems to delay T2 processing after 1 and 2 digits (i.e. with raised expectations), but not after 3 digits (i.e. with full target consolidation). The lack of an effect with a full T1 could relate to the longer than standard SOA of 186 ms: The mask might appear at a late stage of T1 consolidation where interference from bottom-up signals is minimal. However, the key conclusion is that raised expectations, more so than mask interference, have a strong and long-lasting influence on the AB pattern. The AB in the 3 digit full T1 condition is not affected by masking, while the AB in the 1 and 2 digit conditions is. This is in agreement with the RS claim that any factor that enhances the robustness of the stable state emerging from T1 (or partial T1) processing will enhance the AB (Kessler et al., 2005a), which in this paradigm I predicted to be raised and subsequently disappointed expectations. I propose, based on the RS account, that incrementally increasing expectations with partial targets induce an increasingly robust state within the “global workspace” (cf. Dehaene et al., 2003a) of enhanced digit activation that is reflected by the AB effect with 2 digits and with 1 digit. Note, however, that the AB with 1 digit in Experiments 1 and 3 is smaller than in Experiment 2 where 1 digit was a target in itself.

Additionally there was a main effect of practice on the AB magnitude, with an improvement in performance from the first 240 trials to the second 240 trials. The interaction of practice with digit condition revealed that AB performance improved with practice for partial targets (1 digit and 2 digits) but not for the full target (3 digits) (see Figure 35 in Appendix E). This suggests that with enough practice, participants adapt to conditions with partial targets. In the second half, participants may focus less strongly on finding targets. Expectations for the full target may build less strongly with each digit, resulting in a lowered impact on T2 when these expectations are violated. This fits with “overinvestment” findings which show that focusing strongly on finding targets reduces AB performance (Taatgen et al., 2009, Olivers and Nieuwenhuis, 2005, Olivers and Nieuwenhuis, 2006, Arend et al., 2006, Wierda et al., 2010, Shore et al., 2001, McLaughlin et al., 2001). However, it is equally possible that this interaction of practice with digit condition is driven by the differential effects of the mask between the digit conditions: Across the whole experiment, removing the mask only improved performance for partial targets, not for the full target.

My overall explanation depends on the assumption that local expectations within a given trial are raised incrementally and I have argued that these increments would depend on global expectations as induced by relative trial frequencies. One obvious way of confirming this conclusion is to alter the relative frequencies. Global expectations regarding the full T1 should modulate the increments by which local expectations are raised within a trial. That is, increments should be large if 3 digit events are frequent, resulting in high local expectations (cf. Experiments 1 and 3), whereas increments should be small if 3 digit events are rare, resulting in low local expectations. Such a modulation of local by global expectations would further go against the alternative explanation of mere discrimination difficulties of 2 digit events as they are ‘in the middle’ of 1 and 3 digit events. To anticipate, the results in Experiments 3, 6 and 7 rule out this alternative. I will further investigate the influence of global expectations in Experiments 6 and 7. However, next I continue with the investigation of bottom-up influences, by marking the final digit with a colour (Experiment 4) and a sound (Experiment 5): I aim to see whether these perceptual cues could act as signals to switch from built expectations for T1 to the T2.

Chapter 5 - Behavioural Experiments 4 and 5: Bottom-up Switching Signals?

I now investigated whether a salient bottom-up signal could modulate the AB in the case of high expectations (2 digits). The end of the T1 event was marked with salient colour or auditory cues to see whether they could act as switching signals to improve T2 report. That is, I provided participants with an explicit signal for when to switch their expectations from digits to the letter X. There are 3 possible outcomes. Firstly, such cues could strongly counteract the built-up expectations in the partial T1 (1 and 2 digit) trials. The cue concurrent with the last digit could inform participants there are no more digits; in which case, local expectations for the target are no longer necessary. This would facilitate switching to T2, which in turn could strongly attenuate the AB with partial T1s. A second possibility is that the cue could especially capture attention for the T1 event. If that were the case, I might expect a greater AB magnitude with all digit conditions when marked with a colour or sound. A third possibility is that these visual and auditory cues may have little influence on switching: Top-down anticipatory processes may be so built-up that they overshadow any bottom-up influences on switching.

Within the AB, studies have investigated the saliency of targets using colour and sound. Colour can capture attention for the targets, at the expense of T2 processing. In fact, marking a pre-target distractor with colour induced an AB, when targets and distractors were categorically similar (Maki and Mebane, 2006). On the other hand, auditory and colour cues have been shown to considerably improve performance on visual AB tasks. The AB magnitude was reduced when targets were easily discriminated (by colour) from the distractor stream (Hommel and Akyurek, 2005). A tone concurrent with T2 greatly reduced the AB effect, while a tone with T1 improved T1 performance, although a strong blink remained when the sound occurred with T1 (Olivers and Van der Burg, 2008).

The following 2 experiments aimed to further shed light on the dynamics of the bottom-up processes that may influence switching from highly built-up expectations of a composite T1.

Experiment 4: Colour-based Switching Signal

Method

Participants

Twenty participants (9 males, mean age 22.20 years ± 3.69 SD) were recruited.

Apparatus, stimuli, procedure and design

The experiment was similar to the masked condition in Experiment 3, although there were no gaps in the RSVP stream. Additionally, there were 2 colour blocks (black, blue). In the black block, all items in the stream were black, as in previous experiments. In the blue block, the last digit in each sequence was presented in blue (RGB 0, 0, 128), i.e. the only digit in 1 digit trials, the second of 2 digits and the third of 3 digits were blue. Blocks were run consecutively, with breaks given every 15 minutes. Participants were assigned to 2 groups relating to the order of performing the colour blocks: group A (n=10) performed black-blue and group B (n=10) performed blue-black. In the blue block, participants were told that a blue digit marked the end of the digit sequence (T1), after which they should concentrate on detecting the X (T2). In the black block, they were instructed that once the digit sequence had finished, they should look for the X.

It was a 2x4x4 repeated measures design with 3 factors: colour block (black, blue), condition (3 digits + X, 2 digits + X, 1 digit + X and 0 digits + X) and lag (2-5). The relative frequencies of conditions matched Experiments 1, 2 and 3, with trials containing digits and T2 balanced in frequency between those with a full T1 (3 digits) versus those with a partial T1 (1 and 2 digits). In each colour block, there were 18 trials per lag with 3 digits + X, 9 trials per lag with 2 digits + X, 9 trials per lag with 1 digit + X and 18 trials per lag with 0 digits + X (see Table 3 in the Appendix A). The global probability of seeing 3 digits is 0.4, 2 digits is 0.17 and 1 digit is 0.17. The conditional probability of seeing the full T1 (3 digits) increases from 0.55 after a 1st digit has been presented (P(3 digits|1 digit)) to 0.71 after a 2nd digit (P(3 digits|2 digits)). The conditional probability of seeing a 2nd digit after 1 digit is 0.77 (P(2nd digit|1 digit) (See footnote 4 on p30). The experiment consisted of 360 experimental trials in each block, and lasted around 1 hour 35 minutes.

Results

T2|T1 Performance

For T2|T1 performance, the 2x4x4 MANOVA revealed significant main effects of condition (*F* (3, 17)=17.44, *p*< .001, η_p^2 = 0.4900) and lag (*F* (3, 17)=20.01, *p*< .001, η_p^2 = 0.7020), and an interaction effect of condition and lag (*F* (9, 11)=4.91, *p*< .01, η_p^2 = 0.3508). As there were no significant main or interaction effects of the "colour block" factor, I repeated the MANOVA collapsing across this factor. The resulting 4x4 MANOVA, including condition and lag as factors, again revealed significant main effects of condition (*F* (3, 17)=14.73, *p*< .0001, η_p^2 = 0.4943) and lag (*F* (3, 17)=24.11, *p*< .00001, η_p^2 = 0.6914), and an interaction effect of condition and lag (*F* (9, 11)=8.05, *p*< .01, η_p^2 = 0.4190) (Figure 7A).

An AB occurred with 1, 2 and 3 digits. Performance with 1 digit was significantly below baseline at lag 2 (*p*< .0001), while 3 and 2 digit performance was below baseline at lags 2 and 3 (all *p*< .001). Performance with 3 and 2 digits was below 1 digit at lags 2 and 3 (both *p*< .05). The AB with 2 digits was significantly stronger than with 3 digits at lags 2 and 3 (both *p*< .01).

I compared T2|T1 performance in the first and second blocks of the experiment to investigate the effect of learning, while also investigating the effect of the order of performing the colour block (group A performed black-blue and group B performed blue-black). Each block contained 360 trials: note that this is similar to the total number of trials in most of the Behavioural Experiments (see Appendix A Table 3).

The 2x2x4x4 MANOVA consisted of group (A and B) as a between-subjects factor, along with block (1st and 2nd), condition (4 digit levels) and lag (lags 2-5) as within-subjects factors. There was a significant main effect of block (*F* (1, 18)=41.61, *p*< .00001, η_p^2 = 0.6980), with better performance in the 2nd block. The significant main effect of group (*F* (1, 18)=5.37, *p*< .05, η_p^2 = 0.2298) was driven by better performance in group A than group B. There was also a significant interaction effect of group with block (*F* (1, 18)=7.77, $p< .05$, $\eta_p^2 = 0.3014$) driven by better performance in the 1st block in group A (i.e. performing the black block) than group B (performing the blue block) ($p< .05$). There was no significant difference between groups on performance in the 2nd block ($p=.18$). The significant interaction effect of group with lag (*F* (3, 16)=4.30, $p< .05$, $\eta_p^2 = 0.0859$) was driven by better performance in group A than group B at lags 3 and 4 (both $p< .05$) while there was no significant difference at lag 2 ($p= .12$) or lag 5 ($p= .37$). This suggests that group B had a longer lasting AB than group A, which again could relate to the order of performing the colour blocks or could be group effect.

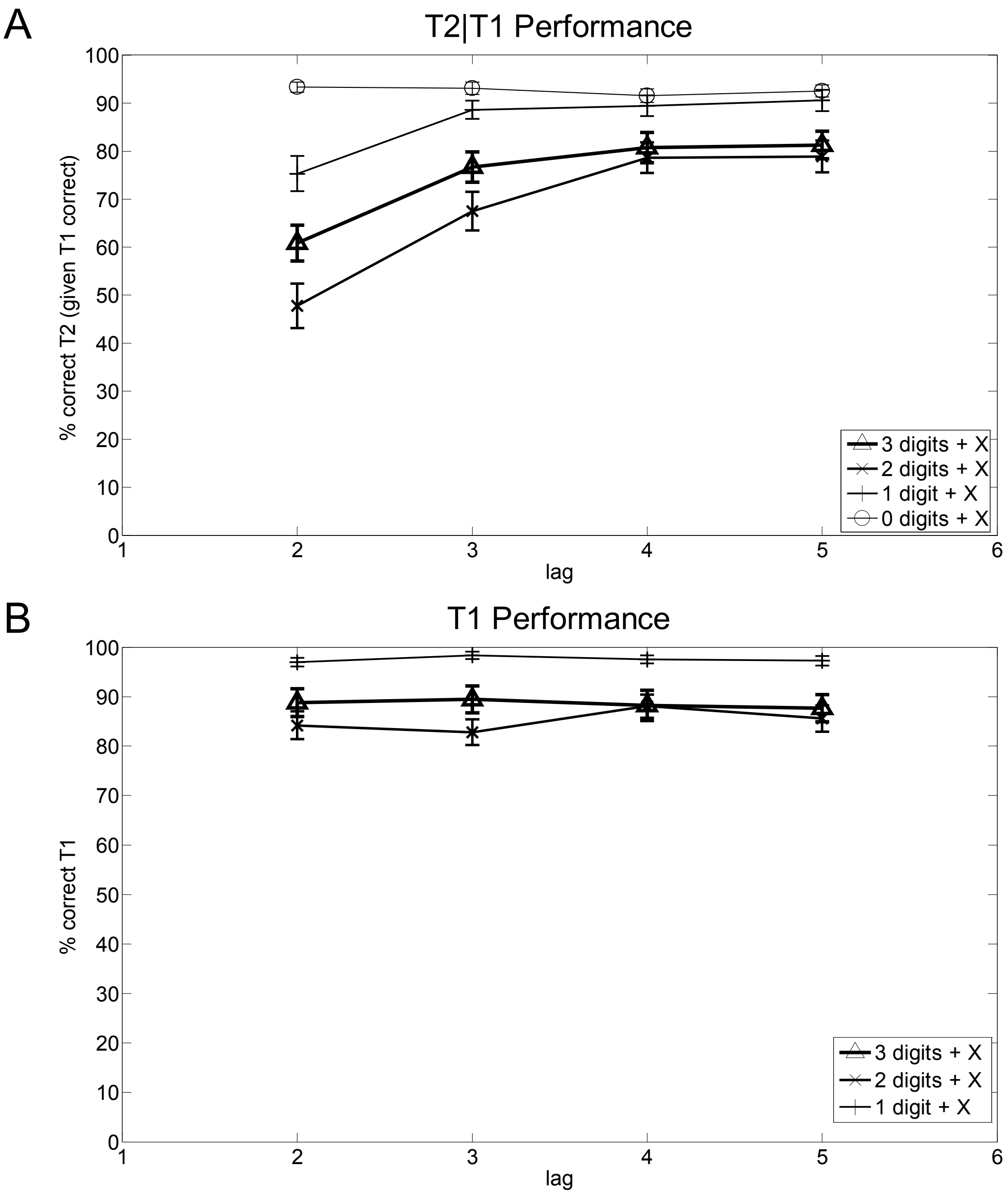

Figure 7 - Experiment 4: Bottom-up Colour Switching Signal. A) T2|T1 performance and B) T1 performance at various levels of T1 compositionality, collapsed across colour block. Error bars show +/- 1 standard error of the mean.

The significant interaction effect of block with lag (*F* (3, 16)=4.28, $p<.05$, $\eta_p^2 = 0.2288$) was driven by better performance in the 2nd block than the 1st block at lag 2 ($p<.001$), lag 3 ($p<.001$) and lag 4 ($p<.01$), while there was no difference at lag 5 ($p=.16$). This shows that practice improves performance within the AB period.

There was a trend towards an interaction between block and condition (*F* (3, 16)=3.14, $p=.054$). In both blocks, 3 digits, 2 digits and 1 digit performance was below baseline (0 digit) (all $p<.05$), and 2 digit performance was below 1 digit ($p<.001$). In block 1 there was no significant difference between 3 digit and 1 digit performance ($p=.48$), while in block 2 performance was higher with 1 digit than 3 digits ($p<.05$). Two digit performance was lower than 3 digit in block 1 ($p<.05$) while there was no significant difference in block 2 ($p=.26$). This suggests that the maximal AB with 2 digits occurred only in the 1st block, with 2 digit performance improving to the level of the 3 digit AB with practice.

Additionally, there were significant main effects of condition and of lag, and a significant interaction of condition and lag, as described in the T2|T1 statistics performed across the whole experiment.

Performance on digit-events

For composite T1 performance in trials with digits and X, a 2x3x4 MANOVA consisted of colour block (black, blue), condition (3 digits + X; 2 digits + X; 1 digit + X) and lag (2-5) (Figure 7B). It revealed a significant main effect of condition (*F* (2, 18)=12.80, $p<.001$, $\eta_p^2 = 0.2617$). This was driven by significantly lower performance in both the 3 digit (89%) and 2 digit (85%) conditions than the 1 digit (98%) condition, collapsed over all lags and colour blocks (both $p<.05$). There was no significant difference between T1 performance in 2 digit and 3 digit trials ($p=.41$). Note that there was no significant main effect of colour block, illustrating that T1 performance was not influenced by marking the final digit with a colour.

Discussion

In summary, I replicated the pattern from Experiments 1 and 3 of a maximal AB with 2 digits, a moderate AB with 3 digits and a mild AB with 1 digit. Over the whole experiment, I found that marking the end of the digits with a colour did not influence the AB magnitude in any digit condition. However, there was an effect of the order of performing the colour blocks. Participants were randomly assigned to one of two groups: Group A performed the black block first and Group B the blue block first. Overall, Group B displayed a stronger AB deficit than Group A. The interaction of group with block further showed that this lower performance for Group B than Group A was limited to the first block. There are 2 alternative explanations for this interaction: it could result from the colour of the final digit or from group differences. Performing the blue block first (Group B) could be detrimental to performance as the blue digit captures attention for the T1 event and hinders switching to T2. Alternatively, Group B may have benefited from practice on the task to a greater extent than Group A, and the interaction could be independent of the digit colour. It is hard to tease apart these 2 possibilities. Each group contained only 10 participants, meaning the result could be skewed by a few outliers. Yet it remains a possibility that the AB magnitude can be deepened by marking the final digit in the T1 event with a salient colour signal. There was, however, no effect of colour when participants have already performed the task without the colour signal (Group A): in this case participants may simply ignore the colour signal. This suggestion that colour can capture attention for T1 fits with Maki and Mebane's (2006) finding that marking a pre-target distractor with colour induced an AB. Overall, however it is unclear whether this results from an effect of colour or group differences. On the other hand, results confirmed that the colour cue was not an effective bottom-up signals to switch expectations from digits to the letter X, since the colour did not attenuate the AB magnitude for partial T1s.

Finally, since this experiment was twice as long as the other experiments, I investigated the effect of practice between the first 360 trials (block 1) and the second 360 trials (block 2). As well as a main effect of practice on the AB magnitude, the key finding was the trend towards an interaction of block with digit condition. The AB with partial targets (1 digit and 2 digits) improved considerably with practice (Figure 36 in Appendix E). Furthermore, the maximal AB with 2 digits occurred only in the first block, with 2 digit performance improving to the level of the 3 digit AB with practice. Like Experiment 3 (which contained 240 trials in each half of the experiment), this suggests that with enough practice, participants may adapt their search for the full target. Local expectations for the full target may build less strongly with each digit, resulting in a lowered impact on T2 when these expectations are violated in trials with partial targets. I discuss this further in the General Discussion. However in the following experiment I will investigate the effect of using a sound cue to mark the end of the digits.

Experiment 5: Sound-based Switching Signal

Method

Participants

Twenty participants (11 males, mean age 20.08 years ± 1.56 SD) were recruited.

Apparatus, stimuli, procedure and design

The experiment was similar to the black block in Experiment 4. Additionally, the final digit was accompanied with a beep sound, analogous to the marking of the last digit with colour in Experiment 4. The sound began with the onset of the final digit and also had a duration of 80 ms. Participants were informed that the sound marked the end of the digit sequence (T1), after which they should look for the letter X (T2).

It was a 4x4 repeated measures design with 2 factors - condition (3 digits + X; 2 digits + X; 1 digit + X; 0 digits + X) and lag (2-5). Trials containing digits and T2 were balanced in frequency between those with a full T1 (3 digits) versus those with a partial T1 (1 and 2 digits). There were 18 trials per lag in the 3 digits + X condition, 9 trials per lag with 2 digits + X, 9 trials per lag with 1 digit + X and 18 trials per lag with 0 digits + X. The global probability of seeing 3 digits is 0.4, 2 digits is 0.17 and 1 digit is 0.17. The conditional probability of seeing the full T1 (3 digits) increases from 0.55 after a 1st digit has been presented (P(3 digits|1 digit)) to 0.71 after a 2nd digit (P(3 digits|2 digits)). The conditional probability of seeing a 2nd digit after 1 digit is 0.77 (P(2nd digit|1 digit) (See footnote 4 on p30). Participants completed 360 experimental trials, and the experiment lasted around 40 minutes with a midway break.

Results

T2|T1 Performance

For T2|T1 performance, the 4x4 MANOVA revealed significant main effects of condition (*F* (3, 17)=13.70, *p*< .0001, η_p^2 = 0.4596) and lag (*F* (3, 17)=28.86, *p*< .00001, η_p^2 = 0.6718) and a significant interaction of condition and lag (*F* (9, 11)=8.11, *p*< .001, η_p^2 = 0.2888) (Figure 8A).

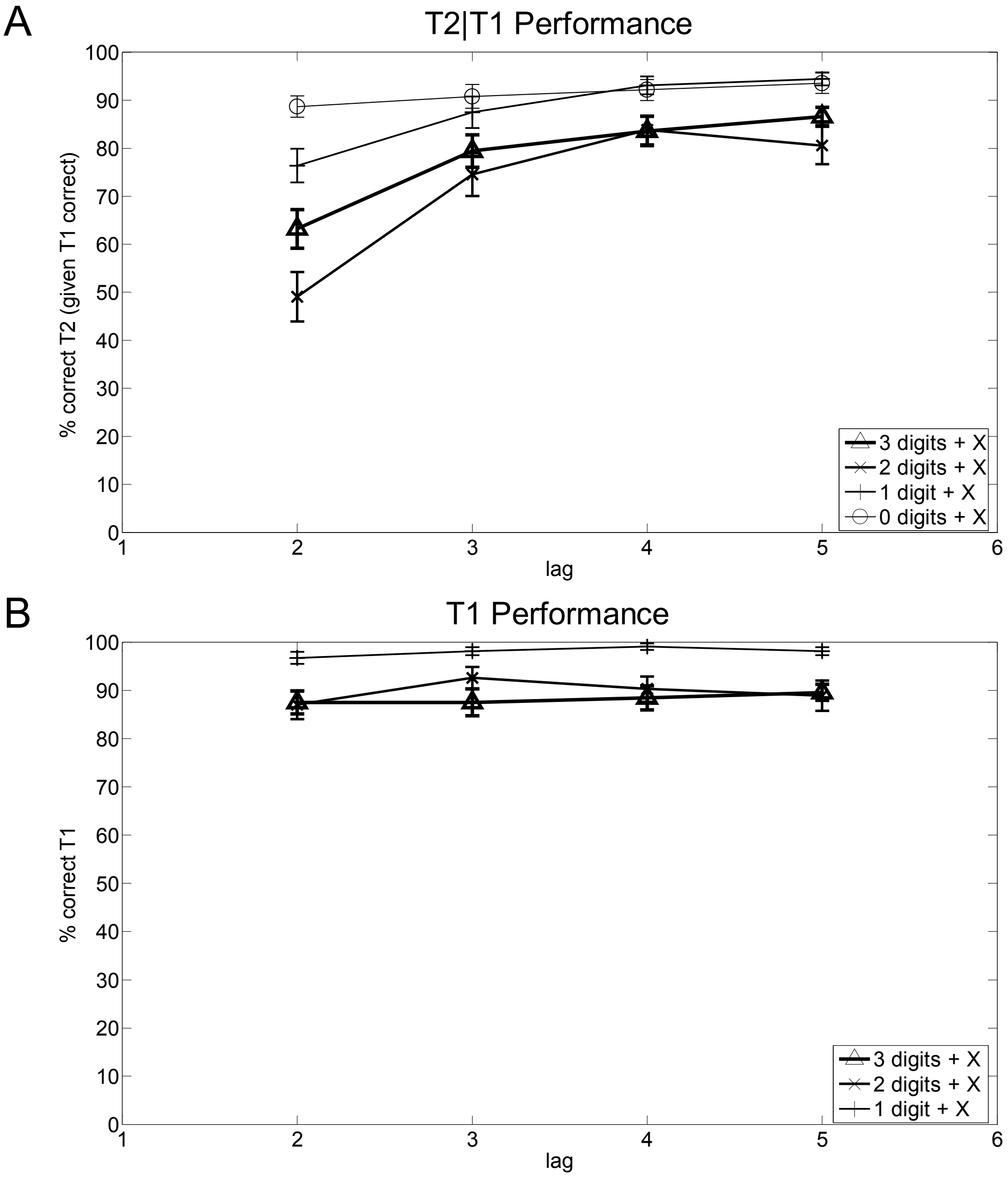

Figure 8 - Experiment 5: Bottom-up Sound Switching Signal. A) T2│T1 performance and B) T1 performance at various levels of T1 compositionality. Error bars show +/- 1 standard error of the mean.

An AB occurred with 1, 2 and 3 digits. One digit performance was significantly below baseline at lag 2 (*p*< .001), while 2 and 3 digit performance was lower than baseline at lags 2 and 3 (all $p< .05$). Performance with 2 and 3 digits was lower than 1 digit at lags 2 and 3 (all $p< .05$). The strongest blink was observed in the 2 digit condition, with 2 digit performance lower than 3 digit performance at lag 2 ($p< .00001$).

I compared T2|T1 performance in the first and second halves of the experiment to investigate the effect of learning. Each half contained 180 trials. The 2x4x4 MANOVA consisted of half (1st, 2nd), condition (4 digit levels) and lag (lags 2-5). The significant main effect of half (F (1, 19)=17.15, $p< .001$, $\eta_p^2 = 0.4744$) was driven by better performance in the 2nd half. The significant interaction of half with lag (F (3, 17)=6.03, $p< .01$, $\eta_p^2 = 0.2026$) was driven by better performance in the 2nd half than the 1st half at lag 2 ($p< .001$), lag 3 ($p< .01$) and lag 4 ($p< .05$) while there was a trend towards this at lag 5 ($p= .06$). Neither the 2-way interaction of half with condition nor the 3-way interaction were significant (all $p> .1$). Additionally the main effects of condition and lag, and interaction of condition with lag were significant, as described in the T2|T1 statistics performed across the whole experiment.

Performance on digit-events

For composite T1 performance in trials with digits and X, a 3x4 MANOVA consisted of condition (3 digits + X; 2 digits + X; 1 digit + X) and lag (2-5). The significant main effect of condition (F (2, 18)=14.85, $p< .0001$, $\eta_p^2 = 0.3608$) was driven by lower performance in both the 3 digit (88%) and 2 digit (90%) conditions than the 1 digit (98%) condition, collapsed over all lags (both $p< .001$), while performance in 3 and 2 digit trials did not differ ($p= .51$) (Figure 8B).

Cross-Experiment Comparisons

To test whether the sound influenced the magnitude of the AB, I compared this experiment (sound) to the black block in Experiment 4 (no sound). Using Experiment (Exp. 4 black block, Exp. 5) as a between-subjects factor, I carried out a 2x4x4 MANOVA on T2|T1 performance. There were significant main effects of condition (F (3, 36)=20.75, $p< .000001$, $\eta_p^2 = 0.3833$) and lag (F (3, 36)=36.55, $p< .000001$, $\eta_p^2 = 0.6501$) and an interaction effect of condition and lag (F (9, 30)=10.70, $p< .000001$, $\eta_p^2 = 0.3136$). However, the factor “Experiment” was not significant in any main or interaction effects, showing that the sound marking the end of the digits did not influence the AB magnitude.

To investigate whether sound affected T1 performance in trials with digits and X, a 2x3x4 MANOVA was performed, with "Experiment" as a between subject factor. It revealed only a significant main effect of condition (F (2, 37)=16.37, $p< .00001$, $\eta_p^2 = 0.2544$). The factor "Experiment" was not significant in any main or interaction effects, showing that sound did not influence performance on T1.

Discussion

Marking the final digit in the T1 composite event with a sound did not influence the AB in any way. Therefore an auditory cue is not an effective bottom-up signal to switch expectations from digits to the letter X, since the AB magnitude was not reduced for partial T1s. Neither did the sound capture attention for the T1 event, which would have resulted in a stronger blink for all digit conditions. Rather, the results suggest that auditory bottom-up signals for T1 have minimal influence on the AB in this paradigm.

My results fit with previous findings of a strong blink when a tone accompanied T1; indeed Olivers and Van der Burg (2008) found that the AB effect with a tone on T1 was similar to trials without a tone. However, I found that performance on the digit event (i.e. T1 performance) was not influenced by the sound, while Olivers and Van der Burg found that T1 performance was significantly improved by the tone on T1. My findings suggest that efficient switching in the context of composite T1s takes time and considerable top-down effort. Even when participants were given a perceptual cue informing them when the digit event had finished, their top-down expectations seemed to dominate.

There was a main effect of practice on the AB magnitude. Performance in all digit conditions improved equally from the first 180 trials to the second 180 trials. The interaction of half with lag shows that practice improved T2 performance within the AB period (lags 2-4), while there was a trend towards improvement at lag 5.

Finally, I have also replicated my finding of a maximal AB with 2 digits, when global expectations are strongest for the full target. In the following 2 experiments, I further investigate the role of global expectations by altering the relative frequencies of the digit events. So far, I have equalised the number of full target (3 digits) versus partial target (1 + 2 digits) events, making 3 digits the most frequent digit event. In Experiment 6, I now equalise the frequencies of all digit events (3 digits = 2 digits = 1 digit).

Chapter 6 - Behavioural Experiment 6: Changing global expectations I (all digit events equally frequent)

In the following two experiments (Experiments 6 and 7), I manipulated the relative frequencies of the digit events to investigate how top-down global expectations contribute to the AB magnitudes. To recap from Chapter 1, this task involves two closely linked aspects of expectation regarding the composite T1: local and global expectation[7]. By "local expectation", I refer to the process of building-up anticipation of a specific event within a given trial. This aspect is new in my paradigm: expectations of a composite target (3 digits) increase at a local level with the presentation of target parts (1st digit, 2nd digit). "Global expectation" refers to the anticipation of a target that is based on the relative frequencies between conditions over the whole experiment. A more frequent condition will result in the expectation at the start of the trial that this event is most likely to occur. In this case, global expectations should affect local expectations by modulating the "size" of the incremental rise of target anticipation by each presented digit. The more the target event is globally expected, the higher the incremental rise.

So far, trials were balanced in frequency between those with a full T1 (3 digits) versus those with a partial T1 (1 and 2 digits). Participants may have quickly learned that after 2 digits have occurred, a 3rd digit is more likely than a distractor, thus enhancing the global and local expectations for the 3 digit full T1. I now equalised trial frequency, so trials could equally contain 1, 2 or 3 digits. A full T1 now occurred only on a third of the trials containing digits. By reducing global target expectation, I aimed to reduce the incremental rise of local expectations within a trial by each digit. This could lead to a reduction of the AB effect in the 1 digit and especially in the 2 digit condition, while the AB with 3 digits could become stronger. In sum, Experiments 6 and 7 could give us insight into the contribution of local expectations for the target, which build within the trial as digits unfold.

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[7] I would like to thank Markus Kiefer for suggesting these terms.

Method

Participants

Twenty participants (10 males, mean age 22.60 years ± 5.84 SD) were recruited.

Apparatus, stimuli, procedure and design

The experiment was similar to the masked condition in Experiment 3 although there were no gaps within the RSVP stream. It was a 4x4 repeated measures design with 2 factors: condition (3 digits + X, 2 digits + X, 1 digit + X and 0 digits + X) and lag (2-5). All conditions were allocated the same number of trials. Participants were now equally likely to see 2 digits (or 1 digit) followed by X as 3 digits and an X. In each condition (3 digits + X, 2 digits + X, 1 digit + X and 0 digits + X) there were 12 trials per lag[8] (see Table 3 in the Appendix A for the number of trials in all conditions). The global probability of seeing 3 digits is 0.25, 2 digits is 0.25 and 1 digit is 0.25. The conditional probability of seeing the full T1 (3 digits) increases from 0.33 after a 1st digit has been presented (P(3 digits|1 digit)) to 0.5 after a 2nd digit (P(3 digits|2 digits)). The conditional probability of seeing a 2nd digit after 1 digit is 0.67 (P(2nd digit|1 digit) (See footnote 4 on p30). The experiment consisted of 11 practice trials and 384 experimental trials, and lasted around 50 minutes with a midway break.

Results

T2|T1 Performance

For T2|T1 performance, the 4x4 MANOVA revealed significant main effects of condition (F (3, 17)=5.46, $p< .01$, $\eta_p^2 = 0.3225$) and lag (F (3, 17)=8.40, $p< .01$, $\eta_p^2 = 0.4997$), and an interaction effect of condition and lag (F (9, 11)=3.95, $p< .05$, $\eta_p^2 = 0.3048$) (Figure 9A).

An AB occurred with 2 digits and 3 digits, but not with 1 digit. One digit performance did not deviate from baseline at lag 2 or 3. On the other hand, 3

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[8] The same data pattern has been replicated in a longer experiment (1 hr 40) with 24 trials per lag in each condition.

digit performance was below baseline at lag 2 (*p*< .0001) but not lag 3, while 2 digit performance was lower at lags 2 and 3 (both *p*< .01). Performance with 3 digits was lower than 1 digit at lag 2 (*p*< .001) but not at lag 3. Two digit performance was below 1 digit at lags 2 and 3 (both *p*< .01). Performance in 2 digit and 3 digit trials did not differ at lag 2 (*p*= .6), while at lag 3 there was lower performance with 2 digits than 3 (*p*< .05).

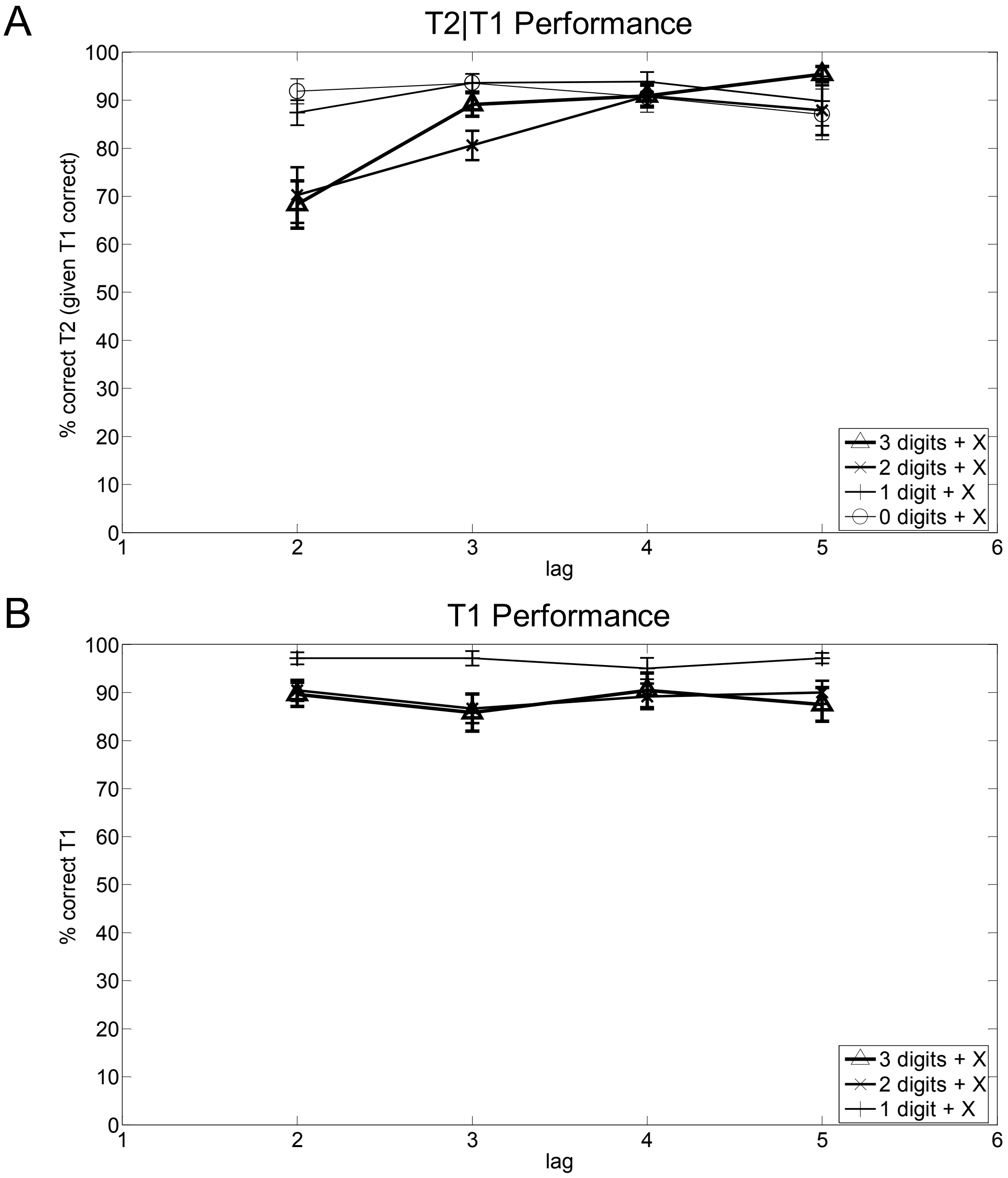

Figure 9 - Experiment 6: Changing global expectations I (all digit events equally frequent). A) T2│T1 performance and B) T1 performance at various levels of T1 compositionality. Error bars show +/- 1 standard error of the mean.

I compared T2|T1 performance in the first and second halves of the experiment to investigate the effect of learning. Each half contained 192 trials. The 2x4x4 MANOVA consisted of half (1st, 2nd), condition (4 digit levels) and lag (lags 2-5). The significant main effect of half (F (1, 19)=13.44, p< .01, η_p^2 = 0.4143) was driven by better performance in the 2nd half. The 2-way and 3-way interactions with half were not significant (all p> .1). Additionally, there were significant main effects of condition and lag, and a significant interaction of condition with lag as described in the T2|T1 statistics performed across the whole experiment.

Performance on digit events

For composite T1 performance in trials with digits and X, a 3x4 MANOVA consisted of condition (3 digits + X; 2 digits + X ; 1 digit + X) and lag (2-5). The significant main effect of condition (F (2, 18)=23.21, p< .0001, η_p^2 = 0.2371) was driven by better performance in 1 digit (97%) than both 2 digit (89%) and 3 digit (88%) trials, collapsed over all lags (both p< .01). Performance did not differ between 2 and 3 digit trials (Figure 9B).

Discussion

I observed an AB in conditions with a full T1 (3 digits) and a 2 digit partial T1, while for the first time, no blink occurred with 1 digit. Of particular note was the finding that the 2 digit AB magnitude now matched the 3 digit AB. Likewise, composite T1 performance revealed comparable accuracy with 2 digits and 3 digits. The lowered global expectations for the full T1 (P(3 digits) = 0.25) seem to have translated into smaller increments of increasing local expectations with each digit – possibly reflected in less incremental pre-activation of digit representations by each occurring digit. In this experiment, the conditional probability of seeing the full T1 (3 digits) increases from 0.33 after a 1st digit has been presented (P(3 digits|1 digit)) to 0.5 after a 2nd digit (P(3 digits|2 digits)). Switching to the letter T2 seems to encounter less resistance and can occur faster, explaining a reduced blink with 2 digits (and 1 digit), while the AB in the 3 digit full T1 condition seems to reflect similar costs for target consolidation as in the previous experiments.

Finally, there was a main effect of practice on the AB magnitude. Performance in all digit conditions improved equally from the first 192 trials to the second 192 trials.

Chapter 7 - Behavioural Experiment 7: Changing global expectations II (2 digit event most frequent)

In this experiment, I further reduced the global expectations for 3 digits, while increasing global expectations for 2 digits. Now trials were balanced in frequency between those with a 2 digit partial T1 versus those with a 3 digit full T1 plus a 1 digit partial T1 (2 digits = 3 digits + 1 digit). In this way, 2 digits were more likely than 3 digits (P(2 digits) = 0.4, while P(3 digits) = 0.17). As described earlier, I expected this change in global expectations to reduce the increments for the build-up of local expectations with each digit. Specifically, after participants have seen 2 digits, their expectations of a 3rd digit should be lower than in Experiment 6. This should result in increased consolidation time if a 3rd digit occurs, while on the other hand, it should lead to an easier switch to T2 with 2 digits.

Method

Participants

Twenty participants (6 males, mean age 22.20 years ± 1.98 SD) were recruited.

Apparatus, stimuli, procedure and design

The experiment was identical to Experiment 6, with the exception of the main change in the relative frequencies of digit conditions. Now 2 digits were as frequent as 1 digit plus 3 digit trials. It was a 4x4 repeated measures design with 2 factors: condition (3 digits + X, 2 digits + X, 1 digit + X and 0 digits + X) and lag (2-5). The experiment consisted of 11 practice trials and 360 experimental trials. There were 9 trials per lag in the 3 digits + X condition, 18 trials per lag with 2 digits + X, 9 trials per lag with 1 digit + X and 18 trials per lag with 0 digits + X (see Table 3 in the Appendix A for the number of trials in all conditions). The global probability of seeing 3 digits is 0.17, 2 digits is 0.4 and 1 digit is 0.17. The conditional probability of seeing the full T1 (3 digits) increases from 0.23 after a 1st digit has been presented (P(3 digits|1 digit)) to 0.29 after a 2nd digit (P(3 digits|2 digits)). The conditional probability of seeing a 2nd digit after 1 digit is 0.77 (P(2nd digit|1 digit) (See footnote 4 on p30). The experiment lasted approximately 40 minutes.

Results

T2|T1 Performance

For T2|T1 performance, the 4x4 MANOVA revealed significant main effects of condition (*F* (3, 17)=10.67, $p < .001$, $\eta_p^2 = 0.3585$) and lag (*F* (3, 17)=11.74, $p < .001$, $\eta_p^2 = 0.5812$), and an interaction effect of condition and lag (*F* (9, 11)=5.29, $p < .01$, $\eta_p^2 = 0.2495$) (Figure 10A). An AB occurred with 1, 2 and 3 digits. Performance on 3 digit and 2 digit trials was significantly below baseline at lags 2 and 3 (all $p < .05$), while 1 digit performance was below baseline at lag 2 ($p < .01$) but not lag 3. Performance with 3 and 2 digits was lower than 1 digit at lag 2 and lag 3 (all $p < .05$). Three digit performance did not differ from 2 digit at lag 2 or lag 3, although collapsed over all lags there was a trend towards a stronger AB with 3 digits (69%) than 2 digits (79%; $p = .08$).

I compared T2|T1 performance in the first and second halves of the experiment to investigate the effect of learning. Each half contained 180 trials. The 2x4x4 MANOVA consisted of half (1st, 2nd), condition (4 digit levels) and lag (lags 2-5). There was a trend towards a main effect of half (*F* (1, 19)=3.69, $p = .07$, $\eta_p^2 = 0.1618$), driven by higher performance in the 2nd half. The 2-way and 3-way interactions with half were not significant (all $p > .2$). Additionally, there were significant main effects of condition and lag, and a significant interaction of condition with lag as described in the T2|T1 statistics performed across the whole experiment.

Performance on digit-events

For composite T1 performance in trials with digits and X, a 3x4 MANOVA consisted of condition (3 digits + X; 2 digits + X; 1 digit + X) and lag (2-5). It revealed a significant main effect of condition (*F* (2, 18)=15.89, $p < .001$, $\eta_p^2 = 0.3456$) and a significant interaction effect of condition and lag (*F* (6, 14)=2.87, $p < .05$, $\eta_p^2 = 0.0915$) (Figure 10B). The main effect was driven by worse performance in the 3 digit condition (74%) than both 2 digit (*p*< .05; 92%) and 1 digit (*p*< .01; 98%) conditions, collapsed over all lags. Performance with 2 digits was also below 1 digit (*p*< .01). The interaction of condition by lag was driven by lower performance with 3 digits than 2 digits at lags 2, 3 and 5 (all *p*< .05), while there was no difference at lag 4. Two digit performance was below 1 digit at lags 3, 4 and 5 (all *p*< .01) but not at lag 2. Three digit performance was below 1 digit at all lags (all *p*< .01).

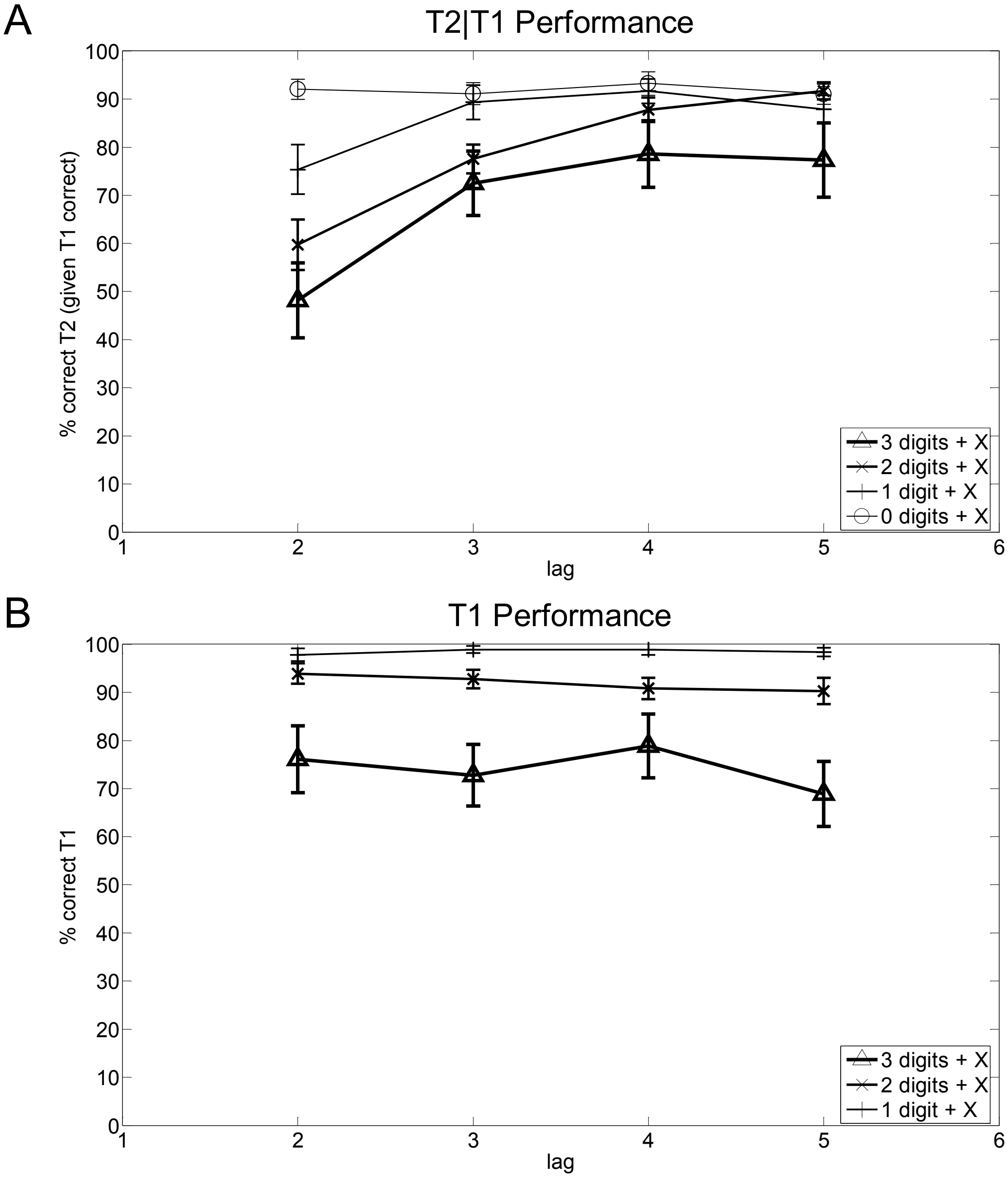

Figure 10 - Experiment 7: Changing global expectations II (2 digit event most frequent). A) T2│T1 performance and B) T1 performance at various levels of T1 compositionality. Error bars show +/- 1 standard error of the mean.

Cross-Experiment Comparisons

I compared 3 experiments which employed different relative trial frequencies: the masked condition of Experiment 3 (3 digit events most frequent: P(3 digits)

= 0.4), Experiment 6 (all digit events equally frequent: P(3 digits) = 0.25) and Experiment 7 (2 digit events most frequent: P(3 digits) = 0.17). The 3x4x4 repeated measures MANOVA contained Experiment (Exp. 3, Exp. 6, Exp. 7) as a between-subjects factor, along with condition (3 digits + X; 2 digits + X; 1 digit + X; 0 digits + X) and lag (2-5) as within-subjects factors. There were significant main effects of condition (*F* (3, 55)=16.50, *p*< .0001, η_p^2 = 0.2626) and lag (*F* (3, 55)=27.02, *p*< .0001, η_p^2 = 0.4906), and interactions of condition and lag (*F* (9, 49)=11.96, *p*< .0001, η_p^2 = 0.2283), and of experiment and condition (*F* (6, 110)=2.83, *p*< .01, η_p^2 = 0.1085). I compared blink magnitudes between experiments using planned comparisons at lags 2 and 3 for each digit level. Comparing Experiment 3 with Experiment 6, there were no differences in AB magnitude (at lag 2 or 3) in 3 digit (both *p*> .4) or 1 digit trials (both *p*> .1). In the 2 digit condition, there was no difference between experiments at lag 3 (*p*> .9), although there was a trend towards a stronger AB at lag 2 in Experiment 3 (54%) than in Experiment 6 (70%; *p*= .08). Comparing Experiment 3 with Experiment 7, there were no significant differences in AB magnitude at lags 2 or 3 in 2 digit (both *p*> .5) or 1 digit trials (both *p*> .5). Importantly, there was a significantly stronger AB with 3 digits in Experiment 7 (48%) than Experiment 3 (74%) at lag 2 (*p*< .01), with a trend in the same direction at lag 3 (*p*= .08). Finally, comparing Experiment 6 with Experiment 7, there were no differences in the 2 digit condition at lags 2 or 3 (both *p*> .2). Performance with 1 digit was lower at lag 2 in Experiment 7 (75%) than Experiment 6 (87%; *p*< .05), while there was no difference at lag 3 (*p*= .4). There was a stronger AB with 3 digits at lags 2 and 3 (both *p*< .05) in Experiment 7 (lag 2 performance: 48%) than Experiment 6 (lag 2 performance: 68%).

Discussion

An AB again occurred in conditions with a full T1 (3 digits) and partial T1 (1 digit and 2 digits). For the first time, the 3 digit AB was numerically stronger than the 2 digit AB, although the difference did not reach significance. However, the cross-experimental comparisons revealed a significantly larger AB with 3 digits in Experiment 7 (P (3 digit)[9] = 17%) than either Experiment 6 (25%) or Experiment 3 (40%), while there was no difference between Experiments 6 and

3. Likewise, in 2 digit trials, there was a larger AB (statistical trend only) in Experiment 3 (P (2 digit as final event) = 17%) than Experiment 6 (25%), while the AB magnitude was not modulated in the transition of global probabilities from 25% (Experiment 6) to 40% (Experiment 7). A similar pattern was apparent with 1 digit trials: The mild AB was lost in the transition from 17% (Experiment 7) to 25% (Experiment 6) global probabilities. Together with the findings across all behavioural experiments, this suggests that global expectations induced by trial frequencies can indeed modulate local expectations regarding the digit event. This relationship does not appear to be linear: The transition from a relatively rare (17%) to an equally frequent (25%) digit event reduces the AB magnitude, while increasing global probability beyond 25% seems to have minimal additional influence. The pattern of results suggests that the processing of an under-expected digit event, in particular, takes its toll on switching to T2. This fits with previous findings of a stronger AB with an infrequent T1 (vs. frequent T1, Crebolder et al., 2002) and invalidly cued T1 (vs. validly cued T1, Martens et al., 2006).

There was a trend towards a main effect of practice on the AB magnitude. Performance in all digit conditions improved equally from the first 180 trials to the second 180 trials.

On a different note, the results from Experiments 6 and 7 also imply that participants did not find any condition perceptually more difficult than the others. For example, the AB with 2 digits could have been lowest in Experiments 1, 3, 4 and 5 because participants found it difficult to distinguish 2 digits from 3 digits. However, I have shown that across all digit conditions the T2 deficit varied considerably with trial frequency, while the perceptual discriminability of digits and the task instructions (3 digits = target) remained constant. This conclusion is further corroborated by Experiment 3, where the presence or absence of the post-digit mask did not affect performance on discriminating 2 digits from 3 digits (T1 performance), while it had a significant effect on AB magnitude (T2|T1 performance) with 2 digits. This dissociation underpins my interpretation in terms of raised and disappointed expectations, while it is hard to account for this by differences in perceptual discriminability.

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[9] unconditional (or global) probability of seeing 3 digits as the final digit event

Summary of Behavioural Findings

In 7 behavioural experiments, I have consistently shown that an AB can be elicited without a full T1 (3 consecutive digits) actually occurring, simply by building local expectations for the target within the trial. In fact, a strong AB was found in trials where expectations were maximally raised but subsequently violated (with 2 digits). The magnitude of the AB for partial targets was modulated by T1 masking. Marking the final digit with a colour or sound cue had minimal influence on performance for any digit level. There was, however, a hint that colour could capture attention for the T1 event, although this effect could equally reflect group differences. On the other hand, global expectations induced before the trial played a strong modulating role in the AB magnitudes for the various digit events. Finally, the findings cannot be explained simply by the act of counting the digits or by participants switching to T2 after the second digit, which adds strength to my claim of incrementally raised expectations strongly influencing the AB. In the following 2 chapters, I investigate the neural correlates of raising expectations for the full T1 event (MEG Experiment 1) and of counting the digits in the T1 event (MEG Experiment 2).

Chapter 8 - MEG Experiment 1: Neural correlates of Expectations

Background to Magnetoencephalography

Magnetoencephalography (MEG) is a non-invasive neuroimaging technique used to detect the magnetic signals from groups of neurons in the cortex. Introduced in the 1970s (Cohen, 1972), MEG systems have progressed from single channel machines to whole-head systems. Like its predecessor, electroencephalography (EEG), MEG has a temporal resolution in the order of milliseconds, allowing us to track neuronal changes in time with high precision. MEEG (MEG and EEG) provide a direct measure of brain activity, in contrast to functional Magnetic Resonance Imaging (fMRI) which records the haemodynamic response, an indirect measure. The spatial resolution of MEG (2-3 cm) is much lower than with fMRI (~1mm) (Kujala et al., 2008), although it can be improved through the use of MEG systems with many sensors, and spatial beamforming filters to localise sources (Konig, 2007).

MEG sensors detect tiny magnetic fields which originate from the electrical currents of cortical neurons. The synchronous activity of thousands of pyramidal neurons becomes summed because groups of neurons are orientated in parallel. The minute signal is picked up by highly sensitive sensors outside the head. In terms of the cellular source of MEEG signals, it is unlikely that they result directly from the firing of action potentials along neurons. Instead, the signal probably originates from excitatory postsynaptic potentials (EPSPs) occurring in the postsynaptic pyramidal cell (Hämäläinen et al., 2002, Del Gratta, 2001). The magnetic field measured at the scalp results from the combination of primary and secondary (volume) currents induced at the cellular level (Baillet et al., 2001, Hämäläinen et al., 1993). The primary current flows intracellularly along the pyramidal cell towards the apical dendrites (where the EPSPs occur). The current loop is completed by the passive secondary current which flows through the extracellular fluid from the synapses back to the body of the neuron. When thousands of neurons are synchronously active in a patch of cortex, the currents become summed and can be measured using MEG.

The orientation of neurons is an important factor which determines whether the magnetic signal can be detected outside the head. Pyramidal neurons are aligned perpendicularly to the surface of the cortex. While an electrical current travels between poles at each end of the neuron, the magnetic current circles the neuron at a right angle to the electrical current (Hämäläinen et al., 1993). Therefore, MEG can optimally detect magnetic currents which originate from neurons within the cortical sulci, while EEG mainly measures from neurons situated in gyri (Cohen et al., 2009).

MEG has some advantages over EEG. The 248 channel MEG system at the Glasgow University Centre for Cognitive Neuroimaging (CCNi) has 7 times more sensors than a typical EEG system, which gives MEG superior spatial resolution. Additionally, less spatial smearing occurs with magnetic than electrical signals. As electrical fields pass through the brain, they are absorbed differentially by various tissues. This distortion of the signal can make EEG source analysis difficult. However, magnetic fields can pass through tissues without disturbance (Konig, 2007).

Each MEG sensor consists of a magnetic pick-up coil coupled to a superconducting quantum interference device (SQUID) (Konig, 2007). The CCNi system uses magnetometers: single coils of wire sitting at right angles to the surface of the helmet. The SQUIDs (Zimmerman, 1977) detect the magnetic current from the magnetometers, and are highly sensitive to the tiny signals when super-cooled in liquid helium. Reference sensors enable differential noise cancellation. The scanner is enclosed in a magnetically shielded room (MSR) to block out the huge external magnetic noise. MEG systems are thus designed to increase the signal-to-noise ratio (SNR), uncovering tiny brain signals (~10^2 to 10^3 femto Tesla (fT)) which would be swamped by the huge biological and environmental magnetic noise (between 10^4 and 10^{11} fT) (Konig, 2007, Baillet et al., 2001). (For more technical details of MEG systems see Hämäläinen et al., 1993.)

MEG data can be analysed in the time- and frequency-domains, and these two approaches inform us of different aspects of brain activity in response to a stimulus. In the time-domain, event-related fields (ERF) emerge from averaging data, and they reflect components evoked by the stimulus which are time-locked to that event. This technique assumes any background activity is merely noise to be eliminated by the averaging process. However, much work has shown that the ongoing, non-stationary activity of the brain is of interest to cognitive processing (cf. Baillet et al., 2001), encouraging analysis in the frequency-, as well as the time-domain. In particular, top-down processes such as expectation and attention can fluctuate over long periods depending on motivation and arousal levels, and so underlying activity may not always relate closely to external stimuli.

However, sensor-level analysis can only roughly inform us about the cortical regions underlying the activity. The inverse problem must be solved in order to localise sources. For a measured magnetic field at the surface, there is no unique solution to the inverse problem, as many current distributions can give rise to the same topography at the sensor-level. So source analysis uses various constraints in the estimation to find a plausible inverse solution (Baillet et al., 2001, Konig, 2007). There are many methods to localise sources in both the time- and frequency-domains (see Michel et al., 2004 for a review). Here source analysis focuses on the frequency domain, where a beamforming approach called Dynamic Imaging of Coherent Sources (DICS) (Gross et al., 2001) can be used. It constrains the estimation by using an adaptive spatial filter to pass activity from a particular source, while minimising activity from all other sources. For further details, see the Analysis Methods further in this chapter.

In summary, MEG offers a direct, non-invasive view of the activity of specific cortical areas, and is well suited to detect the brain's temporal dynamics under rapid visual stimulation.

Introduction to MEG Experiment 1

The behavioural experiments in Chapters 2 to 7 suggest that expectations for a composite T1 build with each successive digit, and when high expectations are violated, there is a detrimental impact on T2 performance. But what are the neural correlates of raised and subsequently violated expectations? In this first MEG experiment, I investigate brain activity in the time- and frequency-domains when participants must detect the composite target (3 digits) without a T2. I predict dissociation in the neural dynamics of raised but violated expectations (2 digits) versus fulfilled expectations and target consolidation (3 digits).

MEEG research into the AB focuses on processing of T1 and T2 in the brain, where targets are single letters or digits. The concept of building local expectations for a composite target (during the trial) is new, and so this experiment is fairly exploratory. The P300 (and its magnetic counterpart, the M300) are consistently modulated in AB experiments. A P300 is observed to each target that is successfully reported (Kessler et al., 2005a, Kessler et al., 2005b, McArthur et al., 1999, Vogel et al., 1998). However if T2 is missed, the T2-P300 is suppressed (Vogel et al., 1998, Kessler et al., 2005a, Shapiro et al., 2006). This evidence fits with the theories that the P300 reflects entry or updating of information in working memory (Donchin and Coles, 1988, Verleger, 1988), or targets accessing the global workspace (Dehaene et al., 2003a). AB masking experiments inform us about effects on the P300 latency. When T2 is unmasked and both targets are reported, the T2-P300 is delayed (Vogel and Luck, 2002), suggesting targets are processed in working memory without time- or processing-constraints from the mask. On no-blink trials, a mask after T1 is associated with an earlier T1-M300 peak but a delayed T2-M300 peak in prefrontal areas, compared to trials with a gap after T1 (Kessler et al., 2005a). This pattern reflects a boost of T1, and a delayed but successful reconfiguration of the system for T2 in response to the intermittent mask.

In this paradigm, the M300 results could inform about where the target decision is made. One possibility is that incoming digits update a low-level counter, and working memory is only recruited once the full target (3 digits) has occurred. This could be reflected by a single M300 to the 3rd digit, along with sources for 3 digits in lateral prefrontal working memory areas (Postle and D'Esposito, 2000), as well as posterior parietal number quantification areas (Dehaene et al., 2003b). In this scenario, M300s would be absent in partial target (1 digits and 2 digit) conditions, and only parietal quantification sources would be observed. Alternatively, all digits could immediately enter working memory as potential parts of the full target. All digits could be held there until the target decision was made. This would manifest in an M300 to each digit, and the involvement of both working memory and quantification areas for all digit levels.

Processing of targets in the AB is also represented in the long-range oscillatory activity of the brain (see Janson and Kranczioch, 2011 for a recent review). A target-related network involves frontal, parietal and temporal regions, as illustrated by MEG (Gross et al., 2004) and fMRI studies (Feinstein et al., 2004, Kranczioch et al., 2005, Marois et al., 2000). Phase synchronization and coherence between sources inform us about network communication (Fries, 2005). Within the AB target-related network, beta-band synchronization differentiates between targets and distractors. In no-blink trials, there is strong synchronization to targets & strong desynchronization to distractors (Gross et al., 2004, Kranczioch et al., 2007, see Kessler et al., 2006 for a review). These fast and dynamic changes could reflect the real-time demands on attention: enhanced processing of relevant information (large-scale synchronization) and suppressed communication of irrelevant information (large-scale desynchronization). In particular, the desynchronization before T2 was essential for T2 report, and could represent the necessary de-coupling of the robust state so the system could switch from processing T1 to T2 (Kessler et al., 2006, Rodriguez et al., 1999, Varela et al., 2001).

On top of the RSVP target detection aspect of the task, I will investigate the neural dynamics of incrementally building expectations for the target. Research into anticipatory temporal attention has been particularly fruitful in the frequency domain, since expectations may not be time-locked to stimuli. Expectations regarding visual targets modulate the alpha (α) (Klimesch et al., 1998, Bastiaansen and Brunia, 2001, Rohenkohl and Nobre, 2011, MacLean and Arnell, 2011) and beta (β) bands (Gross et al., 2006). In the α and β bands, power decreases (relative to a baseline) reflect intense processing, while this is reflected by increases in theta (θ) and gamma (γ) power (cf. Hanslmayr et al., 2011, Klimesch et al., 2007). In the α band, anticipation of performance feedback on a time estimation task resulted in pre-stimulus power decrease over the visual cortex (Bastiaansen and Brunia, 2001). Expectancy for a target was reflected by α power decrease (specifically in the 8.4-10.4 Hz band) in anticipation of the target (Klimesch et al., 1998). Power decreases in α peaked just before a rhythmic target was expected to reappear (Rohenkohl and Nobre, 2011). Anticipatory α power decrease before the RSVP stream was related to performance on the AB (MacLean and Arnell, 2011), with a pre-trial α decrease occurring before T2 was missed at short lags, and before T2 was reported at long lags. Anticipatory α power decreases have been interpreted as increased thalamocortical transfer (cf. Hanslmayr et al., 2011) to prime the relevant sensory cortex, so that when the stimulus does arrive it can be processed quickly and efficiently (Bastiaansen and Brunia, 2001).

Furthermore, expectations about the timing onset of a target were associated with ß-band phase synchronization within the AB target-related network. As the predictability of a single target grew within a trial, there was a greater difference between synchronization to the target (260 ms after target onset) and desynchronization to the pre-target distractor (114 ms after target onset) (Gross et al., 2006), which is of particular interest for my paradigm. This may represent the development of a more vigilant or pre-activated state with increasing expectations, as targets become more available to specialised processors in the global workspace (Dehaene et al., 2003a), while distractors are suppressed. This would increase the efficiency of processing the expected target and of planning its relevant response. But this stability could potentially hinder any subsequent targets (e.g. T2 in the AB), as processing T2 would require a system re-set.

Expectations about upcoming visual inputs are clearly represented in the oscillatory changes in the brain, and this enhanced processing is advantageous when expectations are fulfilled. But what are the neural correlates underlying violated expectations and uncertainty about what you have seen? Dorsolateral PFC and posterior parietal cortex activations increased monotonically with increasing uncertainty in an fMRI study, when participants had to predict the next item in a sequential series of shapes (Huettel et al., 2005). Uncertainty about decisions often activates the posterior fronto-median cortex, including BA 8, BA 6 and the dorsal anterior cingulate cortex (ACC: BA 24, 32) (cf. Volz et al., 2005). The ACC, as well as monitoring for conflict and errors, is active when expectations are violated (Oliveira et al., 2007); the error-related negativity (ERN: an ERP reflecting ACC activity) was observed when performance feedback deviated from participants' judgements of their performance. Regarding this paradigm, if target expectations are, in fact, built-up and violated in 2 digit partial target trials, I might observe strong sources in these regions underlying uncertainty.

To summarise, in this experiment I aim to investigate the neural dynamics of incrementally building target expectations (with 1 digit and 2 digits), maximally violated expectations (2 digits) and full target consolidation (3 digits).

Behavioural AB experiment: pilot study for MEG

A behavioural AB pilot experiment was performed prior to the MEG experiment, to find the optimal settings and timing of the RSVP stream to induce a strong AB. Although the MEG experiment used only the composite T1, I intended it to be a baseline for a future dual target MEG experiment, and so wanted to optimise the settings for the AB. I aimed to induce a blink magnitude of around 50% at lag 2 in the 3 digit + X condition, as it will be important for MEG analysis to have approximately equal numbers of blink and no-blink trials. The RSVP stream was presented more rapidly (SOA=150 ms, ISI=90 ms) than previous behavioural experiments. All digit levels had the same relative frequency to induce a similar magnitude AB with 2 digit and 3 digit trials (like in behavioural Experiment 6). Twenty participants (7 males, mean age 26.30 years ± 5.60 SD) were recruited. All conditions were allocated the same number of trials. In each condition (3 digits + X, 2 digits + X, 1 digit + X and 0 digits + X) there were 20 trials per lag. T2 was presented at lags 2, 3 and 4. All other details were identical to Experiment 6.

T2|T1 Performance

The results illustrate the strong and equal sized AB with 3 digits and 2 digits, with a milder AB with 1 digit (Figure 11A). For T2|T1 performance, a 4x3 repeated measures MANOVA consisted of 2 within-subjects factors: condition (3 digits + X; 2 digits + X; 1 digit + X; 0 digits + X) and lag (2-4). There were significant main effects of condition (F (3, 17)=12.28, $p< .001$, $\eta_p^2 = 0.5570$) and lag (F (2, 18)=36.04, $p< .00001$, $\eta_p^2 = 0.7410$) and a significant interaction of condition and lag (F (6, 14)=5.55, $p< .01$, $\eta_p^2 = 0.2694$). An attentional blink occurred with all partial (1 digit and 2 digits) and full T1 (3 digits) targets. Performance with 1, 2 and 3 digits was significantly lower than baseline (0 digits + X) at lags 2 and 3 (all $p< .05$). In terms of relative blink magnitudes, 3 digit performance was lower than 1 digit at lags 2 and 3 (both $p< .05$). Two digit performance was significantly below 1 digit at lag 2 ($p< .01$), while there was a trend in this direction at lag 3 ($p= .07$). Performance with 2 digits did not differ significantly from 3 digits at any lag (all $p> .8$).

Performance on digit-events

For composite T1 performance in trials with digits and X, a 3x3 MANOVA consisted of condition (3 digits + X; 2 digits + X; 1 digit + X) and lag (2-4) (Figure 11B). It revealed a significant main effect of condition (*F* (2, 18)=67.45, *p*< .00001, $\eta_p^2 = 0.4446$). This was driven by significantly lower performance in both the 3 digit (79%) and 2 digit (82%) conditions than the 1 digit (96%) condition, collapsed over all lags (both *p*< .001). There was no significant difference between T1 performance in 3 digit and 2 digit trials (*p*= .5).

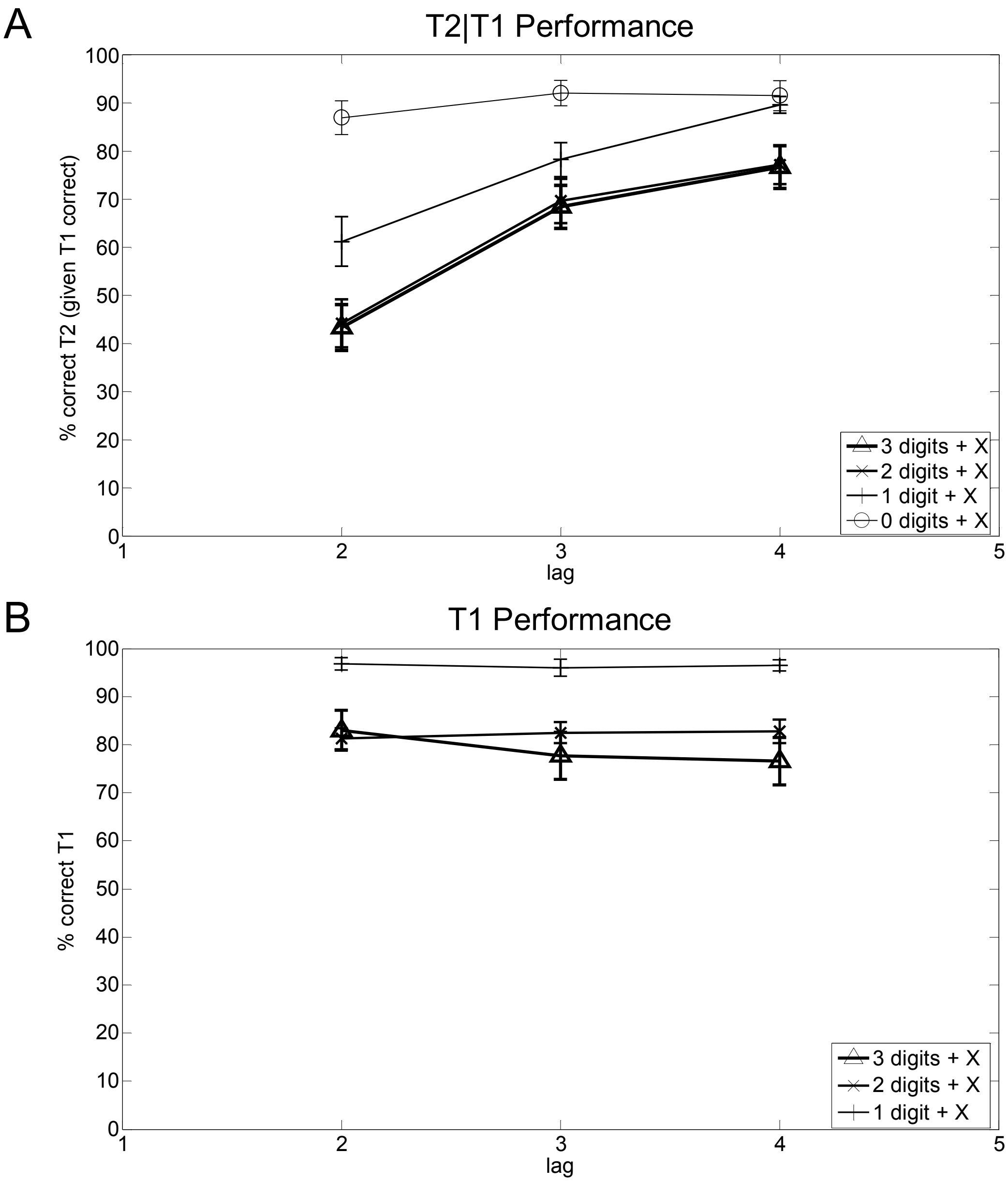

Figure 11 - Fast behavioural pilot AB experiment for the MEG. A) T2│T1 performance and B) T1 performance at various levels of T1 compositionality. Error bars show +/- 1 standard error of the mean.

Methods for MEG experiment

Participants

Sixteen participants were recruited from the University of Glasgow community[10]. Data from 14 participants (6 males, 27 ± 5 years (mean age ± SD), all right-handed with normal or corrected vision) were analysed. The study was conducted in accordance with the declaration of Helsinki, and was approved by the Faculty of Information and Mathematical Sciences (FIMS) ethics committee (FIMS00557) and the CCNi steering committee (Project0038). Participants received a study information sheet, and completed an MRI screening form and MEG/MRI consent form. Participants received £6 per hour for taking part in the experiment. Data were identified using a participant-specific ID code.

Behavioural methodology for MEG experiment

The stimuli used for the MEG experiment were identical to the behavioural AB pilot, except in the MEG I presented a composite digit T1 in an RSVP stream of letter distractors without a T2. The task was to detect 3 digits: after the trial they responded whether or not they saw 3 digits. Participants completed 20 practice and 600 experimental trials. Viewing distance was 185 cm, and stimuli subtended a visual angle of approximately 5°. The resolution of the projector was 1024 x 768 with a colour depth of 32 bits. Trials were self-paced. A central fixation cross occurred for 1500 ms, before the RSVP stream (SOA=150 ms, ISI=90 ms) was presented centrally. Participants were asked to minimise eye movements and blinks during the trial, and remain still in the MEG. They responded with their right hand using a 5 button Lumitouch response pad: pressing their thumb to initiate the trial, index finger for a target (3 digits) and middle finger for no target (0, 1 or 2 digits). If participants reported a target when there were fewer than 3 digits (a false alarm), they received visual feedback about their error. The experiment lasted for approximately 70 mins (4 blocks of ~18 mins) with self-paced breaks between blocks.

It was a repeated measures design with the factor "condition" (3 digit full target, 2 digit partial target, 1 digit partial target and 0 digit baseline

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[10] Two participants were excluded from MEG analysis; one participant performed poorly on 3 digit trials (accuracy < 5%), and I could not obtain a structural MRI for the other participant.

conditions). All conditions contained equal numbers of trials (150 trials per condition) which were mixed throughout the experiment. The onset of the digits was staggered between 3 possible starting points (position 4, 5 and 6) within the 11 item stream, and at least 3 distractors occurred before and after the digits.

MEG methodology

MEG data were collected using the 248-channel whole head magnetometer (4D-Neuroimaging Magnes 3600 WH system, San Diego, CA, USA) at the CCNi at Glasgow University. Online noise cancellation was performed using in-built software. A sampling rate of 508.63 Hz was used. Trigger pulses were delivered through a parallel port connection, to synchronise MEG data collection with experimental events: the start of the trial, the onset and type of digit condition and response accuracy. HPI coils were attached to the participant's head behind the right and left ears, above the nasion, and on the right- and the left-hand side of the forehead. The coil positions and head shape were digitized before the scan using the Polhemus program and stylus (Polhemus Isotrak, Kaiser Aerospace Inc, Colchester, Vermount, USA). Digitization allowed us to localise the head position in the MEG at the start and end of each block (maximum movement tolerated was 0.5 cm), and enabled co-registration with the structural MRI for source localisation. Participants without a structural MRI were scanned using the CCNi 3T Siemens Trio MRI (Siemens Medical Solutions, Erlangen, Germany) by the Research Radiographer Frances Crabbe.

Analysis methods

Preprocessing

Data were analysed using the Matlab toolbox FieldTrip (Oostenveld, 2011). Only trials with correct responses were analysed. Trial definition was based on the onset of the 1st digit (t=0), and the trial length was 2.9s (-1.7:1.2s). Data were preprocessed separately for ERF and TFR analysis.

Event-related fields

Data for ERFs were baseline-corrected (-0.4:0s), detrended, low-pass filtered at 35Hz & padded to a length of 10s. Whole trials were rejected if they contained eye-blinks, muscle or channel jump artifacts. Six channels (A248, A107, A40, A146, A150, A15) were consistently noisy for the group, and were removed. Heart artifacts (1-2 per participant) were removed using independent component analysis (ICA) (Vigário et al., 2000). Individual and subsequently grand average ERFs were calculated for each digit condition by averaging amplitude relative to t=0.

Time-frequency analysis

More detailed preprocessing was applied to data before analysis in the frequency-domain, due to the detrimental influence of line noise on the spectral content of the signal. Data were detrended, dft-filtered (at 50, 100 and 150Hz) and trials were padded to 10s. Trials containing eye-blinks, muscle and channel jump artifacts were excluded. Data were resampled at 500Hz. Data were denoised using PCA to remove line noise components, by regressing out activity common to the magnetometers and the 23 reference channels. Noisy trials and channels were removed. Between 8 and 12 channels were removed for each participant, 5 of which (A248, A107, A40, A146, A134) were consistently bad in all participants. Data were now processed separately for low (2-30Hz: θ, α, β) and high frequencies (30-90Hz: γ[11]). For low time-frequency analysis, I performed ICA with 30 components to remove 1 or 2 heart-related components.

Participant-specific noisy channels were repaired for the sensor-level data, by calculating the average of neighbouring sensors. This step was necessary to preserve a high number of functioning channels for the statistics and plots. Channels were not repaired prior to source-level analysis because repairing channels using an average of the neighbours could induce artificial correlations between sources.

Time-frequency representations (TFRs) of power were estimated for 2-30Hz using a single Hanning taper. A frequency-dependent sliding time window

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[11] High TFR analysis required extremely clean data, so I performed a more thorough rejection of ICA components. As well as rejecting heart-related components, I also excluded any strong noise components. To anticipate the results, I found no statistically significant γ effects, except for smearing from β, and so I do not discuss the γ results.

was used to capture 5 cycles per frequency[12]. The window was moved across the data in 50 ms time steps and 2Hz frequency tiles. The data were Fourier-transformed to give power spectral densities. An absolute baseline (-0.2:0s) was then applied before plotting. Grand average TFRs were calculated for all digit conditions. Main analysis focused on differences between digit (1, 2, 3 digits) versus baseline (0 digit) conditions in theta (θ: 3-7Hz), alpha (α: 9-13Hz) and beta (ß: 17-21Hz) bands[13].

Source analysis of frequency effects

DICS beamformer (Gross et al., 2001) was used for source reconstruction of digit conditions in each participant separately. The DICS method is used to find sources in the frequency domain, and is particularly good at separating nearby sources (Liljeström et al., 2005). This technique uses adaptive spatial filters to localise power. A semi-realistic head model (Nolte, 2003) is first created from the individual's structural MRI. This brain volume is merged with a grid (6mm resolution) and the lead-field matrix calculated for all grid points. The filter is calculated using the cross-spectral density (CSD) matrix and the lead-fields. There are 2 approaches to making filters, each with its own advantages: using a common filter (optimally finds quantitative differences between conditions) and separate filters (optimised for qualitative differences)[14].

Frequency and time windows of interest were identified from the sensor-level statistics. Sources were estimated for low frequency power using a

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[12] With the frequency-dependent time window, the end of the trial was lost for the theta band due to the long time window needed to capture 5 cycles of this slow oscillation. E.g. for 6Hz, I lost information from 0.8:0.9s.

[13] For 30-90Hz analysis, I used 7 multi-tapers to estimate power. The length of the time window chosen represents a compromise between high frequency resolution (long time window) and high temporal resolution (short time window) (Konig & Durka, 2007). In RSVP streams, we are most interested in *when* neural changes occurred, and therefore optimised for good temporal resolution, at the cost of frequency smearing. The length of the time window and the amount of frequency smoothing was dependent on the frequency, with a time window (s) of 10/frequency and a smoothing (in Hz) of 0.4*frequency.

[14] Common filters are made using data from all the conditions you want to compare. The CSD estimate (and thus the filter) is improved by the large amount of data, and so this method is favoured by many MEG researchers. Using a common filter, we assume similar sources in all conditions, and so this method informs us about quantitative differences between conditions. However, I predict that different sources underlie full target consolidation (3 digits) and raised but violated expectations (2 digits). Separate filters can inform us of such qualitative differences. Filters are constructed separately for each digit condition, and so filters are optimally tuned to each specific condition. However, the disadvantage is that source differences between conditions could potentially result from the different filters, and not from real differences in power.

Hanning window on 0.5s of data: θ (6±2Hz, 0.05:0.55s, 3 cycles), α (10±2Hz, 0.4:0.9s, 5 cycles), β (20±4Hz, 0.35:0.85s, 10 cycles). I calculated sources using both a common filter and separate filters for α and β bands, where I observed significant differences between 3 digit, 2 digit and 1 digit conditions at the sensor-level. For θ, there were no sensor-level difference between 3, 2 and 1 digits, so I used only a common filter, collapsed across these conditions, and compared the 321 digit sources to the 0 digit baseline. Sources were identified using the Talairach client (Lancaster et al., 2000).

Cluster-based permutation statistical testing

Non-parametric cluster-based permutation statistics were used to compare 3, 2 & 1 digit levels to the 0 digit baseline condition in a within-subjects design. These cluster-based statistical tests effectively control the Type I error rate for multiple comparisons[15] (Maris and Oostenveld, 2007, Maris, 2004). At the sensor-level (ERFs and TFRs), cluster-based (minimum of 2 sensors per cluster) dependent samples t-tests were performed using Monte Carlo randomization (with 500 randomizations)[16].

For ERFs, statistics were calculated on data from 0.1 to 0.9s. For TF data, statistics were calculated over this time period for the whole frequency range (for low frequencies between 2 and 30Hz, and for high frequencies between 30

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[15] The Multiple Comparison Problem is always an issue when performing statistics on MEG data because of the number of samples to be compared. For example, in the time domain, comparing a stretch of 1 second of data between 2 conditions results in close to 126,000 channel-time samples, as data are collected 508 times per second at 248 MEG channels. Furthermore, in the frequency domain, I evaluate channel-time-frequency samples in around 15 frequency bins. So performing multiple uncorrected t-tests at each sample results in a huge number of false positives, while using a Bonferroni correction is too conservative and leads to many false negatives (depicted in Figure 1 of Maris & Oostenveld, 2007).

[16] An uncorrected 2-way t-test was performed between pairs of conditions at each sample. Samples which exceeded the predefined threshold were selected to form clusters. A cluster represented a group of samples which were temporally and spatially adjacent in ERF data, and which also had spectral adjacency in TFR data. To belong to a cluster, each sample must be adjacent to at least 2 neighbouring sensors which all exceeded the threshold. Clusters were either positive or negative, which informed about the direction of the difference between conditions. These parameters determined the sensitivity of the test. Now I tested the significance of each cluster. The t-values within each cluster were summed, and the cluster with the maximum sum was tested first for its significance using the Monte Carlo random permutation method. Trials from both conditions for all participants were randomly assigned to 2 subsets and the maximum t-value was calculated. This permutation testing was repeated 500 times and a histogram was produced with all test statistics. The original cluster statistic was compared to the histogram to ascertain the Monte Carlo p-value for the cluster, i.e. the proportion of random partitions which gave a higher test statistic. The overall critical p-value of 0.05 was split between positive and negative clusters, i.e. positive clusters were assessed against a p-value of 0.025 and negative clusters were assessed against p of 0.025. Significance testing was repeated for the other clusters.

and 90Hz). Source-level statistics were applied in a similar way. The false detection rate (fdr) was used to correct for multiple comparisons in the Monte Carlo random permutation method (with 1000 randomizations). For α and β, I used dependent sample t-tests to compare each separate digit level to the baseline condition. For θ, I compared the merged 321 digit variable to the 0 digit condition, and used a pooled T statistic instead of a dependent t-test.

Behavioural results

A repeated measures MANOVA consisted of 1 within-subjects factor: condition (3 digits; 2 digits; 1 digit; 0 digits). There was a significant main effect of condition (F (3, 11)=8.70, $p< .01$, $\eta_p^2 = 0.3761$) (Figure 12). Performance with 3 digits (86%) and 2 digits (90%) was significantly lower than the 0 digit baseline (99%, both $p< .01$), while 1 digit (99%) did not differ from baseline ($p= .079$). There was no significant difference between performance with 2 digits and 3 digits ($p= .47$), while 1 digit performance was higher than both 3 digits and 2 digits (both $p< .01$).

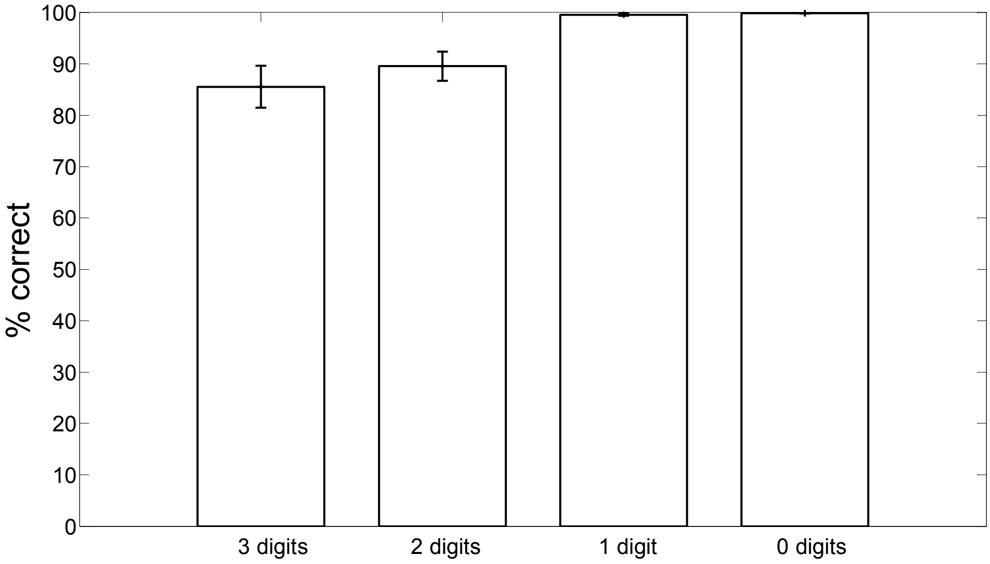

Figure 12 - Behavioural performance on the composite target detection task for 3, 2, 1 and 0 digits. Mean % correct ± 1 standard error is shown.

MEG Results

Event-related fields

Group ERFs (n=14) revealed a moderate amplitude (3.83 to 8.24×10^{-14} T) waveform repeated every 0.146 – 0.154 s in occipital channels (channel A204, Figure 13). There were no significant differences between 3, 2 or 1 digit levels versus the 0 digit baseline condition in occipital channels, suggesting this activity purely reflected visual processing of the incoming RSVP stream, with an

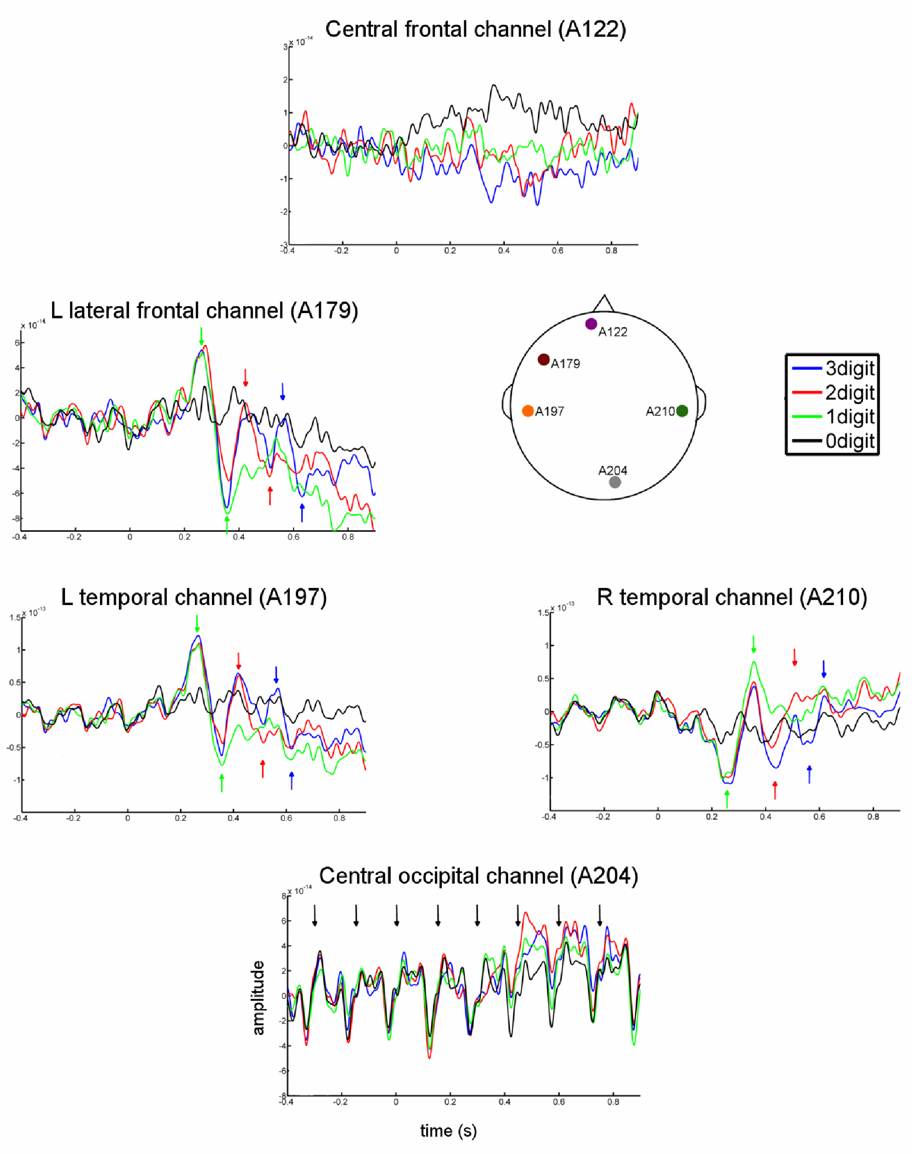

Figure 13 - Grand average ERFs for all digit levels in central frontal (A122), left lateral frontal (A179), left temporal (A197), right temporal (A210) and central occipital (A204) channels. Coloured arrows (green, red and blue) illustrate the M300s to each digit, while black arrows show the onset of items in the RSVP stream.

SOA of 0.15 s. Inspection of the occipital channel ERFs suggests top-down modulation by digits: there was a non-significant upward shift in the baseline for 1, 2 and 3 digits between 0.4 - 0.8 s which was not present occur in the 0 digit condition.

In temporal and lateral frontal channels, there was an M300 component to each incoming digit, occurring approximately 0.32 – 0.39 s after the onset of each digit (Figure 13, Table 1). The polarities of the waveforms were opposite in left- (e.g. temporal channel A197) and right-hand (e.g. temporal channel A210) channels, representing the influx and efflux of the magnetic current. There were no clear evoked components in a central frontal channel (A122); rather I observe a slow wave for 1, 2 and 3 digits which differs from the 0 digit baseline.

Amplitude (* 10^{-14} T)	**1st M300**	**2nd M300**	**3rd M300**
1 digit	12.8		
2 digits	10.1	5.85	
3 digits	12.6	4.37	6.22
Peak latency (s)			
1 digit	0.381		
2 digits	0.376	0.499	
3 digits	0.364	0.517	0.678

Table 1 - Group mean amplitudes and latencies of the M300 in the left lateral frontal channel A179. The unit of amplitude is Tesla (T).

The right temporal channel (A210) clearly shows the activity in the baseline period before the onset of the first digit (Figure 13). From -0.4 to 0 s, there was a component (4.12 to $5.12*10^{-14}$ T) repeated every 0.147 - 0.155 s which did not appear to differ between digit levels and 0 digits. This reflects the onset of the 3 distractors that occur before the 1st digit.

The ERF waveforms and topographies of the M300s were similar in 1, 2 & 3 digit conditions with a broad temporo-parieto-frontal distribution (Figure 14, Table 1). The M300 for 1 digit had a prominent broad temporo-parieto-frontal topography, as well as a focal posterior parietal component. A similar topography emerged for the 1st M300 in 2 & 3 digit conditions with the strong posterior parietal component, as well as a frontal component. Subsequent M300s displayed a strong central topography and the amplitude of the waveforms also decreased (Table 1). For the final M300 with 2 & 3 digits, a broader temporo-parieto-frontal component developed, particularly over left channels. A similar but weaker topography is seen in the 0 digit condition which could reflect the monitoring of the RSVP stream for digits. The 0 digit topography is mainly posterior, while the M300 digit topography has a strong anterior component.

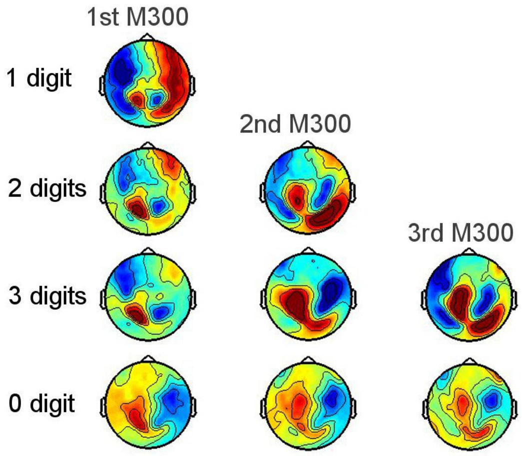

Figure 14 - Absolute topographies for the M300 peaks for each digit level. ERF amplitude is averaged across a 0.1s period for each plot: 1st M300 0.3:0.4 s, 2nd M300 0.45:0.55 s, 3rd M300 0.6:0.7 s.

Time-frequency analysis

Time-frequency analysis in the 4:30 Hz range revealed interesting effects in beta (β), alpha (α) and theta (θ) bands. Group time-frequency representations

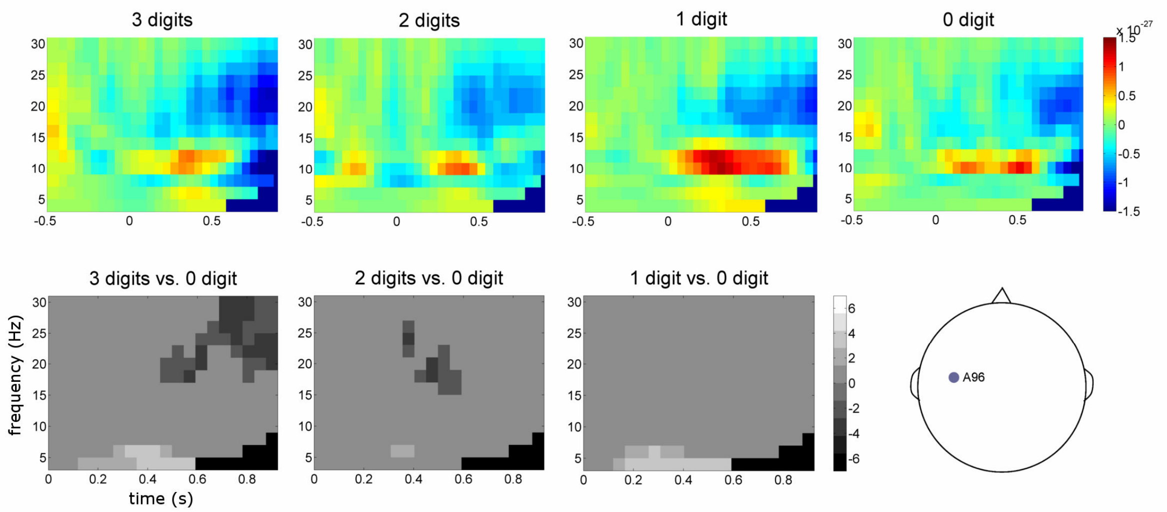

Figure 15 - Group TFR (top row) and statistics (bottom row) for each digit level for a left anterior-temporal channel (A96) in 4 to 30 Hz range. The top row shows TFR relative to baseline (-0.2:0s) for each digit. Red reflects a power increase and blue a power decrease. The bottom row shows the statistically significant effects in time and frequency for 1, 2 and 3 digits vs. 0 digit. White reflects a significant power increase and dark grey a power decrease.

(TFR) for a left anterior-temporal channel (A96) (Figure 15, top row) illustrate the strong differences in ß- and α-bands between digit levels. A ß-band power decrease (relative to baseline) was present in all digit levels, but was strongest and most sustained in the 3 digit condition. In the α-band, there was a strong sustained power increase in the 1 digit and 0 digit conditions, followed by a late power decrease. A more transient power increase was observed in the 3 digit and 2 digit conditions, before the late power decrease. This channel also shows a θ power increase in 1, 2 and 3 digit conditions, which is absent in the 0 digit baseline. Cluster-based statistics were performed across all frequencies and all channels, over a time-window of 0:0.9 s. For temporal channel A96, statistically significant effects were observed for the θ power increase for 1, 2 and 3 digits vs. 0 digit, and for the ß power decrease for 2 and 3 digits vs. 0 digit (Figure 15, bottom row). Significant differences between digit levels were observed in the α-band in posterior channels (as illustrated in Figure 19). Additionally, the TFR for a central occipital channel (A186) illustrates the strong and sustained alpha power decrease during the RSVP stream (relative to baseline) in trials containing 0, 1, 2 and 3 digits (Figure 16). A late α power increase is observed in 1 digit trials. The sensor- and source-level effects for the ß, α and θ bands will now be discussed in detail.

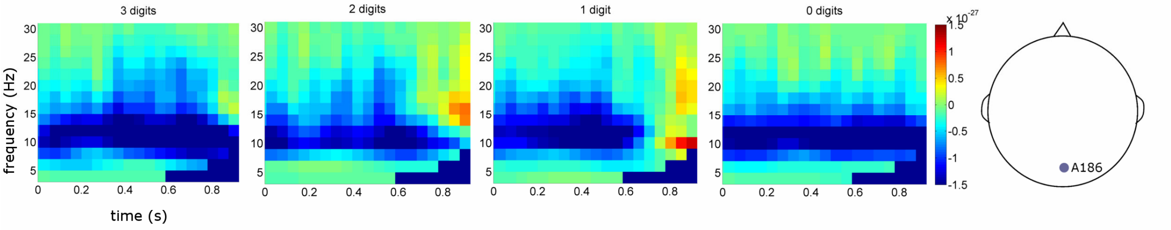

Figure 16 - Group TFR for each digit level for a central occipital channel (A186) in 4 to 30 Hz range. The plots show TFR relative to baseline (-0.2:0 s) for each digit. Red reflects a power increase and blue a power decrease.

Beta band

At the sensor-level, there were clear differences between the digit levels in the ß band (17-21 Hz) (Figure 17). In the 3 digit vs. 0 digit comparison, there was an early and sustained power decrease (2 negative clusters: 0.25:0.65 s, *p*=0.008 & 0.75:0.9 s, *p*=0.01). An early left central cluster (from 0.25 s) was later joined by a right central cluster (~ 0.75 s). The 2 digit vs. 0 digit comparison shows a similar pattern until 0.65 s (negative cluster: 0.35:0.65 s, *p*=0.006), when a late anterior power increase occurred (positive cluster: 0.75:0.9 s, *p*=0.01). A late but non-significant posterior power increase can also be seen in the topographies. There were no significant differences in the 1 vs. 0 digit comparison (all *p*> 0.086), although a late posterior power increase (from 0.7 s) is apparent. Comparing the partial targets, there were no significant differences between 2 and 1 digits (1st positive cluster *p*=0.326 & 1st negative cluster *p*=0.048, not significant (ns)[17]). There was a significant power decrease when comparing 3 digits with 2 digits (0.65:0.9 s, *p*=0) and with 1 digit (0.55:0.9 s,

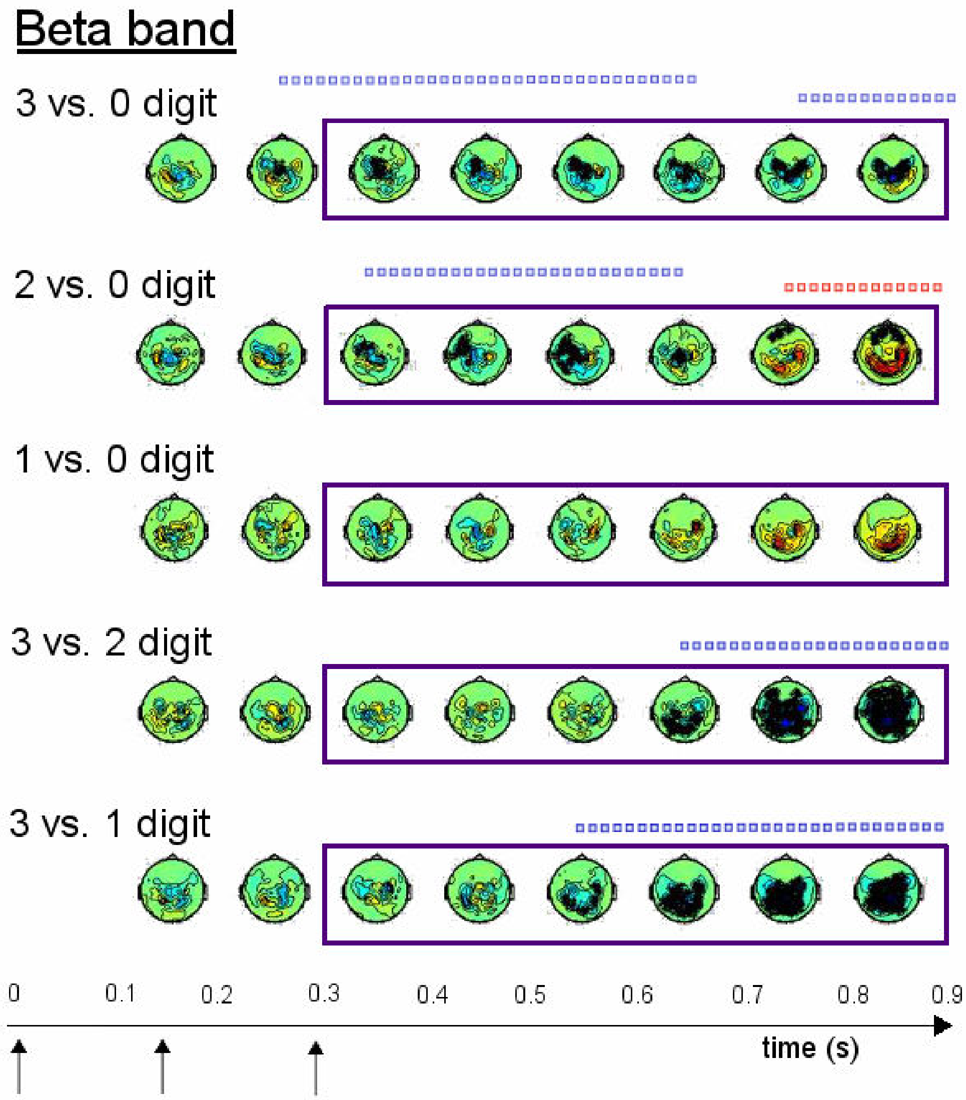

Figure 17 - Difference topographies (eg. 3 digit – 0 digit) with statistics comparing digit levels to the baseline (0 digit) condition in beta band (17-21 Hz). Squares above the topoplots illustrate the timing of significant clusters (red= power increase, blue= power decrease). Black arrows illustrate the onset of the digits. Purple rectangles reflect the time-window used for source analysis.

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[17] The overall p-value (0.05) was split between the positive and negative sides. For example, I assessed significance for negative clusters against a p-value of 0.025.

p=0). The negative cluster for 3 vs. 1 digit occurred bilaterally over parietal and occipital channels, while it also spread to frontal regions for the 3 vs. 2 digit comparison. The key finding from the beta band is that the 2 digit condition is similar to 3 digits from 0.35-0.65 s, after which the 2 digit pattern more closely resembles 1 digit.

I only performed source analysis on a digit level if it differed significantly from the 0 digit condition at the sensor-level, to optimise the filters for locating the strong underlying sources. Therefore, I performed ß source analysis (20 Hz, 0.35:0.85 s time window) for 3, 2 and 0 digits (not for 1 digit), using these 3 conditions to make the common filter[18], as well as using separate filters for each of these digits. For details of all the sources see Tables 5 and 6 in the Appendix B.

The sources with ß power decrease were remarkably similar for the 3 vs. 0 digit and the 2 vs. 0 digit comparisons (Figure 18, 1st & 2nd), with stronger relative power decreases in the 3 digit comparison. These sources were in inferior parietal (3 vs. 0: L/R BA 40, & 2 vs. 0: L BA 40), superior parietal (3 vs. 0: L BA 7, & 2 vs. 0: L/R BA 7), occipito-temporal and middle temporal (3 vs. 0: L/R BA 37, 21, 22, & 2 vs. 0: L/R BA 21,22) and occipital (3 vs. 0: L/R BA 17, 18, 19, & 2 vs. 0: R BA 17) cortices. The 3 vs. 0 digit separate filter statistics additionally revealed power decreases in motor areas (R BA 4, 6) and the inferior part of the right dorsolateral PFC (BA 46). Likewise, there were similar frontal ß power increases for 3 vs. 0 digit and 2 vs. 0 digit comparisons. While bilateral power increases were seen in the 3 digit comparison, the 2 digit sources were strongly right lateralised. The 3 vs. 0 digit common filter analysis showed power increases in the superior part of the dorsolateral PFC (R BA 9), inferior frontal (L BA 10), superior frontal (L BA 8) and the anterior cingulate cortex (ACC) (L BA 6)[19]. For the 2 vs. 0 digit comparison, the common filter analysis revealed increases in the left hemisphere in ventrolateral PFC (BA 47), inferior frontal (BA 10) and superior frontal (BA 6), while the dominant right lateralised source stretched from the dorsolateral PFC (BA 9, 46) to the middle frontal cortex (BA 10). Like 3 digits, there was a ß power increase in the ACC (L BA 32) and superior frontal (L BA 6) for the 2 digit comparison, revealed by the separate filter analysis.

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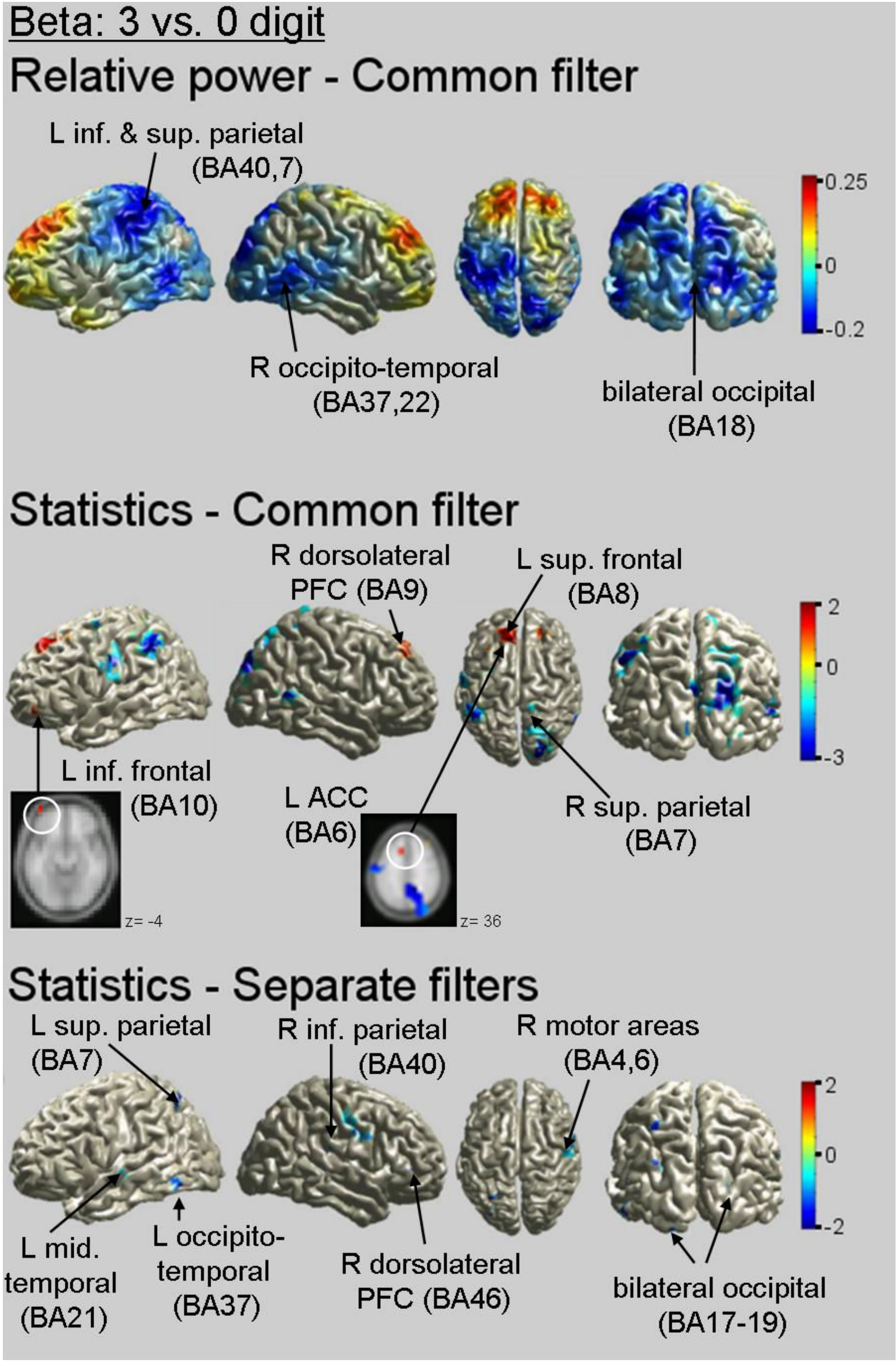
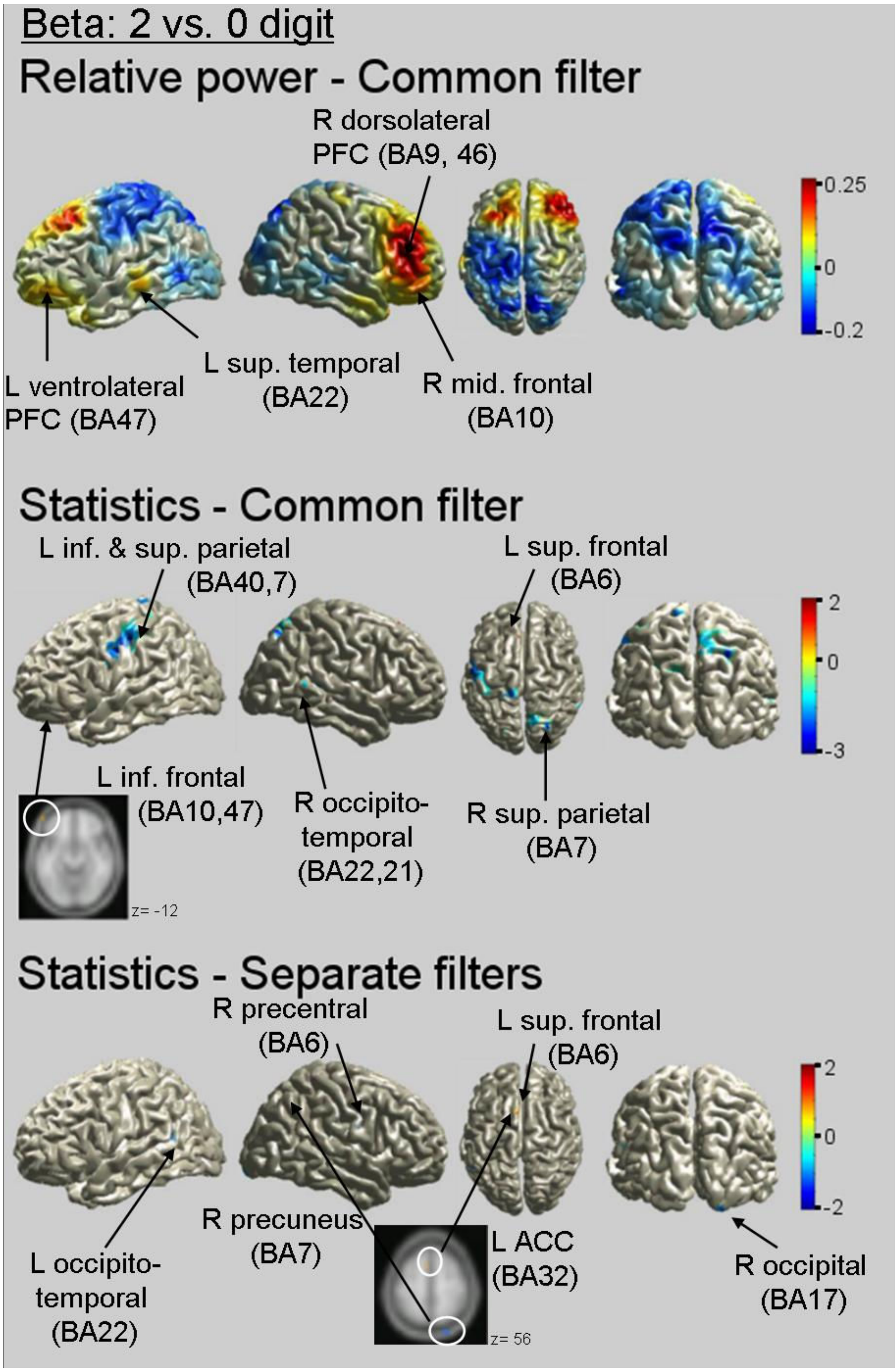
[18] Adding the 1 digit data to the common filter calculation could weaken the source estimation.

[19] The ACC includes BA32, BA24 and deep regions of BA6.

The different filter analyses showed distinct patterns for the comparison of 3 vs. 2 digits (Figure 18, 3rd). In the separate filter analysis, there was a significant frontal decrease in right ventrolateral PFC (BA 47, 45, 11) and left superior medial frontal (BA 8) sources. The common filter statistics revealed a power decrease in the left inferior parietal cortex (BA 40), while the relative power plots also showed the strong power decrease in 3 digits relative to 2 digits across the right PFC (BA 46, 47) and the power increase in the left dorsolateral PFC (BA 46) and right medial frontal (BA 8) sources.




Beta: 2 vs. 0 digit
Relative power - Common filter
R dorsolateral PFC (BA9, 46)
0.25
0
-0.2
L ventrolateral PFC (BA47)
L sup. temporal (BA22)
R mid. frontal (BA10)
Statistics - Common filter
L inf. & sup. parietal (BA40,7)
L sup. frontal (BA6)
2
0
-3
L inf. frontal (BA10,47)
R occipito-temporal (BA22,21)
R sup. parietal (BA7)
z= -12
Statistics - Separate filters
R precentral (BA6)
L sup. frontal (BA6)
2
0
-2
R precuneus (BA7)
L ACC (BA32)
L occipito-temporal (BA22)
R occipital (BA17)
z= 56

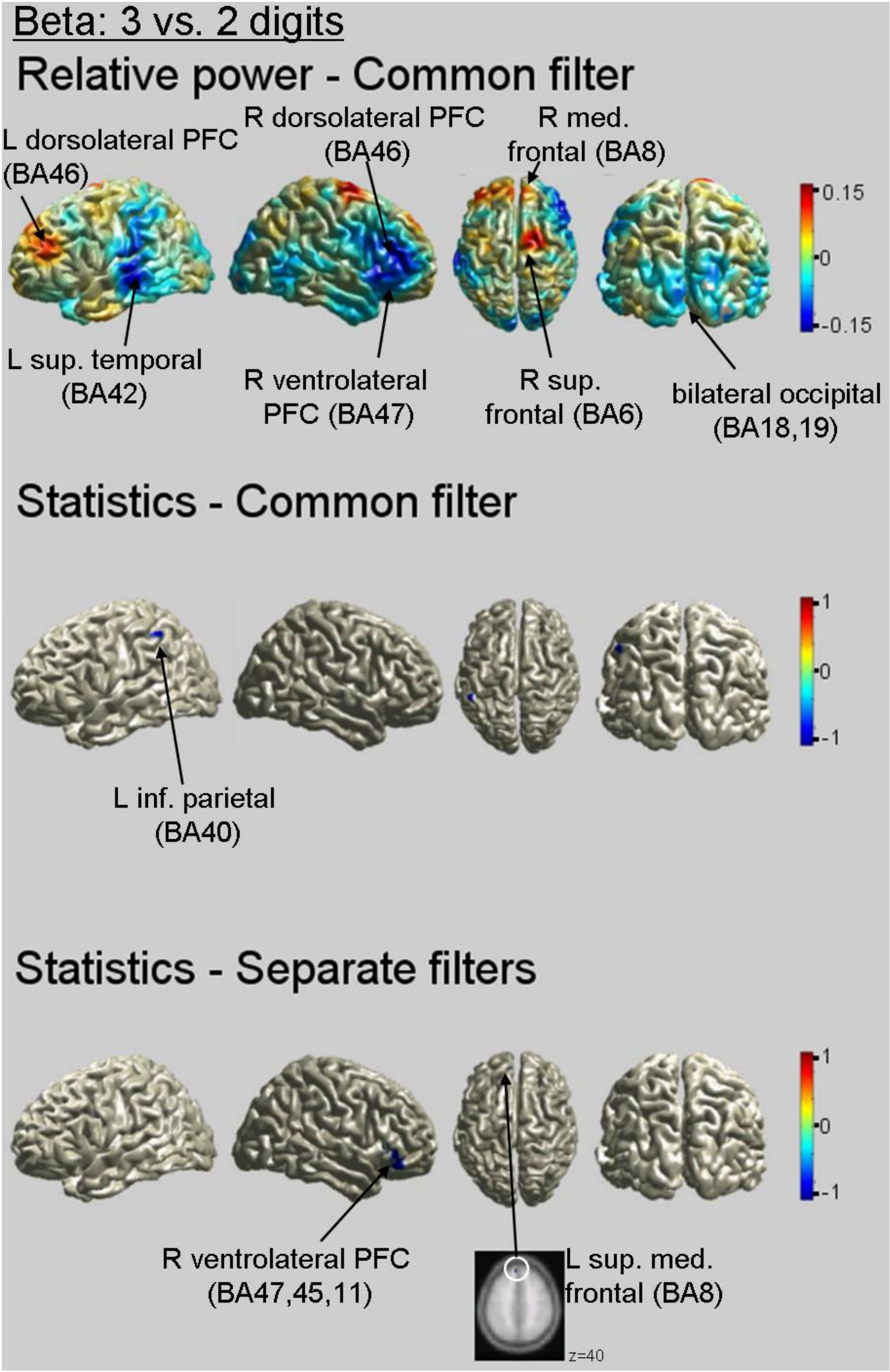


Figure 18 - Group beta band sources for the 3 vs. 0 digit (1st figure) 2 vs. 0 digit (2nd figure) and 3 vs. 2 digit (3rd figure) comparisons. For the common filter analysis, the relative power (e.g. (3 digit – 0 digit)/0digit; top row) and statistics (e.g. 3 vs. 0 digits; middle row) are shown. The separate filter statistics (bottom row) are also shown. Sources are projected onto a surface plot of the brain, with slice plots included for key deep sources and sources that did not project to the surface. From left to right of the page, the views of the brain are: left, right, top and back. Refer to Appendix B Tables 5 and 6 for further details of the sources.

Alpha band

Like β, there were obvious sensor-level differences between the digits in the α band (9-13 Hz) (Figure 19). Effects in the α band were predominantly over posterior channels and dissociate between targets (3 digits) and partial targets (1 and 2 digits). In the 3 digit vs. 0 digit comparison, there was a significant, sustained negative cluster (0.4:0.85 s, p=0.01) over left parietal and bilateral occipital channels. There were no significant differences in the 2 vs. 0 digit comparison (all p>0.104). A late power increase (0.75:0.85 s, p=0.016) was observed in the 1 vs. 0 digit comparison, over bilateral posterior channels. There were no significant differences between the partial digit conditions (2 vs. 1 digit: positive cluster p=0.424, negative cluster p=0.046, ns). There was a significant power decrease when comparing 3 digits with both 2 digits and 1 digit (0.4:0.85 s, p=0 for both comparisons), and this difference started with the onset of the 3rd digit.

I only performed source analysis on a digit level if it differed significantly from the 0 digit condition at the sensor-level, to optimise the filters for locating the underlying sources. Therefore, α source analysis (10 Hz, 0.4:0.9 s time window) was performed for 3, 1 and 0 digits (not for 2 digits[20]), using these 3 conditions for the common filter, as well as using separate filters for each digit. For the 3 vs. 0 digit comparison, there was a pronounced posterior α power decrease, stronger in the left hemisphere, with the common and separate filter analyses (Figure 20, 1st, Tables 7 and 8 in the Appendix B). These sources included inferior and superior parietal (L/R BA 7, 40), middle and superior temporal (L BA 21), occipito-temporal (L BA 19) and posterior cingulate (L BA 23, 31). There were significant lateral prefrontal power decreases in the separate filter analysis in ventrolateral (R BA 47) and dorsolateral PFC (L BA 9, 46), with medial frontal power increases with the common filter in dorsolateral PFC (R BA 9) and middle frontal cortex (L BA 10).

A different pattern emerged for the 1 vs. 0 digit comparison (Figure 20, 2nd), with widespread but left dominant α power increases seen with the common filter in middle frontal (L BA 10), Broca's area (L BA 44), inferior temporal (L BA 20), fusiform gyrus (R BA 19) and precentral cortex (L/R BA 6).

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[20] At the sensor-level, I observed no significant differences between 2 digits and the 0 digit baseline. Therefore I did not perform alpha source analysis with 2 digits.

Power decreases were observed in the primary motor cortex (L BA 4) and precuneus (R BA 7).

For the 3 vs. 1 digit comparison (Figure 20, 3rd), I observed posterior α decreases and mainly frontal power increases. Significant power decreases were more widespread for the separate filter than the common filter analysis. Overlapping sources included inferior and superior parietal (L/R BA 40, 7), temporal (L/R BA 13, 20-22, 37, 41) and occipital (L/R BA 18, 19) regions. There were also power decreases in medial frontal (L/R BA 10) sources in the separate filter statistics. Non-significant power increases can be seen in the common filter relative power plots in dorsolateral PFC (L/R BA 9), pre-motor (L BA 6) and postcentral (L BA 1) cortices.

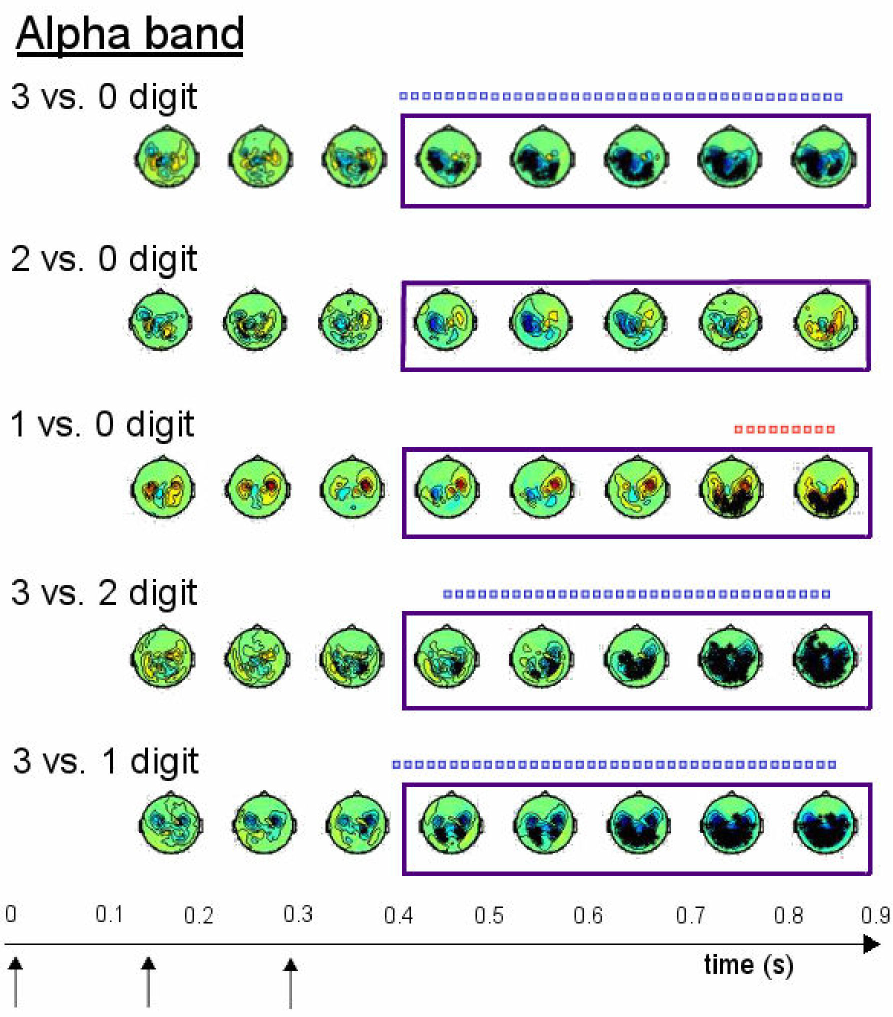
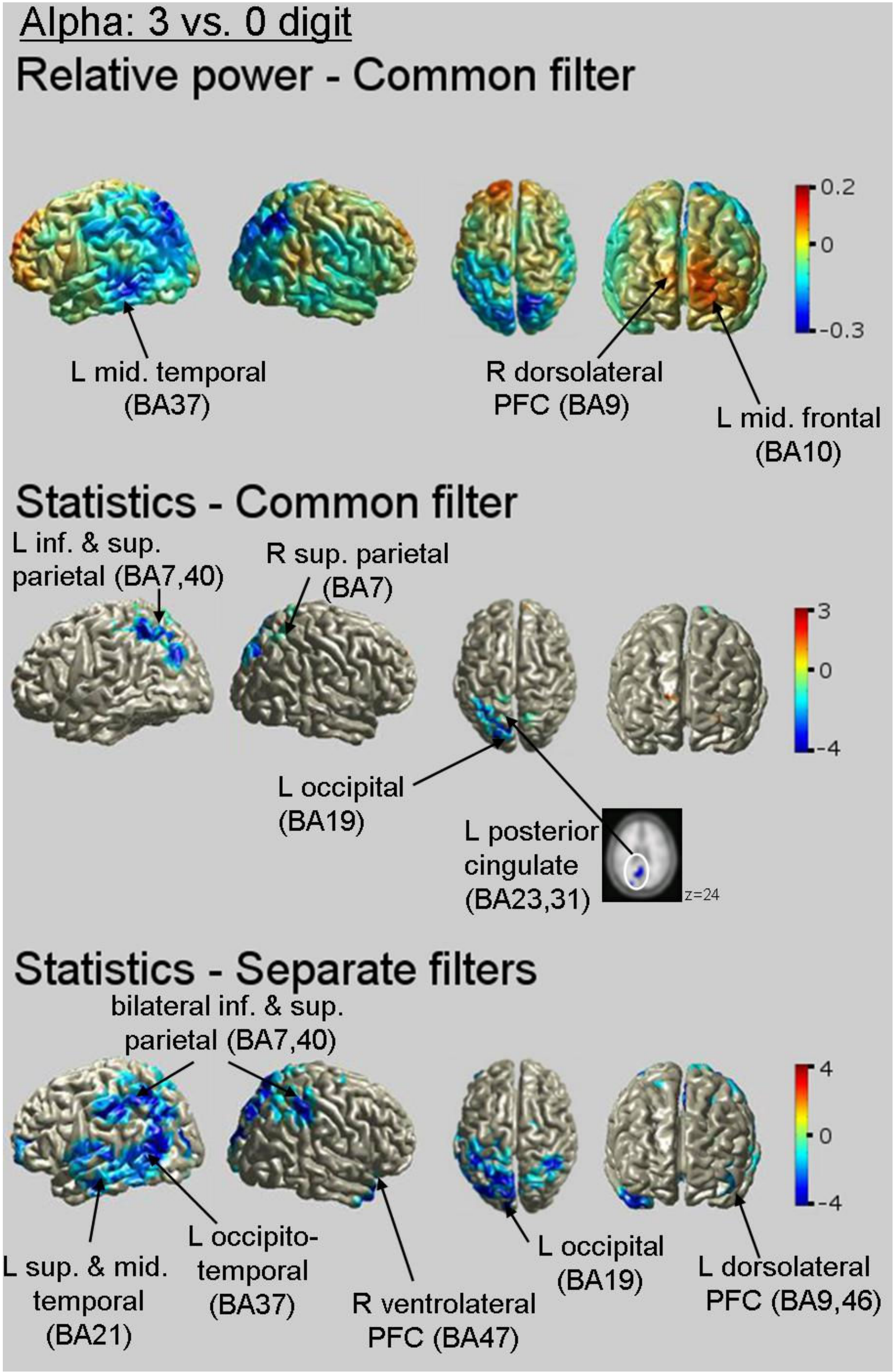
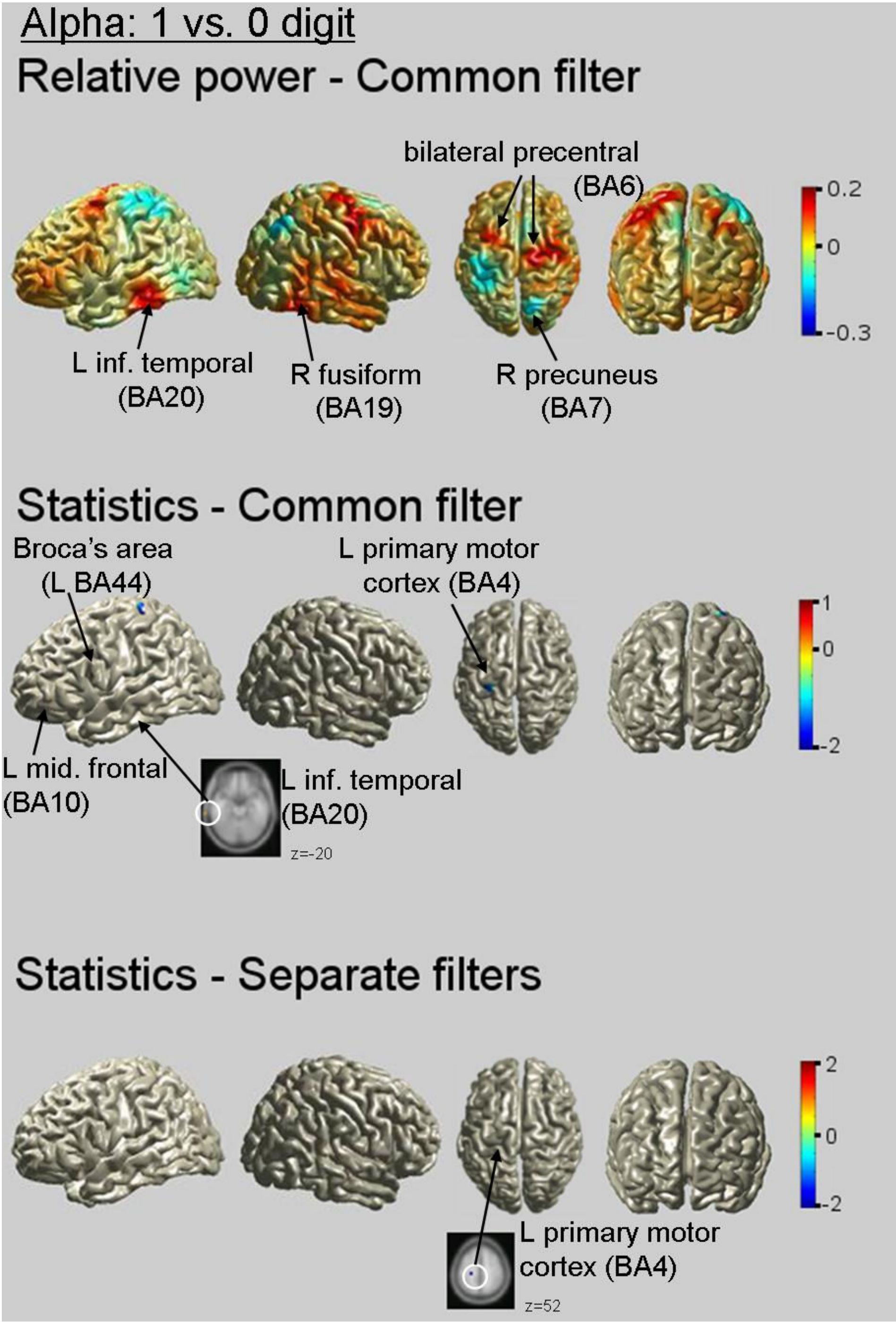


Figure 19 - Difference topographies (eg. 3 digit – 0 digit) with statistics comparing digit levels to the baseline (0 digit) condition in alpha band (9-13 Hz). Squares above the topoplots illustrate the timing of significant clusters (red= power increase, blue= power decrease). Black arrows illustrate the onset of the digits. Purple rectangles reflect the time-window used for source analysis.


Alpha: 3 vs. 0 digit
Relative power - Common filter
L mid. temporal (BA37)
R dorsolateral PFC (BA9)
L mid. frontal (BA10)
0.2
0
-0.3
Statistics - Common filter
L inf. & sup. parietal (BA7,40)
R sup. parietal (BA7)
3
0
-4
L occipital (BA19)
L posterior cingulate (BA23,31)
z=24
Statistics - Separate filters
bilateral inf. & sup. parietal (BA7,40)
4
0
-4
L sup. & mid. temporal (BA21)
L occipito-temporal (BA37)
R ventrolateral PFC (BA47)
L occipital (BA19)
L dorsolateral PFC (BA9,46)


Alpha: 1 vs. 0 digit
Relative power - Common filter
bilateral precentral (BA6)
L inf. temporal (BA20)
R fusiform (BA19)
R precuneus (BA7)
0.2
0
-0.3
Statistics - Common filter
Broca's area (L BA44)
L primary motor cortex (BA4)
L mid. frontal (BA10)
L inf. temporal (BA20)
z=-20
1
0
-2
Statistics - Separate filters
L primary motor cortex (BA4)
z=52
2
0
-2

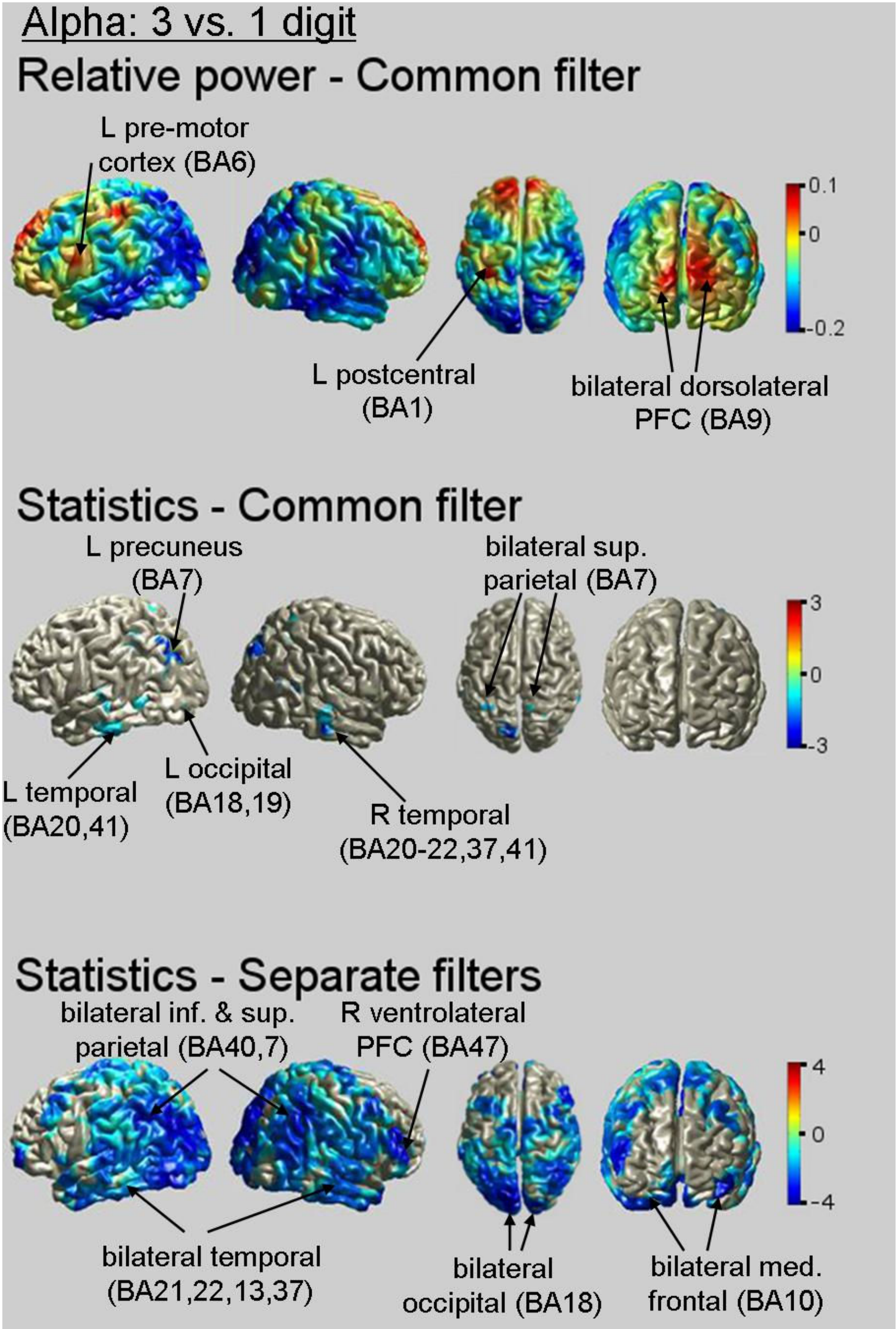


Figure 20 - Group alpha band sources for the 3 vs. 0 digit (1st figure) 1 vs. 0 digit (2nd figure) and 3 vs. 1 digit (3rd figure) comparisons. For the common filter analysis, the relative power (e.g. (3 digit – 0 digit)/0digit; top row) and statistics (middle row) are shown. The separate filter statistics (bottom row) are also shown. Sources are projected onto a surface plot of the brain, with slice plots included for key deep sources and sources that did not project to the surface. From left to right of the page, the views of the brain are: left, right, top and front. Refer to Appendix B Tables 7 and 8 for further details of the sources.

Theta band

At the sensor-level, a similar pattern emerged in 3, 2 and 1 digit conditions in the θ band (3-7 Hz) (Figure 21). When compared to the 0 digit baseline condition, there were only positive significant clusters for all digits: 3 vs. 0 digit (2 clusters: 0.05:0.55 s & 0.1:0.55 s, both *p*=0.002); 2 vs. 0 digit (1 cluster: 0.1:0.55 s, *p*=0); 1 vs. 0 digit (1 cluster: 0:0.55 s, *p*=0). This power increase started with the onset of 1st digit and was sustained bilaterally over anterior channels. There were no significant clusters when comparing 3, 2 and 1 digit pairwise (all *p*> 0.240).

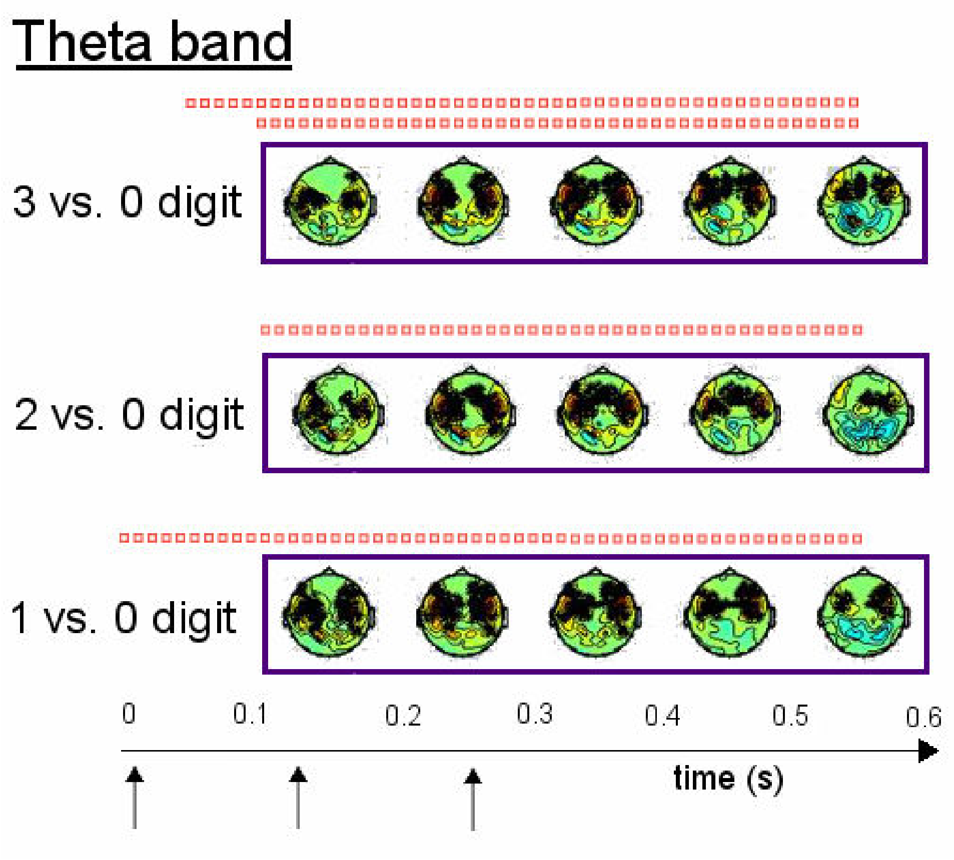


Figure 21 - Difference topographies (eg. 3 digit – 0 digit) with statistics comparing digit levels to the baseline (0 digit) condition in theta band (3-7 Hz). Squares above the topoplots illustrate the timing of significant clusters (red= power increase). Black arrows illustrate the onset of the digits. The purple rectangle reflects the time-window used for source analysis.

I performed θ band (6 Hz) source analysis using a common filter (for all 4 digit levels) on an early time window (0.05:0.55 s) (Figure 22; Appendix B Table 9). Sources showing increased θ power in the 321 digit variable relative to the 0 digit were located in the right dorsolateral PFC (BA 46), left ventrolateral PFC (BA 45), bilateral middle frontal (BA 8, 10), Broca's area (left BA 44), right inferior parietal (BA 40) and right occipito-temporal cortex (BA 37). A power decrease was observed bilaterally in the occipital cortex (BA 18, 19).

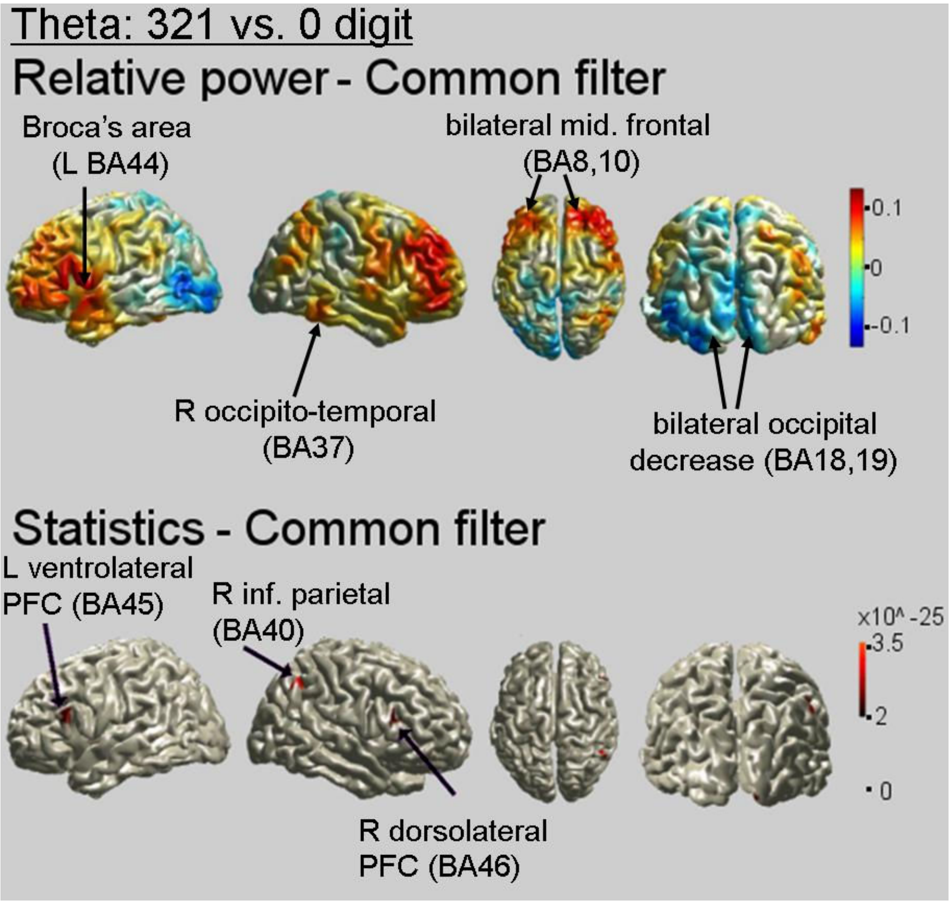


Figure 22 - Group theta band sources for the merged variable 321 digit vs. 0 digit comparison. The common filter relative power (eg. (321 digit – 0 digit)/0digit; top row) and statistics (middle row) are shown. Sources are projected onto a surface plot of the brain. From left to right of the page, the views of the brain are: left, right, top and back. Refer to Appendix B Table 9 for further details of the sources.

Discussion

In terms of ERFs, each digit was associated with a temporo-parieto-frontal M300 (Figure 13). This suggests that each incremental part of the target gains access to the global workspace (cf. Dehaene et al., 2003a), and is updated in working memory (Donchin and Coles, 1988, Verleger, 1988). Thus, processing of composite targets appears to occur online (as digits are revealed) rather than offline (just before the target decision).

Oscillations in the beta band could reflect the building of expectations (power decrease) and the resolution of violated expectations (power increase). The ß power decrease is similar for 3 digits and 2 digits, and absent from the 1 digit condition, when compared to the 0 digit baseline condition. The sensor-level statistics show that the 3 digit and 2 digit ß power decrease is similar in the period from 0.35 - 0.65 s, after which the pattern dissociates into a frontal power increase with 2 digits (0.75 - 0.9 s), while the 3 digit power decrease continues (Figure 17). The timing of the ß power decrease is in a similar range as the findings of Gross and colleagues (2006); a study relating ß band synchronization to anticipation of a target. Network synchronization to the single target peaked 0.26 s after its onset. This was preceded by a decrease in synchronization to the previous distractor (0.114 s after the target onset). The difference between target synchronization and distractor desynchronization increased with growing probability of the target occurring. In the current experiment, the ß power decrease (relative to 0 digits) began 0.25 s after the onset of the 1st digit for 3 digits, and 0.35 s for 2 digits (Figure 17). This suggests that the power decrease with 2 digits began 0.1 s later than with 3 digits. However the direct comparison between 3 digits vs. 2 digits showed the conditions did not differ at this time point: a significant difference was found only after 0.6 s. Overall, the timing of this ß power decrease with 2 digits and 3 digits overlaps with a period during which target anticipation is reflected in ß band synchronization (Gross et al., 2006). Taken alongside the absence of a ß power decrease in the 1 digit condition, this is some evidence that enhanced processing, perhaps reflecting local target expectations, occurs when participants see a 2nd and then a 3rd digit.

The underlying sources for the power decrease with 2 digits and 3 digits are in bilateral parietal, temporal and occipital regions. This fits with the network of sources showing long-range ß band synchronization during dual target processing in the AB (Gross et al., 2004) and with fMRI AB networks (Feinstein et al., 2004, Kranczioch et al., 2005, Marois et al., 2000). The ß power decrease could reflect intense processing that begins with the 2nd incoming digit as expectation for the full composite target builds. The intense processing continues for 3 digits towards the end of the trial as target expectations are fulfilled, and further target-related processing continues.

The late anterior ß power increase with 2 digits could reflect the immediate inhibition of processing when the violation of expectations is registered. At the sensor-level, I observed power increases only in the 2 digit comparison to the 0 digit baseline. Source-level analysis can be more sensitive at detecting differences between conditions than the sensor-level. Thus I observed frontal sources with ß increases in the 3 digit, as well as the 2 digit comparison to baseline. Sources within the left ACC (BA 32 for 2 digits and BA 6 for 3 digits) could relate to error and conflict monitoring (Carter et al., 1998, Cohen, 1998). The ACC has also been linked to deviations in expectation (Oliveira et al., 2007). Error monitoring sources are observed for the 3 digit as well as the 2 digit trials, since conflict must be quickly detected and resolved in the RSVP stream once expectations have been raised. The power increase for the 3 digit and 2 digit comparisons to baseline in right dorsolateral PFC (BA 9, 46) and the left inferior frontal (BA 10) sources could relate to the manipulation of multiple digits in working memory. The dorsolateral PFC is a key area for the manipulation of items held in working memory (Postle and D'Esposito, 2000). The inferior frontal cortex (BA 10) is also involved with performing operations in working memory (Wager and Smith, 2003), such as maintaining existing information while new items (in this case, digits) are being integrated (Koechlin and Hyafil, 2007). Inferior frontal areas are often active alongside posterior fronto-median regions when there is a conflict at the response level (cf. Kranczioch et al., 2005); a response conflict is likely to occur when making the decision about whether you saw 2 or 3 digits in my paradigm. However, the strongly right lateralised power increase (including middle and inferior frontal (BA 10)) is specific to the 2 digit comparison. Neuroimaging and neurophysiological findings suggest that the right inferior frontal cortex, in particular, plays a key role in inhibition (reviewed in Aron et al., 2004). Additionally, a shift to the right hemisphere in frontal activations was observed with increasing uncertainty (Volz et al., 2003), where they found that right BA 8 activation increased with increasing levels of prediction uncertainty. This strongly right lateralised, inferior frontal power increase for 2 digits is the key difference from 3 digits, and could reflect the top-down inhibition necessary to overcome the raised target expectations. This pattern is complemented by the left dorsolateral PFC (BA 46) advantage for 3 digits, hinted at by the non-significant source in the 3 digit comparison to 2 digits (Figure 18 3rd).

The alpha band oscillations dissociate between full targets (3 digits) and partial targets (1 digit and 2 digits). For the 3 digit comparison to 0 digits, the sustained posterior power decrease is the dominant effect, and begins as the 3rd digit is presented. Sources are bilateral but stronger in the left hemisphere, and include prefrontal, parietal, temporal and posterior cingulate cortex. Weaker frontal power increases were observed in the source analysis in the right dorsolateral PFC (BA 9) and left middle frontal cortex (BA 10). Sources are similar to the β band results, and could likewise reflect the intense target processing (power decrease) and the updating of new digit information into working memory (power increase) (cf. Klimesch et al., 2007).

The late widespread α power increase for the 1 digit comparison to baseline is localised to frontal, temporal and parietal sources. The predominately posterior α increase could indicate the top-down inhibition of processing once participants are certain that there is no full target. Response preparation could be reflected by the power decrease in the left primary motor cortex (BA 4). Although the 2 digit condition did not differ significantly from the baseline at the sensor-level, the topoplots suggest α activity is intermediate (Figure 19); a mixture of the left-lateralised power decrease component seen with 3 vs. 0 digits, and the late posterior increase in the 1 vs. 0 digit comparison. It is possible that the power increase for 2 digits could become significant after 0.9s[21].

There is no distinction between digit levels in the theta band, and so I suggest that θ oscillations could code for the working memory requirements of the task. The frontal power increase begins with the onset of the 1st digit and is sustained until all digits have been presented (0.55 s) (Figure 21). The power increase for the collapsed 321 digit variable compared to the baseline condition includes sources in dorsolateral and ventrolateral PFC, as well as middle frontal, Broca's area, inferior parietal and occipito-temporal cortex (Figure 22). Since there are no differences in the θ band relating to digit quantity (1, 2 or 3 digits) or type of target (full or partial target), and yet digits differ from distractor-only (0 digit) trials, it is likely that θ codes for a general processing requirement. The θ power increase could reflect the opening of an event file in working memory with the initial digit (cf. Hommel, 2004, Wyble et al., 2011).

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[21] I cannot analyse the trial beyond 0.9s, since I would encounter a jitter from the end of the RSVP stream.

Digits could be maintained in working memory by ventrolateral PFC, and subsequent digits could update the representation in the event file in dorsolateral PFC (Postle and D'Esposito, 2000), while activity in Broca's area could reflect the sub-vocal rehearsal in verbal working memory (Paulesu et al., 1993). A late decrease of θ power is seen in occipital areas: A non-significant sensor-level power decrease occurs over posterior channels between 0.5 - 0.6 s in the topoplots (Figure 21), and corresponds to significant occipital sources (Figure 22). This top-down inhibition of visual areas could occur once the digits have been consolidated in working memory.

Much research has found a link between the θ oscillations and encoding and maintenance in working memory (see Sauseng et al., 2010 for a recent review). Frontal θ power increases with greater memory load (Jensen and Tesche, 2002) and task difficulty (Gevins et al., 1997). Likewise, long-range θ coupling between prefrontal and parietal regions could reflect integration across the various neural components of working memory (cf. Sauseng et al., 2010). It has further been suggested that θ could be the organisational rhythm during working memory, through θ phase reset, and the nesting of higher frequencies (β, γ) within θ (see Freunberger et al., 2011 for a review) For example, the phase-locking relationship of θ with γ could maintain the correct temporal order of multiple items in working memory (see Jensen, 2006, Lisman, 2010 for reviews).

To summarise, β oscillations seem the most likely candidate to code for the raised and subsequently violated expectations (with 2 digits). Oscillations in the α band seem to reflect more posterior full target (3 digits) processing, and inhibition of processing for 1 digit partial targets. Both the θ and M300 results suggest that all digits enter the global workspace and are consolidated into working memory. However, it is possible that some of my findings relate to the quantification of the digits. Therefore, I performed a 2nd MEG experiment where participants counted the digits. Given the dissociation at the behavioural level between counting and detecting a composite target, I expect differences in the neural patterns.

Chapter 9 - MEG Experiment 2: Neural correlates of Counting

Introduction to MEG Experiment 2

In this chapter, I further investigate the role of counting the digits, using MEG to study the neural dynamics. The behavioural experiments detailed in Chapters 2 and 3 strongly suggest that participants do not simply count the successive digits when detecting the composite T1 event. The subsequent behavioural chapters give further weight to my suggestion that expectation for the full T1 target (3 digits) builds up as digits are presented, leading to a strong AB on trials where expectations are raised but violated (with 2 digits). Conversely, counting the digits is associated with the same blink magnitude with all digit levels: This suggests it is the *act* of counting which induces the AB, as the magnitude isn’t influenced by the *quantity* to be counted. Counting seems to involve consolidation of all digits into working memory as “targets” and so I predict a similar neural signature for all counted digits (1, 2 and 3 digits) in this MEG experiment.

The paradigms used for the current counting task and the target detection task (MEG Experiment 1) are extremely similar. Thus I might expect involvement of a similar fronto-temporo-parietal network for attending to the RSVP stream, inhibiting distractors, selecting digits and storing them in working memory (Hommel et al., 2006). However, the task now explicitly requires number quantification, and therefore could strongly recruit areas specialised for number processing. The posterior parietal cortex is the hub for number processing, with prefrontal involvement for cognitively demanding numerical tasks (Nieder and Dehaene, 2009, Piazza et al., 2006). Numerous fMRI studies have placed the main number quantification centre in the horizontal segment of the intraparietal sulcus (HIPS) (Dehaene et al., 2003b, Nieder and Dehaene, 2009), the sulcus separating the superior (BA 7) and inferior parietal (BA 40) lobules. Activation is typically bilateral, often with a left hemisphere dominance, in agreement with the finding that acalculia is associated with left parietal lesions (Butterworth, 2000). The HIPS is active in a range of numerical tasks, and intraparietal activation is involved in quantifying items in the subitizing (<4 items in spatial array) and counting (>5 items) ranges (Piazza et al., 2002). A meta-analysis (Dehaene et al., 2003b) identified 2 additional parietal areas active in number processing: a left angular gyrus (BA 39) hub for number tasks with a verbal component, and a bilateral superior posterior parietal hub which could represent non-specific attentional aspects of number tasks.

In particular, fMRI studies of counting visual targets in a stream consistently show bilateral intraparietal activation. Silent counting of oddball targets (vs. visual stimulation) within a slow stream (SOA=8s) activated bilateral intraparietal areas (BA 40) and angular gyrus (Linden et al., 1999). Serial counting of coloured squares (vs. a matching task) in a faster, non-rhythmic stream (SOA of 180 or 270 ms) also activated bilateral intraparietal, precentral and motor cortices and the right dorsolateral PFC (Piazza et al., 2006). Silent counting of strings of letters presented serially (SOA=1.5s) activated inferior parietal, as well as middle frontal gyrus and posterior cingulate gyrus (McCarthy et al., 1997).

The few EEG studies into counting also point to a robust parietal number centre. A study into numerosity adaptation in infants revealed sources in right parietal and prefrontal regions (reported in Piazza and Izard, 2009). Silent counting of visual oddball targets evoked a centro-parietal P300, and source localisation revealed parietal (supramarginal gyrus and angular gyrus) and frontal generators (Yamazaki et al., 2001).

In the counting experiment, I predict the recruitment of parietal number processing areas close to the HIPS quantification area. Since I use MEG source analysis, it will not be possible to identify the HIPS with the spatial accuracy of fMRI, but I expect to see sources around this area in the inferior and superior parietal lobules (BA 40 and BA 7). Finally, and most relevant to my research question, I predict a different neural pattern for counting digits compared to the detection task in MEG Experiment 1. The beta band results in Chapter 8 strongly suggest a distinction between processing of the 3 digit full target and the 2 digit partial target: Expectation seems to be built (power decrease) and subsequently suppressed for 2 digits (frontal power increase), while intense target processing (power decrease) continues for 3 digits. I do not expect to see this “violated expectation” signature in the current experiment for any digit level. In fact, the absence of this signature would lend support to my hypothesis that target expectations alone can modulate the AB, and that expectations have a distinct neural signature from counting.

Methods

Except where stated below, this experiment was identical to MEG Experiment 1.

Participants

Sixteen participants were recruited from the University of Glasgow community[22]. Data from 14 right-handed participants (6 males, 26 ± 5 years (mean age ± SD), all with normal or corrected vision) were analysed.

Behavioural methodology for MEG experiment

The apparatus and stimuli were identical to MEG Experiment 1. However, participants were now asked to count the digits (0, 1, 2 or 3 digits) within the RSVP stream. After the trial participants reported the quantity of digits, with the following right hand finger movements: thumb to start the trial, index finger to report 3 digits, middle finger for 2 digits, ring finger for 1 digit and little finger for 0 digits. No error feedback was provided.

Behavioural results

A repeated measures MANOVA revealed a significant main effect of condition (F (3, 11)=8.68, $p< .01$, $\eta_p^2 = 0.5865$) (Figure 23). Performance with 3 digits (77%), 2 digits (93%) and 1 digit (93%) was significantly lower than the 0 digit baseline (99%, all $p< .05$). There was no significant performance difference between 2 digit and 1 digit conditions ($p= .92$), while 3 digit performance was lower than both 2 digits and 1 digit (both $p< .01$). The mistakes made in trials with 3 digits were typically reports of 2 digits (22% of the time), with fewer reports of 1 digit (1%) or 0 digits (<1%).

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[22] Data from 2 participants could not be analysed due to missing trigger information, necessary to identify the trial types. The gradiometer positions were incorrect in a further participant's data but I re-tested that participant.

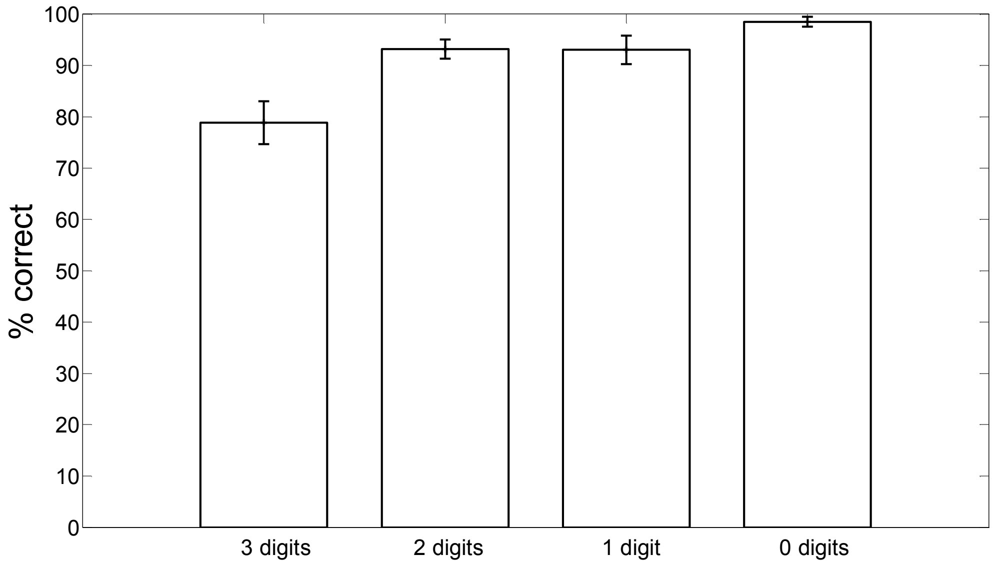

Figure 23 - Behavioural performance for counting the digits. Mean % correct ± 1 standard error is shown.

MEG Results

Event-related fields

Group ERFs (n=14) revealed a moderate amplitude (3.47 to $6.76*10^{-14}$ T) waveform repeated every 0.148 to 0.154 s in occipital channels (channel A204, Figure 24). Note that the SOA was 0.15 s. No significant differences between digits (3, 2, 1 digit) and the baseline condition (0 digits) were observed in occipital channels. Yet there was a visible upward shift in 1, 2 and 3 digit ERFs between 0.27 - 0.88 s, suggesting top-down modulation by the digits.

An M300 to each incoming digit is observed in temporal (A197, A210) and lateral frontal (A179) channels, occurring approximately 0.323 – 0.408 s after the onset of each digit (Figure 24, Table 2). No evoked or slow waves were observed in a central frontal channel (A122), where there were no significant differences between any digit levels.

The M300 topographies were similar for all counted digit (1, 2 and 3 digit) conditions with a focal central parietal and a broad fronto-temporo-parietal component (Figure 25). The strength of the components increased with each digit, as shown by the topography 'snapshot' of the successive M300 peaks in the

Amplitude (* 10^{-14} T)	1^{st} M300	2^{nd} M300	3^{rd} M300
1 digit	12.45		
2 digits	12.51	7.91	
3 digits	10.96	9.07	3.79
Peak latency (s)			
1 digit	0.366		
2 digits	0.362	0.558	
3 digits	0.362	0.511	0.623

Table 2 - Group mean amplitudes and latencies of the M300 in the left lateral frontal channel A179. Amplitude was calculated as the difference in magnetic field strength (T) between the maximum and minimum value of the peak.

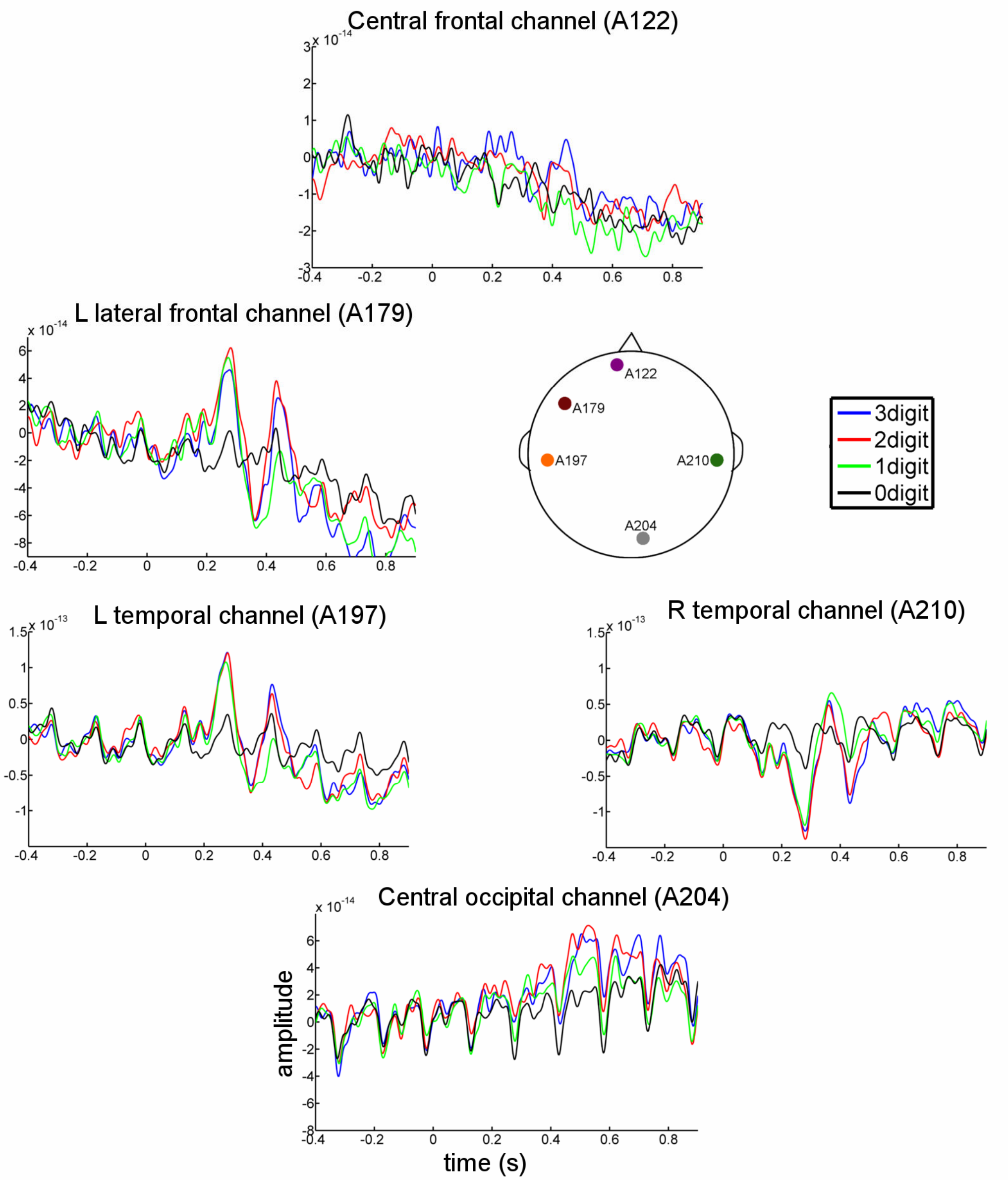

Figure 24 - Grand average ERFs for all digit levels in central frontal (A122), left lateral frontal (A179), left temporal (A197), right temporal (A210) and central occipital (A204) channels.

3 digit condition; although it should be noted that for channel A179, the amplitude decreased with each digit (Table 2). A similar but weaker topography is observed in the 0 digit condition, which could reflect the monitoring of the stream for digits.

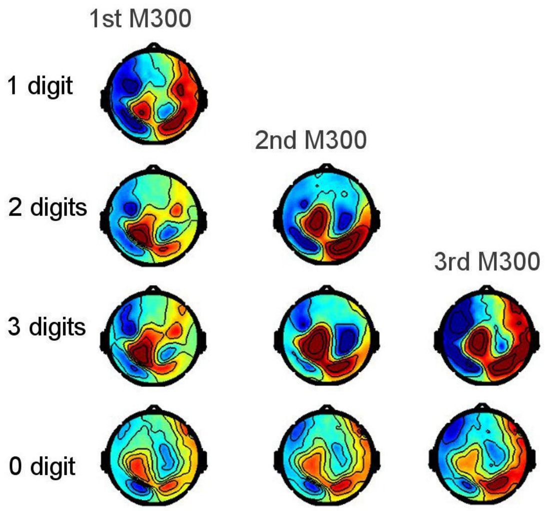

Figure 25 - Absolute topographies for each M300 peak for counting each digit. ERF amplitude is averaged across a 0.1s period for each plot: 1st M300 0.3:0.4 s, 2nd M300 0.45:0.55 s, 3rd M300 0.6:0.7 s.

Time-frequency analysis

Frequency analysis (4:30 Hz) revealed strong components for all digits in beta (ß), alpha (α) and theta (θ) bands. A left anterior-temporal channel (A96) (Figure 26) illustrates the remarkably similar pattern for all counted digits: There was a significant early θ power increase, followed by α and ß power decreases in 1, 2 and 3 digit conditions relative to the 0 digit baseline. It should be noted here that this pattern strongly resembles the TFR statistics for 3 digits (full target) compared to 0 digits in MEG Experiment 1 (Figure 15)[23]. The sensor- and source-level effects in the ß, α and θ bands will now be discussed in detail.

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[23] However, it is important to consider the baseline condition (0 digit) in each experiment. There are stronger power changes within the 0 digit absolute TFR for MEG Experiment 2 (Figure 26, top) than MEG Experiment 1 (Figure 15 top). We must bear this in mind when comparing the experiments.

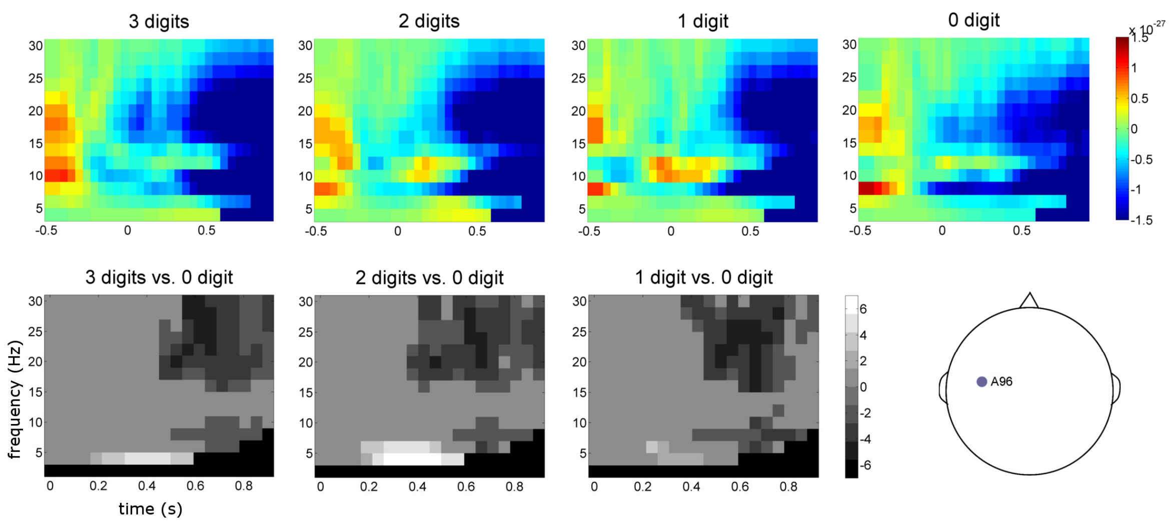

Figure 26 - Group TFR (top row) and statistics (bottom row) when counting digits, for a left anterior-temporal channel (A96) in 4 to 30 Hz range. The top row shows TFR (from -0.5:0.9s) relative to the baseline period (-0.2:0 s) for each digit. Red reflects a power increase and blue a power decrease. The bottom row shows the statistically significant effects in time and frequency for 1, 2 and 3 digits vs. 0 digit, from 0:0.9 s. White reflects a significant power increase and dark grey a power decrease.

Beta band

At the sensor-level, there were remarkably similar early and sustained ß power decreases (17-21 Hz) for all counted digits (1, 2 and 3 digits) compared to the 0 digit baseline (Figure 27) (3 digits: 0.35:0.9 s; 2 digits: 0.35:0.8 s; 1 digit: 0.3:0.8 s; all p=0). These predominately left-lateralised clusters always included parietal channels, and often spread to frontal, temporal and occipital channels. A late right posterior power increase occurred in the 1 digit and 2 digit comparisons to 0 digit (2 digits: 0.7:0.8 s; 1 digit: 0.6:0.9 s; both $p<0.01$), which was absent for 3 digits (p=0.8). Comparing the digits, there were no significant differences between 1 and 2 digits (1st positive cluster p=0.036, ns[24] & 1st negative cluster p=0.65). A significant late power decrease is apparent when comparing 3 digits with both 1 and 2 digits (both 0.6:0.9 s, p=0), seen over right posterior and central channels.

I performed ß band source analysis (20 Hz, 0.35:0.85 s time window) for 3, 2, 1 and 0 digits, using all conditions to make the common filter , as well as making separate filters for each digit level. Sources are shown for the digit vs. 0 digit comparisons. Details of the sources are in Tables 10 and 11 in Appendix C. For all counted digit comparisons to the 0 digit baseline, I observe a similar pattern of left lateralised power decreases and right lateralised power increases

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[24] p=0.025 is used for assessing significance of positive and negative clusters separately. The overall test p=0.05.

(Figure 28. For 1, 2 and 3 digits, strong left power decreases were seen in inferior parietal (BA 40), superior parietal (BA 7), precentral (BA 6), superior temporal (BA 39, BA 22) and occipito-temporal (BA 37, BA 19) sources. Right hemisphere power increases were located in inferior parietal (BA 40), angular gyrus (BA 39), dorsolateral PFC (BA 9), middle frontal (BA 8) for all digits, and also in ventrolateral PFC (BA 47) for 2 and 3 digit comparisons, while in superior frontal (BA 10, 11) for 1 digit. Additionally for 1 and 2 digits (Figure 28 2nd, 3rd), I observe a right occipital (BA 18, 19) power increase and left temporopolar (BA 38) power decrease. There was also a right inferior temporal (BA 20) power increase for 2 and 3 digit comparisons to 0 digits.

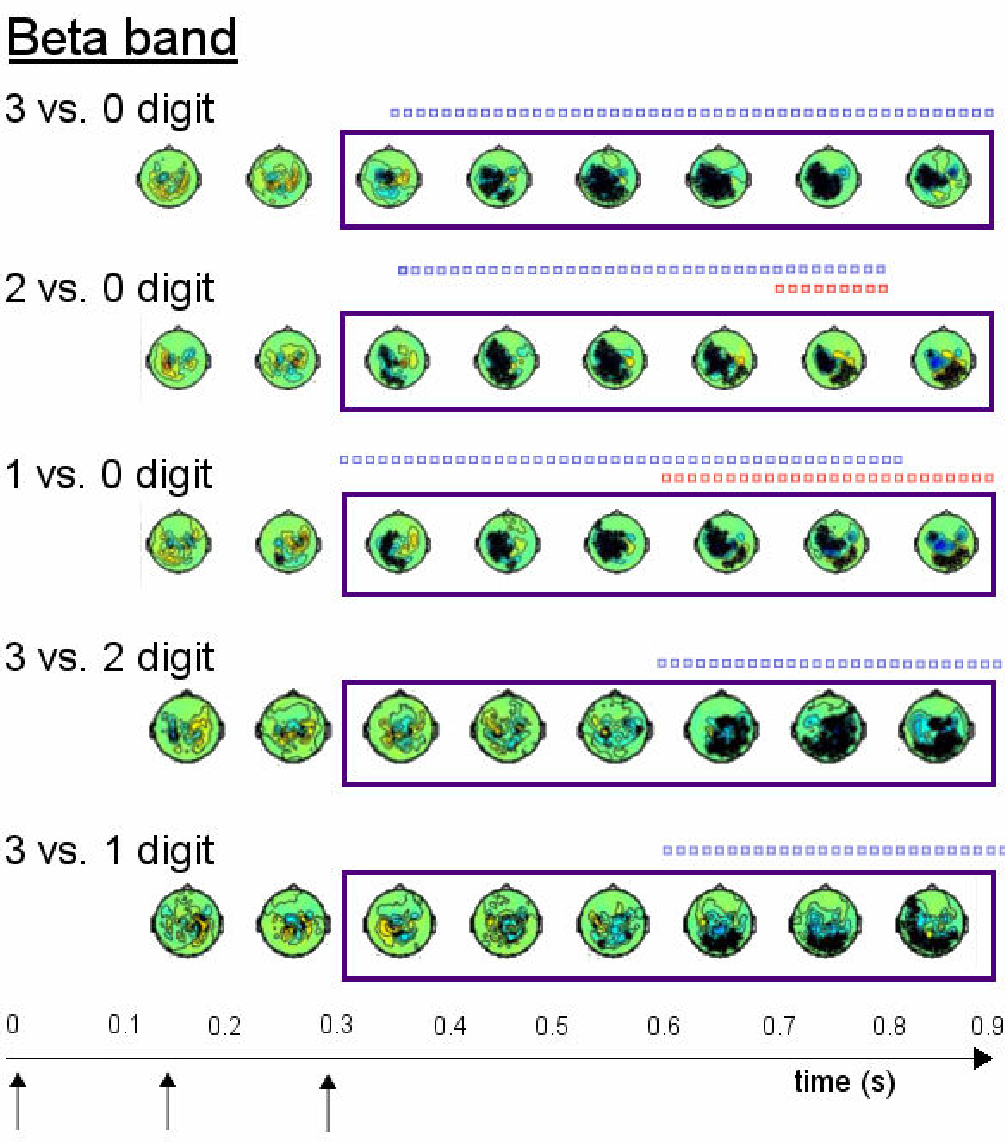
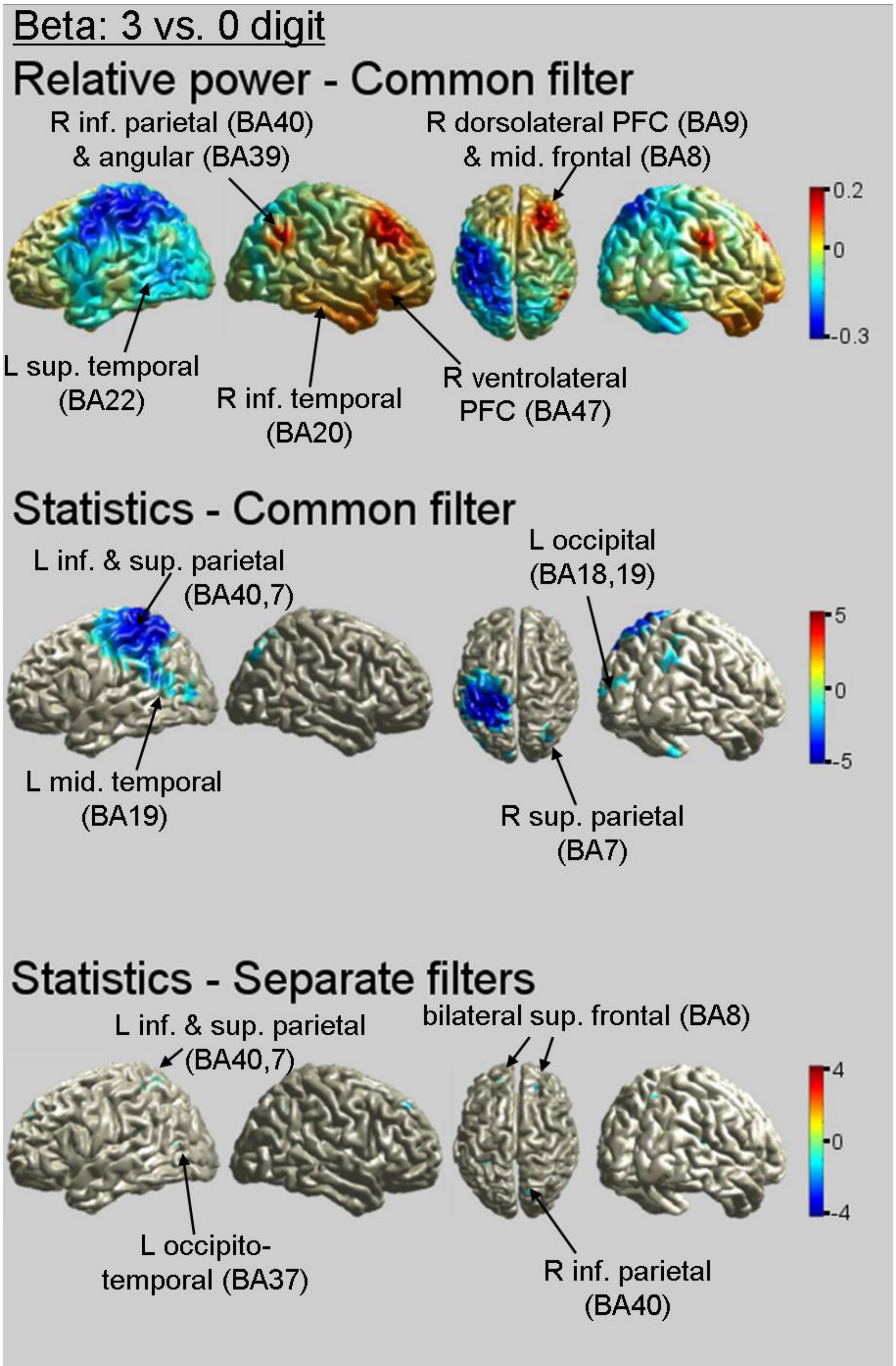
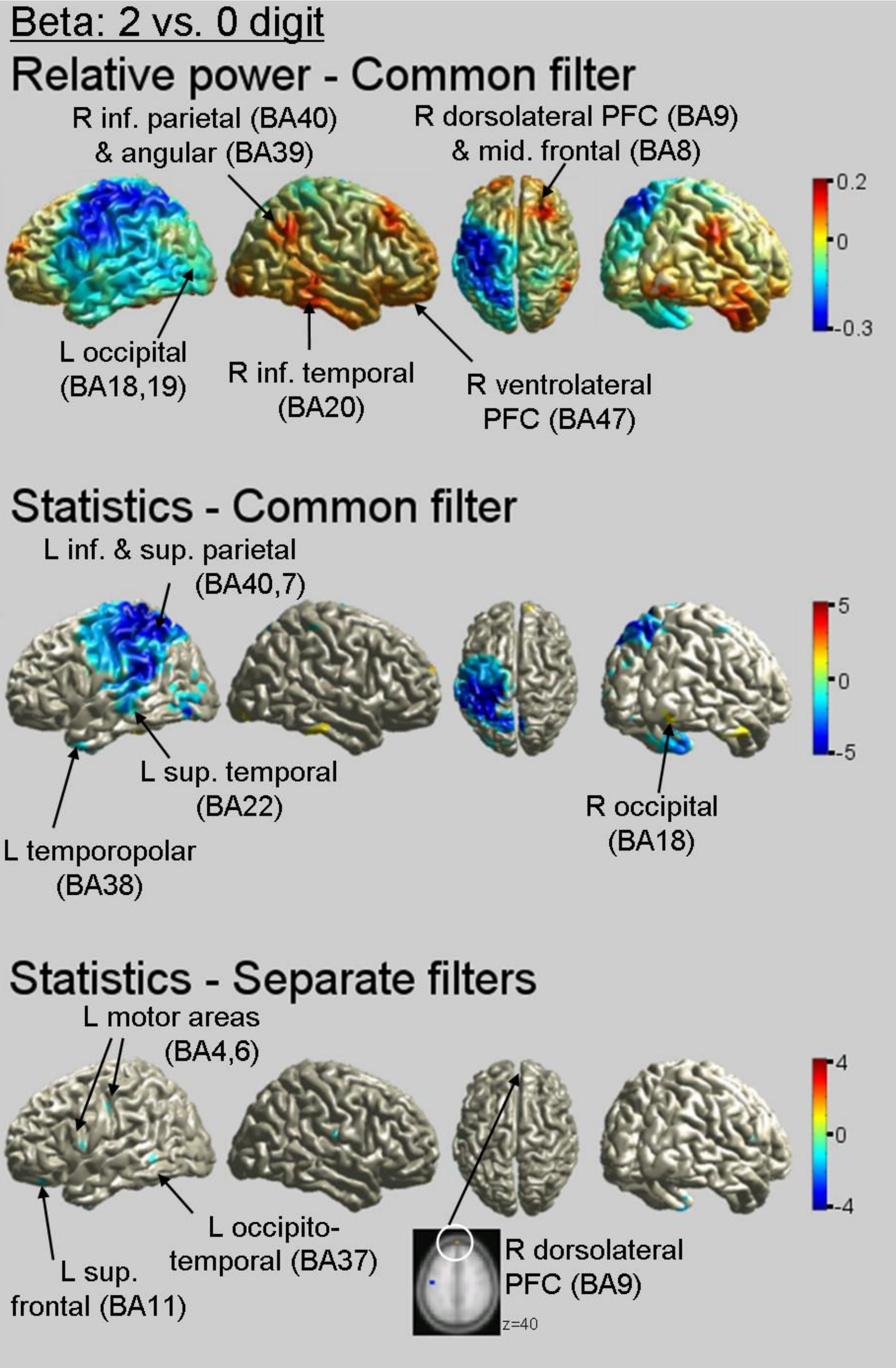


Figure 27 - Difference topographies (eg. 3 digit – 0 digit) with statistics comparing counted digit levels to the baseline (0 digit) condition in beta band (17-21 Hz). Squares above the topoplots illustrate the timing of significant clusters (red= power increase, blue= power decrease). Black arrows illustrate the onset of the digits. Purple rectangles reflect the time-window used for source analysis.


Beta: 3 vs. 0 digit
Relative power - Common filter
R inf. parietal (BA40) & angular (BA39)
R dorsolateral PFC (BA9) & mid. frontal (BA8)
0.2
0
-0.3
L sup. temporal (BA22)
R inf. temporal (BA20)
R ventrolateral PFC (BA47)
Statistics - Common filter
L inf. & sup. parietal (BA40,7)
L occipital (BA18,19)
5
0
-5
L mid. temporal (BA19)
R sup. parietal (BA7)
Statistics - Separate filters
L inf. & sup. parietal (BA40,7)
bilateral sup. frontal (BA8)
4
0
-4
L occipito-temporal (BA37)
R inf. parietal (BA40)


Beta: 2 vs. 0 digit
Relative power - Common filter
R inf. parietal (BA40) & angular (BA39)
R dorsolateral PFC (BA9) & mid. frontal (BA8)
0.2
0
-0.3
L occipital (BA18,19)
R inf. temporal (BA20)
R ventrolateral PFC (BA47)
Statistics - Common filter
L inf. & sup. parietal (BA40,7)
5
0
-5
L sup. temporal (BA22)
L temporopolar (BA38)
R occipital (BA18)
Statistics - Separate filters
L motor areas (BA4,6)
4
0
-4
L occipito-temporal (BA37)
L sup. frontal (BA11)
R dorsolateral PFC (BA9)
z=40

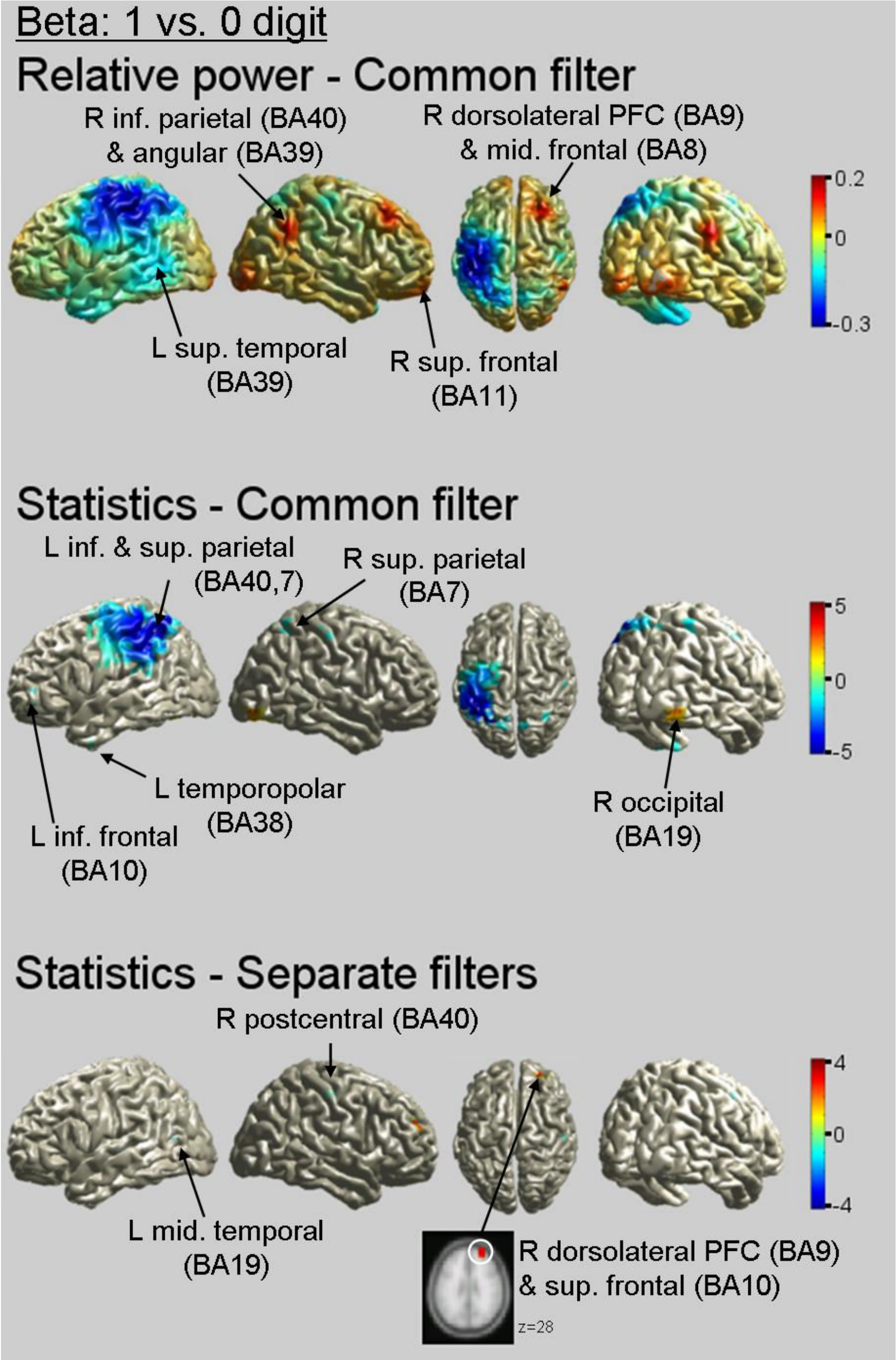


Figure 28 - Group beta band sources for the 3 vs. 0 digit (1st figure), 2 vs. 0 digit (2nd figure) and 1 vs. 0 digit (3rd figure) comparisons for counting the digits. For the common filter analysis, the relative power (eg. (3 digit – 0 digit)/0digit; top row) and statistics (middle row) are shown. The separate filter statistics (bottom row) are also shown. Sources are projected onto a surface plot of the brain, with slice plots included for key deep sources and sources that did not project to the surface. From left to right of the page, the views of the brain are: left, right, top and right back. Refer to Appendix C Tables 10 and 11 for further details of the sources.

Alpha band

Sensor-level α results revealed a similar pattern for all counted digits (1, 2 and 3) compared to the 0 digit baseline (Figure 29). A central parietal, left lateralised power decrease occurred earlier and spread further with increasing digit level (3 digits: 0.35:0.85 s; 2 digits: 0.45:0.85 s; 1 digit: 0.5:0.85 s; all $p<0.014$). The power increase over right posterior and central channels for 1 and 2 digits (seen in the topographies of 1 vs. 0 and 2 vs. 0 digit comparisons) did not reach significance at the sensor-level (both $p>0.2$). Comparing digits, there were no significant α differences between 1 digit compared to 2 digits (positive cluster $p=0.042$, ns, negative cluster, $p=0.568$, ns). There was a significant power decrease over bilateral posterior channels in the 3 vs. 2 digit comparison (0.6:0.85s, $p=0.002$) and a near significant power decrease for the 3 vs. 1 digit comparison (negative cluster, $p=0.028$, ns).

I performed α source analysis (10 Hz, 0.4:0.9 s time window) for all digit levels, with a common filter (containing all 4 digit conditions) and separate filters for each digit. For all counted digits (relative to the 0 digit baseline) I observed a similar pattern of α power changes (Figure 30). For 1, 2 and 3 digits, power decreases were seen strongly in bilateral inferior (BA 40) and superior (BA 7) parietal cortices, as well as in left superior temporal (BA 22, 41) and left occipito-temporal (BA 37) sources. Motor area power decreases were seen in bilateral premotor and SMA cortices (BA 6) for all counted digits, and additionally in bilateral primary motor cortices (BA 4) for 1 digit. Frontal power decreases occurred in left dorsolateral PFC (BA 9, 46) for 1 and 2 digits, and additionally in left ventrolateral PFC (BA 47) for 1 digit, with middle and superior frontal (BA 10) power decreases for 2 and 3 digits. Bilateral occipital (BA 18, 19, 31) power decreases were observed for 2 and 3 digits, while the 1 digit comparison to baseline revealed the occipital power increases (BA 17, 18) that were hinted at by the sensor-level topographies (Figure 29). For 1, 2 and 3 digits, there was a power increase in right dorsolateral PFC (BA 9, 46), with additional superior and middle frontal (BA 10, 11) power increases for 2 and 3 digits. The 1 digit comparison also showed a power increase in right superior and middle temporal (BA 21, 22, 41) sources.

The common and separate filter analysis differed in how much of the brain displayed α power decreases. The common filter analysis revealed quite focal sources for all counted digits (see common filter relative power and statistics in Figure 30). The separate filter relative power (Figure 30) and statistics (Appendix D Figure 34) showed a more spatially extensive α power decrease with increasing digit level, such that most of the brain was significantly different for the 3 vs. 0 digit comparison. This can be accounted for by the strong difference in absolute negative power between the 3 digit and 0 digit conditions (see Appendix D Table 15).

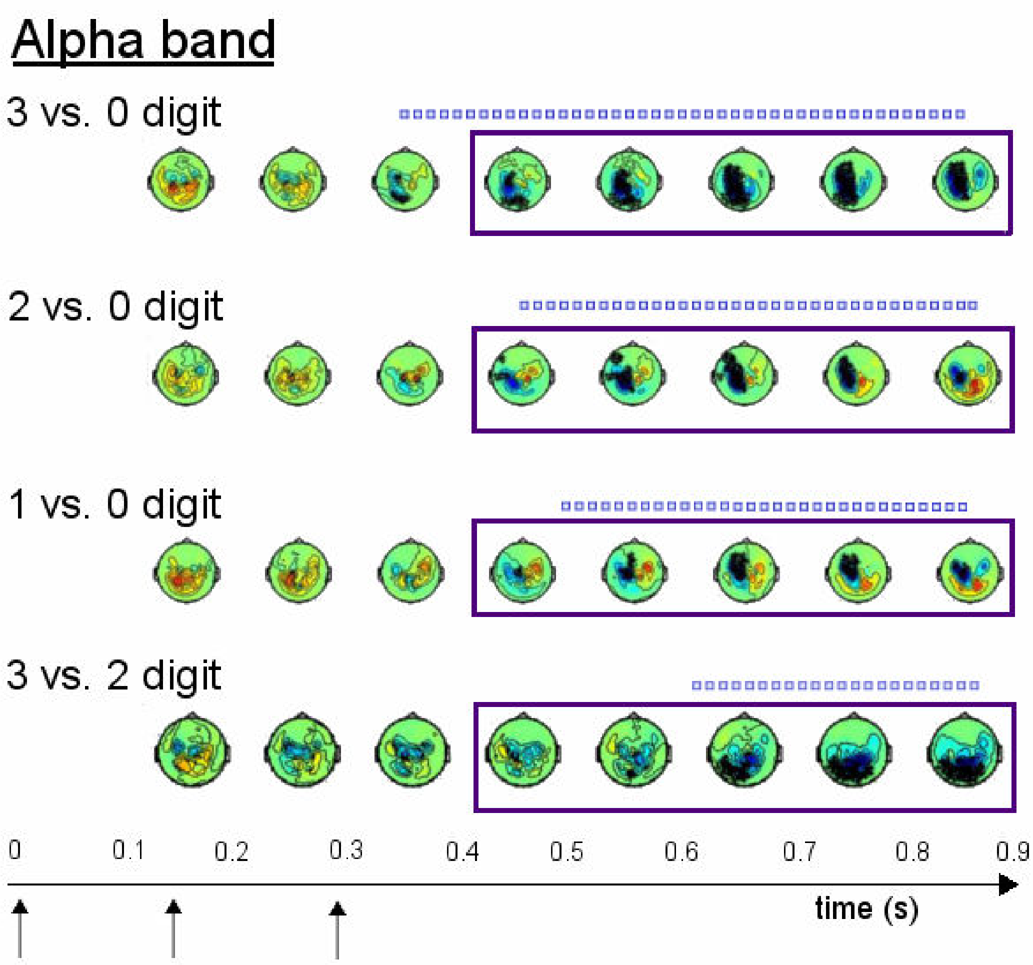
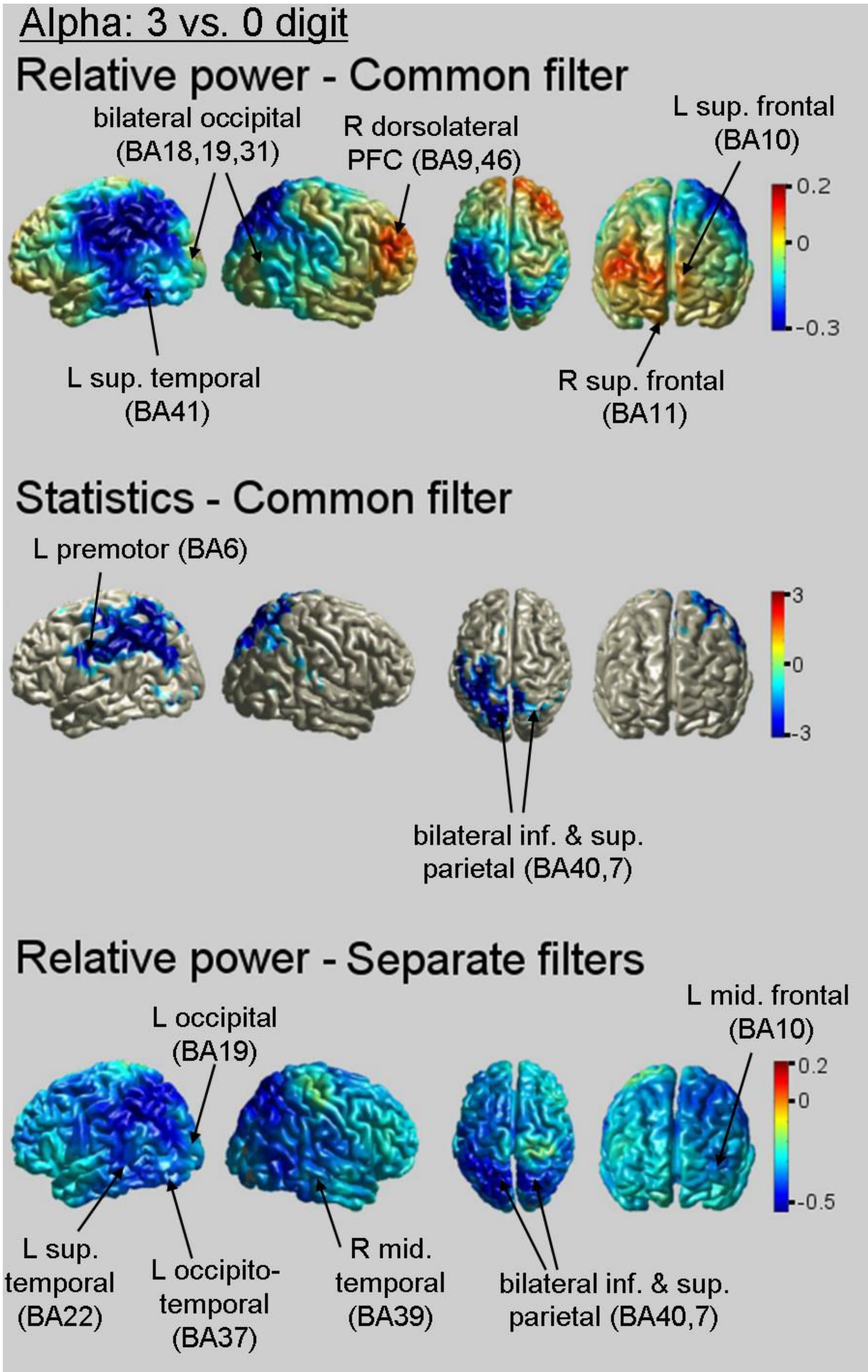
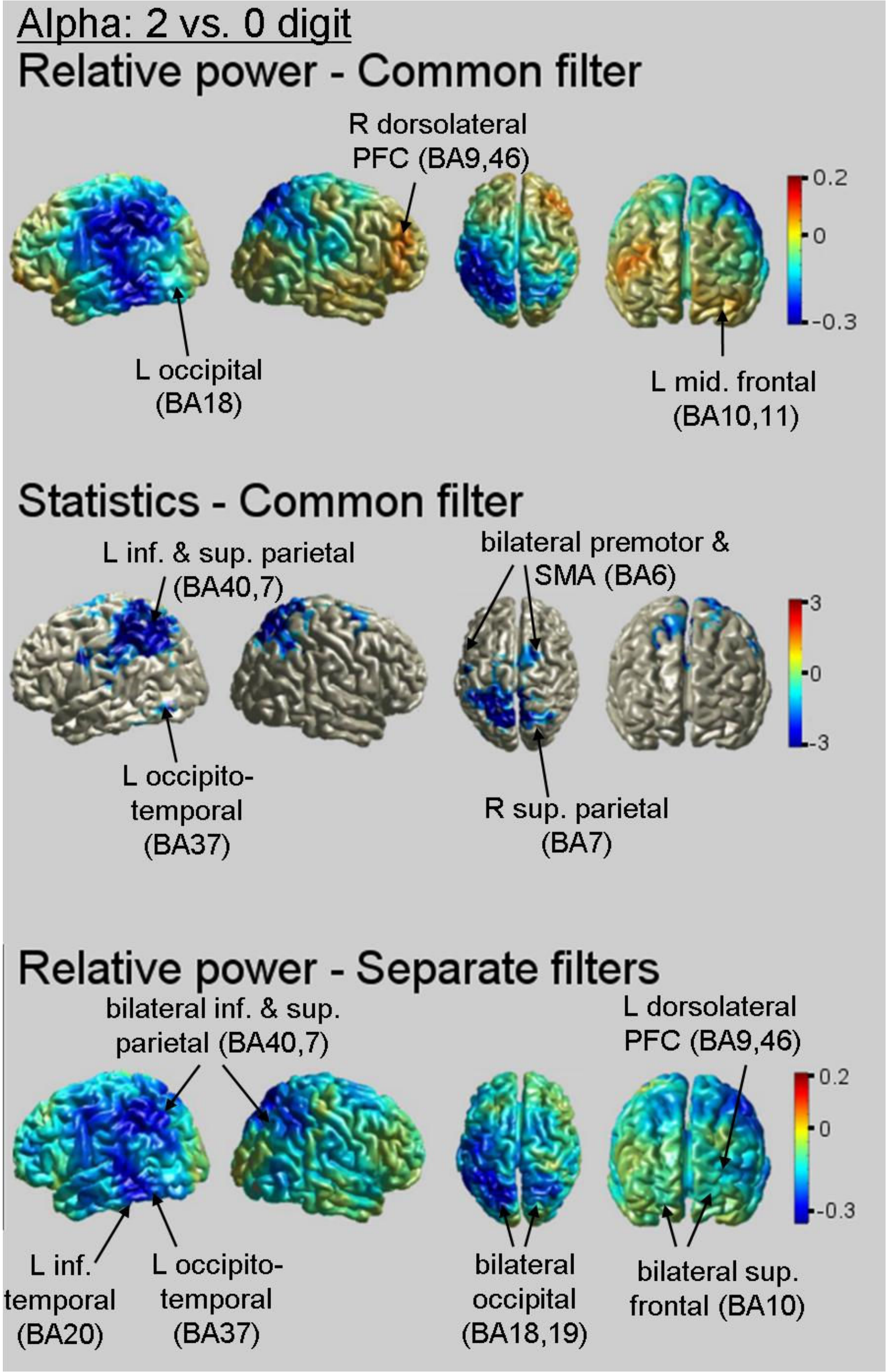


Figure 29 - Difference topographies (eg. 3 digit – 0 digit) with statistics comparing counted digit levels to the baseline (0 digit) condition in alpha band (9-13 Hz). Squares above the topoplots illustrate the timing of significant clusters (red= power increase, blue= power decrease). Black arrows illustrate the onset of the digits. Purple rectangles reflect the time-window used for source analysis.


Alpha: 3 vs. 0 digit
Relative power - Common filter
bilateral occipital (BA18,19,31)
R dorsolateral PFC (BA9,46)
L sup. frontal (BA10)
0.2
0
-0.3
L sup. temporal (BA41)
R sup. frontal (BA11)
Statistics - Common filter
L premotor (BA6)
3
0
-3
bilateral inf. & sup. parietal (BA40,7)
Relative power - Separate filters
L occipital (BA19)
L mid. frontal (BA10)
0.2
0
-0.5
L sup. temporal (BA22)
L occipito-temporal (BA37)
R mid. temporal (BA39)
bilateral inf. & sup. parietal (BA40,7)


Alpha: 2 vs. 0 digit
Relative power - Common filter
R dorsolateral PFC (BA9,46)
0.2
0
-0.3
L occipital (BA18)
L mid. frontal (BA10,11)
Statistics - Common filter
L inf. & sup. parietal (BA40,7)
bilateral premotor & SMA (BA6)
3
0
-3
L occipito-temporal (BA37)
R sup. parietal (BA7)
Relative power - Separate filters
bilateral inf. & sup. parietal (BA40,7)
L dorsolateral PFC (BA9,46)
0.2
0
-0.3
L inf. temporal (BA20)
L occipito-temporal (BA37)
bilateral occipital (BA18,19)
bilateral sup. frontal (BA10)

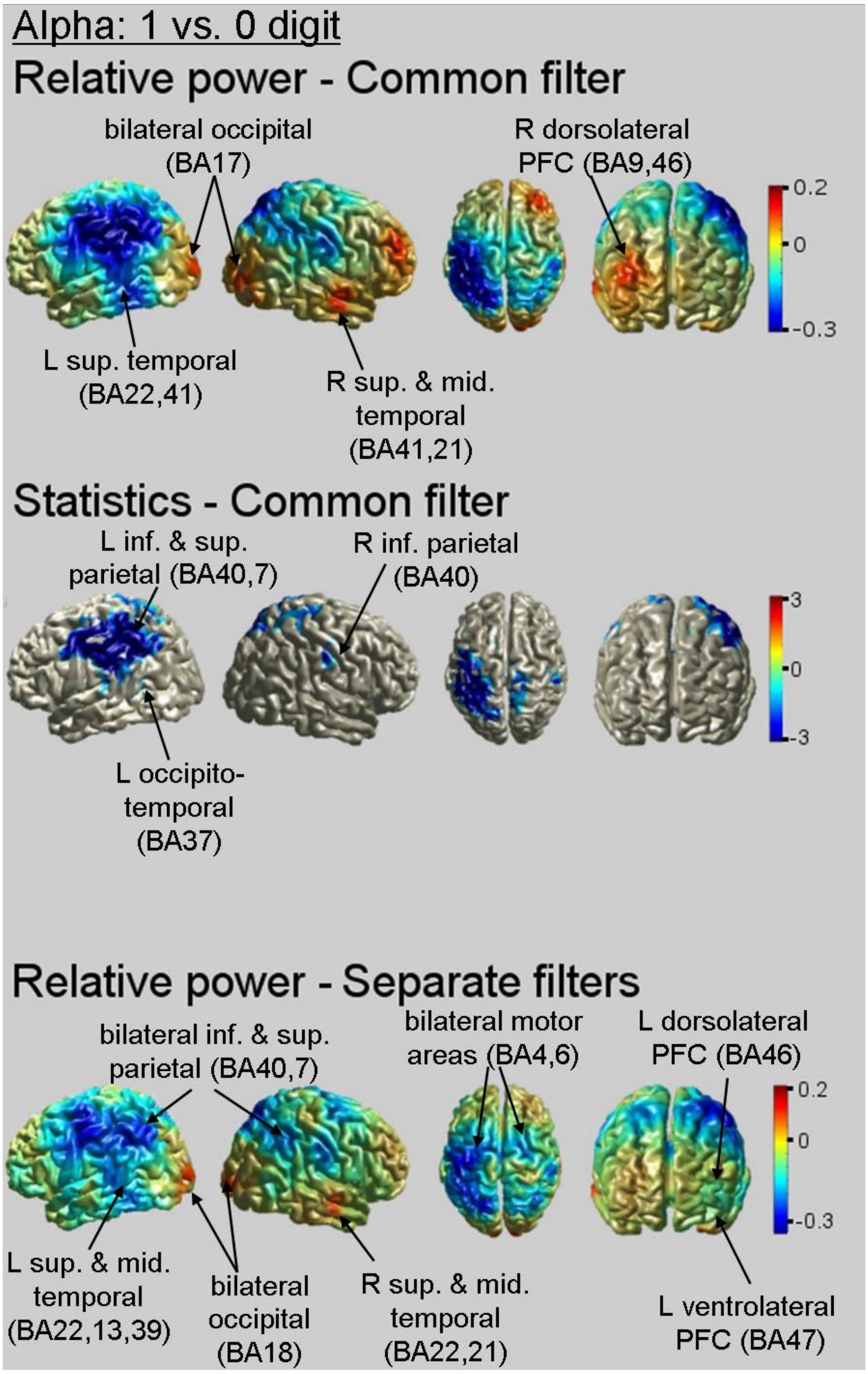


Figure 30 - Group alpha band sources for the 3 vs. 0 digit (1st figure) 2 vs. 0 digit (2nd figure) and 1 vs. 0 digit (3rd figure) comparisons for counting the digits. For the common filter analysis, the relative power (eg. (3 digit – 0 digit)/0digit; top row) and statistics (middle row) are shown. The separate filter relative power (bottom row) is also shown, with corresponding statistics shown in the Appendix D Figure 31. Sources are projected onto a surface plot of the brain. From left to right of the page, the views of the brain are: left, right, top and front. Refer to Appendix C Tables 12 and 13 for further details of the sources.

Theta band

At the sensor-level, an early bilateral θ (3-7 Hz) power increase occurred for all counted digits compared to the 0 digit baseline (Figure 31): 3 vs. 0 digit (0:0.5 s, *p*=0); 2 vs. 0 digit (2 clusters: 0:0.55 s, 0.05:0.55 s, both *p*=0.002); 1 vs. 0 digit (0:0.55 s, *p*=0). The θ power increase began with the 1st digit, and involved bilateral anterior and posterior channels. There were no significant differences when comparing 1, 2 and 3 digits pairwise.

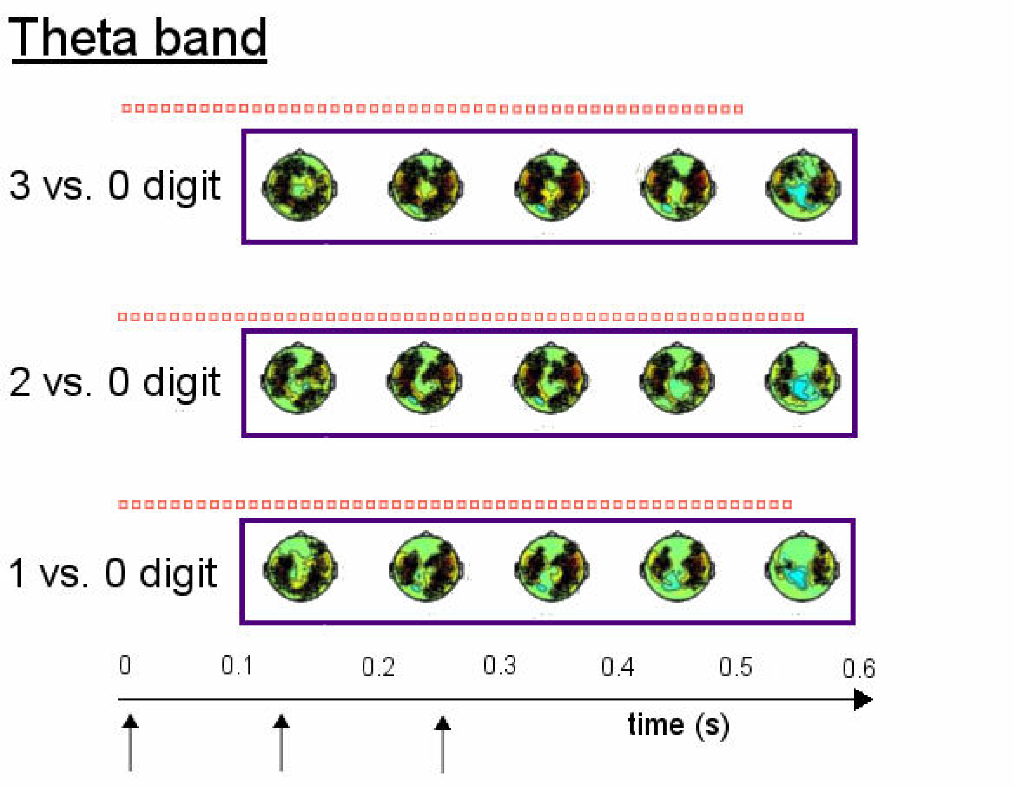


Figure 31 - Difference topographies (eg. 3 digit – 0 digit) with statistics comparing counted digits to the baseline (0 digit) condition in theta band (3-7 Hz). Squares above the topoplots illustrate the timing of significant clusters (red= power increase). Black arrows illustrate the onset of the digits. The purple rectangle reflects the time-window used for source analysis.

I performed θ band (6Hz) source analysis using a common filter (containing all 4 digit levels) on an early time window (0.05:0.55 s) (Figure 32; Appendix C Table 14). Sources showing increased θ power in the merged 321 digit variable relative to the 0 digit were located in the right dorsolateral PFC (BA 46), left ventrolateral PFC (BA 47), left middle frontal (BA 11), left inferior parietal (BA 40), left pre-motor (BA 6), right SMA (BA 6) and right superior and inferior temporal (BA 39, 20). A power decrease was observed in the left occipital cortex (BA 18).

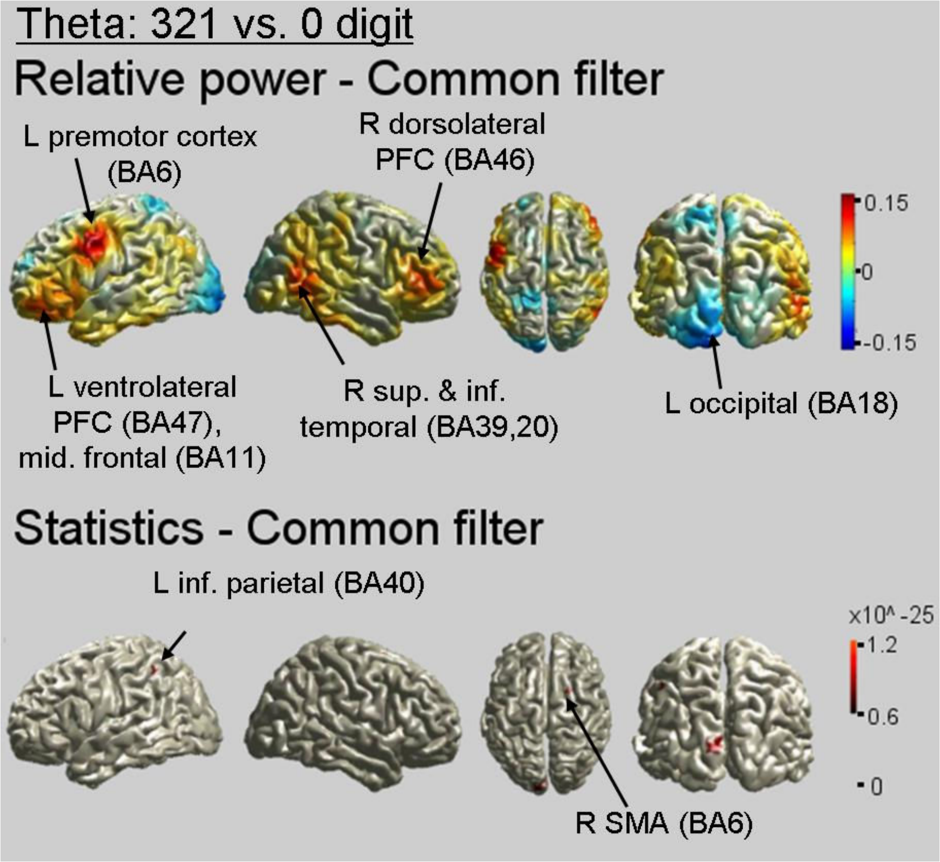


Figure 32 - Group theta band sources for the merged variable 321 digit vs. 0 digit comparison. The common filter relative power (eg. (321 digit – 0 digit)/0digit; top row) and statistics (bottom row) are shown. Sources are projected onto a surface plot of the brain. From left to right of the page, the views of the brain are: left, right, top and back. Refer to Appendix C Table 14 for further details of the sources.

Discussion

The M300 to each counted digit (Figure 24) again suggests all digits gain access to the global workspace (cf. Dehaene et al., 2003a) and subsequently enter working memory (Donchin and Coles, 1988, Verleger, 1988): This pattern resembles the ERF findings from MEG Experiment 1. The M300 results are complemented by the θ-band findings related to working memory discussed below.

However, the key finding is the strong parietal α and β power decrease for all counted digits (1, 2 and 3 digits), relative to the baseline condition. The act of counting is reflected by intense processing in bilateral inferior parietal (BA 40) and superior parietal (BA 7) areas. This could represent activity in the number quantification centre in HIPS (Dehaene et al., 2003b), which is located between inferior and superior parietal cortices. The left-dominated pattern for counting fits with the finding of a left hemisphere dominance for exact numerical judgements, while approximate judgements are typically reflected by a right HIPS advantage (cf. Piazza et al., 2007). Meanwhile a right-hemisphere ß power increase was observed in the inferior parietal cortex (BA 40) and angular gyrus (BA 39).

The left-dominant posterior parietal sources are accompanied by left superior temporal (BA 22, 39, 41) α and ß power decreases for all counted digits, relative to 0 digit. The left superior posterior temporal cortex includes Wernicke's area (BA 22) where language inputs are processed. An fMRI study of over 200 participants found a link between the left lateralisation of the superior temporal sulcus in a language task and of the HIPS in a calculation task (Pinel and Dehaene, 2010). The authors suggested that the superior temporal sulcus could code the abstract representations of numerical symbols, while the HIPS reflects the quantity. Using diffusion tensor imaging, they showed a structural link between these areas. It would be particularly interesting to investigate the synchronisation between these areas using MEG to further understand the direction of communication.

Top-down inhibition of occipital areas is observed for 1 and 2 digits comparisons to baseline. In the ß-band, there is a power increase in right occipital cortex (BA 18, 19) for 1 digit (0.6 – 0.9 s) and 2 digits (0.7 – 0.8 s) (Figures 27 and 28). An occipital α power increase is observed for 1 digit (in bilateral BA 17) (Figure 30), and the sensor-level power increase, although non-significant, suggests this occurs between 0.6 – 0.9 s (Figure 29). This late inhibition could reflect a certainty that there are no further digits to come in the RSVP stream, and could contribute to the higher behavioural performance for counting 1 and 2 digits, compared to 3 digits (Figure 23). It is also possible that this signature develops for 3 digits later in the stream. Frontal power increases are observed at the source-level for all counted digits, in the right dorsolateral PFC (BA 9, 46) in α and ß, and also in the right middle frontal cortex (BA 8) in ß. This could reflect manipulation of the digits in working memory (cf. Postle and D'Esposito, 2000).

The θ power increase for all counted digits (Figure 31) could reflect the opening and sustaining of an event file, beginning with the first digit. This interpretation is supported by sources displaying a θ power increase (although non-significant) in right dorsolateral PFC (BA 46), left ventrolateral PFC (BA 47) and left premotor cortex and right SMA (BA 6) (Figure 32). The lateral PFC sources could reflect the maintenance (ventrolateral) and manipulation (dorsolateral) of digits in working memory (Postle and D'Esposito, 2000). Meanwhile the left premotor source (BA 6) could relate to the sub-vocal rehearsal (Smith et al., 1998) or the maintenance of temporal sequences (Henson et al., 2000) in verbal working memory during counting. There were also θ power increases in the left inferior parietal (BA 40), close to the number quantification centre. In this counting experiment, this region displays intense processing in all frequencies (θ power increases and α/β power decreases), and could be the central node for network communication across the brain. The power decrease in left occipital sources (BA 18) (Figure 32) corresponds to the late non-significant power decrease over posterior sensors (Figure 31). Like MEG Experiment 1, this could reflect top-down inhibition of visual areas following working memory consolidation.

In summary, I found that the act of counting digits in the RSVP stream resulted in intense processing in left posterior parietal cortex (strong α and β power decrease). This pattern was not modulated by the quantity of digits. In this sense, it strongly matches the behavioural outcome for counting digits in the AB in Chapter 3: an equal sized AB was observed when the T1 task was counting 1, 2 or 3 digits. Most importantly, behavioural and neural evidence strongly suggest that counting digits in the T1 composite event is different from detecting the T1 event. Furthermore, I clearly show that the neural signature of counting digits is distinct from the pattern in MEG Experiment 1 for 2 digits. This further strengthens my claim that maximally violated expectations (2 digits), reflected by modulations in the β-band, can induce a strong AB without a full target (3 digits) occurring.

Chapter 10 - General Discussion

The series of behavioural and MEG experiments together strongly suggest that target expectations play an important role in temporal attention. In several behavioural experiments, I investigated the impact of detecting a composite T1 (3 digit full target) on a 2nd target in the AB. I consistently found an AB when digits (1, 2 or 3 digits) were followed by T2. My findings demonstrate for the first time that incrementally building and subsequently violating expectations about a T1 event (in 1 and 2 digit partial target trials) has an impact on switching to a 2nd target. These local expectations built incrementally with each successive digit, such that I consistently observed a stronger AB with 2 digits than 1 digit. The two MEG experiments further show that raised and subsequently violated expectations for T1 have a distinct neural signature, which cannot be accounted for by the act of counting the digits. My novel findings add to the growing knowledge about the dynamics of temporal attention by showing that top-down expectations play an important modulating role. I will discuss this new aspect of expectations with reference to current models of the AB.

Is this really an Attentional Blink?

Firstly I will discuss whether my behavioural findings truly reflect an AB, or whether aspects are accounted for by Repetition Blindness, Psychological Refractory Period or task switching. The paradigm employed here differs in many ways from a standard AB experiment, with a multi-item T1, a two-dimensional task switch and a slower RSVP stream. Typically in the AB, two single item targets (e.g. T1 and T2 are single digits) are presented within an RSVP stream with an SOA of 100 ms. Since T1 and T2 belong to the same category, there is no task switch between targets.

In my paradigm, the RSVP stream could contain 0, 1, 2 or 3 consecutive digits, followed by the letter X (T2). In the target detection experiments (Behavioural Experiments 1 and 3 - 7) participants responded whether or not they saw the full target of 3 digits (T1 task). In the counting experiment (Behavioural Experiment 2) participants responded with the quantity of digits (T1 task). A two-dimensional task switch to T2 (detect the letter X) was necessary during the experiments. Participants switched category from digits (T1) to a letter (T2), while at the same time switching from detecting up to 3 occurrences of the target feature (T1) to detecting one occurrence of the target feature (T2). As predicted, there was no lag 1 sparing with 1, 2 or 3 digits in Behavioural Experiment 1[25]. It has been suggested that the term "AB" is not valid in paradigms employing a task switch, since the T2 deficit could result purely from switching costs or from a mixture of switching and an AB (Potter et al 1998). As mentioned in the General Introduction, several groups disagree with this (Kawahara et al., 2003, Marti et al., 2012); overall suggesting that the key aspect of the AB is the delay in re-engaging attention to the second target. A task switch between targets is a way to lengthen this delay to T2. Furthermore, task switching costs mainly influence performance at lag 1 (cf. Visser et al., 1999, Peterson and Juola, 2000), although it should be noted that a cross-modal AB with lag 1 sparing was found when participants could not prepare for the task switch (Arnell and Larson, 2002). In the current paradigm, the task switch results in a reconfiguration of the task set after T1 (from "digits" to "letter X") which takes time (cf. Rogers and Monsell, 1995). T2 may not be spared at lag 1 as it cannot enter the same attentional episode as T1 (cf. Wyble et al., 2009, 2011, Hommel and Akyurek, 2005). Overall, in my paradigm it is likely that the poor T2 performance for all digit levels at lag 1 reflects mainly switching costs. Yet the T2 deficit at lags 2 to 5 is likely to be a true AB: it is this pattern of relative AB magnitudes with the digit levels that is greatly modulated by local and global target expectations.

The Psychological Refractory Period (PRP) refers to the reaction time delay in responding to a second task that occurs within several hundred ms after a first task, and paradigms tend to employ a task switch (Pashler, 1994). The switch between T1 and T2 in the current paradigm could lead to a delay in processing T2 at short lags. This could result in T2 being blinked on some trials (Jolicoeur et al., 2000, Marti et al., 2012) due to the T2 representation decaying or being substituted by following distractors at a pre-conscious, perceptual level (Enns and Di Lollo, 2000, Giesbrecht and Di Lollo, 1998, Vogel and Luck, 2002). However, since participants respond after the trial in my task and performance is expressed in terms of accuracy (not reaction time), the findings relate more closely to an AB than the PRP.

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[25] lag 1 was only used in Behavioural Experiment 1.

The repetition of digits within the T1 event could have resulted in Repetition Blindness (RB), a deficit in reporting the second repetition of a target within RSVP streams (Kanwisher, 1987, Kanwisher et al., 1996). It can occur when targets are defined purely categorically, e.g. as "digits". There is some evidence that RB could act when participants counted the digits in the T1 event, but not when they detected the 3 digit event. In both the behavioural and MEG counting experiments (Behavioural Experiment 2 and MEG Experiment 2), T1 performance was poorest in the 3 digit condition (~80%), with 1 digit and 2 digit performance at ceiling level. The majority of mistakes with 3 digits were reports of 2 digits. There are 2 alternative explanations for this: guessing and repetition blindness. If participants are uncertain about how many digits they saw, saying 2 digits would be a fair guess: globally around half of all trials contain at least 2 digits[26] (Table 4 in Appendix A) and participants would probably be aware that more than 1 digit had occurred. On the other hand, participants may have been "blinded" by repetition to the third occurrence of a digit, and so report only 2 digits. However, it is unclear why RB would not also act on the second occurrence of a digit, as is typically found in RB experiments (Kanwisher, 1987, Kanwisher et al., 1996). In fact, T1 performance with 2 digits was above 90% in both counting experiments. Taken together, I argue that guesses of 2 digits are a more likely explanation for the reduced performance when counting 3 digits. It should also be noted that participants correctly counted 3 digits on the majority of trials (~80% of the time), so guessing was not prominent. In addition, RB would only have acted within the T1 digit event. It cannot account for the re-engagement of attention to T2 (i.e. the AB) since T2 belongs to a different category.

There is little evidence that RB acted in the target detection experiments (Behavioural Experiments 1, 3-7, MEG Experiment 1). On the whole, T1 performance was above 85% for all digit levels, with the exceptions of Behavioural Experiments 1 and 7. In Experiment 1 (where the global probability of seeing 3 digits was 40% and no feedback was given on false alarms), T1 performance in trials with 2 digits + X was 72%. This improved in subsequent comparable experiments (Experiments 3-5): Here feedback was given when participants said "3 digits" when there was only 1 digit or 2 digits. In

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[26] 57% of trials in Behavioural Experiment 2 and 50% of trials in MEG Experiment 2 contain at least 2 digits.

Experiment 7 the global probability of seeing 3 digits was reduced to 17%. Performance on T1 in trials with 3 digits + X was 74%. The global probabilities of the various digit events seem to influence T1 performance to a small degree. Yet across all experiments, performance on T1 was high.

The rate of presentation of items in the RSVP stream was slower than in a standard AB paradigm (typical SOA is 100 ms), due to the complexity of the T1 event and the task switch. An SOA of 186 ms was employed in the majority of my AB experiments (Behavioural Experiments 1 – 7). However, this is in line with several other groups who used SOAs of 120 – 146 ms with standard single item targets (Gross et al., 2004, Potter et al., 1998) and SOAs of 144 – 250 ms with words and pictures as targets (Duncan et al., 1997, Trippe et al., 2007). When the RSVP stream was faster in the pilot AB experiment for the MEG study (SOA of 150 ms), the AB became stronger for all digit conditions. At the same time, an equal AB magnitude was observed with 2 digits and 3 digits, which matched the pattern from Behavioural Experiment 6[27]. Presenting the stimuli at a faster rate simply deepened the AB for all digit events.

In summary, I show a robust effect of lag on T2 performance in all behavioural experiments when the letter X (T2) follows the digits (T1). My findings most closely resemble an AB, with task switching influencing performance purely at lag 1.

Expectations regarding T1 modulate the AB

I predicted that built-up but unfulfilled target expectations would result in an AB effect, and that it could be even stronger than the effect observed with consolidation of a highly expected target. The paradigm was specifically developed to allow us to manipulate global and local expectations independently. While global expectations are induced by relative trial frequencies and relate to the probability (prior to the trial) of a specific condition occurring, local expectations are induced by the consecutive presentation of target parts (here, digits) that raise the expectation for a full target as a trial unfolds. Indeed, in all experiments the conditional probability

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[27] Note that the MEG behavioural pilot experiment and Behavioural Experiment 6 had the same global frequencies of digit events (all digit events were equally frequent in terms of global probabilities.)

of seeing 3 digits increased from participants seeing 1 digit (P(3 digits|1 digit)) to seeing 2 digits (P(3 digits|2 digits)) (Figure 33). These conditional probabilities for the full T1 seem to translate into target expectations that incrementally build with the presentation of 1 digit and then 2 digits. I further proposed that global expectations modulate local expectations by shaping the size of the increments by which the local expectations are raised by each digit. That is, if full targets (3 digits) are frequent events then the increments with each successive digit are larger than if full targets are infrequent events (compare Figures 33A and 33C). The former was the case in Experiments 1, 3, 4 and 5, while the latter was progressively more the case in Experiments 6 and 7 (i.e. as 3 digit targets became increasingly more rare). Across these experiments I have consistently shown that incrementally raising expectations about a T1 event can result in an AB effect and that its magnitude is modulated by global expectations. I have shown a stable and consistent pattern of blink magnitudes, despite Experiments 1 and 3 having low trial numbers at each lag (see Appendix A, Table 3)[28].

In the initial 5 experiments, the global expectation for 3 digit full T1 events was high (P(3 digits)=0.4), since trial numbers were balanced between full targets (3 digits) and partial targets (1 digit and 2 digits). In this scenario, at the start of a trial participants may highly expect to see 3 digits. In Experiment 1 in trials with 2 digits, strongly built-up but unfulfilled expectations for the full T1 (P(3 digits|2 digits)=0.71) manifested in a large AB. The 2 digit AB was of greater magnitude than in 3 digit trials, where these strong expectations for the full T1 were satisfied. I argued that this pattern was not due to participants switching to T2 after the 2nd digit when the P(3 digits|2 digits) was high. In concordance with the literature, I did not observe lag-1 sparing due to the multidimensional switch between T1 and T2 in my paradigm (cf. Visser et al., 1999). In Experiment 2, I showed that this AB pattern could not be explained simply by the act of counting the digits. When digits were counted, I found a qualitatively different pattern: similar blink magnitudes with 1, 2 and 3 digits at lag 2, and only a marginal effect of global expectations on AB magnitudes at lag

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[28] I have replicated many of our findings in additional experiments. The same data pattern as Experiment 1 was replicated in Experiments 4 and 5, as well as in the masked condition of Experiment 3. A longer replication of Experiment 3 used over 18 trials per lag and revealed the same effect of masking. The pattern in Experiment 6 (same sized AB with 2 and 3 digits) was replicated in another experiment using 24 trials per lag, and also in the behavioural pilot for the MEG with a faster SOA.

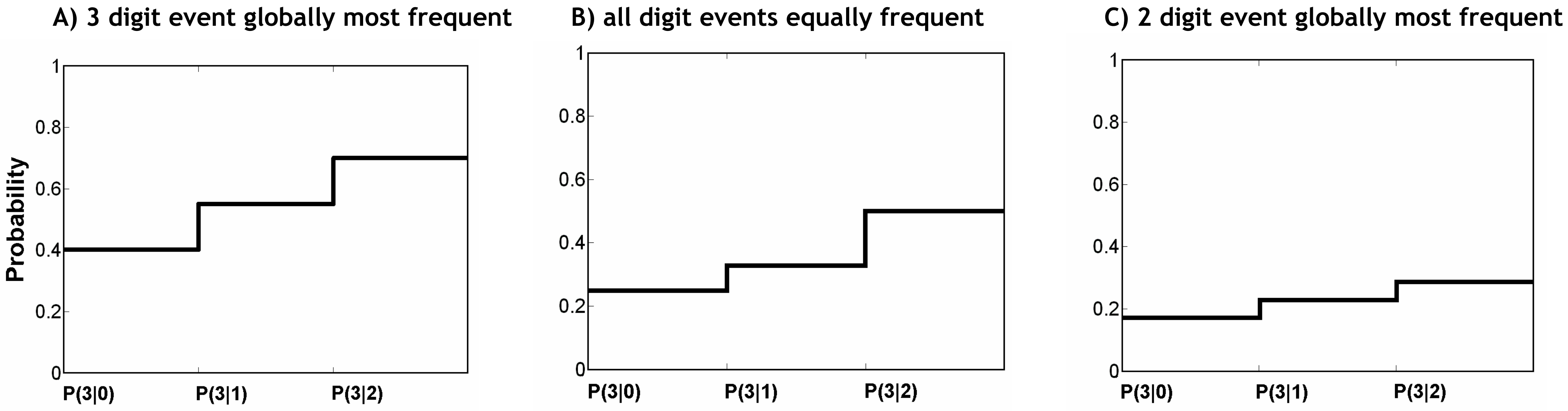

Figure 33 -Conditional probabilities for the 3 digit full T1 following 1 digit and 2 digits, for experiments with different global probabilities of the digit events. Figure A refers to Behavioural Experiments 1, 2, 3, 4 and 5, where the 3 digit event was globally most frequent. Figure B refers to Behavioural Experiment 6, the AB pilot experiment for the MEG study and MEG Experiments 1 and 2, where 1, 2 and 3 digit final events were equally frequent in terms of global probability. Figure C refers to Behavioural Experiment 7, where the 2 digit final event was globally most frequent. The probability values are shown in Table 4 in Appendix A. On each plot, the P(3|0) refers to the global probability of seeing 3 digits at the start of the trial, i.e. when no digits have been seen. The P(3|1) and P(3|2) are the conditional probabilities of seeing the 3 digit full T1, given you have already seen 1 digit and 2 digits respectively.

3. The pattern at lag 3 was even partially reversed compared to Experiment 1: there was a more pronounced AB with 1 digit than 3 digits in Experiment 2.

I then considered the role of the post-digit mask in overcoming expectations in Experiment 3. Replacing this mask with a gap attenuated the AB with partial targets (1 digit and 2 digits). The key finding was that removing the distractor after 2 digits improved performance to the level of the 3 digit AB. This fits with previous findings regarding the interfering role of the mask (Chun and Potter, 1995, Raymond et al., 1992, Grandison et al., 1997, Kessler et al., 2005a, Seiffert and DiLollo, 1997, Nieuwenstein et al., 2009). However, removing the mask after 3 digits did not modulate the AB. Taken together, this suggests that the mask primarily caused interference when expectations for the full target were built up but unfulfilled, while target consolidation with fulfilled expectations was more rapid and not modulated by the mask (in the context of the slow SOA of 186 ms). I have shown that the mask can influence the AB magnitude. Nevertheless, I generally found that top-down expectations exert a stronger influence in this ‘slow’ paradigm than bottom-up signals. On the whole, this was confirmed in Experiments 4 and 5: marking the end of the digit event with acoustic- or colour-based switching-signals had minimal influence on performance for any digit level. There was, however, a hint that colour could capture attention for the T1 event, although this effect could equally reflect group differences. In total, my findings are most compatible with the notion that assumes that various top-down and bottom-up factors can intensify processing of the T1 event (partial or full), which hampers the transition to T2.

In Experiments 6 and 7, I further investigated the top-down influences of global expectations on local expectation increments by lowering the global frequency of full target trials (3 digits). In Experiment 6, global expectations for 2 digits now matched 3 digits, with equal trial frequencies for all digit events (P(3 digits)=0.25). Now the 2 digit AB matched the 3 digit AB, while there was no AB in 1 digit trials. All digit events were globally expected to the same degree, and so local expectations for the full T1 within a trial did not build up at the same rate as in Experiments 1, 3, 4 and 5 (Compare Figures 33B and 33A). In Experiment 7, I further reduced global expectations for 3 digit events (P(3 digits)= 0.17) while raising global expectations for 2 digit events (P(2 digit final event)= 0.4) (Figure 33C). In this experiment, 2 digit event frequency equalled frequencies for 3 digit plus 1 digit events. I now found a stronger AB magnitude with 3 digits compared to the previous experiments. In fact, the AB with 3 digits was numerically stronger than with 2 digits for the first time, while the 2 digit AB magnitude was similar to Experiment 6.

In most experiments there was a main effect of practice on the AB magnitude but no interaction of practice with digit condition: i.e. the pattern of relative blink magnitudes did not change between the first and second halves of the experiment. This suggests that participants quickly learnt the global probabilities of the digit events, since there was a robust effect of global target expectations on the AB within the first half of the experiments. Note that the number of trials in each half of these experiments ranged from 150 - 192. In two longer AB experiments, there was an interaction of practice with digit condition (statistical trend only for Experiment 4). The AB performance improved with practice for partial targets (1 digit and 2 digits) but not for the full target (3 digits) in the masking (Behavioural Experiment 3; 240 trials in each half) and the colour (Behavioural Experiment 4; 360 trials in each half) experiments. This suggests that with enough practice (over 200 trials), participants adapt to conditions with partial targets. In the second half, participants may focus less strongly on finding targets. Expectations for the full target may build less strongly with each digit, resulting in a lowered impact on T2 when these expectations are violated. This fits with "overinvestment" findings which show that focusing strongly on finding targets reduces performance on the AB (Arend et al., 2006, Olivers and Nieuwenhuis, 2005, 2006, McLaughlin et al., 2001, Shore et al., 2001, Taatgen et al., 2009, Wierda et al., 2010).

Finally, in an unreported experiment, I investigated the type of task switch between the composite T1 and single item T2. I aimed to see whether expectations could be incrementally built for a composite T1 consisting of letters, or whether the findings were specific to digits. Strings of digits (e.g. pin and phone numbers) may be more familiar and meaningful to people than strings of letters (cf. Maki and Mebane, 2006); as such, expectations may build more quickly with digits. I carried out an experiment where T1 was 3 consecutive capital letters, while T2 was the number 6 in an RSVP stream of digit distractors. The design of the experiment was otherwise similar to the masked condition of Experiment 3, with trial numbers balanced between full targets (3 letters) and partial targets (1 letter and 2 letters). I replicated the robust finding of a maximal AB with the 2 digits/letters, which suggests that local expectations can build with successive letters as well as digits. The 'size' of the task switch (from letters to a digit) was similar to the other experiments reported here (switching from digits to a letter), which could account for the similar AB magnitudes.

Taken together, my results reveal that global expectations indeed modulate local expectations, but this relationship does not seem to be linear. The AB magnitude with 2 digits was similar in Experiments 6 and 7, although global probability[29] was increased from 25% (Exp. 6) to 40% (Exp. 7). The major difference in AB magnitude for 2 digits (statistical trend only) occurred with a larger AB in Experiment 3 (masked) than Experiment 6, when global probability was raised from 17% to 25% respectively. The 3 digit condition revealed a similarly non-linear relationship to global expectations. The major difference in AB magnitude also occurred between 17% (Exp. 7) and 25% (Exp. 6) global probabilities, with a larger AB in Experiment 7. Likewise, in 1 digit trials, the mild AB was lost in the transition from 17% (Experiment 7) to 25% (Experiment 6) global probabilities. The transition from relatively rare (17%) to equally frequent (25%) events reduces the AB magnitude in 1, 2 and 3 digit trials, but increasing global probability beyond 25% (for 2 and 3 digits) seems to have minimal additional influence. This non-linear pattern suggests that our top-down psychological expectations of various events cannot be entirely attributed to the probabilities of sensory events occurring in the world. The mapping of probabilities onto expectations seems most useful for rare events, but less so when events are highly frequent. Overall this suggests that the AB magnitude, in relation to raised but unfulfilled expectations on the one hand and target consolidation on the other, is influenced by global expectations in a similar non-linear fashion. Nevertheless the most robust finding - since it was replicated in Experiments 1, 3 (masked), 4 and 5 - is the stronger AB with 2 digits than 3 digits when there are high global expectations for the full target (P(3 digits) = 40%). In trials with only 2 digits, target expectations are maximally raised after 2 digits have been seen (P(3 digits|2 digits) = 71%) but are subsequently disappointed by the presentation of a distractor rather than another digit (Figure 33A).

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[29] i.e. the unconditional probability of 2 digits being the final digit event. (See Table 4 in Appendix A).

Local expectations regarding T1 are reflected in the neural signature

The MEG findings complement the behavioural results, and provide insight into the neural correlates of target consolidation and violated expectations, as well as counting successive digits. The first MEG experiment involved participants detecting the composite T1 (3 digits) where there could be 0, 1, 2 or 3 digits, while the second MEG experiment involved counting the digits. Within the AB, activity in the different frequency bands dynamically changes across the trial and relates to whether a blink occurs (see Janson and Kranczioch, 2011 for a recent review). I have likewise shown that theta, alpha and beta have distinct roles when successfully detecting or counting a single composite digit target. The theta band, along with the M300s, seems to represent entry and maintenance of digits in working memory, and the M300 and theta results are remarkably similar in both experiments. An M300 to each digit suggests either entry into working memory (Donchin and Coles, 1988, Verleger, 1988) or access to the global workspace (Dehaene et al., 2003a), and this fits with previous AB findings (Arnell et al., 2004, Kessler et al., 2005a, Kessler et al., 2005b, McArthur et al., 1999, Shapiro et al., 2006, Vogel et al., 1998, Wierda et al., 2010). The theta band power increase is sustained from the onset of the 1st digit until all digits have been presented (0: 0.55s), which suggests that event files in working memory might remain 'open' while there is the possibility of a digit occurring. Digit representations may be maintained in dorsolateral (BA 46, 9) and ventrolateral PFC (BA 47, 45, 12) while the RSVP stream is monitored for subsequent digits. In fact, the PFC may act as a pointer to task-relevant posterior areas, such as the occipito-temporal cortex (BA 37, 19) where visual discrimination of digits from letters could take place (cf. Hommel et al., 2006, Hopf et al., 2002). This indexing by the PFC could temporarily maintain the digit representations, despite continual interference from the RSVP stream (cf. Kessler and Kiefer, 2005).

The alpha band oscillations appears to code for the processing of full targets. A widespread alpha power decrease is observed for all counted digits (1, 2 and 3 digits) in MEG Experiment 2, but only for the 3 digit full target in MEG Experiment 1. In particular, the left inferior parietal cortex (BA 40) shows a strong power decrease for these conditions: This could represent the processing of the digit quantity in regions near to the horizontal segment of the intraparietal sulcus (HIPS; Dehaene et al., 2003b, Nieder and Dehaene, 2009, Piazza et al., 2007). Active processing here (power decrease) does not occur whenever participants encounter a digit, but rather only when they need to class it as a target. Top-down inhibition of occipital areas could be reflected by late alpha increases. In MEG Experiment 1, for the 1 digit condition I observe posterior alpha power increases towards the end of the RSVP stream, corresponding to occipital sources (right BA 19) (Figure 20, 2nd). Meanwhile, in MEG Experiment 2, the 1 and 2 digit conditions revealed power increases (for 1 digit in alpha and beta, and for 2 digits in beta) in occipital sources (BA 17-19) (Figure 28, 2nd, 3rd; Figure 30, 3rd). This signature could reflect the certainty that no more digits will occur. The absence of this occipital inhibition in the 2 digit condition of MEG Experiment 1 is striking, and further fits with my explanation that uncertainty lingers for longer in these trials.

The beta band findings, however, are of greatest relevance to my research question. Beta oscillations seem to code for both the target processing and the rapid changes in local expectation during the trial. They appear to reveal the building of expectations (power decrease) as digits are presented, and the subsequent target consolidation (power decrease) or violation of expectations (frontal power increase). Strong beta power decreases were observed for all counted digits (1, 2 and 3 digits) in MEG Experiment 2 (Figure 27). However in MEG Experiment 1, the beta power decrease was similar for 2 and 3 digits until 0.6 s, when a frontal power increase developed for 2 digits while the 3 digit power decrease continued (Figure 17). Furthermore, there were no significant beta power changes with 1 digit. I tentatively suggest that the 2 digit power increase could represent a late inhibition of processing in right inferior frontal (BA 10) sources, after the left ACC (BA 32) has detected the conflict between the high expectations for a 3rd digit and lag 1 distractor. The source analysis is, however, not time-resolved and it will be necessary to perform synchronisation analysis to ascertain the timing of any communication between 2 such sources. The beta power decreases in both experiments were localised to parietal, temporal and occipital regions, and such networks are involved in target detection and processing under RSVP conditions (Kranczioch et al., 2005, Feinstein et al., 2004, Gross et al., 2004, Marois et al., 2000, Kessler et al., 2006, Hommel et al., 2006).

Beta is the fastest oscillation showing an effect in these experiments. It appears fast enough to code for the rapid changes in expectations which can occur between a digit and the following item in the stream. For example, during the time between one item and the next (SOA of 0.15 s), 3 cycles of 20Hz beta occur: this may be enough cycles in the violated 2 digit condition to indicate that intense processing (beta decrease) must be replaced by active inhibition (beta increase). I did not find effects in the faster gamma rhythm in my experiments. It is possible that beta was fast enough to capture the changes (with the rather slow SOA), while modulations in the gamma-band could have led to the transmission of redundant, error-prone information. For example, 9 cycles of 60Hz gamma would occur during the period of 1 SOA. Redundancy of information would occur with so many cycles of an oscillation, as suggested by Fries' (2005) theory of neuronal communication through coherence, where effective communication between neurons occurs within just 1 cycle. It is also note-worthy that rapidly changing local expectations in my experiment were reflected in the beta band, in concordance with findings by Gross and colleagues (2006). On the other hand, slowly changing global expectations, set up before the trial, were reflected in the alpha band (MacLean and Arnell, 2011). This dissociation between beta and alpha in the literature is highly consistent with the findings reported here.

Post-digit checking: An alternative explanation to expectations?

I have shown consistent behavioural evidence that expectations for the full target strongly influenced AB performance, not only on trials where the full T1 (3 digits) was present, but also on trials with only partial T1s (1 digit and 2 digits). The design of the experiments was such that the conditional probability of 3 digits occurring increased from participants seeing 1 digit (P(3 digits|1 digit)) to seeing 2 digits (P(3 digits|2 digits)). Furthermore, the build-up of expectations within the T1 event and subsequent violation appear to be reflected in modulations of ß band power in the brain. The timing of this ß power decrease with 2 digits and 3 digits overlaps with a period during which target anticipation is reflected in ß band synchronization (Gross et al., 2006).

However, I now explore an alternative explanation, in terms of post-digit checking.

When detecting 3 digit events, participants may experience some uncertainty in trials with 2 digits and 3 digits. On the other hand, participants could be more certain that a 3 digit target did not occur on trials with only 1 digit, suggested by the ceiling level performance on T1 in 1 digit trials. This uncertainty could result in a period of checking following 2 digits and 3 digits, inducing an additional delay in switching to T2 and thus a stronger AB magnitude for 2 digits and 3 digits than for 1 digit. However two aspects of the behavioural findings do not fit with this explanation. Firstly, if uncertainty is strong following 2 digits and 3 digits, but weak following 1 digit, then providing more time after the digits should attenuate the AB in the 2 digit and 3 digit conditions, as checking could proceed in the absence of visual stimulation. At the same time, providing more time may have little influence on the 1 digit condition. However, the results of the masking experiment (Behavioural Experiment 3) do follow this prediction. Rather, providing a gap of 186 ms after the final digit improved performance on the AB in the 1 digit and 2 digit conditions, while there was no change with 3 digits. Secondly, I would not predict that the post-digit checking process would be strongly affected by changes in global probability of the digit events. Taken together, the strong and robust modulation of the AB magnitude by changing the relative frequencies, as well as the effect of masking being limited to partial targets, are better explained in terms of target expectations.

The MEG findings suggest that post-digit checking could be an additional late process following the build-up of target expectations. MEG Experiment 1 involved detecting the 3 digit event. In the absence of a further target (i.e. T2) requiring attention, post-digit checking could occur without any time-constraints. However such checking mechanisms would likely be reflected by a relatively late effect in the brain. The checking of items which have already past could involve the working memory interacting with posterior areas (cf. Hommel et al., 2006, Hopf et al., 2002, Kessler and Kiefer, 2005), such as those involved in digit discrimination. Post-digit checking would likely manifest in a late effect, since it would relate to the final digit in the event: the onset of the 2nd digit occurred at 0.15 s and the 3rd digit at 0.3 s. Given that items enter working memory ~0.3 s after their onset[30], I would expect post-digit checking effects to be apparent from approximately 0.45 s with 2 digits and 0.6 s with 3 digits. While post-digit checking could be an additional process, it cannot account for the earlier effects that are apparent in the ß band (Figure 17). Rather the finding of ß power decreases with 3 digits (from 0.25 s) and 2 digits (from 0.35 s) are better explained by incrementally building expectations for the 3 digit target.

Implications for the AB from MEG findings

The beta band findings in MEG Experiment 1 could help to explain our behavioural results of a strong AB with 2 digits in all target detection experiments where a mask followed the digits. I tentatively suggest that the strong beta power increases in right inferior frontal sources could be the neural correlate of violated expectations which, in turn, could result in the strong 2 digit AB. In a dual target experiment, it would be necessary to overcome this power increase in order to switch to processsing T2 (power decrease). I will discuss this further with reference to AB models, in particular the Robust State account (RS; Kessler et al., 2005a) and the Global Workspace model (GW; Dehaene et al., 1998, Dehaene et al., 2003a).

It is interesting that I observed such a strong frontal "violated expectation" signature for 2 digits, since global expectations for the full target (3 digits) were not extremely high. In MEG experiments, it is optimal to have a similar signal-to-noise ratio (SNR) in all conditions. Therefore, I allocated equal trial numbers to all digit conditions (cf. Behavioural Experiment 6 and the behavioural pilot experiment for the MEG). At the start of the trial, participants may equally expect 1, 2 or 3 digits. I have shown here that, in the absence of strong <u>global</u> expectations for the full target, expectations build <u>locally</u> during the trial. From the beta-band signature, I can conclude that local expectations are minimal as the 1st digit occurs, and build suddenly with the presentation of the 2nd digit. This further suggests that the increments of local expectations do not build linearly with each digit, but rather there is a large step-up with the 2nd digit.

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[30] The M300/P300 is believed to reflect targets entering working memory (Donchin and Coles, 1988, Verleger, 1988).

However, my MEG experiments involved only single targets, and as such, there was no impact of the violated expectations on a T2. Although fast, the tasks were less mentally taxing than an AB experiment, evident by the high performance (above 79%) in both experiments (Figures 12 and 23). It would be necessary to perform a dual target AB experiment in the MEG to ascertain the brain dynamics and sources associated with high and violated expectations impacting on a T2.

In my behavioural AB experiments, I relate the position of T2 (lag) to the final digit in the T1 composite sequence. However, alternatively, lag could be related to the initial digit[31], because it could be argued that the first digit opens an event file in working memory. While the MEG findings indeed suggest that the first digit might open an event file, I also show that each digit, not just the initial one, evokes an M300, i.e. all digits are updated in working memory. I therefore suggest that the entire digit event is only fully encoded after the final digit, and as such it is more appropriate in this case to relate T2 to the end of the digit event.

My findings in relation to current models of the AB

Most existing accounts of the AB would struggle to explain my overall pattern of results, since none were designed to explain raised expectations prior to consolidation, and some were also not designed to take switching between T1 and T2 into account. These results are therefore best understood as providing important boundary conditions for future theoretical developments. My findings extend the implications of “spreading the sparing”. This phenomenon shows that multiple consecutive targets can be reported without the occurrence of a blink, provided they are categorically similar with no intermittent distractors (Di Lollo et al., 2005, Kawahara et al., 2006, Kihara et al., 2008, Nieuwenstein and Potter, 2006, Olivers et al., 2007). In the Temporary Loss of Control (TLC) account (Di Lollo et al., 2005), while the central processor is busy with T1, it loses control of the configuration of the current filter. Distractors which are categorically different from T1 disrupt the filter, which subsequently delays T2 processing. However, a series of categorically similar items can be optimally processed through the same filter, explaining “spreading the sparing” and “lag 1 sparing” findings. The TLC account, in its present form, is mainly designed to optimally account for the outcomes of the counting experiments (Behavioural Experiment 2 and MEG Experiment 2) where all digits are essentially targets, while it cannot explain the modulation of the AB magnitudes by global and local expectations.

Limited capacity accounts of the AB (see Shapiro et al., 1997 for a review, Dux and Marois, 2009) struggle to explain the extended sparing findings. Likewise, with the current paradigm, such accounts might predict a monotonic relationship between the quantity of digits and the size of the blink, i.e. the greatest magnitude AB with 3 digits. However, I found the AB size with 1, 2 and 3 digits was greatly modulated by trial frequency in the 7 target detection experiments here (and in 3 other unreported experiments). Critically, the 3 digit AB was only greatest in magnitude when global expectations for the 3 digit full target were especially low (Experiment 7). Furthermore, the digit counting experiment (Experiment 2) revealed a similarly sized AB with all digit levels, while limited capacity accounts might also predict a monotonic increase with increasing digit levels under such conditions.

Several accounts do capture important aspects of the results. For instance the episodic Simultaneous Type, Serial Token (eSTST, Wyble et al., 2009) and the Robust State (RS, Kessler et al., 2005a) accounts incorporate the basic idea of a transition between T1 and T2 as an essential part of processing; where the cognitive system has to re-engage attention to T2 after T1 (eSTST) or perturb one stable state to be able to generate another (RS). A key aspect of the eSTST model is the encoding of targets in working memory. My theta band findings fit with the idea of multiple successive items (here digits) being encoded in a single attentional episode (cf. Wyble et al., 2011). Furthermore, over-emphasis to a single T1 is detrimental to T2, and this idea is key in the Boost and Bounce (BB, Olivers and Meeter, 2008) and RS accounts. Here I extend this principle of over-emphasis to expectations for a composite T1, which have a detrimental effect on T2 when maximally built but violated.

The Global Workspace model (GW, Dehaene et al., 2003a) implements the interaction between bottom-up and top-down processing, and as such, is highly relevant to my finding that top-down expectations strongly influence the processing of bottom-up targets. To recap on details of the model from Chapter

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[31] I would like to thank Mark Nieuwenstein for this suggestion.

1, the conscious reporting of targets requires a broadcasting of activation from low-level visual areas to specialised processors in high-level association areas across the brain. A state of connectivity (analogous to the stable suppressive state in the RS hypothesis, Kessler et al., 2005a) develops during the broadcasting of T1, such that T2 cannot enter the global workspace during the AB period. Furthermore, expectations play a contextual role in Baars' theatre metaphor for the GW (2005, , 1997). The spotlight of attention shines on the stage of working memory to enable conscious report. Meanwhile, unconscious contexts, such as expectations, intentions and assumptions, influence the spotlight in working memory. MEG findings suggest that expectations could facilitate the access to the GW. With increased target expectations within a trial, there was a greater difference between long-range beta-band synchronization to the target and desynchronization to the pre-target distractor: this was interpreted as "privileged access" to the workspace for expected targets (Gross et al., 2006, p2060). The advantage for expected items could be achieved in the GW model thorough enhanced bottom-up activation or through a lowering of the threshold into the global workspace.

The P300, in this model, is associated with the "global access" of targets (Dehaene et al., 2003a, p8520): the P300 is absent when T2 is not consciously perceived (i.e. T2 is blinked). Thus, my M300 findings suggest that all digits, whether part of a composite target or whether full counted targets in themselves, gain access to the global workspace. My frequency results, however, suggest a slightly different interpretation. The widespread modulations of beta oscillations suggest processing of information by several distant brain regions[32]. In MEG Experiment 2, a widespread beta power decrease was seen for all counted digits. On the other hand, only 2 digit partial targets and 3 digit full targets induced this widespread pattern in MEG Experiment 1. So, although 1 digit partial targets seem to gain access to the GW, the information was not processed by distant cortical regions (at least in terms of beta oscillations). Tentatively, I suggest that local expectations could act within the global workspace, to rapidly influence the broadcasting of information to specialised processors. Incrementally built expectations must exceed a threshold (in this case, 2 digits) before they affect broadcasting in this way.

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[32] I must, however, be cautious in my interpretation, since a demonstration of phase synchrony or coherence would be necessary to suggest broadcasting in the global workspace (i.e. network communication), as discussed in the Limitations.

In the following, I will sketch out necessary features of an AB account that could explain the reported data pattern. I will formulate these features based on the RS account, in relation to the wider GW framework, as it appears to be closest to explaining the observed data pattern from the behavioural and MEG experiments. The RS account is also the easiest to extend, largely due to the disadvantage that it is, at present, not based on an implemented model like the GW, eSTST and BB accounts, and is therefore less constrained but also less precise in its mechanisms. Nevertheless, the RS hypothesis inherently contains the framework to explain the build-up of target expectations and how this would affect the downstream T2. Originally, the RS account (Kessler et al., 2005b, Kessler et al., 2005a, Kessler et al., 2006) was proposed to explain the impact of the T1-mask: By competing with T1, the mask can lead to a boost of T1 processing, by enhanced excitation of T1 while the mask and any other non-T1 items are suppressed. This results in a robust stable state to T1 which hampers the transition to T2 processing. The basic concept of the RS implies two important things. Firstly if T2 is further away from T1 in state-space (e.g. different category and colour) then the transition will be more effortful, as in this case with a multidimensional switch. Secondly, the T1-mask is not the only factor that may induce a robust state in the global workspace that is hard to perturb and generates an AB (Kessler et al., 2005a, p. 1038). In agreement with the general “over-investment” view (Olivers & Nieuwenhuis, 2006), any factor that puts too much emphasis on T1 processing will enhance the AB by making the T1-state harder to perturb and, thus, hampering the transition to T2. The transition period from T1 to T2 directly depends on the robustness of T1 processing (i.e. how hard it is to perturb) and the distance between T1 and T2 in state-space.

Applying these ideas to the current paradigm, each digit presented in succession (1st and 2nd) enters the global workspace, and would lead to a progressively more stable state, through excitation of digit and inhibition of letter representations; an idea that is generally shared with the BB account (Olivers and Meeter, 2008). When top-down expectations for a full T1 are especially built up (i.e., when 2 digits have occurred and the global expectation for 3 digits is high), there is a strong pre-activation of the digit representations in anticipation of the 3rd digit. If the final piece arrives, digit matching can be accomplished very quickly, and T1 consolidation begins, while the incoming mask generates only a moderate amount of interference especially with a long SOA. It takes time to perturb the stability in the global workspace to switch to T2, due to T1 complexity – reflected by the low performance at lag 1 – but all aspects of processing can be resolved efficiently when the actual outcome matches the expected outcome. This explains why the mask following 3 digits did not influence T2 performance: The window of opportunity to interfere with a full T1 had already passed; T1 processing was fast as it was primed by the pre-activation to the previous digits, along with the long SOA.

Conversely, when a distractor rather than a digit follows 2 digits, there is strong competition between the highly enhanced digit representations and the suppressed letters. In order for the letters to "win" and the system to switch to T2, top-down efforts are required that would take a long "system" time. Accordingly, a larger magnitude AB was observed with a 2 digit partial T1 compared to the 3 digit full T1 whenever there was interference between the mask after 2 digits and highly built-up expectations for a 3rd digit. When participants globally expected 3 digits as much as 2 digits, the potentially lowered expectations for a full T1 resulted in a weaker enhancement of the 2nd digit and the resulting competition would be resolved more easily to switch to T2. Similarly, omitting the mask after 2 digits could allow expectations to decay in the absence of new digit input, while there was no distractor interference.

I suggest that network dynamics should be taken into consideration for a full explanation of the AB (RS hypothesis, Kessler et al., 2005a, e.g. GW model, Dehaene et al., 2003a). The RS hypothesis, like the GW model, is envisaged as a recurrent spreading activation network (cf. Houghton and Tipper, 1996, Rumelhart and McClelland, 1986) and is based on neurophysiological findings regarding the dynamics of excitation and suppression within the attentional network during the AB (Kessler et al., 2006, Gross et al., 2006, Hommel et al., 2006, Janson and Kranczioch, 2011). Within the beta-band, phase synchronization to targets and desynchronization to distractors was observed on trials without a blink (Gross et al., 2004, Kranczioch et al., 2007). The desynchronization before T2 was essential for T2 report: It could represent the necessary de-coupling of the robust state within the global workspace, enabling the transition from T1 to T2 (Fries, 2005, Kessler et al., 2006, Rodriguez et al., 1999, Varela et al., 2001). Most relevant to my findings, target anticipation was reflected by this beta-band oscillatory coupling to the target and de-coupling to the distractor (Gross et al., 2006). Oscillations seem to be enhanced with raised expectations, possibly reflecting the build-up of pre-activation within the global workspace with increasing expectations.

As mentioned above, the MEG Experiment 1 findings are in agreement with the idea of pre-activation with 2 digits in anticipation of a 3rd digit. In particular, the beta band power decrease (0.35 – 0.65 s) is seen with 2 digits and 3 digits (but critically not with 1 digit) (Figure 17), and could represent the pre-activation of digit representations and the development of a stable suppressive state in the global workspace. When expectations are fulfilled (3 digits), the beta power decrease persists as target processing continues, and the pre-activation may aid efficient processing in this case. However, when expectations are violated (2 digits), the late anterior beta power increase could represent the competition between pre-activated digit representations and the incoming distractor. In this single target experiment, there is no impact of a T1 stable state on switching to a subsequent target as in the AB. But extending previous findings, it is possible that oscillatory stability could strongly hinder a switch to a subsequent target if T1 expectations are unfulfilled, as the transition to T2 would require the global workspace to de-stabilize the enhanced synchronization through strong desynchronization (cf. Gross et al., 2004, Gross et al., 2006, Kessler et al., 2006). My findings suggest that incrementally building expectations may alone induce a stable suppressive state in the global workspace, without the full target being presented.

Limitations

The MEG frequency findings, based on power changes between conditions, cannot inform us about communication within a network, or concretely show the development of a robust state in the global workspace. Power is calculated by squaring the amplitude of the oscillation. It gives an indication of the number of synchronously active neurons (cf. Hanslmayr et al., 2011). However, observing two cortical sources with beta power decreases, for example, does not mean that there is communication between these sources. To understand network communication, it is necessary to perform coherence or synchronisation analysis (Fries, 2005, Rodriguez et al., 1999, Varela et al., 2001, Gross et al., 2006, Gross et al., 2004). This estimates the phase-coupling relationship between sources or sensors: a consistent phase difference between areas is taken to represent functional connectivity. Follow-up analyses with this paradigm will investigate this, as I am particularly interested in whether the expectation-related beta power changes will translate into enhanced beta synchronisation with building expectations for T1 (cf. Gross et al., 2006).

Conclusions

I have shown that building up expectations about the T1 event within a trial can alone induce an AB. Participants seem to implicitly build local expectations about what they are likely to see in real-time as they perceive the world. Alongside this, participants are strongly influenced by their global expectation for events, which they extract from the frequencies or probabilities of these events. High expectations are beneficial when they are, in fact, satisfied. However, when built-up expectations are violated, there are detrimental effects for switching to downstream targets. In this sense, it is harder ‘to let go’ when expectations remain unfulfilled. The enhanced top-down target expectations can be partially overcome by removing the competition from subsequent distracting events (i.e. a mask). Overall, performance is maximal when participants are not biased towards expecting any specific event (equal digit event frequencies). This gives us insight into the flexibility of top-down attentional influences on processing visual stimuli. Furthermore, raised expectations regarding T1 seem to be optimally reflected by modulations of beta band oscillations, and could represent the pre-activation of digit representations in anticipation of the full target. I have shown that target expectations clearly influence the processing of visual information at high speeds. I envisage this novel aspect of expectations complementing the growing knowledge of the AB, and emphasising the importance of network dynamics as a metaphor for the parallel distributed processing in the brain.

Appendix

A. Trial numbers for each condition and probabilities of digit events in Behavioural and MEG Experiments

		Condition								
		3 digits + X	**2 digits + X**	**1 digit + X**	**0 digits + X**	**3 digits**	**2 digits**	**1 digit**	**0 digits**	**total n**
Behavioural Experiments										
Exp 1		12 (60)	6 (30)	6 (30)	12 (60)	(60)	(20)	(20)	(20)	300
Exp 2		18 (72)	9 (36)	9 (36)	18 (72)	(72)	(24)	(24)	(24)	360
Exp 3	**mask**	12 (48)	6 (24)	6 (24)	12 (48)	(48)	(16)	(16)	(16)	240
	unmask	12 (48)	6 (24)	6 (24)	12 (48)	(48)	(16)	(16)	(16)	240
Exp 4	**Black**	18 (72)	9 (36)	9 (36)	18 (72)	(72)	(24)	(24)	(24)	360
	Blue	18 (72)	9 (36)	9 (36)	18 (72)	(72)	(24)	(24)	(24)	360
Exp 5		18 (72)	9 (36)	9 (36)	18 (72)	(72)	(24)	(24)	(24)	360
Exp 6		12 (48)	12 (48)	12 (48)	12 (48)	(48)	(48)	(48)	(48)	384
Exp 7		9 (36)	18 (72)	9 (36)	18 (72)	(24)	(72)	(24)	(24)	360
MEG Experiments										
Exp 1						(150)	(150)	(150)	(150)	600
Exp 2						(150)	(150)	(150)	(150)	600

Table 3 - Number of trials per condition in Behavioural Experiments 1-7 (Chapters 2-7) and MEG Experiments 1-2 (Chapters 8-9). The value before the brackets is the number of trials per lag (where applicable), while the value in brackets is the total number of trials per condition. See footnotes 3 and 8 for details of replications of these experiments with more trials per lag.

<table>
<tr><th colspan="2"></th><th colspan="4">Unconditional probability of final digit event</th><th colspan="4">Proportion of trials with digit occurrence</th><th colspan="4">Conditional probabilities</th></tr>
<tr><th>Global trial frequencies</th><th>Experiment</th><th>3 d</th><th>2 d</th><th>1 d</th><th>0 d</th><th>3 d only</th><th>≥ 2 d</th><th>≥ 1 d</th><th>0 d only</th><th>2nd d|1st d</th><th>2 d final event|1 d</th><th>3 d final event|1 d</th><th>3 d final event|2 d</th></tr>
<tr><td>3 digit event most frequent</td><td>Beh. Exps. 1, 2, 3, 4 & 5</td><td>0.40</td><td>0.17</td><td>0.17
[A]</td><td>0.27</td><td>0.40</td><td>0.57</td><td>0.73
[B]</td><td>0.27</td><td>0.77
[E]</td><td>0.23
[D]</td><td>0.55
[C]</td><td>0.71</td></tr>
<tr><td>all digit events equally frequent</td><td>Beh. Exp. 6, MEG Exps. 1 & 2</td><td>0.25</td><td>0.25</td><td>0.25</td><td>0.25</td><td>0.25</td><td>0.50</td><td>0.75</td><td>0.25</td><td>0.67</td><td>0.33</td><td>0.33</td><td>0.50</td></tr>
<tr><td>2 digit event most frequent</td><td>Beh Exp. 7</td><td>0.17</td><td>0.40</td><td>0.17</td><td>0.27</td><td>0.17</td><td>0.57</td><td>0.73</td><td>0.27</td><td>0.77</td><td>0.55</td><td>0.23</td><td>0.29</td></tr>
</table>

Table 4 - Probabilities of 0, 1, 2 and 3 digit events for experiments with different global trial frequencies. Calculations for these values are shown below.

Calculations for unconditional and conditional probabilities for the occurrence of the 0, 1, 2 and 3 digit events in Table 4.

I have focused on the T1 digit event, irrespective of the occurrence of T2, to investigate my claim that local expectations for the full T1 event build within the trial as 1 digit and 2 digits are revealed.

Referring to trial numbers in Table 3, and using Experiment 1 and the 1 digit condition as an example:

There are 50 trials in total where 1 digit occurs in the RSVP stream as the final digit event (30 trials with a T2 and 20 trials without T2):

n trials with 1 digit as final digit event = 30 + 20
= 50

1 digit occurred as the final digit event within a trial on 17% of all trials (value [A] in Table 4):

unconditional probability of 1 digit being final digit event = 50 / 300
= 0.167

However, participants will see a first digit on trials containing 2 digits and 3 digits, i.e. on 73% of all trials (value [B] in Table 4):

unconditional probability of seeing at least 1 digit = P(1d) + P(2d) + P(3d)
= 0.1667 + 0.1667 + 0.4
= 0.733

The conditional probability of seeing the full target event (3 digits) given that you have already seen 1 digit (P(3d final event|1d)) is 0.545, i.e. if a participant has seen 1 digit they have a 50% chance of seeing the 3 digit target event (value [C] in Table 4):

unconditional probability of seeing 3 digits as the final event = 0.4
unconditional probability of seeing at least 1 digit = 0.733
conditional probability of seeing 3 digits given 1 digit (3d final event|1d) = 0.4 / 0.733
= 0.545

The conditional probability of seeing 2 digits as the *final digit event*, given that you have already seen 1 digit (P(2d final event|1d) is 0.227 (value [D] in Table 4):

unconditional probability of seeing 2 digits as the final event = 0.1667
unconditional probability of seeing at least 1 digit = 0.733
conditional probability of seeing 2 digits given 1 digit (2d final event|1d) = 0.1667 / 0.733
= 0.227

The conditional probability of seeing a *2nd digit*, given that you have already seen 1 digit (P(2nd d|1st d) is 0.773 (value [E] in Table 4). This probability is greater than value [D] since trials with 2 digits and 3 digits as final events contain a 2nd digit:

unconditional probability of seeing at least 2 digits = 0.567
unconditional probability of seeing at least 1 digit = 0.733
conditional probability of seeing a 2nd digit given 1 digit (2nd d|1st d) = 0.567 / 0.733
= 0.773

B. MEG Experiment 1 Locations of sources for beta, alpha and theta bands

Area	**Brodmann area**	**Talairach-MNI coordinates**	**t-value**
3 digits vs. 0 digit			
power decrease			
R Middle Frontal Gyrus*	BA46	(54, 46, 8)	-2.79
L Superior Parietal Lobule*	BA7	(-38, -66, 56)	-2.29
R Inferior Parietal Lobule*	BA40	(70, -30, 24)	-1.8
R Precentral Gyrus – Frontal*	BA4	(46, -10, 44)	-1.41
R Precentral Gyrus – Frontal*	BA6	(58, 2, 36), (58, -10, 40),	-1.81, -1.48
L Middle Temporal Gyrus*	BA21	(-70, -10, 0)	-1.52
L Inferior Temporal Gyrus*	BA37	(-58, -58, -8)	-2.35
L Lingual Gyrus – Occipital*	BA18	(-18, -94, -16)	-2.76
L Cuneus – Occipital*	BA19	(-30, -86, 32)	-1.78
R Middle Occipital Gyrus*	BA18	(22, -98, 24)	-1.78
R Lingual Gyrus – Occipital*	BA17	(14, -102, -12)	-1.88
L Cerebellum*	none	(-62, -66, -16)	-2.77
R Cerebellum*	none	(2, -42, 0)	-1.24
2 digits vs. 0 digit			
power decrease			
L Precentral Gyrus – Frontal*	BA4	(-46, -14, 40)	-2.42
R Precentral Gyrus – Frontal*	BA6	(70, -6, 28)	-2.74
R Precuneus – Parietal*	BA7	(22, -78, 56)	-1.18
L Superior Temporal Gyrus*	BA22	(-62, -54, 20)	-2.03
R Lingual Gyrus – Occipital*	BA17	(22, -102, -12)	-1.73
R Cerebellum*	none	(10, -34, -28)	-2.43
power increase			
L Medial Frontal Gyrus*	BA32	(-2, 10, 44)	1.5
L Superior Frontal Gyrus*	BA6	(-6, 14, 56), (-10, 10, 60)	1.71, 1.94
3 digits vs. 2 digit			
power decrease			
L Superior Frontal Gyrus*	BA8	(-10, 50, 40)	-2.31
L Medial Frontal Gyrus*	BA8	(-6, 50, 40)	-1.96
R Inferior Frontal Gyrus*	BA45	(58, 30, 4)	-2.30
R Inferior Frontal Gyrus*	BA47	(50, 30, 0)	-1.73
R Middle Frontal Gyrus*	BA11	(46, 42, -12)	-1.44

Table 5 - Locations of significant sources for MEG experiment 1 beta (20Hz) source analysis. Separate filters were used for source analysis of each digit condition. The time window used for source analysis was 0.35:0.85s. Sources relate to Figure 18 in Chapter 8.

Area	**Brodmann area**	**Talairach-MNI coordinates**	**Relative power**
3 digits vs. 0 digit			
power decrease			
L Middle Frontal Gyrus*	BA6	(-34, 2, 64)	-0.083
L Medial Frontal Gyrus	BA6	(-10, -22, 68)	-0.147
L Precentral Gyrus - Frontal*	BA6	(-66, -10, 32)	-0.111
L Postcentral Gyrus - Parietal	BA2	(-62, -22, 52)	-0.214
R Paracentral Lobule - Parietal*	BA4	(10, -38, 72)	-0.089
L Superior Parietal Lobule*	BA7	(-22, -50, 72)	-0.092
R Superior Parietal Lobule*	BA7	(22, -62, 56), (34, -74, 56)	-0.13, -0.101
R Precuneus - Parietal*	BA7	(10, -54, 36)	-0.13

L Inferior Parietal Lobule*	BA40	(-50, -42, 56)	-0.18
R Posterior Cingulate*	BA30	(10, -46, 24)	-0.11
L Cingulate Gyrus - Limbic*	BA31	(-6, -42, 28)	-0.125
R Cingulate Gyrus - Limbic*	BA31	(6, -42, 32)	-0.126
L Precuneus - Parietal*	BA31	(-2, -66, 24)	-0.079
R Precuneus - Parietal*	BA31	(22, -74, 28)	-0.138
R Middle Temporal Gyrus*	BA37	(54, -62, 8)	-0.106
R Superior Temporal Gyrus*	BA22	(58, -46, 12)	-0.129
R Cuneus - Occipital*	BA18	(10, -74, 16)	-0.104
L Cuneus - Occipital*	BA18	(-6, -102, 8)	-0.123
power increase			
R Superior Frontal Gyrus*	BA9	(26, 38, 28)	0.14
R Middle Frontal Gyrus	BA9	(42, 50, 40)	0.21
L Superior Frontal Gyrus*	BA8	(-10, 42, 56), (-10, 54, 44)	0.15, 0.19
L Middle Frontal Gyrus*	BA10	(-46, 58, -4)	0.11
L Cingulate Gyrus - Frontal*	BA6	(-14, 26, 36)	0.13
L Middle Temporal Gyrus	BA21	(-54, 2, -36)	0.083
R Superior Frontal Gyrus	BA6	(18, -6, 72	0.094
R Postcentral Gyrus- Parietal	BA5	(38, -42, 64)	0.095
2 digits vs. 0 digit			
power decrease			
L Precentral Gyrus - Frontal*	BA4	(-34, -22, 48)	-0.15
L Precentral Gyrus - Frontal*	BA6	(-34, -10, 36)	-0.128
L Paracentral lobule*	BA2	(-14, -34, 84)	-0.111
L Postcentral Gyrus - Parietal*	BA3	(-54, -10, 44)	-0.125
L Superior Parietal Lobule*	BA7	(-22, -42, 76)	-0.113
R Superior Parietal Lobule*	BA7	(22, -70, 60), (22, -62, 44)	-0.128, -0.111
L Precuneus - Parietal*	BA7	(-18, -62, 36)	-0.121
R Precuneus - Parietal*	BA7	(22, -58, 48)	-0.104
L Inferior Parietal Lobule*	BA40	(-62, -18, 44)	-0.111
L Angular Gyrus - Parietal*	BA39	(-26, -54, 32)	-0.103
L Middle Temporal Gyrus	BA21	(-66, -54, 8)	-0.125
R Superior Temporal Gyrus*	BA22	(58, -42, 8)	-0.073
R Middle Temporal Gyrus*	BA21	(50, -42, 12)	-0.068
R Cerebellum*	none	(26, -54, -56)	-0.1
power increase			
L Middle Frontal Gyrus*	BA10	(-50, 54, -12)	0.141
L Middle Frontal Gyrus*	BA47	(-54, 50, -12)	0.134
L Superior Frontal Gyrus*	BA6	(-10, 38, 60)	0.124
R Middle Frontal Gyrus*	BA9	(38, 46, 40)	0.236
R Middle Frontal Gyrus	BA46	(42, 34, 16)	0.269
R Middle Frontal Gyrus	BA10	(34, 38, 8)	0.207
L Superior Temporal Gyrus	BA22	(-70, -18, 0)	0.133
R Inferior Temporal Gyrus	BA20	(54, -2, -28)	0.09
3 digits vs. 2 digit			
power decrease			
R Inferior Frontal Gyrus	BA46	(38, 34, 8)	-0.175
R Middle Frontal Gyrus	BA46	(46, 26, 24)	-0.133
R Middle Frontal Gyrus	BA47	(46, 38, -4)	-0.127
L Inferior Parietal Lobule*	BA40	(-58, -42, 52)	-0.118
L Superior Temporal Gyrus	BA42	(-66, -22, 8)	-0.149
L Middle Occipital Gyrus	BA18	(-10, -90, 12)	-0.092
R Lingual Gyrus - Occipital	BA18	(30, -98, -4)	-0.106
R Cuneus - Occipital	BA19	(30, -90, 32)	-0.117

power increase			
L Middle Frontal Gyrus	BA46	(-46, 46, 24)	0.093
R Medial Frontal Gyrus	BA8	(6, 50, 44)	0.082
R Superior Frontal Gyrus	BA6	(14, 2, 68)	0.123

Table 6 - Locations of significant and peak relative power sources for MEG experiment 1 beta (20Hz) source analysis. A common filter was used for source analysis, using data from 3 digit, 2 digit and 0 digit conditions. The time window used for source analysis was 0.35:0.85s. Relative power was calculated as (3 digit – 0 digit)/0digit for example. Sources relate to Figure 18 in Chapter 8.

Area	**Brodmann area**	**Talairach-MNI coordinates**	**t-value**
3 digits vs. 0 digit			
power decrease			
L Middle Frontal Gyrus*	BA9	(-26, 18, 32):	-2.47
L Middle Frontal Gyrus*	BA11	(-38, 54, -12)	-3.61
L Inferior Frontal Gyrus*	BA46	(-46, 46, 4)	-3.27
R Superior Frontal Gyrus*	BA6	(22, -2, 72)	-2.31
R Inferior Frontal Gyrus*	BA47	(30, 10, -20)	-2.74
L Precentral Gyrus – Frontal*	BA6	(-26, -10, 48)	-2.55
L Precentral Gyrus – Frontal*	BA4	(-26, -22, 64)	-2.58
L Postcentral Gyrus – Parietal*	BA2	(-50, -22, 28)	-2.44
L Superior Parietal Lobule*	BA7	(-14, -62, 64)	-3.22
L Precuneus – Parietal*	BA7	(-10, -62, 32)	-3.84
L Inferior Parietal Lobule*	BA40	(-46, -38, 48)	-3.56
R Superior Parietal Lobule*	BA7	(34, -50, 60)	-2.97
R Precuneus – Parietal*	BA7	(2, -54, 40)	-3.07
R Inferior Parietal Lobule*	BA40	(50, -42, 44)	-2.66
L Superior Temporal Gyrus*	BA21	(-50, -22, 0)	-2.49
L Middle Temporal Gyrus*	BA21	(-50, -10, -12)	-2.12
L Middle Temporal Gyrus*	BA37	(-50, -62, 8)	-2.13
R Superior Temporal Gyrus*	BA38	(50, 18, -32)	-2.79
L Precuneus – Occipital*	BA31	(-14, -58, 24)	-3.67
L Cuneus – Occipital*	BA19	(-10, -98, 24)	-3.81
L Lentiform Nucleus, Lateral Globus Pallidus*	none	(-22, -14, -8)	-2.26
R Cerebellum*	none	(6, -66, -44)	-2.07
1 digits vs. 0 digit			
power decrease			
L Precentral Gyrus – Frontal*	BA4	(-26, -26, 52)	-2.72
3 digits vs. 1 digit			
power decrease			
L Middle Frontal Gyrus*	BA10	(-50, 54, -8)	-3.39
R Inferior Frontal Gyrus*	BA47	(54, 34, -12):	-2.60
R Medial Frontal Gyrus*	BA10	(2, 70, -4)	-2.88
R Precentral Gyrus – Frontal*	BA4	(42, -18, 68)	-1.16
L Precentral Gyrus – Frontal*	BA6	(-14, -18, 68)	-1.92
L Superior Parietal Lobule*	BA7	(-42, -58, 52)	-2.72
L Precuneus – Parietal*	BA7	(-22, -82, 52):	-3.04
L Inferior Parietal Lobule*	BA40	(-50, -34, 52):	-1.81
R Superior Parietal Lobule*	BA7	(38, -54, 56)	-3.18
R Inferior Parietal Lobule*	BA40	(50, -54, 52):	-2.71
L Superior Temporal Gyrus*	BA22	(-66, -42, 20):	-2.49
L Middle Temporal Gyrus*	BA21	(-66, -6, -16):	-2.38
R Superior Temporal Gyrus*	BA13	(50, -46, 16)	-2.21
R Middle Temporal Gyrus*	BA21	(50, -14, -12)	-2.20
R Fusiform Gyrus – Temporal*	BA37	(30, -38, -12)	-1.99
R Posterior Cingulate*	BA23	(10, -58, 16)	-3.16
L Parahippocampal Gyrus*	BA36	(-38, -22, -12)	-2.4

L Inferior Occipital Gyrus*	BA18	(-38, -90, -8)	-3.43
R Middle Occipital Gyrus*	BA18	(10, -98, 16):	-2.64
L Cerebellum*	none	(-22, -86, -32)	-2.41
R Cerebellum*	none	(18, -86, -28)	-2.07

Table 7 - Locations of significant sources for MEG experiment 1 alpha (10Hz) source analysis. Separate filters were used for source analysis of each digit condition. The time window used for source analysis was 0.4:0.9s. Sources relate to Figure 20 in Chapter 8.

Area	**Brodmann area**	**Talairach-MNI coordinates**	**Relative power**
3 digits vs. 0 digit			
power decrease			
L Postcentral Gyrus - Parietal*	BA5	(-18, -42, 72)	-0.102
L Inferior Parietal Lobule*	BA40	(-50, -42, 56)	-0.158
L Superior Parietal Lobule*	BA7	(-34, -58, 56)	-0.171
R Superior Parietal Lobule*	BA7	(18, -70, 56)	-0.278
L Precuneus - Parietal*	BA7	(-14, -54, 40)	-0.104
L Middle Temporal Gyrus	BA37	(-54, -62, 4)	-0.250
L Precuneus - Occipital*	BA31	(-14, -58, 28)	-0.115
L Cuneus - Occipital*	BA19	(-34, -90, 32)	-0.138
L Cingulate Gyrus - Limbic*	BA31	(-2, -54, 28)	-0.114
L Posterior Cingulate*	BA23	(-2, -42, 24)	-0.075
power increase			
L Middle Frontal Gyrus*	BA10	(-34, 66, 12)	0.089
R Superior Frontal Gyrus*	BA9	(14, 62, 32)	0.067
1 digit vs. 0 digit			
power decrease			
L Precentral Gyrus - Frontal*	BA4	(-30, -22, 56)	-0.096
L Postcentral Gyrus - Parietal*	BA3	(-22, -30, 56)	-0.094
R Precuneus - Parietal	BA7	(10, -74, 56)	-0.131
power increase			
L Middle Frontal Gyrus*	BA10	(-46, 50, -8)	0.098
L Inferior Frontal Gyrus*	BA44	(-62, 18, 16)	0.066
L Middle Frontal Gyrus	BA6	(-34, 10, 60)	0.119
R Precentral Gyrus - Frontal	BA6	(42, -14, 64)	0.211
L Inferior Temporal Gyrus*	BA20	(-66, -30, -20)	0.155
R Superior Temporal Gyrus	BA41	(58, -26, 8)	0.087
R Fusiform Gyrus - Temporal	BA19	(50, -66, -12)	0.129
R Cerebellum		(38, -70, -28)	0.130
3 digits vs. 1 digit			
power decrease			
L Superior Parietal Lobule*	BA7	(-38, -54, 60), (-26, -54, 60)	-0.136, -0.071
R Superior Parietal Lobule*	BA7	(30, -62, 64), (10, -58, 80)	-0.181, -0.157
L Precuneus - Parietal*	BA7	(-14, -78, 52)	-0.147
L Superior Temporal Gyrus*	BA41	(-54, -26, 8)	-0.145
L Inferior Temporal Gyrus*	BA20	(-54, -30, -16)	-0.174
L Parahippocampal Gyrus - Limbic*	BA36	(-34, -30, -12)	-0.142
L Fusiform Gyrus - Temporal*	BA20	(-50, -38, -20)	-0.184
R Middle Temporal Gyrus*	BA22	(50, -38, 0)	-0.197
R Superior Temporal Gyrus*	BA41	(50, -30, 12)	-0.185
R Inferior Temporal Gyrus*	BA37	(50, -38, -16)	-0.144
R Fusiform Gyrus - Temporal*	BA20	(50, -18, -20)	-0.125
R Middle Temporal Gyrus*	BA21	(66, -42, -12)	-0.135
L Cuneus - Occipital*	BA19	(-14, -82, 36)	-0.163
L Middle Occipital Gyrus*	BA18	(-26, -86, 0)	-0.168

L Cerebellum*		(-26, -54, -16)	-0.142
power increase			
L Superior Frontal Gyrus	BA9	(-14, 62, 28)	0.056
R Superior Frontal Gyrus	BA9	(10, 62, 28)	0.065
L Precentral Gyrus - Frontal	BA6	(-62, -10, 28)	0.042
L Postcentral Gyrus - Parietal	BA1	(-38, -38, 72)	0.084

Table 8 - Locations of significant and peak relative power sources for MEG experiment 1 alpha (10Hz) source analysis. A common filter was used for source analysis, using data from 3 digit, 1 digit and 0 digit conditions. The time window used for source analysis was 0.4:0.9s. Relative power was calculated as (3 digit – 0 digit)/0digit for example. Sources relate to Figure 20 in Chapter 8.

Area	**Brodmann area**	**Talairach-MNI coordinates**	**Relative power**
321 digits vs. 0 digit			
power increase			
R Superior Frontal Gyrus	BA8	(18, 46, 40)	0.1
R Middle Frontal Gyrus	BA10	(46, 58, -8)	0.1
R Middle Frontal Gyrus*	BA46	(46, 46, 24)	0.1
R Middle Frontal Gyrus*	BA8	(50, 30, 44)	0.12
L Middle Frontal Gyrus	BA8	(-34, 38, 40)	0.08
L Middle Frontal Gyrus	BA10	(-42, 54, 4)	0.09
L Precentral Gyrus - frontal	BA44	(-66, 14, 4)	0.14
L Inferior Frontal Gyrus*	BA45	(-62, 26, 20)	0.09
L Supramarginal Gyrus - parietal	BA40	(-66, -46, 28)	0.06
R Inferior Parietal Lobule*	BA40	(50, -62, 48)	0.08
R Superior Parietal Lobule	BA7	(22, -62, 64)	0.07
L Superior temporal gyrus	BA38	(-62, 14, -8)	0.11
L Fusiform Gyrus - temporal	BA20	(-50, -2, -24)	0.06
R Fusiform Gyrus - temporal	BA37	(46, -46, -16)	0.07
R Parahippocampal Gyrus*	BA37	(34, -42, -8)	0.06
R Superior Frontal Gyrus	BA8	(18, 46, 40)	0.1
power decrease			
L Middle Occipital Gyrus*	BA19	(-42, -90, 20)	-0.02
R Lingual Gyrus - Occipital*	BA18	(6, -98, -8)	-0.05

Table 9 - Locations of significant and peak relative power sources for MEG experiment 1 theta (6Hz) source analysis. A common filter was used for source analysis, using data from 3 digit, 2digit, 1 digit and 0 digit conditions. Data for 3 digit, 2 digit and 1 digit were merged, and compared to 0 digits. Relative power was calculated as (321 digit – 0 digit)/0digit. The time window used for source analysis was 0.05:0.55s. Sources relate to Figure 22 in Chapter 8.

C. MEG Experiment 2 Locations of sources for beta, alpha and theta bands

Area	Brodmann area	Talairach-MNI coordinates	t-value
3 digits vs. 0 digit			
power decrease			
L Superior Frontal Gyrus*	BA8	(-14, 50, 44)	-2.92
R Superior Frontal Gyrus*	BA8	(18, 38, 44)	-3.82
L Middle Occipital Gyrus*	BA37	(-50, -66, -8)	-2.13
L Superior Parietal Lobule*	BA7	(-22, -54, 64)	-1.56
L Precuneus – Parietal*	BA7	(-2, -78, 52)	-2.01
L Postcentral Gyrus – Parietal*	BA7	(-18, -58, 68)	-2.13
L Inferior Parietal Lobule*	BA40	(-46, -46, 60)	-2.42
R Precuneus – Parietal*	BA7	(10, -78, 52)	-3.13
R Inferior Parietal Lobule*	BA40	(50, -66, 52)	-2.94
L Cerebellum*		(-58, -66, -16)	-2.73
2 digits vs. 0 digit			
power decrease			
L Superior Frontal Gyrus*	BA11	(-26, 46, -24)	-2.65
L Precentral Gyrus – Frontal*	BA4	(-50, -10, 36)	-2.81
L Precentral Gyrus – Frontal*	BA6	(-58, -10, 40), (-66, 6, 12)	-2.73, -2.49
R Postcentral Gyrus – Parietal*	BA1, BA2	(66, -18, 24), (70, -18, 24)	-2.25, -2.24
L Uncus - Limbic Lobe*	BA38	(-26, 2, -40)	-3.55
L Inferior Temporal Gyrus*	BA37	(-62, -58, -4)	-1.02
L Thalamus*		(-2, -22, 8)	-1.90
power increase			
R Medial Frontal Gyrus*	BA9	(6, 58, 40)	1.54
1 digit vs. 0 digit			
power decrease			
R Postcentral Gyrus – Parietal*	BA1	(54, -22, 56)	-2.00
R Postcentral Gyrus – Parietal*	BA40	(62, -22, 56)	-2.06
L Precuneus – Parietal*	BA19	(-34, -86, 44)	-2.62
L Middle Temporal Gyrus*	BA19	(-38, -78, 24)	-1.94
L Cerebellum*			-2.45
power increase			
R Superior Frontal Gyrus*	BA9	(30, 46, 28)	2.52
R Superior Frontal Gyrus*	BA10	(26, 54, 24)	3.38

Table 10 - Locations of significant sources for MEG experiment 2 beta (20Hz) source analysis. Separate filters were used for source analysis of each digit condition. The time window used for source analysis was 0.35:0.85s. Sources relate to Figure 28 in Chapter 9.

Area	Brodmann area	Talairach-MNI coordinates	Relative power
3 digits vs. 0 digit			
power decrease			
L Precentral Gyrus - Frontal*	BA6	(-34, -14, 56)	-0.217
L Postcentral Gyrus - Parietal*	BA2	(-54, -22, 48)	-0.216
L Superior Parietal Lobule*	BA7	(-18, -62, 64)	-0.242
L Inferior Parietal Lobule*	BA40	(-46, -50, 60)	-0.228
L Supramarginal Gyrus - Temporal*	BA40	(-66, -50, 28)	-0.114
R Superior Parietal Lobule*	BA7	(30, -66, 56)	-0.109
R Precuneus - Parietal*	BA7	(26, -62, 36)	-0.080
R Precuneus - Parietal*	BA19	(30, -82, 36)	-0.106
L Superior Temporal Gyrus	BA22	(-58, -54, 8)	-0.157
L Middle Temporal Gyrus*	BA19	(-50, -62, 16)	-0.151
L Middle Occipital Gyrus*	BA18	(-42, -86, 12)	-0.127

L Cuneus - Occipital*	BA19	(-10, -98, 24)	-0.091
L Cingulate Gyrus - Limbic*	BA31	(-14, -22, 44)	-0.114
L Cerebellum*	none	(-26, -62, -36)	-0.092
power increase			
R Middle Frontal Gyrus	BA8	(30, 26, 40)	0.179
R Middle Frontal Gyrus	BA9	(30, 38, 32)	0.129
R Inferior Frontal Gyrus	BA47	(50, 38, -16)	0.084
R Inferior Temporal Gyrus	BA20	(50, -2, -36)	0.076
R Inferior Parietal Lobule	BA40	(50, -54, 40)	0.117
R Angular Gyrus - Parietal	BA39	(58, -62, 40)	0.201
<u>2 digits vs. 0 digit</u>			
power decrease			
L Middle Frontal Gyrus*	BA6	(-26, 6, 40)	-0.147
R Postcentral Gyrus - Parietal*	BA2	(42, -34, 60)	-0.080
L Postcentral Gyrus - Parietal*	BA5	(-22, -38, 72)	-0.140
L Superior Parietal Lobule*	BA7	(-34, -50, 64)	-0.225
L Precuneus - Parietal*	BA7	(-14, -50, 48)	-0.151
L Inferior Parietal Lobule*	BA40	(-50, -42, 60)	-0.231
L Superior Temporal Gyrus*	BA22	(-46, -22, 4)	-0.118
L Superior Temporal Gyrus*	BA38	(-30, 6, -32):	-0.094
L Fusiform Gyrus - Temporal*	BA20	(-38, -10, -24)	-0.113
L Superior Occipital Gyrus*	BA19	(-34, -86, 24)	-0.072
L Inferior Occipital Gyrus*	BA18	(-46, -86, 0)	-0.114
L Cerebellum*	none	(-46, -74, -28)	-0.073
power increase			
R Superior Frontal Gyrus*	BA9	(10, 58, 24)	0.056
R Middle Frontal Gyrus	BA8	(26, 30, 44)	0.122
R Inferior Frontal Gyrus	BA47	(50, 30, -12)	0.075
R Inferior Temporal Gyrus*	BA20	(58, -30, -20)	0.130
R Inferior Parietal Lobule	BA40	(54, -54, 44)	0.128
R Angular Gyrus - Parietal	BA39	(58, -62, 40)	0.142
R Fusiform Gyrus - Occipital*	BA18	(30, -90, -16)	0.106
R Inferior Occipital Gyrus*	BA18	(30, -94, -4)	0.100
R Cerebellum*	none	(30, -34, -28)	0.123
<u>1 digit vs. 0 digit</u>			
power decrease			
L Inferior Frontal Gyrus*	BA10	(-34, 42, 0)	-0.075
L Middle Temporal Gyrus*	BA38	(-42, 2, -44)	-0.138
L Precentral Gyrus - Frontal*	BA6	(-42, -14, 64)	-0.283
L Postcentral Gyrus - Parietal*	BA5	(-42, -50, 64)	-0.219
L Postcentral Gyrus - Parietal*	BA2	(-66, -22, 32)	-0.137
R Postcentral Gyrus - Parietal*	BA2	(58, -22, 56)	-0.084
L Superior Parietal Lobule*	BA7	(-34, -50, 64)	-0.202
L Precuneus - Parietal*	BA7	(-2, -74, 56)	-0.113
R Superior Parietal Lobule*	BA7	(38, -62, 56)	-0.068
L Inferior Parietal Lobule*	BA40	(-42, -54, 52), (-50, -34, 52)	-0.194, -0.294
L Supramarginal Gyrus - Parietal*	BA40	(-66, -46, 28)	-0.156
L Superior Temporal Gyrus	BA39	(-54, -54, 8)	-0.125
power increase			
R Middle Frontal Gyrus	BA8	(22, 30, 36)	0.119
R Superior Frontal Gyrus	BA9	(34, 34, 32)	0.073
R Superior Frontal Gyrus	BA11	(14, 58, -16)	0.083
R Inferior Parietal Lobule	BA40	(54, -54, 36)	0.138
R Angular Gyrus - Parietal	BA39	(54, -66, 32)	0.095
R Fusiform Gyrus - Occipital*	BA19	(30, -66, -8)	0.081

R Inferior Occipital Gyrus*	BA18	(46, -86, -8)	0.080
R Cerebellum*	none	(22, -66, -16)	0.102

Table 11 - Locations of significant and peak relative power sources for MEG experiment 2 beta (20Hz) source analysis. A common filter was used for source analysis, using data from 3 digit, 2 digit, 1 digit and 0 digit conditions. The time window used for source analysis was 0.35:0.85s. Relative power was calculated as (3 digit – 0 digit)/0digit for example. Sources relate to Figure 28 in Chapter 9.

Area	**Brodmann area**	**Talairach-MNI coordinates**	**t-value**	**Relative power**
3 digits vs. 0 digit				
power decrease				
L Middle Frontal Gyrus*	BA10	(-38, 46, 12)	-3.01	-0.370
L Precentral Gyrus - Frontal*	BA6	(-58, -14, 40)	-2.63	-0.427
L Middle Frontal Gyrus*	BA6	(-22, 10, 60)	-3.44	-0.401
R Precentral Gyrus - Frontal*	BA6	(18, -14, 60)	-3.51	-0.412
L Superior Parietal Lobule*	BA7	(-22, -70, 60)	-2.70	-0.521
L Inferior Parietal Lobule*	BA40	(-34, -46, 44)	-2.87	-0.475
L Precuneus - Parietal*	BA19	(-34, -70, 40)	-2.69	-0.446
L Precuneus - Parietal*	BA7	(-22, -66, 52)	-2.77	-0.525
R Superior Parietal Lobule*	BA7	(26, -58, 44)	-2.66	-0.438
R Inferior Parietal Lobule*	BA40	(34, -42, 44)	-2.56	-0.406
L Supramarginal Gyrus - Temporal*	BA40	(-58, -46, 20)	-3.02	-0.444
L Inferior Temporal Gyrus*	BA37	(-58, -66, 0)	-3.07	-0.435
L Inferior Temporal Gyrus*	BA37	(-54, -66, 0)	-2.96	-0.451
L Superior Temporal Gyrus*	BA22	(-58, -42, 12)	-2.97	-0.419
R Middle Temporal Gyrus*	BA39	(46, -74, 12)	-2.73	-0.455
R Middle Occipital Gyrus*	BA37	(42, -66, 4)	-2.66	-0.439
L Cuneus - Occipital*	BA19	(-22, -90, 28)	-2.54	-0.489
L Cerebellum*		(-26, -26, -36)	-2.77	-0.420
R Cerebellum*		(34, -54, -24)	-3.08	-0.403
2 digits vs. 0 digit				
power decrease				
L Superior Frontal Gyrus*	BA9	(-14, 58, 36)	-3.99	
L Middle Frontal Gyrus*	BA46	(-50, 50, 16)	-4.14	
L Superior Frontal Gyrus*	BA10	(-26, 58, 24)	-4.25	
L Middle Frontal Gyrus*	BA10	(-22, 70, 8)	-2.44	
R Superior Frontal Gyrus*	BA10	(26, 70, -12)	-2.78	
L Superior Frontal Gyrus*	BA6	(-6, 10, 68)	-3.42	
R Medial Frontal Gyrus*	BA6	(18, 6, 48)	-3.02	
L Postcentral Gyrus - Parietal*	BA3	(-18, -34, 64)	-3.38	
R Postcentral Gyrus - Parietal*	BA5	(18, -42, 64)	-2.62	
L Superior Parietal Lobule*	BA7	(-38, -62, 56)	-2.71	
L Precuneus - Parietal*	BA7	(-18, -50, 56)	-3.13	
L Inferior Parietal Lobule*	BA40	(-46, -38, 48)	-3.02	
R Superior Parietal Lobule*	BA7	(34, -58, 56)	-2.16	
R Precuneus - Parietal*	BA7	(18, -54, 52)	-2.58	
R Inferior Parietal Lobule*	BA40	(54, -34, 44)	-3.04	
L Inferior Temporal Gyrus*	BA37	(-62, -62, -12)	-2.52	
L Middle Temporal Gyrus*	BA37	(-50, -62, 4)	-2.50	
L Middle Temporal Gyrus*	BA37	(-46, -58, 4)	-2.79	
L Inferior Temporal Gyrus*	BA20	(-38, -14, -40)	-2.68	
L Middle Occipital Gyrus*	BA18	(-34, -94, 4)	-2.81	
R Middle Occipital Gyrus*	BA19	(54, -78, 8)	-2.35	
L Thalamus - Sub-lobar*		(-2, -30, 4)	-3.09	
L Cerebellum*		(-38, -46, -36)	-2.85	
R Cerebellum*		(42, -70, -36)	-2.91	
1 digit vs. 0 digit				
power decrease				

L Middle Frontal Gyrus*	BA46	(-50, 54, 8)	-3.93	
L Inferior Frontal Gyrus*	BA47	(-58, 26, -4)	-3.00	
R Superior Frontal Gyrus*	BA6	(18, -10, 64)	-3.05	
L Precentral Gyrus - Frontal*	BA6	(-62, 2, 40)	-2.47	
L Precentral Gyrus - Frontal*	BA4	(-38, -26, 72)	-2.84	
R Precentral Gyrus - Frontal*	BA4	(22, -22, 60)	-3.12	
R Paracentral Lobule - Frontal*	BA31	(10, -30, 44)	-3.69	
R Cingulate Gyrus - Limbic*	BA31	(10, -30, 36)	-4.10	
L Postcentral Gyrus - Parietal*	BA2	(-46, -22, 44)	-3.51	
R Postcentral Gyrus - Parietal*	BA2	(50, -26, 60)	-2.78	
L Superior Parietal Lobule*	BA7	(-22, -58, 64)	-3.15	
L Inferior Parietal Lobule*	BA40	(-54, -38, 48)	-3.07	
L Precuneus - Parietal*	BA7	(-26, -74, 52)	-2.63	
R Superior Parietal Lobule*	BA7	(22, -66, 60)	-2.49	
R Inferior Parietal Lobule*	BA40	(50, -66, 48)	-2.82	
R Angular Gyrus - Parietal*	BA39	(58, -66, 36)	-2.67	
L Superior Temporal Gyrus*	BA22	(-70, -42, 12)	-2.72	
L Superior Temporal Gyrus*	BA13	(-42, -46, 24)	-4.10	
L Middle Temporal Gyrus*	BA39	(-46, -62, 24)	-3.12	
L Middle Occipital Gyrus*	BA19	(-26, -86, 20)	-2.37	
L Thalamus - Sub-lobar*		(-2, -10, 0)	-3.15	
L Cerebellum*		(-18, -34, -44)	-2.80	
R Cerebellum*		(22, -66, -44)	-3.08	
power increase				
R Middle Temporal Gyrus	BA21	(62, -18, -8)	ns	0.099
R Superior Temporal Gyrus	BA22	(62, -18, 0)	ns	0.099
L Lingual Gyrus - Occipital	BA18	(-6, -102, -8)	ns	0.147
R Cuneus - Occipital	BA18	(14, -102, 8)	ns	0.108

Table 12 - Locations of significant and peak relative power sources for MEG experiment 2 alpha (10Hz) source analysis. Separate filters were used for source analysis of each digit condition. Much of the brain was significantly different in the 3 digit vs. 0 digit comparison, so only the sources with the peak negative relative power (< -0.35) are included in the table. The time window used for source analysis was 0.4:0.9s. Sources relate to Figure 30 in Chapter 9.

Area	**Brodmann area**	**Talairach-MNI coordinates**	**Relative power**
<u>3 digits vs. 0 digit</u>			
power decrease			
L Precentral Gyrus - Frontal*	BA6	(-58, -2, 48)	-0.179
L Postcentral Gyrus - Parietal*	BA2	(-58, -18, 28)	-0.180
L Superior Parietal Lobule*	BA7	(-30, -62, 56)	-0.393
L Inferior Parietal Lobule*	BA40	(-46, -62, 48)	-0.299
R Superior Parietal Lobule*	BA7	(34, -66, 56)	-0.204
R Inferior Parietal Lobule*	BA40	(54, -34, 24)	-0.122
L Precuneus - Parietal*	BA7	(-18, -46, 44)	-0.223
L Precuneus - Parietal*	BA31	(-18, -74, 24)	-0.163
L Precuneus - Occipital*	BA31	(-14, -62, 24)	-0.153
R Precuneus - Parietal*	BA7	(22, -74, 44)	-0.161
L Superior Temporal Gyrus*	BA41	(-42, -34, 16)	-0.190
L Cuneus - Occipital*	BA19	(-14, -86, 32)	-0.212
L Middle Occipital Gyrus*	BA19	(-38, -86, 8)	-0.150
R Middle Occipital Gyrus*	BA19	(42, -86, 16)	-0.108
R Lingual Gyrus - Occipital*	BA18	(6, -86, -8)	-0.120
L Thalamus - Sub-lobar*		(-2, -18, 12)	-0.139
L Insula - Sub-lobar*	BA13	(-34, -30, 24)	-0.186
power increase			
L Superior Frontal Gyrus	BA10	(-10, 66, 20)	0.066
R Superior Frontal Gyrus	BA11	(10, 66, -16)	0.071

R Superior Frontal Gyrus	BA9	(10, 62, 28)	0.100
R Middle Frontal Gyrus	BA46	(46, 30, 24)	0.110
2 digits vs. 0 digit			
power decrease			
L Superior Frontal Gyrus*	BA6	(-26, -2, 72)	-0.115
R Superior Frontal Gyrus*	BA6	(2, 2, 72)	-0.096
L Postcentral Gyrus - Parietal*	BA5	(-26, -38, 64)	-0.204
L Postcentral Gyrus - Parietal*	BA7	(-26, -50, 72)	-0.237
L Superior Parietal Lobule*	BA7	(-30, -50, 64)	-0.287
L Precuneus - Parietal*	BA7	(-14, -78, 48)	-0.214
L Inferior Parietal Lobule*	BA40	(-42, -38, 56)	-0.273
R Superior Parietal Lobule*	BA7	(2, -66, 56)	-0.178
L Precuneus - Parietal*	BA31	(-14, -46, 36)	-0.176
R Precuneus - Parietal*	BA7	(10, -66, 48)	-0.130
R Precuneus - Parietal*	BA31	(10, -46, 28)	-0.135
L Fusiform Gyrus - Temporal*	BA37	(-50, -62, -16)	-0.227
L Middle Temporal Gyrus*	BA37	(-42, -54, 0)	-0.259
L Middle Occipital Gyrus*	BA18	(-34, -82, 0)	-0.135
R Anterior Cingulate - Limbic*	BA25	(2, 10, -8)	-0.111
R Cingulate Gyrus - Limbic*	BA24	(2, -2, 36)	-0.120
L Parahippocampal Gyrus*	BA19	(-42, -46, 0)	-0.233
L Thalamus - Sub-lobar*		(-2, -10, 12)	-0.094
power increase			
L Middle Frontal Gyrus	BA11	(-34, 38, -12)	0.065
L Medial Frontal Gyrus	BA10	(-2, 66, 16)	0.050
R Middle Frontal Gyrus	BA9	(34, 46, 36)	0.069
R Middle Frontal Gyrus	BA46	(54, 34, 24)	0.078
1 digit vs. 0 digit			
power decrease			
L Superior Frontal Gyrus*	BA6	(-10, 14, 72)	-0.070
R Precentral Gyrus - Frontal*	BA6	(18, -18, 68)	-0.081
R Precentral Gyrus - Frontal*	BA4	(18, -22, 56)	-0.108
L Postcentral Gyrus - Parietal*	BA1	(-58, -18, 52)	-0.292
L Postcentral Gyrus - Parietal*	BA3	(-30, -22, 44)	-0.186
L Postcentral Gyrus - Parietal*	BA5	(-38, -46, 64)	-0.301
L Postcentral Gyrus - Parietal*	BA40	(-58, -26, 56)	-0.331
R Postcentral Gyrus - Parietal*	BA2	(54, -26, 56)	-0.205
R Postcentral Gyrus - Parietal*	BA5	(18, -42, 64)	-0.096
R Postcentral Gyrus - Parietal*	BA7	(14, -50, 68)	-0.115
L Superior Parietal Lobule*	BA7	(-38, -62, 56)	-0.296
L Inferior Parietal Lobule*	BA40	(-58, -38, 48)	-0.314
R Inferior Parietal Lobule*	BA40	(54, -38, 48)	-0.189
L Middle Temporal Gyrus*	BA19	(-38, -58, 12)	-0.165
L Middle Temporal Gyrus*	BA37	(-42, -58, 4)	-0.193
L Superior Temporal Gyrus*	BA41	(-42, -42, 12)	-0.175
L Superior Temporal Gyrus*	BA22	(-66, -42, 20)	-0.168
L Cingulate Gyrus - Limbic*	BA23	(-10, -14, 32)	-0.124
R Cingulate Gyrus - Limbic*	BA31	(18, -26, 40)	-0.112
L Thalamus - Sub-lobar*		(-10, -18, 12)	-0.110
power increase			
R Superior Frontal Gyrus	BA9	(34, 46, 28)	0.109
R Middle Frontal Gyrus	BA46	(42, 46, 16)	0.086
R Middle Temporal Gyrus	BA21	(70, -18, -4)	0.145
R Superior Temporal Gyrus	BA41	(54, -18, 4)	0.086
R Cuneus - Occipital	BA17	(18, -90, 4)	0.092
L Cuneus - Occipital	BA17	(-10, -98, 4)	0.057

Table 13 - Locations of significant and peak relative power sources for MEG experiment 2 alpha (10Hz) source analysis. A common filter was used for source analysis, using data from 3 digit, 2 digit, 1 digit and 0 digit conditions. The time window used for source analysis was 0.4:0.9s. Relative power was calculated as (3 digit – 0 digit)/0digit for example. Sources relate to Figure 30 in Chapter 9.

Area	**Brodmann area**	**Talairach-MNI coordinates**	**Relative power**
321 digits vs. 0 digit			
power increase			
R Superior Frontal Gyrus*	BA6	(18, 10, 72)	0.04
L Middle Frontal Gyrus	BA6	(-58, 6, 40)	0.15
L Middle Frontal Gyrus	BA47	(-42, 38, -8)	0.09
L Middle Frontal Gyrus	BA11	(-38, 42, -16)	0.1
R Inferior Frontal Gyrus	BA46	(50, 38, 8)	0.09
R Superior Temporal Gyrus	BA39	(54, -54, 8)	0.1
R Fusiform Gyrus - Temporal	BA20	(38, -30, -16)	0.08
R Inferior Temporal Gyrus	BA20	(54, -34, -16)	0.07
R Parahippocampal Gyrus	BA35	(22, -30, -12)	0.07
L Parahippocampal Gyrus - Hippocampus	none	(-26, -14, -16)	0.06
L Inferior Parietal Lobule*	BA40	(-54, -54, 52)	0.05
L Inferior Parietal Lobule	BA39	(-50, -70, 44)	0.06
power decrease			
L Cuneus*	BA18	(-14, -94, 20)	-0.06
L Middle Occipital Gyrus*	BA18	(-30, -94, 4)	-0.06
L Uvula - Cerebellum*		(-6, -94, -28)	-0.1

Table 14 - Locations of significant and peak relative power sources for MEG experiment 2 theta (6Hz) source analysis. A common filter was used for source analysis, using data from 3 digit, 2digit, 1 digit and 0 digit conditions. Data for 3 digit, 2 digit and 1 digit were merged, and compared to 0 digits. Relative power was calculated as (321 digit – 0 digit)/0digit. The time window used for source analysis was 0.05:0.55s. Sources relate to Figure 32 in Chapter 9.

D. Alpha band differences in power between conditions in MEG Experiment 2 are revealed in the separate filter statistics

The maximum absolute power for 10Hz separate filter analysis was in a similar range for 0, 1, 2 and 3 digits (Table 15). However, the minimum absolute power was much stronger for 3 digits than the other digit levels. This could account for why most of brain was statistically significant for the 3 digit vs. 0 digit comparison (Figure 34). Differences in absolute power between conditions affect the outcome of significant sources only when using separate filter. The common filter analysis seems to average out strong power differences between conditions (as seen in Figure 30 (1st) in the Chapter 9), so that only peak differences are seen.

Digit	Min absolute power	Max absolute power
3 digit	$8.7*10^{-28}$	$4.3*10^{-26}$
2 digit	$1.1*10^{-27}$	$5.2*10^{-26}$
1 digit	$1.1*10^{-27}$	$5.8*10^{-26}$
0 digit	$1.2*10^{-27}$	$6.9*10^{-26}$

Table 15 - Absolute minimum and maximum alpha power for separate filter source analysis.

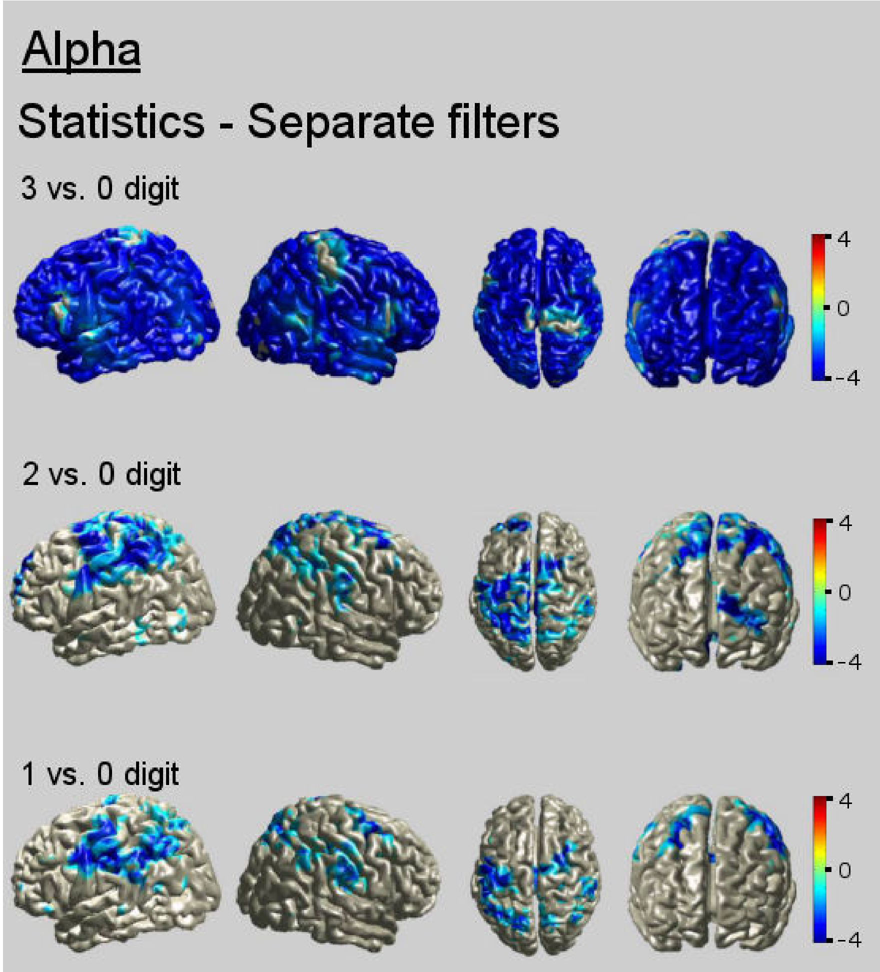

Figure 34 - Group alpha band sources for the separate filter statistics for experiment 2. The 3 vs. 0 digit (top row), 2 vs. 0 digit (middle row) and 1 vs. 0 digit (bottom row) comparisons are shown. These figures relate to Figure 30 in the text. Sources are projected onto a surface plot of the brain. From left to right of the page, the views of the brain are: left, right, top and front.

E: Effect of practice on AB performance with partial targets (1 digit and 2 digits) in long experiments

In most behavioural experiments there was a main effect of practice on the AB magnitude but no interaction of practice with digit condition: i.e. the pattern of relative blink magnitudes did not change between the first and second halves of the experiment. This suggests that participants quickly learnt the global probabilities of the digit events, since there was a robust effect of global target expectations on the AB within the first half (150 – 192 trials) of the experiments. In two longer AB experiments, there was an interaction of practice with digit condition (statistical trend only for Experiment 4). The AB performance improved with practice for partial targets (1 digit and 2 digits) but not for the full target (3 digits) in the masking (Behavioural Experiment 3; 240 trials in each half) (Figure 35A and B) and the colour experiments (Behavioural Experiment 4; 360 trials in each half) (Figure 36A and B).

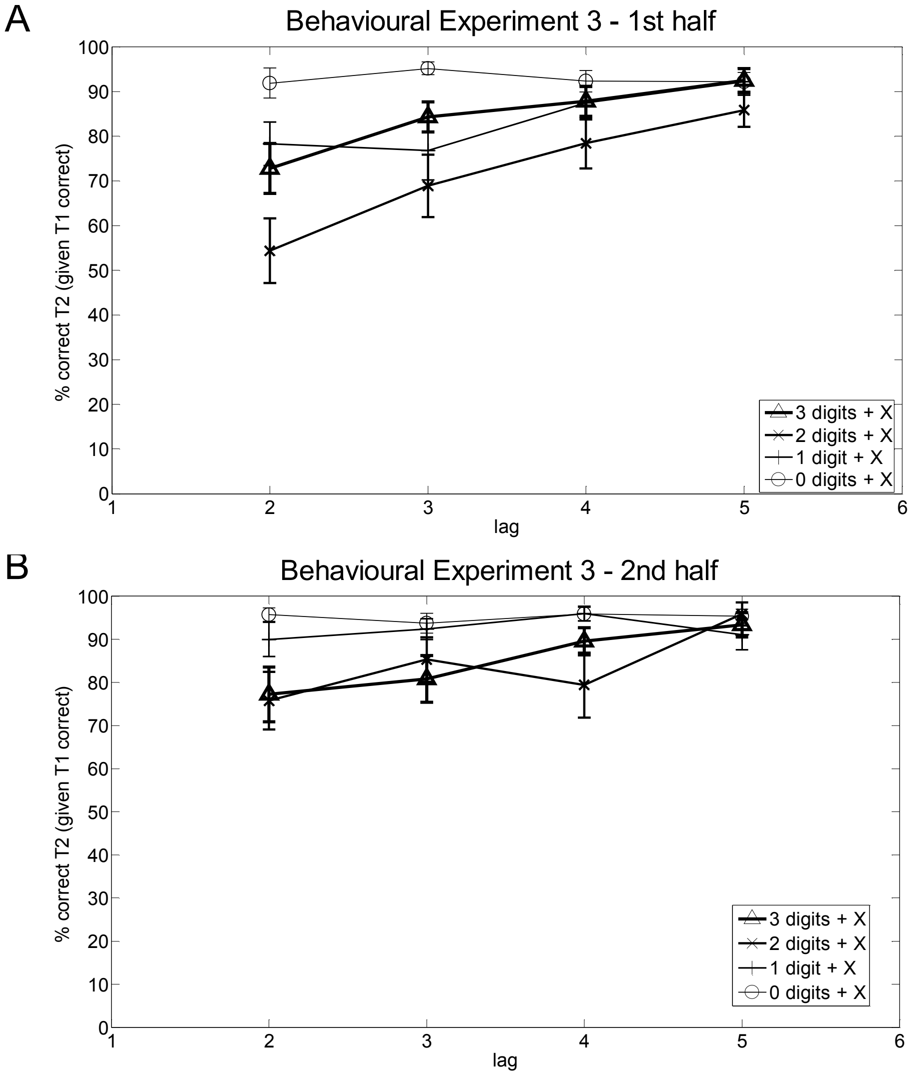

Figure 35 - Experiment 3: The digit-event mask. T2|T1 performance at various levels of T1 compositionality for masked and unmasked conditions during A) the first half and B) the second half of the experiment. Error bars +/- 1 standard error of the mean.

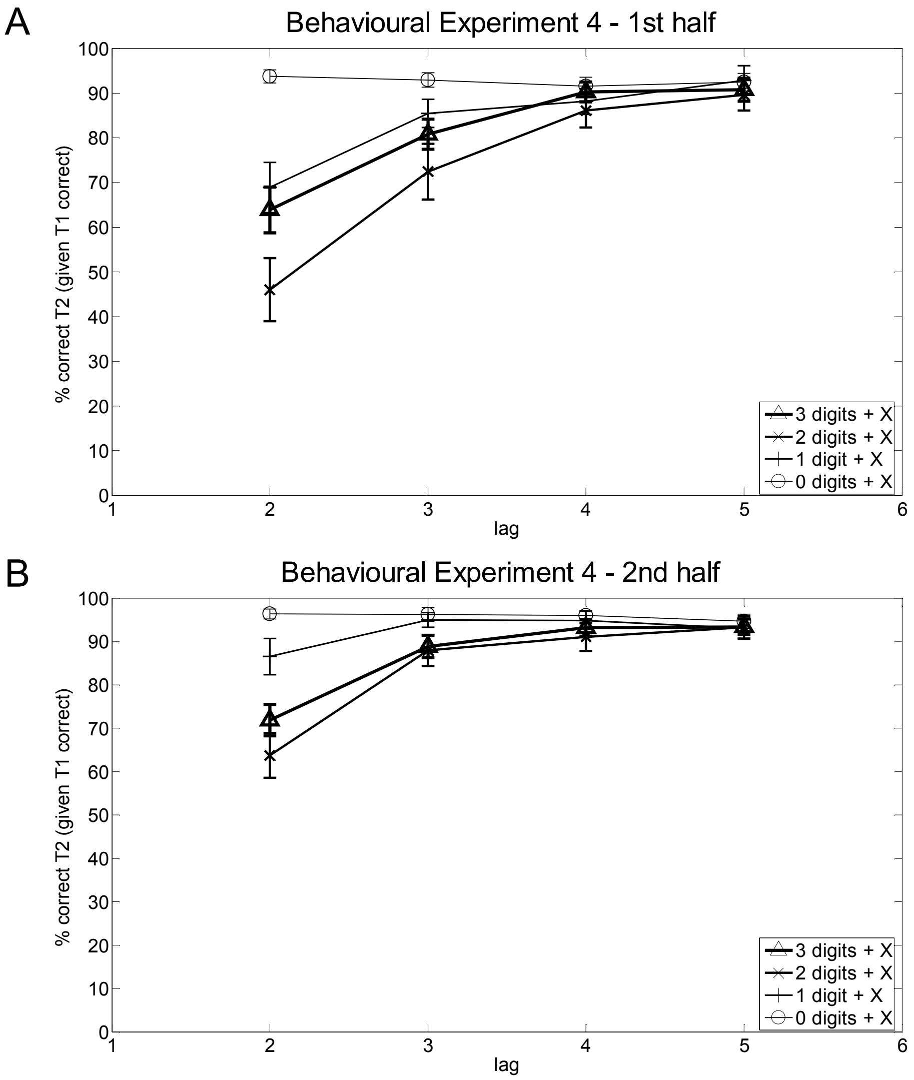

Figure 36 - Experiment 4: Colour marking final digit. T2│T1 performance at various levels of T1 compositionality for black and blue conditions during A) the first half and B) the second half of the experiment. Error bars +/- 1 standard error of the mean.

List of References

AREND, I., JOHNSTON, S. & SHAPIRO, K. (2006) Task-irrelevant visual motion and flicker attenuate the attentional blink. *Psychonomic Bulletin & Review,* 13, 600-607.

ARNELL, K. M., HELION, A. M., HURDELBRINK, J. A. & PASIEKA, B. (2004) Dissociating sources of dual-task interference using human electrophysiology. *Psychonomic Bulletin & Review,* 11, 77-83.

ARNELL, K. M. & LARSON, J. M. (2002) Cross-modality attentional blinks without preparatory task-set switching. *Psychonomic Bulletin & Review,* 9, 497-506.

ARNELL, K. M. & SHAPIRO, K. L. (2011) Attentional blink and repetition blindness. *Wiley Interdisciplinary Reviews: Cognitive Science,* 2, 336-344.

ARON, A., ROBBINS, T. & POLDRACK, R. (2004) Inhibition and the right inferior frontal cortex. *Trends in Cognitive Sciences,* 8, 170-177.

BAARS, B. J. (1997) In the Theatre of Consciousness. Global Workspace Theory, A Rigorous Scientific Theory of Consciousness. *Journal of Consciousness Studies,* 4, 292-309.

BAARS, B. J. (2005) Global workspace theory of consciousness: toward a cognitive neuroscience of human experience. IN STEVEN, L. (Ed.) *Progress in Brain Research.* Elsevier.

BAILLET, S., MOSHER, J. C. & LEAHY, R. M. (2001) Electromagnetic brain mapping. *Ieee Signal Processing Magazine,* 18, 14-30.

BASTIAANSEN, M. C. M. & BRUNIA, C. H. M. (2001) Anticipatory attention: an event-related desynchronization approach. *International Journal of Psychophysiology,* 43, 91-107.

BOWMAN, H. & WYBLE, B. (2007) The simultaneous type, serial token model of temporal attention and working memory. *Psychological Review,* 114, 38-70.

BROADBENT, D. E. & BROADBENT, M. H. P. (1987) From Detection to Identification - Response to Multiple Targets in Rapid Serial Visual Presentation. *Perception & Psychophysics,* 42, 105-113.

BUTTERWORTH, B. (2000) *The Mathematical Brain,* London, Macmillan.

CARTER, C., BRAVER, T., BARCH, D., BOTVINICK, M., NOLL, D. & COHEN, J. (1998) Anterior Cingulate Cortex, Error Detection, and the Online Monitoring of Performance. *Science,* 280, 747-749.

CHUN, M. M. (1997) Types and tokens in visual processing: a double dissociation between the attentional blink and repetition blindness. *J Exp Psychol Hum Percept Perform,* 23, 738-55.

CHUN, M. M. & POTTER, M. C. (1995) A 2-Stage Model for Multiple-Target Detection in Rapid Serial Visual Presentation. *Journal of Experimental Psychology: Human Perception and Performance,* 21, 109-127.

COHEN, D. (1972) Magnetoencephalography: Detection of the brain's electrical activity with a superconducting magnetometer. *Science,* 175, 664-666.

COHEN, D., HALGREN, E. & LARRY, R. S. (2009) Magnetoencephalography. *Encyclopedia of Neuroscience.* Oxford, Academic Press.

COHEN, J. D. (1998) Anterior cingulate cortex, error detection, and the online monitoring of performance. *Science* 280, 747-749.

CREBOLDER, J. M., JOLICOEUR, P. & MCILWAINE, J. D. (2002) Loci of Signal Probability Effects and of the Attentional Blink Bottleneck. *Journal of Experimental Psychology: Human Perception and Performance,* 28, 695-716.

DEHAENE, S., KERSZBERG, M. & CHANGEUX, J. P. (1998) A neuronal model of a global workspace in effortful cognitive tasks. *Proceedings of the National Academy of Sciences of the United States of America,* 95, 14529-14534.

DEHAENE, S., PIAZZA, M., PINEL, P. & COHEN, L. (2003b) Three parietal circuits for number processing. *Cognitive Neuropsychology* 20, 487-506.

DEHAENE, S., SERGENT, C. & CHANGEUX, J. P. (2003a) A neuronal network model linking subjective reports and objective physiological data during conscious perception. *Proc Natl Acad Sci,* 100, 8520-5.

DEL GRATTA, C. P., V; TECCHIO, F; ROMANI, GL (2001) Magnetoencephalography—a noninvasive brain imaging method with 1 ms time resolution. *Reports on Progress in Physics,* 64, 1759-1814.

DI LOLLO, V., KAWAHARA, J., GHORASHI, S. M. S. & ENNS, J. T. (2005) The attentional blink: Resource depletion or temporary loss of control? *Psychological Research,* 69, 191-200.

DONCHIN, E. & COLES, M. G. H. (1988) Is the P300 Component a Manifestation of Context Updating. *Behavioral and Brain Sciences,* 11, 357-374.

DUNCAN, J., MARTENS, S. & WARD, R. (1997) Restricted attentional capacity within but not between sensory modalities. *Nature,* 387, 808-10.

DUX, P. E. & MAROIS, R. (2009) The attentional blink: A review of data and theory. *Attention, Perception, & Psychophysics,* 71, 1683-1700.

ENNS, J. T. & DI LOLLO, V. (2000) What's new in visual masking? *Trends in Cognitive Sciences,* 4, 345-352.

FEINSTEIN, J. S., STEIN, M. B., CASTILLO, G. N. & PAULUS, M. P. (2004) From sensory processes to conscious perception. *Consciousness and Cognition,* 13, 323-335.

FREUNBERGER, R., WERKLE-BERGNER, M., GRIESMAYR, B., LINDENBERGER, U. & KLIMESCH, W. (2011) Brain oscillatory correlates of working memory constraints. *Brain Research,* 1375, 93-102.

FRIES, P. (2005) A mechanism for cognitive dynamics: neuronal communication through neuronal coherence. *Trends in Cognitive Sciences,* 9, 474-480.

GEVINS, A., SMITH, M. E., MCEVOY, L. & YU, D. (1997) High-resolution EEG mapping of cortical activation related to working memory: effects of task difficulty, type of processing, and practice. *Cerebral Cortex,* 7, 374-385.

GIESBRECHT, B. & DI LOLLO, V. (1998) Beyond the attentional blink: Visual masking by object substitution. *Journal of Experimental Psychology: Human Perception and Performance,* 24, 1454-1466.

GRANDISON, T. D., GHIRARDELLI, T. G. & EGETH, H. E. (1997) Beyond similarity: Masking of the target is sufficient to cause the attentional blink. *Perception & Psychophysics,* 59, 266-274.

GROSS, J., KUJALA, J., HAMALAINEN, M., TIMMERMANN, L., SCHNITZLER, A. & SALMELIN, R. (2001) Dynamic imaging of coherent sources: Studying neural interactions in the human brain. *Proceedings of the National Academy of Sciences of the United States of America,* 98, 694-699.

GROSS, J., SCHMITZ, F., SCHNITZLER, I., KESSLER, K., SHAPIRO, K., HOMMEL, B. & SCHNITZLER, A. (2004) Modulation of long-range neural synchrony reflects temporal limitations of visual attention in humans. *Proceedings of the National Academy of Sciences of the United States of America,* 101, 13050-13055.

GROSS, J., SCHMITZ, F., SCHNITZLER, I., KESSLER, K., SHAPIRO, K., HOMMEL, B. & SCHNITZLER, A. (2006) Anticipatory control of long-range phase synchronization. *European Journal of Neuroscience,* 24, 2057-2060.

HÄMÄLÄINEN, M., HARI, R., ARTHUR, W. T. & JOHN, C. M. (2002) Magnetoencephalographic Characterization of Dynamic Brain Activation:

Basic Principles and Methods of Data Collection and Source Analysis. *Brain Mapping: The Methods (Second Edition)*. San Diego, Academic Press.

HÄMÄLÄINEN, M., HARI, R., ILMONIEMI, R. J., KNUUTILA, J. & LOUNASMAA, O. V. (1993) Magnetoencephalography - Theory, Instrumentation, and Applications to Noninvasive Studies of the Working Human Brain. *Reviews of Modern Physics,* 65, 413-497.

HANSLMAYR, S., GROSS, J., KLIMESCH, W. & SHAPIRO, K. L. (2011) The role of alpha oscillations in temporal attention. *Brain Research Reviews,* 67, 331-343.

HENSON, R. N., BURGESS, N. & FRITH, C. D. (2000) Recoding, storage, rehearsal and grouping in verbal short-term memory: an fMRI study. *Neuropsychologia,* 38, 426-40.

HOMMEL, B. (2004) Event files: feature binding in and across perception and action. *Trends in Cognitive Sciences,* 8, 494-500.

HOMMEL, B. & AKYUREK, E. G. (2005) Lag-1 sparing in the attentional blink: Benefits and costs of integrating two events into a single episode. *Quarterly Journal of Experimental Psychology Section a-Human Experimental Psychology,* 58, 1415-1433.

HOMMEL, B., KESSLER, K., SCHMITZ, F., GROSS, J., AKYÜREK, E., SHAPIRO, K. & SCHNITZLER, A. (2006) How the brain blinks: towards a neurocognitive model of the attentional blink. *Psychological Research,* 70, 425-435.

HOPF, J.-M., VOGEL, E., WOODMAN, G., HEINZE, H.-J. & LUCK, S. J. (2002) Localizing Visual Discrimination Processes in Time and Space. *Journal of Neurophysiology,* 88, 2088-2095.

HOUGHTON, G. & TIPPER, S. P. (1996) Inhibitory Mechanisms of Neural and Cognitive Control: Applications to Selective Attention and Sequential Action. *Brain and Cognition,* 30, 20-43.

HUETTEL, S. A., SONG, A. W. & MCCARTHY, G. (2005) Decisions under Uncertainty: Probabilistic Context Influences Activation of Prefrontal and Parietal Cortices. *The Journal of Neuroscience,* 25, 3304-3311.

JANSON, J. & KRANCZIOCH, C. (2011) Good vibrations, bad vibrations: Oscillatory brain activity in the attentional blink. *Advances in Cognitive Psychology,* 7, 92-107.

JENSEN, O. (2006) Maintenance of multiple working memory items by temporal segmentation. *Neuroscience,* 139, 237-249.

JENSEN, O. & TESCHE, C. D. (2002) Frontal theta activity in humans increases with memory load in a working memory task. *Eur J Neurosci,* 15, 1395-9.

JOLICOEUR, P. (1999a) Dual-Task Interference and Visual Encoding. *J Exp Psychol Hum Percept Perform,* 25, 596-616.

JOLICOEUR, P. (1999b) Concurrent Response-Selection Demands Modulate the Attentional Blink. *J Exp Psychol Hum Percept Perform,* 25, 1097-1113.

JOLICOEUR, P., DELL'ACQUA, R. & CREBOLDER, J. (2000) Multitasking performance deficits: Forging links between the Attentional Blink and the Psychological Refractory Period. IN MONSELL, S. & DRIVER, J. (Eds.) *Control of Cognitive Processes: Attention and Performance XVIII.* The MIT Press, p309-330.

KANWISHER, N. G. (1987) Repetition blindness: Type recognition without token individuation. *Cognition,* 27, 117-143.

KANWISHER, N. G., KIM, J. W. & WICKENS, T. D. (1996) Signal detection analyses of repetition blindness. *Journal of Experimental Psychology-Human Perception and Performance,* 22, 1249-1260.

KAWAHARA, J. I., KUMADA, T. & DI LOLLO, V. (2006) The attentional blink is governed by a temporary loss of control. *Psychonomic Bulletin & Review,* 13, 886-890.

KAWAHARA, J. I., ZUVIC, S. M., ENNS, J. T. & DI LOLLO, V. (2003) Task switching mediates the attentional blink even without backward masking. *Perception & Psychophysics,* 65, 339-351.

KESSLER, K., GROSS, J., SCHMITZ, F. & SCHNITZLER, A. (2006) Cortical dynamics and synchronization related to multiple target consolidation under rapid-serial-visual-presentation conditions. *Journal of Physiology-Paris,* 99, 21-28.

KESSLER, K. & KIEFER, M. (2005) Disturbing visual working memory: Electrophysiological evidence for a role of the prefrontal cortex in recovery from interference. *Cerebral Cortex,* 15, 1075-1087.

KESSLER, K., SCHMITZ, F., GROSS, J., HOMMEL, B., SHAPIRO, K. & SCHNITZLER, A. (2005a) Target consolidation under high temporal processing demands as revealed by MEG. *Neuroimage,* 26, 1030-1041.

KESSLER, K., SCHMITZ, F., GROSS, J., HOMMEL, B., SHAPIRO, K. & SCHNITZLER, A. (2005b) Cortical mechanisms of attention in time: neural correlates of the Lag-1-sparing phenomenon. *European Journal of Neuroscience,* 21, 2563-2574.

KIHARA, K., KAWAHARA, J. & TAKEDA, Y. (2008) Electrophysiological evidence for independent consolidation of multiple targets. *Neuroreport,* 19, 1493-1496.

KLIMESCH, W., DOPPELMAYR, M., RUSSEGGER, H., PACHINGER, T. & SCHWAIGER, J. (1998) Induced alpha band power changes in the human EEG and attention. *Neuroscience Letters,* 244, 73-76.

KLIMESCH, W., SAUSENG, P. & HANSLMAYR, S. (2007) EEG alpha oscillations: The inhibition-timing hypothesis. *Brain Research Reviews,* 53, 63-88.

KOECHLIN, E. & HYAFIL, A. (2007) Anterior Prefrontal Function and the Limits of Human Decision-Making. *Science,* 318, 594-598.

KONIG, R. S., C; DURKA, P J (2007) Tiny Signals from the Human Brain: Acquisition and Processing of Biomagnetic Fields in Magnetoencephalography. *Journal of Low Temperature Physics,* 146, 697-718.

KRANCZIOCH, C., DEBENER, S., MAYE, A. & ENGEL, A. K. (2007) Temporal dynamics of access to consciousness in the attentional blink. *Neuroimage,* 37, 947-955.

KRANCZIOCH, C., DEBENER, S., SCHWARZBACH, J., GOEBEL, R. & ENGEL, A. K. (2005) Neural correlates of conscious perception in the attentional blink. *Neuroimage,* 24, 704-714.

KUJALA, J., GROSS, J. & SALMELIN, R. (2008) Localization of correlated network activity at the cortical level with MEG. *Neuroimage,* 39, 1706-1720.

LANCASTER, J., WOLDORFF, M., PARSONS, L., LIOTTI, M., FREITAS, C., RAINEY, L., KOCHUNOV, P., NICKERSON, D., MIKITEN, S. & FOX, P. (2000) Automated Talairach Atlas labels for functional brain mapping. *Human Brain Mapping,* 10, 120-131.

LILJESTRÖM, M., KUJALA, J., JENSEN, O. & SALMELIN, R. (2005) Neuromagnetic localization of rhythmic activity in the human brain: a comparison of three methods. *NeuroImage,* 25, 734-745.

LINDEN, D. E. J., PRVULOVIC, D., FORMISANO, E., VOLLINGER, M., ZANELLA, F. E., GOEBEL, R. & DIERKS, T. (1999) The Functional Neuroanatomy of Target Detection: An fMRI Study of Visual and Auditory Oddball Tasks. *Cerebral Cortex,* 9, 815-823.

LISMAN, J. (2010) Working Memory: The Importance of Theta and Gamma Oscillations. *Current Biology,* 20, R490-R492.

MACLEAN, M. H. & ARNELL, K. M. (2011) Greater attentional blink magnitude is associated with higher levels of anticipatory attention as measured by alpha event-related desynchronization (ERD). *Brain Research,* 1387, 99-107.

MAKI, W. S. & MEBANE, M. W. (2006) Attentional capture triggers an attentional blink. *Psychonomic Bulletin & Review,* 13, 125-131.

MARIS, E. (2004) Randomization tests for ERP topographies and whole spatiotemporal data matrices. *Psychophysiology,* 41, 142-151.

MARIS, E. & OOSTENVELD, R. (2007) Nonparametric statistical testing of EEG- and MEG-data. *Journal of Neuroscience Methods,* 164, 177-190.

MAROIS, R., CHUN, M. M. & GORE, J. C. (2000) Neural correlates of the attentional blink. *Neuron,* 28, 299-308.

MARTENS, S., ELMALLAH, K., LONDON, R. & JOHNSON, A. (2006) Cuing and stimulus probability effects on the P3 and the AB. *Acta Psychologica,* 123, 204-218.

MARTENS, S. & WYBLE, B. (2010) The attentional blink: Past, present, and future of a blind spot in perceptual awareness. *Neuroscience & Biobehavioral Reviews,* 34, 947-957.

MARTI, S., SIGMAN, M. & DEHAENE, S. (2012) A shared cortical bottleneck underlying Attentional Blink and Psychological Refractory Period. *NeuroImage,* 59, 2883-2898.

MCARTHUR, G., BUDD, T. & MICHIE, P. (1999) The attentional blink and P300. *Neuroreport,* 10, 3691-3695.

MCCARTHY, G., LUBY, M., GORE, J. & GOLDMAN-RAKIC, P. (1997) Infrequent Events Transiently Activate Human Prefrontal and Parietal Cortex as Measured by Functional MRI. *Journal of Neurophysiology,* 77, 1630-1634.

MCLAUGHLIN, E. N., SHORE, D. I. & KLEIN, R. M. (2001) The attentional blink is immune to masking-induced data limits. *Quarterly Journal of Experimental Psychology Section a-Human Experimental Psychology,* 54, 169-196.

MICHEL, C. M., MURRAY, M. M., LANTZ, G., GONZALEZ, S., SPINELLI, L. & DE PERALTA, R. G. (2004) EEG source imaging. *Clinical Neurophysiology,* 115, 2195-2222.

MILLER, G. A. (1956) The magical number seven, plus or minus two: some limits on our capacity for processing information. *Psychological Review,* 63, 81-97.

NIEDER, A. & DEHAENE, S. (2009) Representation of number in the brain. *Annual Review in Neuroscience,* 32, 185-208.

NIEUWENSTEIN, M. R. & POTTER, M. C. (2006) Temporal limits of selection and memory encoding - A comparison of whole versus partial report in rapid serial visual presentation. *Psychological Science,* 17, 471-475.

NIEUWENSTEIN, M. R., POTTER, M. C. & THEEUWES, J. (2009) Unmasking the Attentional Blink. *Journal of Experimental Psychology-Human Perception and Performance,* 35, 159-169.

NOLTE, G. (2003) The magnetic lead field theorem in the quasistatic approximation and its use for magnetoencephalography forward calculation in realistic volume conductors. *Phys. Med. Biol. ,* 48, 3637-3652.

O'BRIEN, R. G. & KAISER, M. K. (1985) MANOVA Method for Analyzing Repeated Measures Designs: An Extensive Primer. *Psychological Bulletin,* 97, 316-333.

OLIVEIRA, F. T. P., MCDONALD, J. J. & GOODMAN, D. (2007) Performance Monitoring in the Anterior Cingulate is Not All Error Related: Expectancy Deviation and the Representation of Action-Outcome Associations. *Journal of Cognitive Neuroscience,* 19, 1994-2004.

OLIVERS, C. N. L. & MEETER, M. (2008) A Boost and Bounce Theory of Temporal Attention. *Psychological Review,* 115, 836-863.

OLIVERS, C. N. L. & NIEUWENHUIS, S. (2005) The beneficial effect of concurrent task-irrelevant mental activity on temporal attention. *Psychological Science,* 16, 265-269.

OLIVERS, C. N. L. & NIEUWENHUIS, S. (2006) The beneficial effects of additional task load, positive affect, and instruction on the attentional blink. *Journal of Experimental Psychology: Human Perception and Performance,* 32, 364-379.

OLIVERS, C. N. L. & VAN DER BURG, E. (2008) Bleeping you out of the blink: Sound saves vision from oblivion. *Brain Research,* 1242, 191-199.

OLIVERS, C. N. L., VAN DER STIGCHEL, S. & HULLEMAN, J. (2007) Spreading the sparing: against a limited-capacity account of the attentional blink. *Psychological Research,* 71, 126-139.

OOSTENVELD, R., FRIES, P., MARIS, E., & SCHOFFELEN, J. (2011) FieldTrip: Open Source Software for Advanced Analysis of MEG, EEG, and Invasive Electrophysiological Data. *Computational Intelligence and Neuroscience,* 2011, 1-9.

PASHLER, H. (1994) Dual-Task Interference in Simple Tasks - Data and Theory. *Psychological Bulletin,* 116, 220-244.

PAULESU, E., FRITH, C. D. & FRACKOWIAK, R. S. J. (1993) The neural correlates of the verbal component of working memory. *Nature,* 362, 342-345.

PETERSON, M. S. & JUOLA, J. F. (2000) Evidence for distinct attentional bottlenecks in attention switching and attentional blink tasks. *J Gen Psychol,* 127, 6-26.

PIAZZA, M. & IZARD, V. (2009) How Humans Count: Numerosity and the Parietal Cortex. *The Neuroscientist,* 15, 261-273.

PIAZZA, M., MECHELLI, A., BUTTERWORTH, B. & PRICE, C. J. (2002) Are Subitizing and Counting Implemented as Separate or Functionally Overlapping Processes? *NeuroImage,* 15, 435-446.

PIAZZA, M., MECHELLI, A., PRICE, C. J. & BUTTERWORTH, B. (2006) Exact and approximate judgements of visual and auditory numerosity: an fMRI study. *Brain Research,* 1106, 177-88.

PIAZZA, M., PINEL, P., LE BIHAN, D. & DEHAENE, S. (2007) A magnitude code common to numerosities and number symbols in human intraparietal cortex. *Neuron,* 53, 293-305.

PINEL, P. & DEHAENE, S. (2010) Beyond Hemispheric Dominance: Brain Regions Underlying the Joint Lateralization of Language and Arithmetic to the Left Hemisphere. *Journal of Cognitive Neuroscience,* 22, 48-66.

POSTLE, B. R. & D'ESPOSITO, M. (2000) Evaluating models of the topographical organization of working memory function in frontal cortex with event-related fMRI. *Psychobiology,* 28, 132-145.

POTTER, M. C., CHUN, M. M., BANKS, B. S. & MUCKENHOUPT, M. (1998) Two Attentional Deficits in Serial Target Search: The Visual Attentional Blink and an Amodal Task-Switch Deficit. *Journal of Experimental Psychology: Learning, Memory, and Cognition,* 24, 979-992.

RANGANATH, C. & RAINER, G. (2003) Neural mechanisms for detecting and remembering novel events. *Nature Reviews Neuroscience,* 4, 193-202.

RAYMOND, J. E., SHAPIRO, K. L. & ARNELL, K. M. (1992) Temporary Suppression of Visual Processing in an Rsvp Task - an Attentional Blink. *Journal of Experimental Psychology: Human Perception and Performance,* 18, 849-860.

RODRIGUEZ, E., GEORGE, N., LACHAUX, J. P., MARTINERIE, J., RENAULT, B. & VARELA, F. J. (1999) Perception's shadow: long-distance synchronization of human brain activity. *Nature,* 397, 430-433.

ROGERS, R. D. & MONSELL, S. (1995) Costs of a Predictable Switch between Simple Cognitive Tasks. *Journal of Experimental Psychology-General,* 124, 207-231.

ROHENKOHL, G. & NOBRE, A. C. (2011) Alpha Oscillations Related to Anticipatory Attention Follow Temporal Expectations. *The Journal of Neuroscience,* 31, 14076-14084.

RUMELHART, D. E. & MCCLELLAND, J. L. (1986) Parallel Distributed Processing: Explorations in the Microstructure of Cognition. *MIT Press, Cambridge (USA).*

SAUSENG, P., GRIESMAYR, B., FREUNBERGER, R. & KLIMESCH, W. (2010) Control mechanisms in working memory: a possible function of EEG theta oscillations. *Neurosci Biobehav Rev,* 34, 1015-22.

SEIFFERT, A. E. & DILOLLO, V. (1997) Low-level masking in the attentional blink. *Journal of Experimental Psychology: Human Perception and Performance,* 23, 1061-1073.

SERGENT, C., BAILLET, S. & DEHAENE, S. (2005) Timing of the brain events underlying access to consciousness during the attentional blink. *Nature Neuroscience,* 8, 1391-1400.

SHAPIRO, K., ARNELL, K. & RAYMOND, J. (1997) The attentional blink. *Trends in Cognitive Sciences,* 1, 291-296.

SHAPIRO, K., SCHMITZ, F., MARTENS, S., HOMMEL, B. & SCHNITZLER, A. (2006) Resource sharing in the attentional blink. *Neuroreport,* 17, 163-166.

SHORE, D. I., MCLAUGHLIN, E. N. & KLEIN, R. M. (2001) Modulation of the attentional blink by differential resource allocation. *Canadian Journal of Experimental Psychology* 55, 318-324.

SMITH, E. E., JONIDES, J., MARSHUETZ, C. & KOEPPE, R. A. (1998) Components of verbal working memory: Evidence from Neuroimaging. *Proceedings of the National Academy of Sciences,* 95, 876-882.

TAATGEN, N. A., JUVINA, I., SCHIPPER, M., BORST, J. P. & MARTENS, S. (2009) Too much control can hurt: A threaded cognition model of the attentional blink. *Cognitive Psychology,* 59, 1-29.

TRIPPE, R. H., HEWIG, J., HEYDEL, C., HECHT, H. & MILTNER, W. H. R. (2007) Attentional Blink to emotional and threatening pictures in spider phobics: Electrophysiology and behavior. *Brain Research,* 1148, 149-160.

VARELA, F., LACHAUX, J. P., RODRIGUEZ, E. & MARTINERIE, J. (2001) The brainweb: Phase synchronization and large-scale integration. *Nature Reviews Neuroscience,* 2, 229-239.

VERLEGER, R. (1988) Event-related potentials and cognition: a critique of the context updating hypothesis and an alternative interpretation of P3. *Behav. Brain Sci.* , 11, 343- 427.

VIGÁRIO, R., JAAKKO, S., JOUSMÄKI, V., HÄMÄLÄINEN, M. & OJA, E. (2000) Independent component approach to the analysis of EEG and MEG recordings. *IEEE Transactions on Biomedical Engineering,* 47, 589-593.

VISSER, T. A. W., BISCHOF, W. F. & DI LOLLO, V. (1999) Attentional switching in spatial and nonspatial domains: Evidence from the attentional blink. *Psychological Bulletin,* 125, 458-469.

VOGEL, E. K. & LUCK, S. J. (2002) Delayed working memory consolidation during the attentional blink. *Psychonomic Bulletin & Review,* 9, 739-743.

VOGEL, E. K., LUCK, S. J. & SHAPIRO, K. L. (1998) Electrophysiological evidence for a postperceptual locus of suppression during the attentional blink. *Journal of Experimental Psychology: Human Perception and Performance,* 24, 1656-1674.

VOLZ, K., SCHUBOTZ, R. & VON CRAMON, D. Y. (2003) Predicting events of varying probability: uncertainty investigated by fMRI. *NeuroImage,* 19 271-280.

VOLZ, K. G., SCHUBOTZ, R. I. & VON CRAMON, D. Y. (2005) Variants of uncertainty in decision-making and their neural correlates. *Brain Research Bulletin,* 67, 403-12.

WAGER, T. D. & SMITH, E. E. (2003) Neuroimaging studies of working memory: A meta-analysis. *Cognitive, Affective & Behavioral Neuroscience,* 3 255-274.

WARD, R., DUNCAN, J. & SHAPIRO, K. (1996) The Slow Time-Course of Visual Attention. *Cognitive Psychology,* 30, 79-109.

WEICHSELGARTNER, E. & SPERLING, G. (1987) Dynamics of automatic and controlled visual attention. *Science,* 778-780.

WIERDA, S. M., VAN RIJN, H., TAATGEN, N. A. & MARTENS, S. (2010) Distracting the mind improves performance: an ERP Study. *PLoS One,* 5, e15024.

WYBLE, B., BOWMAN, H. & NIEUWENSTEIN, M. (2009) The Attentional Blink Provides Episodic Distinctiveness: Sparing at a Cost. *Journal of Experimental Psychology: Human Perception and Performance,* 35, 787-807.

WYBLE, B., POTTER, M. C., BOWMAN, H. & NIEUWENSTEIN, M. (2011) Attentional Episodes in Visual Perception. *Journal of Experimental Psychology: General,* 140, 488-505.

YAMAZAKI, T., KAMIJO, K.-I., KIYUNA, T., TAKAKI, Y. & KUROIWA, Y. (2001) Multiple Dipole Analysis of Visual Event-Related Potentials During Oddball Paradigm with Silent Counting. *Brain Topography,* 13, 161-168.

ZIMMERMAN, J. E. (1977) Squid Instruments and Shielding for Low-Level Magnetic Measurements. *Journal of Applied Physics,* 48, 702-710.